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CHARACTERISTICS OF HORNBILL-DISPERSED FRUITS IN LOWLAND DIPTEROCARP FORESTS OF SOUTHERN THAILAND

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***ABSTRACT*. –** Interactions among fruits and a hornbill assemblage are presented from a 42-month study in the dipterocarp forests of the Budo Su-Ngai Padi National Park and Hala-Bala Wildlife Sanctuary in southern Thailand. This community-level approach allowed us to determine fruit selection by hornbills and to evaluate their potential role in seed dispersal. We studied the interactions between fruit species and seven hornbill species (*Buceros bicornis*, *B. rhinoceros*, *B. vigil*, *Aceros comatus*, *A. corrugatus*, *Anorrhinus galeritus*, and *Rhyticeros undulatus*). Fruit characteristics were determined for 458 species in 75 families. Of these, 244 fruit species (53%) were casually observed to be eaten by frugivores. Hornbills consumed at least 93 fruit species from 33 families (15 spp. in Moraceae, 12 spp. in Lauraceae, 11 spp. in Myristicaceae, and 8 spp. each in Annonaceae and Meliaceae). Hornbills tended to ignore winged-fruits (Dipterocarpaceae) and acorns (Fagaceae) and fruits of shrubs (Annonaceae, Arecaceae, and Rubiaceae). Although various kinds of fruits were available in the dipterocarp forests, hornbills had clear feeding preferences for fruits with certain traits related to their life form, fruit protection, fruit colour, and seed diameter. The number of possible pairs of fruits and frugivores is enormous in the tropics, but fruit–hornbill relationships are structured in certain ways, so only a subset of the possible interactions actually occurs. This study provides a preliminary inventory of fruit–hornbill interactions in lowland dipterocarp forests of southern Thailand, allowing for comparisons across different forest types where different hornbill species perform similar roles.

This paper was presented at the 5th International Hornbill Conference jointly organised by the National Parks Board (Singapore) and the Hornbill Research Foundation (Thailand), in Singapore on 22nd–25th March 2009.

***KEY WORDS*. –** hornbill, fruit dispersal, diet, Thailand.

INTRODUCTION

Most tropical rain forest plants are adapted to seed dispersal by animals. Many birds, mammals and insects, and occasionally reptiles and amphibians, consume rain forest fruits, but they differ in foraging behaviour, ability to manipulate seeds, and, hence, seed dispersal effectiveness (Howe & Smallwood, 1982; Herrera & Pellmyr, 2002; Wang & Smith, 2002). Given their highly frugivorous diet and ability to swallow and regurgitate large seeds, hornbills are considered important seed dispersers in Asia (Kinnaird, 1998; Datta & Rawat, 2003; Kitamura et al., 2004a; Kitamura et al., 2004c, Kitamura et al., 2006; Kinnaird & O'Brien, 2007; Kitamura et al., 2008; Sethi & Howe, 2009; Velho et al., 2009) and Africa (Whitney et al., 1998; Whitney & Smith, 1998; Jensch & Ellenberg, 1999; Holbrook & Smith, 2000;

Holbrook et al., 2002; Poulsen et al., 2002). Their role may be particularly important in degraded landscapes, owing to the disproportionate extinction of large frugivorous vertebrates following human disturbances (Sodhi et al., 2004; Corlett, 2007a, 2007b).

In Southeast Asia, lowland dipterocarp forests are one of the most important habitats for hornbills, where up to ten species of hornbills can inhabit a given site (Gale & Thong-Aree, 2006; Kemp et al., 2007; Kinnaird & O'Brien, 2007). Southeast Asia is dominated by members of one family of large trees, the Dipterocarpaceae, which formerly formed the most extensive habitats in Peninsular Malaysia (Whitmore, 1984). However, large areas of dipterocarp forests have disappeared, and changes in land use, such as the establishment of rubber/oil-palm plantations and orchards, are still increasing (Fitzherbert et al., 2008). Additionally, selective logging has disturbed most of the remaining natural forests. These human disturbances not only directly affect the community structure of forests, but also may indirectly influence the frugivore community. This indirect effect is probably quite strong with respect to Asian hornbills because they depend on forest trees for both food and nesting sites. Therefore, hornbills are likely particularly sensitive indicators of forest condition and human disturbance.

The presence or absence of hornbills is now fairly well documented for remaining dipterocarp forests and other forests of Thailand (Round, 1988; Poonswad, 1993). However, the diets of hornbills inhabiting lowland dipterocarp forests of southern Thailand are still unknown. Knowledge of the dietary composition of hornbill species is required to predict the consequences of changes in the hornbill assemblage on seed dispersal because the role that a hornbill species plays in the dispersal of seeds from a plant species depends upon whether it consumes fruits from that plant. Recent technical innovations such as aerial photographs and satellite images allow comparisons between past and present forest coverage. However, no data are available on the interactions between fruits and hornbill assemblages associated with these changes.

The aim of this study was to collect diet information for hornbills from field observations in order to better understand their potential role as seed dispersers for lowland dipterocarp forests in southern Thailand. The following two questions were addressed: (1) Which plant species are included in the fruit diet of the hornbills present in lowland dipterocarp forests? and (2) Which morphological fruit and seed characteristics do hornbills base their food selection upon, and are certain feeding preferences prevalent?

