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ORIGINAL ARTICLE

Estimation of nutrients delivered to nest inmates by four sympatric species of hornbills in Khao Yai National Park, Thailand

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ORNITHOLOGICAL SCIENCE

Abstract Hornbills are omnivorous and the breeding male delivers all food required by the nest-confined female and chicks. The contributions of different food types, in terms of breeding nutrition, have not previously been documented. In Khao Yai National Park, Thailand, we sampled the identity and number of food items delivered daily to the nest, during each week of the nesting cycle, by two small and two large sympatric species of hornbills. We then recorded the mass and estimated the nutrient content of each food type from analyses of protein, fat, carbohydrate, calcium, and energy. The overall pattern of nutrient delivery during the nesting cycle was the same for each of the four hornbill species, and was related to sequential demands for egg, feather, and chick development. The two larger species delivered mainly carbohydrates (Great *Buceros bicornis* 50%, Wreathed *Aceros undulatus* 57%) and less fat and protein. The smallest, Oriental Pied Hornbill *Anthracoceros albirostris*, also delivered mostly carbohydrate (45%), but the small White-throated Brown Hornbill *Anorrhinus austeni* delivered equivalent proportions of protein (32%), fat (30%), and carbohydrate (37%). Comparison of the incubation and nestling phases showed that more protein was delivered during the nestling phase for all species, except for Great Hornbill where the compression of egg production, incubation, and molt had to be completed by midway through the nestling phase and so high levels of fat and protein were delivered during incubation. We confirmed that fruits are an important source of all nutrients, especially fat, for all four hornbill species, but suggest that delivery of animal protein may be linked, in some way, to breeding success. Oriental Pied Hornbill broods, that received protein at about 1.05% of brood mass per day, had the highest breeding success (96%) whereas Wreathed Hornbills received only 0.57% protein and had only 67% success, while the other two species delivered intermediate amounts of protein and had intermediate breeding success.

Key words Breeding nutrition, Frugivore, Hornbill, Nesting diet, Omnivore, Thailand

Breeding hornbills, like many other birds, must collect sufficient food to satisfy both their own nutritional requirements and those of any offspring they raise. In hornbills, provision of these nutrients is the responsibility of the male because the female seals herself into the nest and is fed by the male throughout the egg-laying, incubation and, with the chick(s), the nestling phase (Kemp 1995). In most hornbill species, the breeding female, after a phase of courtship feeding by the male, seals herself into the nest cavity about a week before egg-laying and, once laying commences, starts her annual molt of rectrices and remiges, further increasing the nutritional demand imposed on the male (Poonswad 1993; Kemp 1995).

There is some variation between hornbill species in the timing of the female's emergence or whether assistance is available to the male from members of a group. Species also differ in size, duration of the nesting cycle and number of eggs laid and chicks raised (Poonswad et al. 1987; Kemp 1995), all of which influence the nutrient requirements of nest inmates. Food delivered to the nest also varies between

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species, habitats, seasons and phases of the nesting cycle. It may depend in part on availability, but also on nutrient demands, such as calcium for egg or skeleton formation, or particular amino acids for feather growth.

The diets of many bird species are predominately either frugivorous or carnivorous during breeding, but in omnivores, such as forest hornbills, both food types occur regularly in the diet (Poonswad et al. 1987; Kemp 1995). The proportion of nutrients contributed by different food types at different phases of the nesting cycle has not previously been recorded for hornbills. Four species of hornbills breed in Khao Yai National Park, central Thailand, two large species, Great Hornbill *Buceros bicornis* and Wreathed Hornbill *Aceros undulatus*, and two smaller species, White-throated Brown Hornbill *Anorrhinus austeni* and Oriental Pied Hornbill *Anthracoceros albirostris*. Their dietary choices have been reported (Poonswad et al. 1987, 1998), as have differences in their size, nesting cycle and breeding biology (Poonswad 1993; Table 1). Here, we concentrate on intra-specific patterns and sources of nutrients delivered to nest inmates during the incubation and nestling phases of the nesting cycle, based on the identity and analysis of food items delivered to the nest inmates; an attempt at inter-specific comparisons is also presented.

