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FOOD CONSUMED BY GREAT HORNBILL AND RHINOCEROS HORNBILL IN TROPICAL RAINFOREST, BUDO SU-NGAI PADI NATIONAL PARK, THAILAND

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ABSTRACT. – Great and Rhinoceros Hornbills are omnivorous. Food consumed by these two species was studied during the breeding season (January to July of 2003 and 2004) in tropical rainforest, Budo Su-Ngai Padi National Park. The results showed that the Great and the Rhinoceros Hornbills had similar duration of every phase in the breeding cycle, i. e. nest visiting, sealing, incubation, early nestling and late nestling. However, considering the entire breeding cycle, Great Hornbill had significantly shorter cycle (110.6±6.7 days) than that of the Rhinoceros Hornbill (121.7±10.4 days). Total food consumption rate of Great Hornbill was significantly less than (47.0 g/Obs.h.) that of the Rhinoceros Hornbill (62.5 g/Obs.h.), and the diet was comprised of fig (53.6%), non-fig (41.5%) and animal (4.9%). Proportion of fig in the diet of Rhinoceros Hornbill was also significantly higher (72.3%), but similar proportion of non-fig (23.5 %) and animal (4.2%). Of the total 21 species of non-fig diet of both Great and Rhinoceros Hornbills in this study, *Polyalthia* sp. (family Annonaceae) and *Aglaia spectabilis* (family Meliaceae) dominated fruit food by weight, while millipede dominated animal food. There was no difference in diversity of non-fig fruit species consumed during all phases between both hornbills except during late nestling. In general, the diet of Great Hornbill has significantly higher diversity than that of Rhinoceros Hornbill. From similarity coefficient, it was indicated that they used the same food resources which were mainly available during the study period.

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KEY WORDS. – Food consumption, Great Hornbill, Rhinoceros Hornbill, Thailand.

INTRODUCTION

Hornbills play important ecological roles as seed dispersers and predators (Poonswad, 1999). Although they are omnivorous, fruits are their main food. They spend much time on searching for fruiting resources (Poonswad & Tsuji, 1994). Hornbills are distributed throughout forested areas of the country. They are found from the mountainous evergreen forest to low land evergreen forests, including tropical rain forest (Lekagul & Round, 1991). These vegetation types provide healthy food sources and nest sites. Presently, in Thailand, there are a few number of studies on food of sympatric hornbill species, including Great (*Buceros bicornis*), Wreathed (*Rhyticeros undulates*), White-throated Brown (*Ptilolaemus austeni*) and Oriental Pied Hornbills (*Anthracoceros albirostris*) studied at Khao Yai national Park in breeding season (Poonswad et al., 1998a). Savini (2007) studied food overlap and fruit selection among four sympatric hornbill species during different phases of their annual cycle. Chimchome et al. (1998) listed food of Rufous-necked Hornbill (*Aceros nipalensis*), while Ouithavon et al. (2005a,b) reported feeding ecology and some characteristics of food of two sympatric species, i.e. Rufous-necked and Great Hornbills of Huai Kha Khaeng Wildlife Sanctuary. Other than these, there are some studies on food of Great, Malabar Grey (*Ocyceros griseus*), Malabar Pied Hornbills (*Anthracoceros coronatus*) and Narcondam Hornbill (*Rhyticeros narcondami*) in India (Balasubramanian et al., 2004; Datta, 2001; Hussain 1984; 1993; Kannan, 1994; Kannan & James, 1997; 1999; Mudappa & Kannan, 1997; Reddy & Basalingappa, 1993). Food of some island species was studied, including Wreathed Billed hornbill (*Aceros waldeni*) and Visayan Tarictic Hornbill (*Penelopides panini panini*) (Kauth et al., 1998, Curio, 2005). Klop et al. (1999) studied diet composition of Visayan Tarictic Hornbill in breeding season, and Suryadi et al. (1998) studied food preferences of Sulawesi Red-knopped Hornbill (*Aceros cassidix*) in non breeding season. Hadiprakarsa & Kinnaird (2004) studied the diets of four Sumatran hornbill species. Most of those studies were for individual species. There was no diet study that compared between sympatric species of the same genus, such as Great and Rhinoceros hornbills (*B. rhinoceros*) which high similarity will be expected because they are expected to obtain food from the same source. Leighton (1986) studied the pattern of feeding among sympatric Bornean hornbills, including Rhinoceros Hornbill, but did not intensively compare their diet. General information on food of Great and Rhinoceros Hornbills was documented in Ali & Ripley (1989) and Smythies (1981). In Thailand, sympatric Great and Rhinoceros Hornbills are found in Peninsular Thailand. They are also found in the tropical rainforest of Budo Su-Ngai Padi National Park situated in the farthest South of Thailand border to Malaysia. During 1994–2000, the percentage of nesting hornbills in Budo Su-Ngai Padi National Park had decreased from the highest (80.9%) in 1997 to the lowest (36.4%) in 2000. Serious threats to hornbill population by human in this national park include illegal logging and slash and burn for cultivation (Poonswad et al., 2001) that decrease potential nest trees and food sources. This will inevitably increase competition for nest trees and food sources, particularly between the hornbill species, which are similar in size and closely related as the Great and the Rhinoceros Hornbills. Thus, this research presents comparative study on species richness, diversity, similarity and feeding rate of the diets during the breeding season of these two sympatric species.