METHODS

Study site. – This research was conducted for 42 months, from May 2004 to November 2007, in Budo Su-Ngai Padi National Park (hereafter BSPNP) and Hala-Bala Wildlife Sanctuary (HBWS) in Narathiwat Province at the southern tip of Thailand close to the Malaysian border. Both are newly protected areas and were, until recently, controlled by Muslim separatists. BSPNP is comprised of the Budo (189 km^2) and Su-Ngai Padi sectors (152 km^2) in southern Thailand (6°00'–40'N, 101°30'–55'E). These areas support a Malaysian flora that has not been logged commercially since 1989 but still experiences illegal logging, despite being designated a national park in 1999. In our study site in the Budo sector, people appear to be the main threat to hornbills (e.g., poaching, illegal logging, and forest clearance), and involvement of the local community in conservation is the main countermeasure (Poonswad et al., 2005).

HBWS, established in 1996, covers a total of 433 km^2 and is actually two sites with markedly different attributes. Our study site, the Bala sector (5°44'–57'N, 101°46'–51'E) in Narathiwat Province, is an isolate of roughly 111 km^2, surrounded on all sides by agriculture and human settlements. The much larger Hala sector in Yala Province is contiguous both with Belum on the Malaysian side and with other areas of forest outside the wildlife sanctuary on the Thai side, and it represents one of the largest and most significant forests remaining in the Thai-Malay Peninsula.

Average annual rainfall at Narathiwat Airport (TMD weather station 583201; 6°31'N, 101°44'E, 10 km west of Budo sector) is about 2,400 mm (2004–2008), with a marked rainy season from October to December and a clear dry season from February to April (Fig. 1). However, rainfall in the mountains of BSPNP and HBWS appears subjectively to be higher than on the flats at Narathiwat Airport. The mean monthly temperature is 27.2°C, and the minimum temperature is relatively constant (23.6°C average) throughout the year (Fig. 1). Fruit production is highly seasonal, with a peak in abundance from July to September and with periods of fruit scarcity that differ notably between years (S. Kitamura, unpublished data).

Hornbill species studied. – In total, ten species of hornbills occur in HBWS, but only six of these are found in BSPNP. These six species are the White-crowned Hornbill *Aceros comatus*, Wreathed Hornbill *Rhyticeros undulatus*, Bushy-crested Hornbill *Anorrhinus galeritus*, Great Hornbill *Buceros bicornis*, Rhinoceros Hornbill *B. rhinoceros*, and Helmeted Hornbill *B. vigil*. In addition, the Wrinkled Hornbill *Aceros corrugatus* was included in our study because this is the rarest of the hornbills in Thailand, and because one of the authors (S. Thong-Aree) had closely observed their breeding behaviour at HBWS. All of these species are of international and/or national conservation concern: *B. rhinoceros*, *B. bicornis*, *B. vigil*, *A. comatus*, and *A. corrugatus* are all listed as Near Threatened (IUCN, 2008); *R. undulatus* and *A. galeritus* are unlisted internationally, but are considered Near Threatened nationally (Sanguansombat, 2005). In HBWS, hornbill density is relatively low compared with densities in similar forests at other study sites (Gale & Thong-Aree, 2006). Density estimates for these hornbills were 2.7 individuals/km^2 for *B. rhinoceros*, 1.21 for *B. vigil*, 0.69 for *R. undulatus*, 0.64 for *A. galeritus*, 0.12 for *B bicornis*, 0.08 for *A. comatus*, and 0.08 for *A. corrugatus* (Gale & Thong-Aree, 2006).

In this study, hornbill-dispersed fruits are defined as fruit species that were consumed by at least one hornbill species in a given study site (Kitamura et al., 2004b). We did not consider variation in diet among hornbill species, although the overlap in resource requirements, competition, and the potential for compensatory change are expected to be greatest among closely related hornbill species (Leighton, 1982; Poonswad et al., 1998; Poulsen et al., 2002; Hadiprakarsa & Kinnaird, 2004). Feeding observations were gathered while monitoring plant phenology along existing transects (two 1,000 m × 10 m transects at each study site, including 2,581 plants over 10 cm in diameter at breath height) and from opportunistic observations made while conducting other fieldwork. Additional data were collected by more indirect methods such as seeds collected underneath active hornbill nests during the breeding season in HBWS for *A. corrugatus* (Thong-Aree, 2007) and in BSPNP for *B. bicornis* and *B. rhinoceros* (Chaisuriyanane, 2005). The number of known nest trees in BSPNP varied among hornbill species. Compared with those of *B. bicornis*, *B. rhinoceros*, and *R. undulatus*, known nest trees of *B. vigil*, *A. galeritus*, and *A. comatus* were rare (P. Poonswad, *unpublished data*). Therefore we recognized that the sampling efforts for compiling each hornbill diets were biased to some well-studied species.

***Plant species studied*. –** Whenever possible, ripe fruits were collected in the study area. Morphological characteristics were then measured at a field station. Plant nomenclature follows the Tree Flora of Malaya I–V (Whitmore, 1972, 1973; Ng, 1978, 1989) or the incomplete series of the Flora of Thailand when the studied group was covered therein. Plant specimens were collected as often as possible and matched with herbarium specimens from the Royal Forest Department in Bangkok (BKF). Voucher specimens were deposited in our laboratory in BSPNP.

Life form was defined as follows: Liana, lianas and epiphytes; Shrub, herbs and arboreal shrubs (<7 m); Treelet (7–15 m); or Tree (> 15 m). Fruit protection was defined as follows: D, dehiscent fruit; I, indehiscent fruit with a thin husk; T, indehiscent fruit with a thick husk; or N, nuts (winged fruits of Dipterocarpaceae and acorns of Fagaceae). Fruit colour was noted as black, brown, green, purple, pink, red, white, yellow, or orange. Hornbills can perceive a wider range of colours than humans can, and the colours noted here are those perceptible to humans (as perceived by the first author).