METHODS

We conducted this study in the 70 km^2 Khao of Yai National Park (ca. 14°15–30′N, 101°20–24′E), Thailand, an area of tall monsoon forest (62 km^2) with patches of open grassland (8 km^2; Poonswad et al. 1998). We observed hornbill nests during the breeding seasons (January–June) of 1982–1985 and recorded all food items delivered (0700–1700) to the nesting female and/or chicks by the breeding male and any other helpers. We observed each hornbill species at 2–10 day intervals, to provide weekly samples of full-day observations that covered the whole nesting cycle (Table 2). Breeding success, i.e. the number of chicks fledging per nest, was also recorded.

We observed food items delivered to the nest using binoculars (8×30), a spotting scope (×20 and ×40), or took photographs (using 400–800 mm telephoto lenses), depending on the distance from the nest. We identified items as fruit or animal and classified them by direct observation, by collection of debris below

Table 1. Attributes of size and breeding biology for four species of hornbills that breed in Khao Yai National Park, Thailand (from Poonswad 1993 unpublished data; Kemp 1995, 2001).

Hornbill species	Median female mass (g)	Nesting cycle, weeks (incubation/nestling) (ratios)	Clutch size, range (mean)	Mean brood size, (range, sample)	Female + mean brood mass, g (ratios)	Egg volume (cc)	Exceptional breeding biology
Great	2,211	20 (7/13) (1.4)	1–4	1 (0, N=66)	3,316 (2.1)	71	Female emerges 6 weeks after chicks hatch
Wreathed	1,950	20 (7/13) (1.4)	1–3	1 (0, N=27)	3,900 (2.5)	60	
White-throated Brown	755	15 (5/10) (1.1)	1–5	2.6 (1–4, N=15)	2,718 (1.7)	29	Cooperative group, 1–5 helpers for male at nest
Oriental Pied	624	14 (5/9) (1.0)	1–3	1.5 (1–2, N=12)	1,560 (1.0)	29	

Table 2. Sample sizes for observations at nests of four sympatric species of hornbills in Khao Yai National Park, Thailand. Incubation and nestling phases were determined from direct observation or published information, and the incubation phase was assumed to include the pre-laying interval of one week (Poonswad 1993; Kemp 1995).

Hornbill species	No. of pair-years	Total no. of days observation	No. of full-day observations, mean days/week and phase duration					
			Incubation phase			Nestling phase		
			Full-days	Days/week	Phase duration	Full-days	Days/week	Phase duration
Great	16	437	78	11.1	Weeks 1–7	119	9.2	Weeks 8–20
Wreathed	9	227	35	5.0	Weeks 1–7	63	4.8	Weeks 8–20
White-throated Brown	14	258	46	9.2	Weeks 1–5	92	9.2	Weeks 6–15
Oriental Pied	24	449	62	12.4	Weeks 1–5	157	17.4	Weeks 6–14

the nest, or by comparison with specimens collected nearby. Some plant samples were sent for further identification to the Forest Herbarium, Royal Forest Department, Bangkok, Thailand.

Using an average weight for each food item, we estimated the total wet weight consumed for each item per day. Average weights of fruits were obtained from samples dropped below nests or collected later from fruiting trees. Average weights of animals were obtained from fresh specimens dropped below nests or from specimens of similar size caught elsewhere in the study area (of the same group but not always of the same species, due to the difficulty of collecting and identifying most small animals in tropical forest).

We also determined nutritional values in g/wet weight (protein, fat, carbohydrate (CHO), calcium, and energy content) for each type of food. Fruits were analyzed by the Food Analysis Laboratory, Institute of Nutrition, Mahidol University at Salaya, Nakhon Pathom, Thailand. A few animal food items were also sent there for analysis, but most values for animal foods were obtained from published sources (Department of Health 1978, 1984; Puwastien & Sungpuag 1983). Samples of specific animals were difficult to obtain from the forest, so, where necessary, data for animals of the same genus or family as those identified as hornbill food items were substituted in the analyses.