METHODS

Study area. **–** The study was carried out within an approximately 50 km^2 area in a tropical rainforest of Budo Mountain (189 km^2; location 6°2'–6°37'N and 101°30'–101°41'E), a sector of Budo Su-Ngai Padi National Park (340 km^2) which comprises two unconnected sections, Su-Ngai Padi and Budo Mountains (Fig. 1). Its elevation ranges from 100 to 825 m asl. The vegetation lies within the Malaysian floral region which is dominated by Dipterocarpaceae (Poonswad et al., 1999; Chaisuriyanun, 2005). At Budo Mountain, six sympatric hornbill species include Great, Rhinoceros, Helmeted (*Rhinoplax vigil*), Wreathed, White-crowned (*Berenicornis comatus*) and Bushy-crested Hornbills (*Anorrhinus galeritus*) (Poonswad et al., 2005). The area experiences heavy illegal logging even after the designation as a national park in 1999 (Poonswad et al., 2005). Mean annual rainfall was 2,900 mm (1998-2003) with a marked wet season from the end of August to January and a dry season from February to August. Minimum rainfall was recorded in April (101.5 mm) and maximum was in December (736 mm). Mean monthly temperature ranged from 25.3°C (December and January) to 29.4°C (April and May). The average monthly relative humidity ranged from 77% (April, May and July) to 88% (November) (Narathiwat Climatologic Station, Meteorological Department 2004).

Studied species. **–** Ten nests of Great and Rhinoceros Hornbills, five each, were selected from the existing 43 nests of Great and 33 nests of Rhinoceros Hornbill (found during 1994-2002 by villagers who have been working for the Thailand Hornbill Project) based on location, which was at least one km away from fruit orchards and human settlements as shown in Fig. 1. Those nests may not all be active during the study period. We observed a total of 17 breeding pairs in two breeding seasons between January and July of 2003 and 2004. In 2003, we were able to observe seven breeding pairs, five of Great and two of Rhinoceros Hornbills. In 2004, ten breeding pairs, five Great and five Rhinoceros Hornbills were observed.

Data collection. **–** These Great and Rhinoceros Hornbills have slightly different breeding strategy from others by having imprisoned females emerge from the nest cavity after chicks hatch for about six weeks (Poonswad et al., 2004; Reilly, 1989). The observation on food consumed by these studied hornbills throughout the breeding cycle, which was defined as the period when a pair visited their nest until the chick fledged, was done at nest sites. The breeding cycle is divided into nest visiting, nest sealing, incubation, early nestling and late nestling phases. Phases in the entire breeding cycle were defined as follows, and the duration of each phase was determined for both species.

- Nest visiting phase was defined when a pair visited a nest cavity until the female entered to seal the nest. This phase was indicated by the presence of fresh faeces on

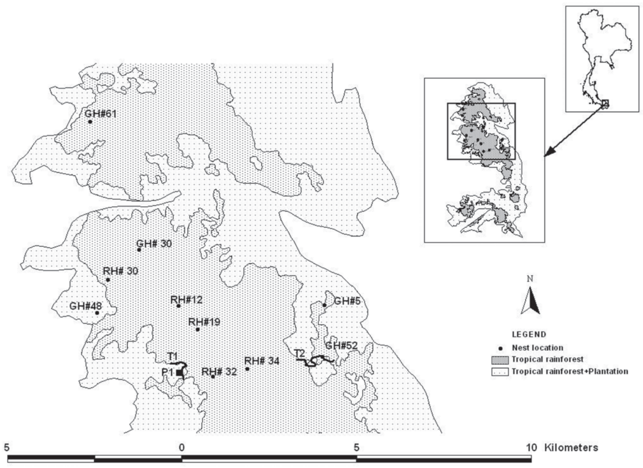

Fig. 1. Study area; nest locations of Great and Rhinoceros hornbills (GH and RH) and site of vegetation survey; a one hectare plot (P1) and two transects (T1 and T2) in Budo Mountain; Budo Su-Ngai Padi National Park, Southern Thailand.

the ground or leaves under the nest cavity and around the nest tree.

- Nest sealing phase was defined when the female began to seal the nest entrance until the sealing was complete.
- Incubation phase was after the female was imprisoned for one week until the chick hatched (Poonswad, 1993). Due to difficulty in detecting the actual hatching, the incubation period was then estimated according to Poonswad et al. (2004) who reported the incubation period of Great Hornbill at Khao Yai National Park, i.e. seven weeks after female has imprisoned.
- Early nestling phase was the period after chick hatching until female emerging.
- Late nestling phase was the period after female emerging until chick fledging.

Number of days and hours spent on each breeding phase was summarized in Table 1.

***Food and feeding*. –** At each nest, observations on food species and quantity of each feeding were made from a blind for about 5–9 hour per day (starting between 0800–1000 hours until 1500–1700 hours depending on distance and terrain of nest location) at 3–4 days interval.

The blinds were built as close to the nest as possible, depending on the surrounding and sensitivity of the breeding pair, but far enough not to disturb their regular activities (usually 10–20 m from the nest tree). Food items brought for each meal by the male were classified as fruit or animal, and identified and counted by direct observation assisted by a spotting scope or a pair of binoculars or digital video camera recorder. The identified fruit species, except for those of figs (*Ficus* spp.), was confirmed by regurgitated seeds collected from beneath the nest cavity. The seeds of unknown species found under the nest were counted and identified by comparison with the seeds of fallen fruit under a mother tree. In order to obtain a total wet weight of fruit food consumed per hour, mean weight of pulp from 15–160 ripe fruits of each species collected under the mother tree was calculated depending on the size of fruit. Abundance of fruit food trees within the study area was checked by setting a plot of 1 ha (100m × 100m) and two transects (1km × 10m each) (Fig. 1). In the plot, we recorded the number of food trees with dbh ≥ 10 cm, and along these transects all food trees with such size were recorded. No attempt was made to study the phenology of those food plants. For known animal-food items, we collected 10–20 individuals of each animal food species to obtained mean weight for the calculation of a total animal food consumed per hour. However, due to the difficulty in identification of animal food items, no further attempt had been made to classify them.