Continuous variables included fruit and seed weight, length, and diameter, and seed number per fruit. Fresh fruits and seeds were weighed using electronic balances and measured using callipers with 0.01 g and 0.01 mm precision, respectively. All characterizations were based on the original classifications by Kitamura et al. (2002). Data were collected on a maximum of 30 samples for each fruit species. In the case of several dehiscent fruits such as *Aglaia spectabilis* (Meliaceae), we treated arillate seeds as the dispersal units because they separate quite easily in the ripe fruit and are apparently removed individually by hornbills (Kitamura et al., 2002). Fruits with obvious damage were excluded from the measurements. No attempt was made to look at variation among individuals within species; samples were chosen to represent the typical size range. These measurements were performed within a day of fruit collection. Some seeds were kept as a reference collection against which seeds collected under active hornbill nests could be compared.

***Data analysis*. –** Most of the variables measured had highly skewed distributions; thus, the median value is given instead of the mean. To determine the influence of fruit traits on hornbill consumption, we fitted generalized linear models (GLM) to the data using the GLM function in R (R Development Core Team, 2008). For the GLM analyses, we checked for correlations between the fruit traits; strongly correlated parameters were eliminated to avoid multicollinearity. Dietary data were used as binomial response variables (0 = non-diet, 1 = diet) and each fruit trait (fruit diameter, seed diameter, number of seeds per fruit, fruit protection, life form, fruit colour, fruit odour, and seed hardness) as a linear predictor (fixed effects), assigning each model a binomial error distribution and a logit link function. For analyses, yellow and orange fruits were categorized as yellow-orange.

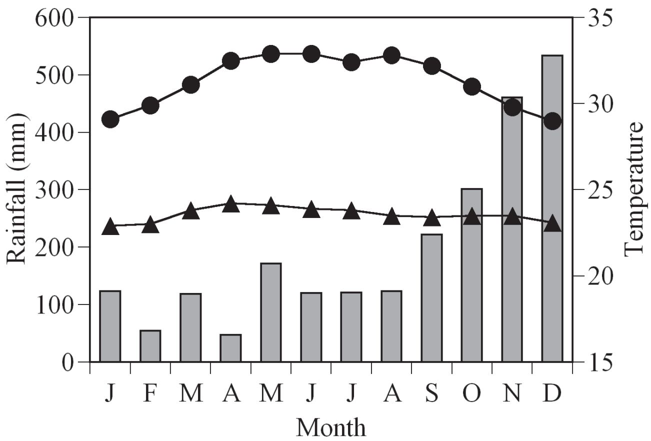

Fig. 1. Monthly average rainfall (columns) and temperature (solid circle: maximum temperature, solid triangle: minimum temperature) from 2004 to 2008 at the Narathiwat Airport in Narathiwat Province, southern Thailand.

RESULTS

***Characteristics of fruits at the community level*. –** In total, fruit characteristics were determined for 458 species of 227 genera from 75 families. The median fruit weight was 2.65 g (range 0.01–1380.0 g), and the median fruit diameter was 16.4 mm (1.9–152.8 mm). The median seed weight was 0.48 g (0.01–173.8 g), and the median seed diameter was 9.1 mm (0.2–77.0 mm). Fruit species with a single seed predominated (65%). The most common fruit colours were red and yellow-orange (23% each), followed by black (19%) and brown (11%). Most fruits did not have a strong odour (84%). Indehiscent with a thin husk was the most common fruit protection type (65%; mostly Annonaceae, Rubiaceae), followed by dehiscent (19%; Euphorbiaceae, Meliaceae, and Myristicaceae), and indehiscent with a thick husk (11%; Arecaceae, Clusiaceae, and Euphorbiaceae). Lianas

Table 1. Characteristics or hornbill-dispersed fruits in lowland dipterocarp forests in Southern Thailand. FW = Fruit weight (g); FL = Fruit length (mm); FD = Fruit diameter (mm); CO = Colour of fruit; NO = number of seeds per fruit; SW = seed weight (g); SL = seed length (mm); SD = Seed diameter (mm). ND = no data; Fruit Type: D = dehiscent; I = indehiscent fruit with thin husk; T = indehiscent fruit with thick husk; N = nut; Life forms: Liana = epiphyte liana; Shrub = herbs, shrub (<7m); Treelet (7-15 m); Tree (>15m). HD = Hardness of seed : H = hard, M = medium; S = soft; Hornbill species: BCH = Bushy-crested hornbill; GH = great hornbill; HH = Helmeted hornbill; RH = Rhinoceros hornbill; WCH = white crowned hornbill; WH = wreathed hornbill; WRH = wrinkled hornbill; X = eaten by hornbills; NA = data are not available.