Food samples were weighed, to obtain the wet weight in grams, blended with an ordinary mixer; then frozen for 24 hours before being transferred into a freeze drier, if the sample was to be analyzed later. Nutritional values, including protein, fat, and calcium were determined by Kjeldahl AOAC 981.10, Soxhlet AOAC 945.16, and atomic absorption AOAC 975.03, respectively. Carbohydrate was obtained by subtracting the sum of moisture (drying AOAC 925.45), protein, fat, and ash (dry ashing) from 100. Energy was calculated using the general factors of 16.7, 37.5, and 16.7 kJ/g from protein, fat, and carbohydrate, respectively.

A comparison of the quantities of food and nutrients delivered to nest inmates among these four hornbill species, involves correcting for differences in female body mass, clutch and brood sizes, and the length of nesting cycle and its phases (Table 1). Therefore, although mean daily delivery rates of food types and nutrients are compared within species as absolute amounts, useful for ecological comparisons, biological comparison requires some sort of correction for inter-specific differences. In an attempt at correction, ratios were calculated between values for each species by taking the species with the lowest values, the smallest Oriental Pied Hornbill (Table 1), as one unit. The mean values for each species were then adjusted using either ratios of the mean mass of nest inmates or ratios of the duration of the total nesting cycle. The mean mass of nest inmates for each species was calculated as the sum of the median female mass plus the mean brood size multiplied by the median female mass, except for Great Hornbill where the female leaves the nest early in the nestling phase and is scored for only half of her mass contribution (Table 1). Chick mass at different ages and growth curves were unavailable for any of the hornbill species, so the mass of the adult female, less than the adult male, was substituted for the mass of a chick at fledging. Any excess of the adult female mass over the real fledgling mass would offset any additional nutritional requirements of chicks during their development.