***Data analysis*. –** We analyzed food consumption by both species according to phases in the breeding cycle including only incubation, early and late nestling phases. We categorized food delivered to the brood into fig, non-fig and animal. Diversity of food, the Shannon-Wiener index (H′) (Shannon and Weaver 1949) and Simpson's reciprocal index (1/D) (Simpson, 1949) were applied to indicate the diversity of the non-fig and animals in the diet of these two studied species of hornbills. To determine the similarity of the diet consumed by these two hornbill species, coefficient of similarity was modified from Kemp (1976).

RESULTS

***Breeding cycle*. –** The breeding season of the studied hornbills in Peninsular Thailand began in March and ended in July, the driest months. The breeding season of the Great Hornbill started about one week earlier than the Rhinoceros Hornbill (Fig. 2). However, both species had similar breeding scheme, i.e. nest visiting began as early as late December until mid January, female imprisonment began during early to late March, emergence during mid- to late- June, and the only chick fledged during late-June to late-July (Fig. 2). The duration of each phase of both species was relatively similar, but the entire breeding cycle was significantly different (Mann-Whitney *U*-test, $U = 12.0$, $P = 0.024$) and about ten days difference (Table 2).

***Species richness and diversity of diet.* –** Great and Rhinoceros Hornbills were found to be omnivorous, consuming both fruits and animals. The different types of fruit and animal food and weight consumed during various phases in the breeding cycle by both species are given in Tables 3 and 4. The diet was categorized into fig, non-fig and animal (in methods). There were at least eight species of figs found, but no attempt to identify further. Among non- fig food items, there were 18 identified species from 13 genera in nine non-fig families and three unknown species recorded. The Great Hornbill consumed 17 species of 12 genera in nine families and three unknown species, whereas Rhinoceros Hornbill consumed less number of species, 13 species of 11 genera in eight families (Table 3). We did not include *Artrocarpus* sp. in the calculation for food plant diversity and weight due to such fruit consumed by only one nest of Great Hornbill, for which data was inadequate. Therefore data from such nest was omitted, except for food species recorded. Of animal food items, the Great Hornbill consumed at least 17 taxa, whereas the Rhinoceros Hornbill consumed at least 15 taxa (Table 4).

There was no difference of diversity of non-fig fruit consumed during each phase of Great and Rhinoceros Hornbills for both indices (Table 5). Overall, diversity of animal food

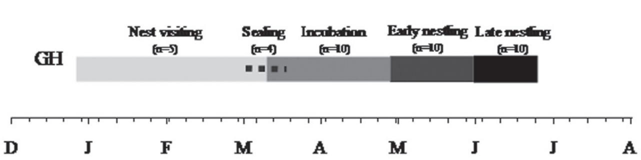

Fig. 2. Breeding cycle of Great and Rhinoceros Hornbill at Budo Mountain, 2003-2004.

Table 1. Number of hour (day) observation and phase duration of Great and Rhinoceros hornbills on each breeding phase (GH = Great hornbills and RH = Rhinoceros hornbills).

Hornbill species	No.of pair-year	Total no. of hour (day) observation	No.of hour (day) observation and phase duration									
			Nest visiting		Nest sealing		Incubation		Early nestling		Late nestling	
			No.of hour (day) observation	Phase duration	No.of hour (day) observation	Phase duration	No.of hour (day) observation	Phase duration	No.of hour (day) observation	Phase duration	No.of hour (day) observation	Phase duration
GH	10	1,489 (220)	119.5 (33)	8 weeks before Female impresoned date	16.1 (5)	weeks 1-2	474.0 (65)	weeks 3-8	449.6 (63)	weeks 9-13	429.5 (54)	weeks 14-17
RH	7	811 (128)	43.0 (14)	8 weeks before female impresoned date	27.0 (6)	week 1	244.2 (36)	weeks 2-7	253.3 (36)	weeks 8-13	243.7 (36)	weeks 14-18

consumed by both species differed indicated significantly by both indices. Considering all three phases, it appeared that only during late nestling phase, the Great Hornbill consumed significantly higher diversity than that of Rhinoceros Hornbill (Table 5).

***Contribution of non-fig and animal food species in the diet*. –** Among the non-fig diet, it was found that *Polyalthia* sp. was the major component that contributed for 40% and 50% by weight of total non-fig fruits consumed by Great and Rhinoceros Hornbills respectively, and followed by *Aglaia spectabilis* (16.5% and 20.4%, respectively) for entire breeding cycle (Table 3). Considering non-fig fruit consumed by phase, *Polyalthia* dominated in all phases of the Great Hornbill, except for the incubation phase which was dominated by *Litsea grandis* (24%). Similarly to that of Rhinoceros Hornbill, *Polyalthia* dominated in all phases, except for incubation phase which was dominated by *Aglaia spectabilis* (46%) instead (Table 3).

In total, both species consumed similar weights of animal food (Table 4). Among 18 taxa of animal food, millipede was most commonly consumed by both hornbills (the Rhinoceros Hornbill consumed at least 67% by weight of total animals eaten), and the second most common animal food item is the flying horned lizard (9.2%). For the Great Hornbill, although millipede dominated in animal food, it contributed only 30% by weight and skink was the second most common food item (19%) (Table 4).