Family	Species	FP	LF	FW	FL	FD	CO	NO	SW	SL	SD	HD	OD	Hornbill species						
														BCH	GH	HH	RH	WCH	WH	WRH
Agavaceae	*Dracaena* sp.SK048	I	Tree	5.6	22.6	22.0	Red	1.0	1.6	15.1	16.9	M	A							X
Alangiaceae	*Alangium kurzii*	I	Treelet	0.9	15.6	10.9	Black	1.0	0.2	10.2	5.3	M	A	X					X	
Annonaceae	*Cyathostemma* sp.1	I	Liana	0.6	15.0	9.2	Red	1.0	0.4	12.3	7.3	M	A		X					
	Desmos chinensis	I	Liana	0.3	8.2	7.2	Black	1.0	0.1	6.3	4.8	M	A	X	X		X		X	
	D. cochinchinensis	I	Liana	0.5	11.9	9.2	Black	1.0	0.2	8.8	6.9	H	A		X				X	
	Polyalthia cauliflora	I	Treelet	18.8	37.1	30.0	Black	2.3	1.1	16.4	12.1	M	A	X						
	P. clavigera	I	Treelet	17.4	45.8	27.1	Red	1.0	4.9	31.5	16.0	M	A						X	
	P. lateriflora	I	Tree	29.0	55.8	32.0	Red	1.0	6.3	33.6	17.2	M	A		X		X		X	
	Uvaria lurida	I	Liana	12.3	50.1	19.1	Red	6.7	0.6	12.9	11.5	M	A	X					X	
	Xylopia malayana	D	Tree	0.2	8.7	6.7	White	1.0	0.2	8.4	6.3	M	A		X				X	X
Arecaceae	*Oncosperma horridum*	I	Tree	6.3	21.2	23.0	Black	1.0	4.0	18.2	20.4	H	A	X	X		X		X	X
Bombacaceae	*Neesia malayana*	D	Tree	1.2	24.1	11.1	Orange	1.0	1.1	20.0	11.1	M	A	X						
Burseraceae	*Santiria laevigata*	I	Tree	2.1	15.4	15.8	Black	1.0	1.2	14.2	13.1	M	A						X	
Celastraceae	*Bhesa robusta*	D	Tree	1.1	18.6	11.2	Orange	1.2	0.4	15.2	8.1	M	A				X	X		
Chrysobalanaceae	*Maranthes corymbosa*	I	Tree	9.4	34.5	24.3	Black	1.0	4.1	30.8	17.9	M	A		X		X		X	
Connaraceae	*Agelaea trinervis*	D	Liana	1.0	15.9	10.3	Yellow	1.0	0.9	14.9	10.3	M	A						X	
	Rourea minor	D	Liana	0.9	14.7	10.4	Red	1.0	0.4	11.6	8.0	S	A	X						
Ctenolophonaceae	*Ctenolophon parvifolius*	D	Tree	1.2	19.4	10.4	Orange	1.0	0.9	19.0	9.7	M	A						X	
Elaeocarpaceae	*Elaeocarpus petiolatus*	I	Shrub	0.8	14.5	9.4	Blue	1.0	0.3	13.2	6.8	M	A	X						
Euphorbiaceae	*Bridelia insulana*	I	Tree	0.5	10.2	9.3	Purple	1.0	0.3	8.7	5.8	M	A						X	
	Macaranga gigantea	D	Tree	0.0	2.9	4.2	Purple	1.0	0.0	2.7	3.6	M	A		X					
	Neoscortechinia philippinensis	D	Treelet	4.0	32.9	19.6	Red	1.0	1.7	22.8	15.0	S	A	X				X	X	
Flacourtiaceae	*Hydnocarpus ilicifolia*	T	Treelet	1.0	16.3	11.7	White	1.0	0.8	15.4	11.0	M	A		X					
Gnetaceae	*Gnetum cuspidatum*	I	Liana	3.3	25.2	16.2	Red	1.0	1.8	22.6	12.5	M	A	X						
	G. microcarpum	I	Liana	1.1	18.0	10.5	Red	1.0	0.8	16.2	8.8	M	A	X						
Icacinaceae	*Platea latifolia*	I	Tree	4.5	30.6	16.9	Orange	1.0	1.8	28.4	13.2	M	A						X	
Lauraceae	*Beilschmiedia* sp.BN472	I	Tree	13.9	48.7	22.7	Black	1.0	11.9	47.8	20.2	M	A						X	
	B. sp.L1N800	I	Treelet	6.5	32.0	20.3	Black	1.0	4.9	30.7	18.0	M	A		X					
	Cinnamomum iners	I	Treelet	0.6	11.2	8.8	Purple	1.0	0.2	9.2	6.6	M	A	X						
	C. sintoc	I	Tree	6.0	19.5	22.3	Black	1.0	2.6	15.0	17.2	M	A						X	
	Dehaasia longipetiolata	I	Tree	9.6	35.0	21.3	Black	1.0	4.7	32.4	16.5	M	A				X	X		
	D. sp.12N101	I	Treelet	3.8	31.4	14.7	Black	1.0	2.9	30.1	13.2	M	A						X	
	Litsea castanea	I	Tree	0.5	11.5	9.3	Red	1.0	0.2	8.9	6.8	M	A	X						
	L. costalis	I	Tree	9.9	24.0	27.3	Orange	1.0	2.6	15.8	17.6	H	A	X	X	X	X		X	
	L. grandis	I	Tree	0.5	10.9	7.7	Black	1.0	0.2	8.9	5.6	M	A		X		X		X	
	L. robusta	I	Tree	8.6	19.8	30.5	Red	1.0	3.3	17.1	23.7	M	A	X						
	L. sp2	I	Tree	20.8	42.0	30.4	Red	1.0	13.6	39.3	23.2	M	A						X	
	Nothaphoebe umbelliflora	I	Tree	15.5	41.7	26.9	Black	1.0	7.4	31.4	20.7	M	A		X		X		X	