Statistical analyses were performed with SigmaSta

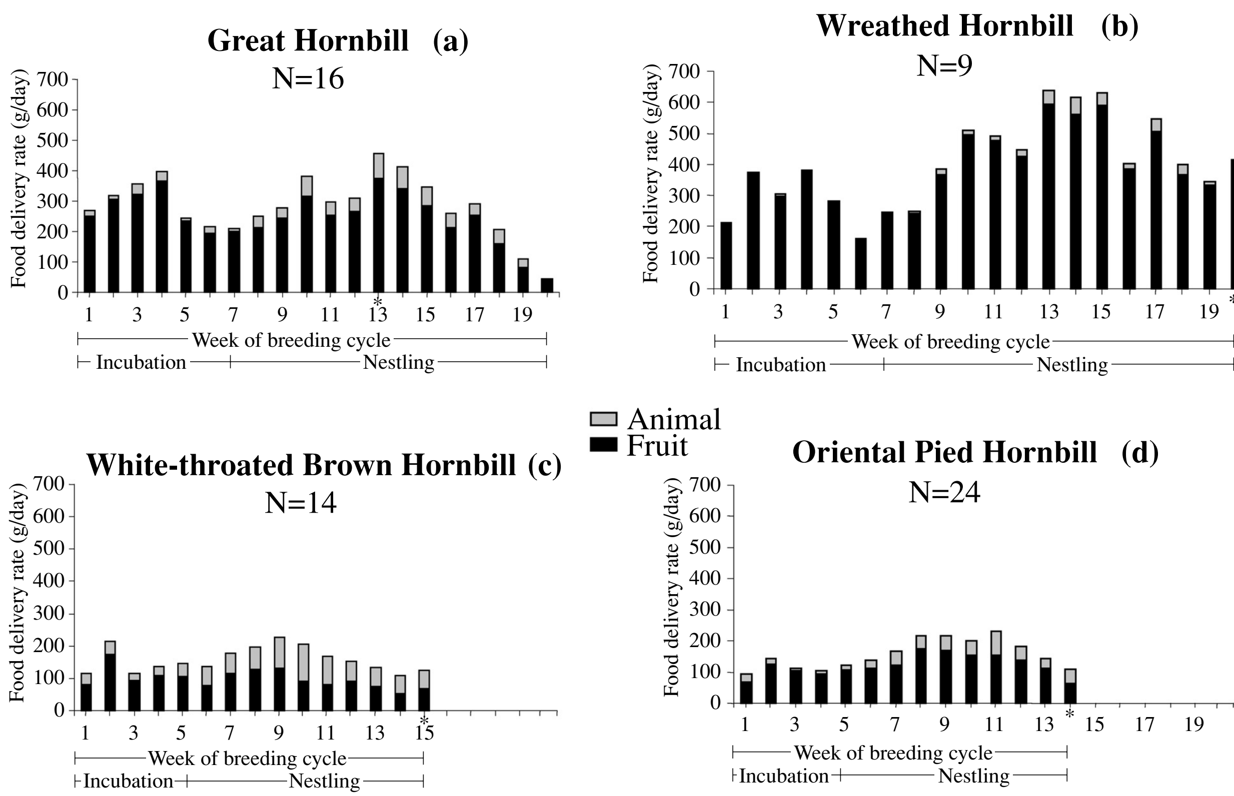

Fig. 1. Quantity of food (estimated g/day) and proportion as fruits and animals delivered by wet weight to the nest inmates of four hornbill species: Great Hornbill (a), Wreathed (b), White-throated (c), and Oriental Pied (d) in Khao Yai National Park, Thailand, at weekly intervals during the nesting cycle. * time of female emergence.

2.0 (Jardel Corporation 1995) We used Mann-Whitney Rank Sum Test (T, for medians) for intra-specific comparisons of each phase of the nesting cycle and the Kruskal-Wallis ANOVA (F, for means) or One Way ANOVA on Ranks (H, for medians) for All Pairwise Multiple Comparison Procedures (Dunn's Method, for significance at $P<0.05$) of inter-specific values.

RESULTS

1) Intra-specific patterns of food delivery by mass and food type during the incubation and nestling phases

The weekly pattern of food delivery over the whole nesting cycle was similar for each hornbill species (Fig. 1), taking into account the differences in the lengths of their nesting cycles (Table 1). There were two main peaks, the first during early incubation and the second midway through the nestling phase, even though the quantities and proportions of fruits and animals in the diet varied between species.

Great Hornbill food delivery rose to a peak halfway through the incubation phase (Week 4) and nestling phase (Week 13, also the time of the female's emergence) but then dropped off markedly until fledging (Fig. 1a). Only the delivery of animal food was significantly higher after hatching ($T=5121.5$, $N_1=78$, $N_2=119$, $P<0.001$), whereas fruit delivery showed no significant change between the incubation and nestling phases. The female Great Hornbill would have consumed all animal food delivered during incubation, but once she emerged from the nest, all animal food would have become available to the chick.

Wreathed Hornbill food delivery also showed a low peak midway through incubation (Weeks 2–4), a drop before hatching, but then a high and sustained feeding rate throughout the nestling phase with a peak in Weeks 13–15, all of it supplied by the male alone to the female and a single chick (Fig. 1b). The incubating female received little animal food, but there was a significant increase in animals and fruits once the chick had hatched ($T=913.0$, $N_1=35$, $N_2=63$, $P<0.001$ and $T=1322.0$, $N_1=35$, $N_2=63$, $P=0.002$, respectively), the increase in animals sufficiently obvious to confirm hatching.

White-throated Brown Hornbill food delivery by the male and nest helpers appeared to increase markedly during egg-laying (Week 2), especially for fruits (Fig. 1c), although there was no significant difference in the rates of fruit delivery before and after hatching. Food delivery peaked again midway through the nestling phase (Week 9), probably through the significantly higher delivery rate to the female and several chicks of animal foods after hatching ($T=2126.0$, $N_1=46$, $N_2=92$, $P<0.001$), and then declined towards fledging.