***Food similarity*. –** As both the Great and Rhinoceros Hornbills live in sympatry, they were expected to use similar food resources. The fig species consumed by both hornbills were similar but the degree of similarity was not calculated because the species could not be identified. The non-fig and animal proportions in the diet of both hornbills showed relatively high similarities, especially in the late nestling phase (Table 6). Of the 21 species of non-fig food items, 12 species (57%) were eaten by both hornbill species. Eight species (38%) were eaten only by Great Hornbill, and only one species (5%) was eaten only by Rhinoceros Hornbill (Table 3). Of the 18 animal food items, 14 (78%) were eaten by both hornbill species. Rat and squirrel were occasionally eaten only by Great Hornbill, while earthworms were eaten only by Rhinoceros Hornbill, but in small amounts (Table 4). The overall degree of similarity between years within species was less than that between species (Table 6). When considering diet in each breeding phase, the degree of similarity among Great Hornbill breeding pairs between years in the late nestling phase was high for both non-fig and animal food items (Table 6).

***Food consumption rate*. –** The average of overall feeding rate for the entire breeding cycle of Rhinoceros Hornbill was significantly higher than that of Great Hornbill. The proportions of the three food categories, indicate that the fig features highly for the Rhinoceros Hornbill (72.3%), while Great Hornbill consumed greater proportion of non-fig food item (41.5%); and both species consumed similar proportion of animal food items (4.2% and 4.9%, respectively) (Table

Table 2. The length of various breeding phases and the entire breeding cycle of Great and Rhinoceros hornbills in breeding seasons.

Hornbill species	The phase duration in the breeding cycle (days)					
	Nest visiting	Nest sealing	Incubation	Early nestling	Late nestling	Entire cycle
GH mean ± sd	60.6 ± 13.6 (n=5)	14 ±12.8 (n=4)	42*	34.1 ± 5.9 (n=10)	27.5 ± 5.7 (n=10)	110.6 ± 6.7 (n=10)
RH mean ± sd	58.6 ± 20.8 (n=5)	9.3 ± 7.9 (n=4)	37- 46**	38.9 ± 9.2 (n=7)'	33.9 ± 11.4 (n=7)	121.7 ± 10.4 (n=7)

* The duration estimated follows Poonswad (1999)
** The duration estimated follows Reilly (1989)

7). Overall, the feeding rates of the three food categories by both species during different phases did not differ, except for the proportion of fig of all phases and animal during incubation phase (Table 7). If the feeding rate of total food is considered, there was significant difference for the late nestling phase and the entire breeding cycle.

DISCUSSION

Diet diversity, composition and similarity. – It is obvious that both the Great and Rhinoceros Hornbills were frugivorous, with over 95% of total weight consisting of fruits (Table 3). In general, the diversity of diet (fruits and animals) of the Great Hornbill studied at Khao Yai National Park (KY) and Huai Kha Khaeng Wildlife Sanctuary (HKK) are more diverse than this study (Poonswad et al., 1998a; Ouithavon et al., 2005a). The diversity of fruit and animal diet eaten by Great Hornbill studied at KY and HKK is similar as indicated by Shannon Weiner index (H′) (KY: H′=1.95, Poonswad et al. 1998a and HKK: H′=2.27, Ouithavon et al. 2005a) but higher than this study (H′=1.61). The Great Hornbill in this study seemed to feed on larger amount of certain diet species than the Rhinoceros Hornbill (Table 5), i.e. the Great Hornbill fed on species which were more abundant. The Shannon-Wiener and Simpson's reciprocal indices in this study suggest that the diversity of non-fig fruits consumed by both Great and Rhinoceros hornbills was similar (Table 5). Whereas the animal diet diversity as measured by the Shannon-Wiener index and the Simpson's reciprocal index suggest that the Great Hornbill consumed greater diversity of diet than that of Rhinoceros Hornbill which consumed larger proportion on certain species, e.g. millipedes (Table 5).

The diet of the Rhinoceros Hornbill is clearly dominated by figs (72%) as compare with that of the Great Hornbill (54%), while both species also consumed animal diet. The proportion of fig category consumed by Rhinoceros Hornbill in this study is similar to that of Rhinoceros Hornbill studied in Sumatra (77%) (Hadiprakarsa & Kinnaird, 2004). Leighton (1986) reported that Bornean Rhinoceros Hornbill consumed more non-fig than fig but did not specify the proportion or percentage. From the consumption rate of figs (Table 7), it can be speculated that figs were available throughout the breeding cycle. It seems that hornbills that feed on figs with great proportion tends to eat less dietary diversity. The diet composition of Great Hornbill observed in this study (54%) is similar to that of Great Hornbill at Khao Yai National Park (KY) (56%) (Poonswad et al., 1998a), but both are greater than that of Great Hornbill at Huai Kha Khaeng Wildlife Sanctuary (HKK) (46%) (Ouithavon et al., 2005a observed from only two pairs). It should be noted that the proportion of animal food consumed by the Great Hornbill at KY and HKK are much higher (14% and 21%, respectively, Poonswad et al., 1998a, Ouithavon et al., 2005a). In this study, the delivery of non-fig fruits and animals (degree of similarity) were relatively similar between Great and Rhinoceros hornbills, and is similar to those of four sympatric hornbill species studied at KY (Poonswad et al., 1998a). Hence, they obtained food from the same source.

The total diet of both the Great and Rhinoceros Hornbills in this study was dominated by *Polyalthia* sp. (family Annonaceae) and *Aglaia spectabilis* (family Meliaceae) by weight. This is similar to those of the Great Hornbill at KY and HKK (Poonswad et al., 1998a; Ouithavon et al., 2005a). Although the Great and Rhinoceros Hornbills fed on similar fruit species, however, the difference in degree of consumption and proportion of different species of fruits (fig and non-fig fruit) suggests that these two closely related species clearly avoid competition over food resources. Hence, they may have foraged in different parts of habitat and their niche selection is forced by competition (McFarland, 1981).