Table 1. Cont'd

Family	Species	FP	LF	FW	FL	FD	CO	NO	SW	SL	SD	HD	OD	Hornbill species						
														BCH	GH	HH	RH	WCH	WH	WRH
Magnoliaceae	*Magnolia elegans*	D	Tree	0.6	11.9	12.4	Pink	1.0	0.2	9.6	9.3	M	A		X				X	X
Meliaceae	*Aglaia rubiginosa*	D	Tree	15.1	45.8	27.2	Orange	1.0	13.4	41.1	25.4	S	A	X						
	A. spectabilis	D	Tree	9.8	39.6	23.8	Red	1.0	6.7	30.0	20.8	M	A		X		X		X	
	A. sp.BalaL3	D	Treelet	21.2	43.4	29.4	Red	1.0	19.9	42.3	28.2	M	A	X						
	Aphanamixis polystachya	D	Treelet	1.3	17.4	12.9	Red	1.0	1.0	14.6	11.7	S	A						X	X
	Chisocheton ceramicus	D	Tree	11.9	18.5	33.4	Orange	1.0	8.7	16.1	32.3	M	A	X	X		X	X	X	
	Dysoxylum grande	D	Tree	3.9	25.9	19.4	Brown	1.0	2.5	22.4	16.7	S	A		X				X	
	D. macrocarpum	D	Tree	19.9	49.3	30.4	Brown	1.0	14.4	43.6	27.4	M	A		X				X	
	D .rigidum	D	Tree	3.8	22.1	17.6	Red	1.0	3.2	21.0	16.6	M	A	X	X	X	X	X	X	X
Menispermaceae	*Tinomiscium petiolare*	I	Liana	12.7	32.9	26.5	Yellow	1.0	2.6	27.5	18.4	H	A		X					
Moraceae	*Antiaris toxicaria*	I	Tree	5.7	26.2	21.7	Red	1.0	1.9	17.7	14.9	M	A		X					
	Artocarpus elasticus	T	Tree	1.3	15.2	11.0	White	1.0	0.4	12.4	9.1	S	P		X				X	
	A. lacucha	I	Tree	39.2	37.3	44.1	Yellow	9.0	0.1	7.3	5.4	S	A						X	
	A. lanceifolius	T	Treelet	4.3	25.7	17.9	Orange	1.0	1.2	19.6	11.1	S	P		X				X	
	A. rigidus	T	Tree	5.6	26.0	19.9	Orange	1.0	0.8	17.2	10.0	S	P		X				X	X
	Ficus aurantiacea	I	Liana	103.5	68.1	68.2	Purple	900.0	0.0	2.2	0.9	S	A		X					
	F. benjamina	I	Tree	4.3	21.6	20.6	Purple	NA	NA	NA	NA	S	P		X	X	X		X	
	F. caulocarpa	I	Tree	0.1	6.3	6.6	White	119.9	0.0	0.9	0.8	S	A				X	X		X
	F. chartacea	I	Shrub	0.7	10.1	10.9	Red	71.8	0.0	1.7	1.0	S	A		X		X	X	X	
	F. cucurbitina	I	Tree	5.8	36.8	14.4	Red	NA	NA	NA	NA	S	A			X				
	F. deltoidea	I	Liana	0.3	7.5	8.1	Purple	4.1	0.0	3.8	2.2	S	A		X				X	
	F. dubia	I	Tree	15.5	32.8	31.7	Red	NA	NA	NA	NA	S	A	X	X	X	X		X	X
	F. microcarpa	I	Tree	0.4	8.4	9.7	Black	NA	NA	NA	NA	S	A		X					
	F. sundaica	I	Tree	0.8	11.9	12.3	Red	NA	NA	NA	NA	S	A		X	X	X		X	X
	F. vasculosa	I	Shrub	1.0	13.9	12.8	Red	38.0	0.0	1.0	0.8	S	A		X				X	
Myristicaceae	*Endocomia macrocoma*	D	Tree	10.4	34.3	23.1	Red	1.0	5.7	31.9	19.3	M	A		X				X	
	Gymnacranthera farquhariana	D	Treelet	1.7	17.6	14.8	Pink	1.0	1.2	15.0	12.0	S	A						X	
	Horsfieldia irya'	D	Tree	2.5	21.1	15.9	Orange	1.0	1.4	15.8	12.8	M	A		X					
	H. sucosa	D	Tree	9.5	34.2	24.8	Orange	1.0	6.7	27.6	21.6	M	A		X			X	X	X
	H. tomentosa	D	Tree	6.7	30.3	22.1	Orange	1.0	4.3	22.4	19.3	S	A	X	X	X			X	X
	Knema furfuracea	D	Treelet	3.6	22.8	16.0	Red	1.0	2.5	21.2	14.0	M	A		X		X	X	X	
	K. globularia	D	Tree	0.6	11.7	10.4	Red	1.0	0.1	7.2	6.4	M	A	X	X				X	X
	K. hookeriana	D	Tree	10.5	38.0	20.3	Red	1.0	6.8	33.2	17.6	M	A	X						
	K. pseudolaurina	D	Shrub	6.5	27.3	23.3	Red	1.0	3.5	23.6	15.5	M	A		X					
	Myristica elliptica	D	Tree	22.6	53.0	28.8	Red	1.0	16.0	50.3	26.4	H	A	X				X	X	
	M. iners	D	Tree	21.1	45.8	29.8	Red	1.0	16.4	38.0	28.4	M	A	X	X		X	X	X	
Myrtaceae	*Cleistocalyx nervosum*	I	Treelet	0.7	12.7	10.3	Purple	1.0	0.3	7.9	7.1	S	A	X	X				X	
	Syzygium sp.3	I	Tree	3.8	19.1	20.6	Purple	1.0	1.8	13.0	15.7	M	A	X						X
Oleaceae	*Chionanthus ramiflorus*	I	Treelet	3.2	23.0	15.3	Black	1.0	1.1	19.7	9.8	M	A						X	
Passifloraceae	*Adenia* sp.1	D	Liana	0.5	11.2	10.8	White	1.0	0.2	9.9	8.4	M	A	X				X		
Rubiaceae	*Canthium hirtellum*	I	Tree	17.7	33.9	30.7	Green	2.0	1.0	28.9	13.0	H	P		X				X	
Rutaceae	*Luvunga* sp.SK408	I	Treelet	14.1	38.1	25.7	Yellow	1.0	6.0	33.2	17.4	M	P		X					