Oriental Pied Hornbill food delivery also peaked during egg-laying (Week 2) and then, after hatching, rose steadily to an extended peak midway through the nestling phase (Weeks 8–11) before declining towards fledging (Fig. 1d). The Oriental Pied Hornbill delivered significantly more fruit and animal foods

Table 3. Statistical comparison of daily rates (range, mean, SD, median) of protein, fat, carbohydrate, calcium, and energy delivered to nest inmates by wet weight during the incubation and nestling phases for four sympatric species of hornbills in Khao Yai National Park, Thailand. GH=Great Hornbill, WH=Wreathed Hornbill, BH=White-throated Brown Hornbill, PH=Oriental Pied Hornbill.

	Incubation phase				*Nestling phase*			
	GH	WH	BH	PH	GH	WH	BH	PH
N (weeks)	7	7	5	5	13	13	10	9
Protein (g/day)								
Range	6.1–23.8	3.2–9.0	6.1–11.3	4.7–6.5	1.8–28.3	7.2–25.7	9.8–22.0	5.7–15.1
Mean	11.0	6.5	8.6	5.5	17.2	15.6	14.5	10.9
SD	6.1	2.3	2.5	0.7	7.8	5.6	4.1	3.1
Median	9.5	6.4	7.9	5.3	16.3	15.6	13.6	10.5
					T=48.5	T=31.0	T=19.0	T=17.00
					P=0.05	P<0.001	P=0.01	P=0.008
Fat (g/day)								
Range	6.5–56.1	4.5–35.2	7.2–11.6	6.0–9.2	1.7–14.9	8.9–61.6	8.6–17.9	7.4–14.0
Mean	19.7	19.7	9.6	7.5	11.3	21.6	12.1	10.8
SD	16.4	11.2	1.7	1.2	3.5	14.3	2.7	2.1
Median	15.2	18.8	10.2	7.3	12.3	20.0	12.1	10.9
					T=100.00	T=73.0	T=25.0	T=18.0
					P=0.04	P=1.0	P=0.08	P=0.01
Carbohydrate (g/day)								
Range	20.7–61.0	15.5–43.0	11.1–19.3	7.7–19.2	5.9–39.2	37.3–79.3	7.1–19.0	4.4–22.9
Mean	32.6	30.1	13.8	13.3	26.3	53.2	13.3	15.5
SD	13.9	10.7	3.3	4.1	10.1	14.1	3.8	6.0
Median	26.3	30.6	12.5	13.1	26.9	49.5	13.4	16.9
					T=78.0	T=36.0	T=40.5	T=29.0
					P=0.75	P=0.003	P=1.0	P=0.29
Calcium (g/day)								
Range	0.39–1.95	0.49–0.90	0.27–0.78	0.30–0.42	0.02–2.74	0.82–2.21	0.40–1.22	0.51–1.05
Mean	1.13	0.72	0.48	0.36	1.43	1.37	0.73	0.74
SD	0.56	0.13	0.25	0.06	0.77	0.45	0.26	0.18
Median	0.85	0.72	0.31	0.40	1.3	1.4	0.67	0.76
					T=61.0	T=29.00	T=28.0	T=15.0
					P=0.34	P<0.001	P=0.16	P=0.003
Energy (kJ/day)								
Range	706–3,520	481–2,187	572–894	485–754	192–1,652	1,186–3,945	605–1,334	620–1,067
Mean	1,469	1,353	735	596	1,150	1,959	917	845
SD	937	625	137	99	401	789	210	156
Median	1,131	1,323	711	593	1,111	1,764	889	851
					T=77.0	T=55.0	T=26.0	T=17.0
					P=0.81	P=0.15	P=0.10	P=0.008

Table 4. Mean daily rates (from Table 2) and proportions of energy-producing protein, fat, and carbohydrate delivered to nest inmates by wet weight during the incubation and nestling phases for four sympatric species of hornbills in Khao Yai National Park, Thailand.* % of nutrients delivered, not including crude ash, present in the actual food remains.