Diet consumption rate and breeding cycle. – The Rhinoceros Hornbill had significantly higher total food and fig consumption rate than that of the Great Hornbill (Table 7). Interestingly, although total food consumption rate of Rhinoceros Hornbill was higher than that of Great Hornbill, we expected the former species would have shorter nestling phase, but in contrary, the average total duration of nestling phase of Great Hornbill was shorter (62 days and 73 days, respectively; Tables 2 and 7). From the feeding rate of three diet categories, the Rhinoceros Hornbill fed much more on fig than the Great Hornbill, where as the rest were similar. Although the nestling phase of Rhinoceros Hornbill was longer, the average weight of Rhinoceros Hornbill nestling was lighter than that of the Great Hornbill (1.3 and 1.9 kg). Is the growth rate of Great Hornbill chick faster than that of the Rhinoceros Hornbill? It is sensible that the breeding cycle of Great Hornbill at KY takes longer period (120 days) than this study (111 days), and total consumption rate is much lower (KY: 305 g/day or 30.5 g/hr; this study: 47.0

Table 3. List of non-fig food plants species, weight and percentage (in bracket) of fruit species consumed by Great and Rhinoceros hornbills during different phases and a total (a=inadequate data not for weight calculation but was included in food list, INC= Incubation phase, EN=Early Nestling phase and LN=Late Nestling phase).

Non-fig fruit diet species		**Mean weight (g/Obs.h) and percentage of non-fig fruit diet**							
		GH				**RH**			
		INC	**EN**	**LN**	**Total**	**INC**	**EN**	**LN**	**Total**
Annonaceae	*Desmos cochinchinensis*	0.003 (0.02)	0.01 (0.04)		0.01 (0.02)				
	Polyalthia sp.	**2.77 (21.1)**	**11.59 (47.0)**	**5.96 (42.6)**	**20.00 (39.9)**		**4.28 (35.0)**	**20.83 (66.1)**	**22.14 (49.6)**
Lauraceae	*Litsea grandis*	**3.18 (24.2)**	0.37 (1.5)		3.15 (6.3)	**0.53 (9.9)**		**3.32 (10.5)**	3.37 (7.5)
	Litsea sp.01	1.73 (13.2)	1.5 (6.1)		3.02 (6.0)				
Meliaceae	*Aglaia lawii*			0.15 (1.1)	0.15 (0.3)		0.12 (1.0)	0.08 (0.3)	0.18 (0.4)
	Aglaia spectabilis	1.03 (7.8)	**3.58 (14.5)**	**3.79 (27.1)**	**8.27 (16.5)**	**2.47 (46.1)**	**3.55 (29.1)**	**3.57 (11.3)**	**9.08 (20.3)**
	Chisocheton erythrocarpus		0.16 (0.6)		0.16 (0.3)			0.1 (0.3)	0.09 (0.2)
	Dysoxylum macrocarpum	0.06 (0.5)	1.28 (5.2)	**1.88 (13.4)**	3.21 (6.4)	0.18 (3.4)	0.28 (2.3)	1.16 (3.7)	1.46 (3.3)
	Dysoxylum sp.01	0.01 (0.1)	0.09 (0.4)	0.07 (0.5)	0.17 (0.3)			0.14 (0.4)	0.12 (0.3)
Moraceae	*Artocarpus* spp.	a		a	a	0.18 (3.4)			0.18 (0.4)
Myristicaceae	*Knema* sp.01		0.14 (0.6)	0.18 (1.3)	0.33 (0.7)		0.56 (4.6)	0.36 (1.1)	0.86 (1.9)
	Knema sp.02			0.04 (0.3)	0.04 (0.1)				
	Myristica elliptica							0.6 (1.9)	0.6 (1.3)
Myrtaceae	*Syzygium claviflora*		0.09 (0.4)		0.09 (0.2)				
	Syzygium sp.01	0.28 (2.1)	0.39 (1.6)	0.11 (0.8)	0.75 (1.5)	0.2 (3.7)			0.2 (0.4)
Palmae	*Oncosperma horridum*	0.94 (7.2)	0.43 (1.7)	0.47 (3.4)	1.72 (3.4)	**1.8 (33.6)**	**3.43 (28.1)**	0.39 (1.2)	**5.56 (12.5)**
Rubiaceae	*Canthium hirtellum*	**2.9 (22.1)**	2.13 (8.6)		**4.66 (9.3)**				
Sterculiaceae	*Sterculia parviflora*		0.09 (0.4)	0.31 (2.2)	0.41 (0.8)			0.94 (3.0)	0.81 (1.8)
Unknown	unknown1-30	0.01 (0.1)			0.01 (0.02)				
	unknown2-30	0.21 (1.6)			0.18 (0.4)				
Unknown	unknown3-30		**2.82 (11.4)**	1.03 (7.4)	3.85 (7.7)				
Total mean weight		**13.1**	**24.7**	**14.0**	**50.2**	**5.4**	**12.2**	**31.5**	**44.7**
Total no. species		**13**	**15**	**12**	**20**	**6**	**6**	**11**	**13**

Table 4. List of animal taxa, weight and percentage (in bracket) of each taxa consumed by Great and Rhinoceros hornbills during different phases and a total.