Table 1. Cont'd

Family	Species	FP	LF	FW	FL	FD	CO	NO	SW	SL	SD	HD	OD	Hornbill species						
														BCH	GH	HH	RH	WCH	WH	WRH
Sapotaceae	*Palaquium impressinervium*	I	Tree	5.5	31.3	20.6	Green	1.5	2.0	26.7	13.7	M	P					X		
	Payena acuminata	I	Tree	7.3	25.6	22.9	Green	1.0	2.0	20.2	13.9	H	A	X						
	Payena sp.1	I	Tree	12.6	45.7	23.7	Green	1.0	1.7	32.2	12.3	M	P	X						
	Payena sp.P5N899	I	Tree	5.1	25.0	19.7	Green	1.0	1.2	19.7	11.6	M	P					X		
Sterculiaceae	*Sterculia balanghas*	D	Treelet	0.5	11.2	8.4	Black	1.0	0.4	10.7	7.8	M	A		X		X		X	
	S. macrophylla	D	Tree	2.6	22.2	16.4	Black	1.0	2.0	19.7	14.5	M	A						X	
	S. parviflora	D	Tree	3.2	26.2	16.6	Black	1.0	3.0	26.1	16.5	M	A	X	X				X	
Symplocaceae	*Symplocos cerasifolia*	I	Tree	7.7	36.1	20.1	Blue	1.0	2.0	29.6	15.5	M	A		X				X	
Theaceae	*Ternstroemia wallichiana*	D	Tree	1.9	21.0	15.1	Red	1.0	1.9	21.4	15.8	H	A		X				X	
Thymelaeaceae	*Gonystylus maingayi*	D	Tree	4.3	32.8	18.2	Yellow	1.0	2.2	24.7	15.6	M	A						X	
Tiliaceae	*Microcos tomentosa*	I'	Treelet	1.4	19.2	12.7	Orange	1.0	0.7	16.4	9.4	M	A							X
Ulmaceae	*Gironniera hirta*	I	Tree	0.1	7.9	6.9	Orange	1.0	0.0	5.2	4.9	M	A		X				X	X
Miscellenea	Unknown sp.1	I	Liana	0.3	9.5	7.8	Red	1.3	0.1	5.7	5.2	M	P		X					
33 families	93 species													31	49	7	20	14	57	16

Table 2. Parameter estimates for generalized linear models (GLM) determining the probability that a fruit species is included in the diet of hornbills. Parameters shown in bold indicate significant (P<0.05) predictors.

Parameters	Df	Deviance	Resid. Df	Resid. Dev	P(>|Chi|)
NULL			435	438.6	
Fruit diameter	1	2.26	434	436.3	0.130
Number	1	0.55	433	435.8	0.460
Seed diameter	1	7.33	432	428.4	**0.010**
Fruit protection	3	31.26	429	397.2	**0.000**
Life form	3	77.41	426	319.8	**0.000**
Fruit colour	6	19.46	420	300.3	**0.003**
Odour	1	0.04	419	300.2	0.840
Seed hardness	2	5.47	417	294.8	0.060

comprised 13% of collected fruit species, shrubs 32%, treelets 21%, and trees 34%.

Characteristics of hornbill-dispersed fruits. – Of the 458 fruit species examined, 245 (53%) were casually observed to be eaten by animals. Of these, hornbills consumed at least 93 fruit species of 55 genera from 33 families (Table 1). The number of fruit species consumed by each hornbill species varied from 7 for *B. vigil* to 57 for *R. undulatus* (Table 1). In hornbill diets, the most species-rich families were Moraceae (15 spp.), Lauraceae (12 spp.), Myristicaceae (11 spp.), Annonaceae (8 spp.), and Meliaceae (8 spp.). Within these families, *Ficus* (Moraceae) was the most species-rich genus (10 spp.), followed by *Litsea* (5 spp.) and *Knema* (4 spp.). Median fruit weight for the species eaten by hornbills was 3.9 g (range 0.03–103.5 g), and the median fruit diameter was 17.6 mm (4.2–68.2 mm). The median weight of consumed seeds was 1.60 g (0.01–19.9 g), and the median diameter was 12.9 mm (0.8–32.3 mm).

Of eight variables that we examined, four (seed diameter, fruit protection, life form, and fruit colour) differed significantly between diet and non-diet fruits (Table 2). Hornbills consumed various fruits in terms of the size of the fruit/seed; however, the smallest and largest fruits available in the forest were not consumed (Fig. 2). Hornbills were never observed eating nuts and were only rarely observed eating indehiscent fruits with a thick husk, but they ate dehiscent fruits and indehiscent fruits with a thin husk (Fig. 3a). Hornbills tended to consume fruits from trees and avoid fruits from shrubs (Fig. 3b). Hornbills preferred to consume red or black fruits, but not brown fruits (Fig. 3c).