Animal Taxa	**Mean weight (g/Obs.h.) and percentage of animal diet**							
	GH				**RH**			
	INC	EN	LN	Total	INC	EN	LN	Total
Beetle	0.007	0.012	0.006	0.025	0.014		0.021	0.032
(Scarabaeidae)	(1.0)	(0.4)	(0.2)	(0.4)	(0.9)		(0.5)	(0.5)
Centipede		0.06	**0.437**	0.498	0.132			0.132
Scolopendra spp.(Scolopendridae)		(2.1)	**(14.3)**	(7.6)	(9.0)			(1.9)
Cicada	0.019	0.014	0.021	0.052	0.01	0.012	0.065	0.078
(Cicadidae)	(2.9)	(0.5)	(0.7)	(0.8)	(0.7)	(0.6)	(1.6)	(1.1)
Earthworm					0.058			0.058
(Octochaetidae)					(3.9)			(0.8)
Grass snake	**0.083**	0.228	0.197	0.497			**0.259**	0.222
Chrysopelea ornata (Colubridae)	**(12.5)**	(7.8)	(6.5)	(7.6)			**(6.5)**	(3.2)
Grasshopper	0.012	0.078	0.074	0.162	0.024	0.072	0.108	0.188
(Orthoptera)	(1.8)	(2.7)	(2.4)	(2.5)	(1.6)	(3.5)	(2.7)	(2.7)
Horned lizard	0.033	**0.461**	0.104	**0.594**	**0.203**	**0.238**	0.146	**0.567**
Acanthosaura spp. (Agamidea)	5.0)	**(15.7)**	(3.4)	**(9.1)**	**(13.8)**	**(11.7)**	(3.7)	**(8.0)**
Flying horned lizard	0.031	0.136	0.217	0.379	0.119	**0.128**	**0.319**	**0.648**
Draco maculatus (Agamidea)	(4.6)	(4.6)	(7.1)	(5.8)	(8.1)	**(6.3)**	**(8.1)**	**(9.2)**
Insect	0.018	0.009		0.025				
	(2.7)	(0.3)		(0.4)				
Millipede	**0.317**	**0.622**	**1.043**	**1.942**	**0.901**	**1.569**	**2.61**	**4.707**
(Polydesmidae)	**(47.7)**	**(21.2)**	**(34.2)**	**(29.6)**	**(61.1)**	**(77.0)**	**(65.8)**	**(66.9)**
Phasmida sp.		0.021	0.098	0.118			0.027	0.023
(Coleoptera)		0.7)	(3.2)	(1.8)			(0.7)	(0.3)
Rat		0.158		0.158				
Rattus sp. (Muridae)		(5.4)		(2.4)				
Scorpion	0.027	0.015	0.13	0.169			0.085	0.073
(Scorpionidae)	(4.1)	(0.5)	(4.3)	(2.6)			(2.1)	(1.0)
Skink	**0.117**	**0.604**	**0.548**	**1.254**			0.113	0.097
(Scincidae)	**(17.6)**	**(20.6)**	**(18.0)**	**(19.1)**			(2.9)	(1.4)
Snake		0.061	0.111	0.172			0.209	0.179
(Serpentes)		(2.1)	(3.6)	(2.6)			(5.3)	(2.5)
Spider		0.006	0.006	0.012	0.014			0.014
(Arachnida)		(0.2)	(0.2)	(0.2)	(0.9)			(0.2)
Squirrel		0.414		0.414				
(Sciuridae)		(14.1)		(6.3)				
Walking stick		0.034	0.06	0.094		0.019		0.019
(Phasmatidae)		(1.2)	(2.0)	(1.4)		(1.0)		(0.3)
Total mean weight	**0.665**	**2.934**	**3.051**	**6.567**	**1.474**	**2.038**	**3.964**	**7.038**
Total no. taxa	**10**	**17**	**15**	**17**	**9**	**6**	**11**	**15**

g/hr). Further more, if the protein in the animal food is to accelerate the growth of chick, then the KY Great Hornbill chick should have grown faster and fledged faster as to compare the feeding rate (feeding rate: KY = 4.3 g/hr, this study = 2.3 g/hr). On the other hand, the Great Hornbill at HKK has the similar breeding cycle to both at KY and this study (data from two breeding pairs: 110 and 118 days), and total consumption rate (385.1 g/day or about 38.5 g/hr) is slightly higher than that of at KY, but still lower than this study. However, Poonswad et al. (1998a) found no correlation between consumption rate and the length of breeding cycle in any of four hornbill species at KY, including the Great Hornbill. The nestling phase of Great Hornbill at KY takes 91 days (Poonswad et al., 2004) which is longer than that of this study (62 days), but the average weight of fledgling is similar (KY: 2.04 kg, this study:1.91 kg).

Abundance of fruit food resources for hornbills. – Figs dominate the diets of Great and Rhinoceros Hornbills (Poonswad et al. 1998a, Hadiprakarsa and Kinnaird 2004, Ouithavon et al., 2005a) and the Fig trees produce fruit almost or all year round (Poonswad et al. 1998b, Plongmai

Table 5. Diversity of diet and inter-specific comparison of mean diversity indices; Shannon-Wiener index (H') and Simpson's index (1/D) of non- fig and animal food consumed by Great and Rhinoceros hornbills in three breeding phases.

	Diversity of diet								Mann-Whitney U-Test (Corrected for ties)				
	Incubation phase		Early nestling phase		Late nestling phase		Total			Incubation phase	Early nestling phase	Late nestling phase	Total
	GH	RH	GH	RH	GH	RH	GH	RH					
Non-fig diet													
H' Mean	0.78	0.23	0.89	0.42	0.63	0.42	1.11	0.74	Mann-Whitney U	8.5	13.5	17.0	16.0
sd	0.54	0.33	0.59	0.43	0.46	0.38	0.59	0.39	Asymp. Sig. (2-tailed)	0.070	0.155	0.364	0.165
1/D Mean	2.18	1.21	2.45	1.57	1.91	1.33	2.90	1.89	Mann-Whitney U	8.5	13.5	15.0	15.0
sd1.	03	0.37	1.27	0.64	0.79	0.34	1.56	0.63	Asymp. Sig. (2-tailed)	0.070	0.155	0.243	0.132
n	7	6	7	7	8	6	8	7					
Animal diet													
H' Mean	0.50	0.28	0.86	0.44	1.18	0.69	1.32	0.80	Mann-Whitney U	8.0	10.0	7.5	11.0
sd	0.80	0.56	0.59	0.39	0.54	0.43	0.39	0.43	Asymp. Sig. (2-tailed)	0.592	0.197	**0.033**	**0.049**
1/D Mean	1.81	1.31	2.27	1.42	3.09	1.68	3.27	1.82	Mann-Whitney U	8.0	10.0	6.5	7.0
sd	1.48	0.67	1.17	0.42	1.16	0.52	1.27	0.54	Asymp. Sig. (2-tailed)	0.592	0.197	**0.024**	**0.015**
n	4	5	6	6	8	6	8	7					
Total													
H' Mean	0.97	0.77	1.28	0.82	1.29	0.79	1.61	1.18	Mann-Whitney U	15.0	12.5	12.0	10.0
sd	0.60	0.39	0.71	0.59	0.43	0.46	0.50	0.50	Asymp. Sig. (2-tailed)	0.685	0.125	0.064	0.071
1/D Mean	2.49	1.90	3.54	2.25	3.14	1.79	4.13	2.66	Mann-Whitney U	12.0	13.5	11.0	10.0
sd	1.10	0.69	1.83	1.12	1.52	0.58	1.67	1.04	Asymp. Sig. (2-tailed)	0.372	0.159	**0.049**	0.071
n	7	5	7	7	8	7	8	6					

Table 6. Degree of similarity (C value) of non-fig and animal food consumed by Great and Rhinoceros hornbills during the breeding seasons. [a] indicates the similarity of the same species between years, otherwise comparisons between species were based on both seasons combined.

Incubation phase	Food type	Species	Degree of similarity	
	Non-fig		GH	RH
		GH	0.50[a]	0.56
		RH		0.29[a]
	Animal		GH	RH
		GH	0.33[a]	0.63
		RH		0.20[a]
Early nestling phase	Food type		Degree of similarity	
	Non-fig		GH	RH
		GH	0.32[a]	0.67
		RH		0.45[a]
	Animal		GH	RH
		GH	0.21[a]	0.52
		RH		0.67[a]
Late nestling phase	Food type		Degree of similarity	
	Non-fig		GH	RH
		GH	0.59[a]	0.70
		RH		0.53[a]
	Animal		GH	RH
		GH	0.70[a]	0.85
		RH		0.31[a]
All phases combined	Food type		Degree of similarity	
	Non-fig		GH	RH
		GH	0.57[a]	0.73
		RH		0.56[a]
	Animal		GH	RH
		GH	0.79[a]	0.88
		RH		0.42[a]

et al., 2005; Ouithavon et al., 2005b). High number of ripe crops produced is corresponded with hornbill chick raising period at KY (Poonswad et al., 1998b). Density of fig trees (6.5 trees/ha; transect survey; Chaisuriyanun, 2005) in this study area is similar to the density in other geographical area, e.g. Kalimantan (6.6 trees/ha) (Leighton, 1982) where food of Rhinoceros Hornbill was studied. These densities appeared to be much higher than that at KY (1.5 trees/ha; Poonswad et al., 1998b), at Bukit Barisan Selatan National Park, Sumatra (0.51 trees/ha; Anggraini et al., 2000) and at Peninsular Malaysia (2.0 trees/ha; Johns, 1983). In addition, along the hornbill census trails (other than vegetation study plot and the two transects) in this study area, up to 10 fig trees/ha were calculated. Hence fig trees in our study area are relatively abundant. The availability in abundance of fruit food may enhance the consumption of hornbills. The abundance of *Polyalthia* sp. occurred in our study area at density of 8.5 trees/ha corresponded with feeding rate. Similarly, *Oncosperma horridium* occurred in relatively high density (9 trees/ha) and was ranked first among the non-fig species consumed by Rhinoceros Hornbill. In contrast, density of *Syzygium* sp. 1 was the highest (11.5 trees/ha) and *Artrocarpus* sp. (10.5 trees/ha), both were consumed at similar rates (Table 3 and Appendix 1). More interestingly, those species ranked within the top five species consumed by weight including, *Lisea grandis*, , *Canthium hirtellum* and *Aglaia spectabilis* were not found in both 1 ha plot and along transects (2 ha) (Table 3 and Appendix 1). While *Dysoxylum macrocarpum* had only one tree in 1 ha plot. Moreover, it is documented that *Dysoxylum macrocarpum* and *Aglaia spectabilis* provide few ripe fruit per day, but fruit of both species are lipid and carbohydrate-rich species (Leighton, 1982; Poonswad, 1993). *Polyalthia viridis* and *Syzygium cumini* in KY documented by Poonswad et al. (1998a) provide relatively low calories (90.97 kcal and 87.57 kcal, respectively) as compared to *Dysoxylum* sp. (250.9 kcal) but in the diet of Great Hornbill ranjed as 1, 7 and 4, respectively. However, they did not state the density of those species occurring in KY. It is likely that hornbills sought for fruits of these species in this study, and therefore, it is rather contradictory to Poonswad et al. (1998a) who concluded that abundance is more importance than nutritional value in fruit selection. The quality of nutrition contents, such as lipid-rich fruit species, although with thin aril, significantly provide sufficient energy requirement for a hornbill (Leighton, 1982). However, considering cost and benefit, the lipid- rich fruit, as

Table 7. Intra- and inter-specific comparison of delivery rate of three food categories of Great and Rhinoceros hornbills in three breeding phases.