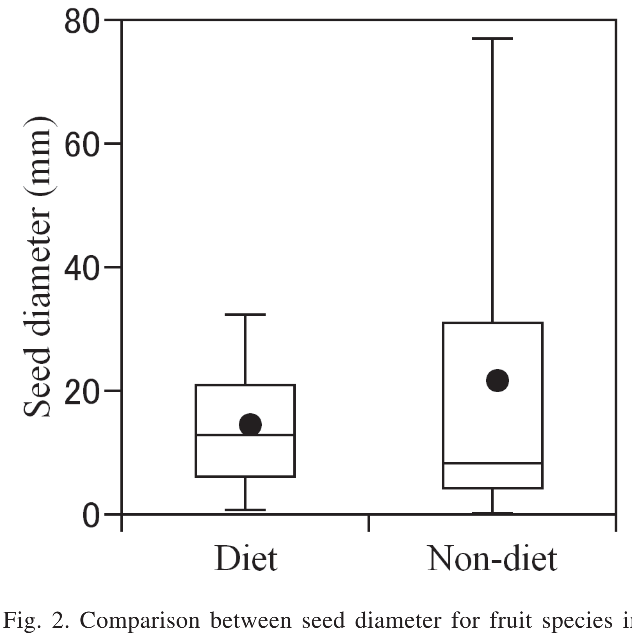

Fig. 2. Comparison between seed diameter for fruit species in hornbill diets (N=93) and non-diet fruit species (N=365) collected in this study.

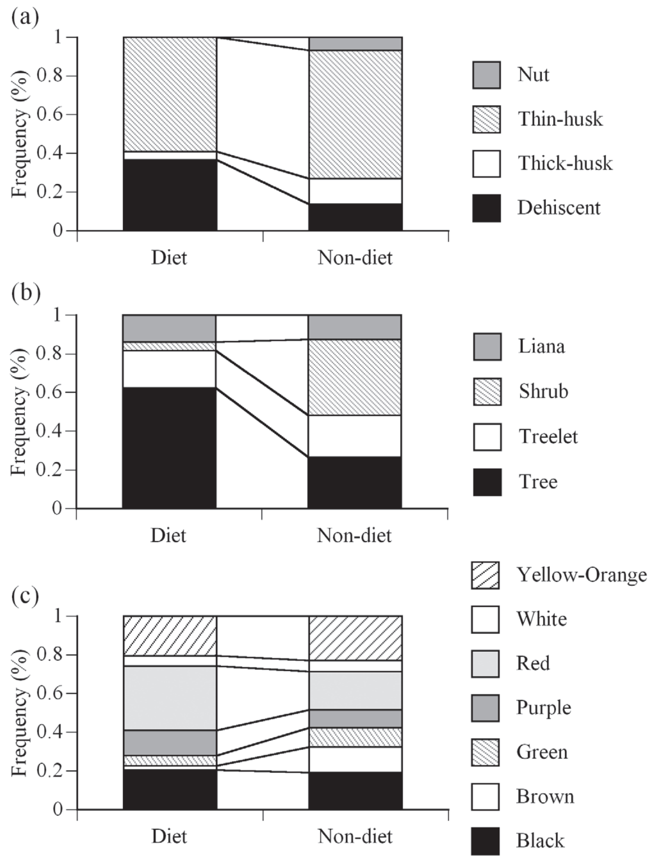

Fig. 3. Comparison between the percentage of plant species (% species) with specific fruit traits in hornbill diets (N=93) and non-diet fruit species collected in this study (N=365). (a) fruit protection; (b) life form; (c) fruit colour.

Table 3. Dietary diversity for Asian hornbills found in this study compared with those studies elsewhere in tropical Asia.

Hornbill Species	Study location	Fruit Diversity			Source
		Family	Genus	Species	
Anorrhinus galeritus	Borneo	19	30	93	(Leighton 1982)
	Sumatra	12	21	42	(Kinnaird and O'Brien 2007)
	S-Thailand	16	24	31	This study
Buceros bicornis	NE-Thailand	23	38	55	(Poonswad et al. 1998, Kanwatanakid-Savin et al. 2009)
	S-India	14	16	19	(Kannan and James 1997)
	NE-India	9	12	19	(Datta and Rawat 2003)
	S-Thailand	19	31	49	This study
B. rhinoceros	Borneo	10	14	41	(Leighton 1982)
	Sumatra	11	15	31	(Kinnaird and O'Brien 2007)
	S-Thailand	9	15	20	This study
B.vigil	Borneo	1	1	6	(Leighton 1982)
	Sumatra	1	1	6	(Kinnaird and O'Brien 2007)
	S-Thailand	4	4	7	This study
Aceros comatus	Borneo	7	10	22	(Leighton 1982)
	Sumatra	10	16	18	(Kinnaird and O'Brien 2007)
	S-Thailand	8	12	14	This study
A. corrugatus	Borneo	9	11	26	(Leighton 1982)
	S-Thailand	10	13	16	This study
Rhyticeros undulatus	NE-Thailand	26	40	58	(Poonswad et al. 1998, Kanwatanakid-Savini et al. 2009)
	Sumatra	13	36	56	(Kinnaird and O'Brien 2007)
	India	17	24	34	(Datta and Rawat 2003)
	orneo	14	23	57	(Leighton 1982)
	S-Thailand	23	38	57	This study

DISCUSSION

We recorded 93 fruit species belonging to 33 families in hornbill diets in dipterocarp forests of southern Thailand. The diet list given here is unlikely to be complete; for example, at least 60 fig species were collected in the Bala sector of HBWS (Chantarasuwan & Thong-Aree, 2006), but we only collected 21 species of figs in this study. Nevertheless, we believe that this list was generated over a sufficient time period (our results and the opportunistic observations of other authors) to allow a preliminary comparison between the traits of fruits in hornbill diets and traits of fruits in their habitat.