	Food delivery rate (g/Obs.h.)								Kruskal-Wallis Test			Mann-Whitney U- test (Corrected for ties)				
	Incubation phase		Early nestling phase		Late Nestling phase		Entire three phases						Incubation phase	Early nestling phase	Late Nestling phase	Entire three phases
	GH	RH	GH	RH	GH2	RH	GH	RH		GH	RH					
N (Nests)	7	7	8	7	8	6	8	7								
Fig (g/Obs.h.)																
Range	0-47.9	0-137.8	6.2-82.2	8.0-115.5	0-56.9	0-150.5	0-82.2	0-152.1	Chi-Square	9.85	9.22	Mann-Whitney U	721	681.5	381	5229.5
Mean	20	34	29.2	42.2	27	54.3	25.2	45.2	df	2	2	Z	-2.14	-3.02	-4.13	-5.67
SD	11.8	29.9	17.5	22.6	12.9	34.5	14.8	31.6	Asymp.Sig.	0.007	0.01	Asymp. Sig. (2-tailed)	0.032	0.003	0	0
%	59.5	80.9	48.7	74.3	55.9	64.3	53.6	72.3	P	<0.01	<0.05	P (df = 1)	<0.05	<0.01	<0.001	<0.001
Non-fig (g/Obs.h.)																
Range	0- 69.3	0-32.6	0-117.3	0-90.7	0-94.9	0-258.0	0-117.3	0-258.0	Chi-Square	8.07	4.76	Mann-Whitney U	852	840	801	7788.5
Mean	13	6.3	27.5	12.4	18.1	26.3	19.5	14.7	df	2	2	Z	-1.14	-1.83	-0.22	-1.68
SD	18.2	9.6	32.5	19.5	24.7	53.4	26.4	33.4	Asymp.Sig.	0.017	0.093	Asymp. Sig. (2-tailed)	0.253	0.067	0.825	0.092
%	38.7	15	45.9	21.8	37.5	31.1	41.5	23.5	P	<0.05	>0.05	P (df = 1)	>0.05	>0.05	>0.05	>0.05
Animal (g/Obs.h.)																
Range	0-8.6	0-12.9	0-41.7	0-9.6	0-14.7	0-14.5	0-41.7	0-14.5	Chi-Square	31.46	8.53	Mann-Whitney U	809	1005	764	8243.5
Mean	0.6	1.7	3.2	2.2	3.2	3.9	2.3	2.6	df	2	2	Z	-1.98	-0.6	-0.58	-1.02
SD	1.9	3.2	6	2.8	3.4	4.1	4.3	3.5	Asymp.Sig.	0	0.014	Asymp. Sig. (2-tailed)	0.047	0.55	0.564	0.308
%	1.8	4.1	5.4	3.9	6.6	4.6	4.9	4.2	P	<0.001	<0.05	P (df = 1)	<0.05	>0.05	>0.05	>0.05
Total (g/Obs.h.)																
Range	6.8-77.0	0-137.8	11.6-171.0	15.5-167.0	12.2-136.5	9.4-3.3.7	6.8-171.0	2.4-303.7	Chi-Square	18.82	14.97	Mann-Whitney U	818	1042	429	6798
Mean	33.6	42.1	59.9	56.9	48.2	84.5	47.0	62.5	df	2	2	Z	-1.36	-0.29	-3.69	-3.21
SD	17.8	28.9	34.9	33.5	30.1	57.2	30.5	44.8	Asymp.Sig.	0	0.001	Asymp. Sig. (2-tailed)	0.174	0.774	0	0.001
%	100	100	100	100	100	100	100	100	P	<0.001	<0.01	P (df = 1)	>0.05	>0.05	<0.001	<0.01
Kruskal-Wallis Test																
Chi-Square	76.94	49.51	72.46	63.65	55.86	44.23	201.11	160.61								
Asymp. Sig.	0	0	0	0	0	0	0	0								
P (df = 2)	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001								

fruit of *Dysoxylum* sp. of which only a few ripen at a time, may cost consumers, such as hornbills, more energy searching those fruit than the abundant fruit of *Polyalthia* that may provide sufficient daily energy requirement. Nevertheless, other subtle factors should be looked at or studied.

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Appendix 1. List of fruit (fig and non-fig) eaten by Great and Rhinoceros hornbills during the breeding season (ND=no data, - = not identified).

Fruit species	Hornbill species seen feeding on item	Fruiting trees found during vegetation survey			
		Plot; 1 ha		2 transects; 2 ha	
		No. of trees	No. of species	No. of trees	No. of species
Moraceae					
Ficus spp.	GH, RH	1	1	11	7
Artocarpus spp.	GH, RH	18	5	21	6
Annonaceae					
Desmos cochinchinensis	GH	ND	ND	ND	ND
Polyalthia spp.	GH, RH	7	7	17	9
Lauraceae					
Litsea grandis	GH, RH	0	0	0	0
Litsea sp.01	GH	1	1	1	1
Meliaceae					
Aglaia lawii	GH, RH	0	0	0	0
Aglaia spectabilis	GH, RH	0	0	0	0
Chisocheton erythrocarpus	GH, RH	3	1	0	0
Dysoxylum macrocarpum	GH, RH	1	1	0	0
Dysoxylum sp.01	GH, RH	1	1	3	1
Myristicaceae					
Knema sp.01	GH, RH	–	–	1	1
Knema sp.02	GH	–	–	1	1
Myristica elliptica'	RH	1	1	0	0
Myrtaceae					
Syzygium claviflora	GH	1	1	0	0
Syzygium sp.01	GH, RH	21	1	23	1
Palmae					
Oncosperma horridum	GH, RH	0	0	18	1
Rubiaceae					
Canthium hirtellum	GH	1	1	0	0
Sterculiaceae					
Sterculia parviflora	GH, RH	0	0	1	1
Unknown					
unknown1-30	GH	–	–	–	–
unknown2-30	GH	–	–	–	–
unknown3-30	GH	–	–	–	–
Total		**56**	**21**	**97**	**29**