The number of fruit species recorded within the diet of Asian hornbills at a given study site varies widely. For example, 121 species in 22 families were recorded in the diet of five hornbill species (*B. rhinoceros, B. vigil*, *R. undulatus*, *A. galeritus*, and *Anthracoceros albirostris*) in a Bornean forest (Leighton. 1982), 64 species in 15 families were in the diet of four species of hornbills (*B. rhinoceros*, *B. vigil*, *R. undulatus*, and *A. galeritus*) in a Sumatran forest (Hadiprakarsa & Kinnaird, 2004), 52 species in 12 families for *Aceros cassidix* in a Sulawesi forest (Kinnaird & O'Brien, 1993; Suryadi et al., 1994), 73 species in 32 families for four species of hornbills (*B. bicornis*, *R. undulatus*, *Anorrhinus austeni*, and *Anthracoceros albirostris*) in a Thai forest (Kitamura et al., 2002; Kitamura et al., 2004b), and 79 species in 22 families for three species of hornbills (*B. bicornis*, *R. undulatus*, and *A. albirostris*) in an Indian forest (Datta, 2001; Datta & Rawat, 2003). The dietary diversity of hornbills recorded in our study (93 species) is relatively high compared with previous findings, except for hornbills in Borneo.

The number of fruit species eaten by hornbills does not in itself demonstrate the importance of hornbills as seed dispersers. The relative importance of hornbills as seed dispersers almost certainly differs among seasons and among different parts of the habitat. One method of identifying the relative importance of hornbills in a given frugivore community is to hypothesize that highly frugivorous species that disperse a large number of different plant taxa will have consistently greater impacts on regeneration in tropical forest communities than will species that disperse fewer plant taxa (Whitney et al. 1998). Following this definition, hornbills in our study sites were observed to disperse 20% of the fruits collected. This is at the lower end of the range of values reported for other hornbill study sites elsewhere. In other study sites, hornbills consumed and presumably dispersed at least 22% of plants with flesh-covered seeds in a Cameroon forest (Whitney et al., 1998) and 27%, 28%, 32%, and 39% in forests in Thailand, India, Sumatra, and Sulawesi, respectively (Kitamura et al., 2002; Kinnaird & O'Brien, 2005; Datta & Rawat, 2008).

In species-rich systems, understanding of ecological interactions is constrained by the high number of potential interactions between species. Both of our study sites are dominated by dipterocarp trees, but many animal-dispersed plants are present. Of these, obviously, hornbills eat only a subset of the animal-dispersed fruits. Our GLM analysis revealed that seed diameter, fruit protection, life form, and fruit colour were important factors for fruit selection by hornbills. In Sulawesi, Red-knobbed Hornbills (*Aceros cassidix*) preferentially select fruits that ripen to red, purple, or black (Suryadi et al., 1994). Similarly, hornbill-dispersed fruits from northeastern Thailand are: 1) large, 2) easily accessible within the canopy, 3) red, purple, or black, and 4) dehiscent or indehiscent with a thin husk (Kitamura et al., 2004b). We obtained similar selection criteria for our focal hornbills in dipterocarp forests in southern Thailand. Although fruit diversity varies highly among these study sites, hornbills in lowland dipterocarp forests of southern Thailand consumed similar fruits reported elsewhere in Southeast Asia. The influence of seed diameter and fruit protection on fruit selection may reflect the fact that hornbills cannot easily manipulate well-protected fruits, but are less constrained by size. Small plants seemed to negatively affect fruit selection by hornbills, possibly because the small crop size offered by these shrubs decreases their visibility to foraging birds.

Despite the wide range of fruit species included in this study, we acknowledge certain research limitations that enabled us to examine in greater depth the relative importance of hornbills as seed dispersers in their habitat. First, we concentrated on morphological fruit traits. Other factors, such as crop size (Kinnaird et al., 1996; Hadiprakarsa & Kinnaird, 2004), phenology (Whitney & Smith, 1998; Holbrook et al., 2002; Poulsen et al., 2002), tree distribution (Kinnaird et al., 1996), and nutrients in fruit pulp (O'Brien et al., 1998; Poonswad et al., 1998; Poonswad et al., 2004; Kanwatanakid-Savini & Poonswad, 2007) also influence fruit preference by hornbills. Second, our approach was predicated on the assumption that all seven species of hornbills consume similar fruits and therefore disperse similar seeds. Different hornbill species may have different dispersal methods. Larger hornbills tend to perch in the upper canopy, but smaller hornbills tend to perch in the middle or lower canopy levels, as well as in the upper canopy in the forest (Datta & Rawat, 2003; Hadiprakarsa & Kinnaird, 2004). These different habitat uses in the forest may affect the chances that a seed will be dispersed to a favourable site in an unpredictable location (Wheelwright & Orians, 1982). Third, we used a general linear model to determine the influence of fruit traits on consumption by hornbills without considering the effect of phylogeny. Species are phylogenetic units with shared evolutionary histories and are not therefore statistically independent units (Felsenstein, 1985). In future studies, a complete phylogeny of the study plants should be used.

The number of possible pairs of fruits and frugivores is enormous in the tropics, but fruit–hornbill relationships are structured so that only a subset of the possible interactions actually occurs. Even a preliminary assessment of the impact of disperser losses on plants and changes in fruit supply on animals requires information about the animal species that eat fruits and disperse seeds (Corlett, 1998). However, the collection of such information is extremely time-consuming, especially in diverse tropical forests, and we are frequently asked to inform management decisions in the absence of comprehensive data (Dennis & Westcott, 2006; Moran et al., 2009). This study provides a preliminary inventory of fruit-hornbill interactions in lowland dipterocarp forests of southern Thailand, allowing for comparisons across forest types in which different hornbill species perform similar roles.

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