Hornbill species	Protein		Fat		Carbohydrate		Total	
	g/day	%	g/day	%	g/day	%	g/day	%*
Incubation phase								
Great	11.0±6.1	17.4	19.7±16.4	31.1	32.6±13.9	51.5	63.3	100
Wreathed	6.5±2.3	11.5	19.7±11.1	35.0	30.1±10.7	53.5	56.3	100
White-throated Brown	8.6±2.5	26.9	9.6±1.7	30.0	13.8±3.3	43.1	32.0	100
Oriental Pied	5.5±0.7	20.9	7.5±1.2	28.5	13.3±4.1	50.6	26.3	100
Nestling phase								
Great	17.2±7.8	31.4	11.3±3.5	20.6	26.3±10.0	48.0	54.8	100
Wreathed	15.6±5.6	17.3	21.6±14.3	23.9	53.2±14.1	58.8	90.4	100
White-throated Brown	14.5±4.1	36.3	12.1±2.7	30.3	13.3±3.8	33.3	39.9	100
Oriental Pied	10.9±3.1	29.3	10.8±2.1	29.0	15.5±6.0	41.7	37.2	100
Total								
Great	28.2	23.9	31.0	26.2	58.9	49.9	118.1	100
Wreathed	22.1	15.1	41.3	28.2	83.3	56.7	146.7	100
White-throated Brown	23.1	32.1	21.7	30.2	27.1	36.7	71.9	100
Oriental Pied	16.4	25.8	18.3	28.8	28.8	45.4	63.5	100

during the nestling phase than the incubation phase ($T=4394.5$, $N_1=57$, $N_2=142$, $P<0.001$ and $T=4319.5$, $N_1=62$, $N_2=157$, $P<0.001$, respectively), to the female and several chicks.

2) Intra-specific patterns of nutrient delivery during the incubation and nestling phases

The estimated weekly pattern of nutrients delivered to nest inmates over the whole nesting cycle varied considerably by nutrient type and hornbill species (Tables 3 & 4, Figs. 2–5).

Great Hornbill nutrient delivery comprised similar proportions overall of protein (23.9%) and fat (26.2%) but more carbohydrate (49.9%) (Table 4). Significantly more fat was delivered during incubation than the nestling phase (Table 3), possibly an anomaly due to a peak soon after egg-laying (Week 3, Fig. 2b). There were no significant differences for other nutrients, including energy (Table 3), even though all other nutrients also appeared to peak in Week 3 (except for calcium, Fig. 2d) and the delivery rates for protein, calcium and to a less extent carbohydrate rose again midway through the nestling phase (Fig. 2a, d, and c). The peak in Week 3 of fat derived mainly from lipid-rich fruits, the peak of protein derived from similar quantities of fruit and animal foods and the peak of carbohydrate from fruit (Fig. 2b, a, and c respectively).

Wreathed Hornbill nutrient delivery was low overall in protein (15.1%), medium in fat (28.2%) and high in carbohydrate content (56.7%) (Table 4). Mean delivery rates of protein, carbohydrate, and calcium were significantly higher during the nestling phase (Table 3, Fig. 3a, c, and d), and although apparently also higher for fat and energy these were not significant.

White-throated Brown Hornbill nutrient delivery yielded similar proportions overall of protein (32.1%), fat (30.2%), and carbohydrate (36.7%) (Table 4). Only protein increased significantly during the nestling phase (Table 3, Fig. 4a), although other nutrients also appeared to increase during the same phase (Fig. 4).

Oriental Pied Hornbill nutrient delivery yielded similar proportions overall of protein (25.8%) and fat (28.8%) but higher carbohydrate (45.4%) (Table 4). There were significant increases during the nestling phase for all nutrients (protein, fat, energy, and calcium) except carbohydrate (Table 3, Fig. 5).

3) Intra-specific patterns of nutrient delivery by food type

Fruit and animal foods contributed to all nutrient classes measured in this study. However, the proportions of these foods delivered to nest inmates and the quantities of their contributions to the main nutrient classes, varied among hornbill species (Figs. 2–5).

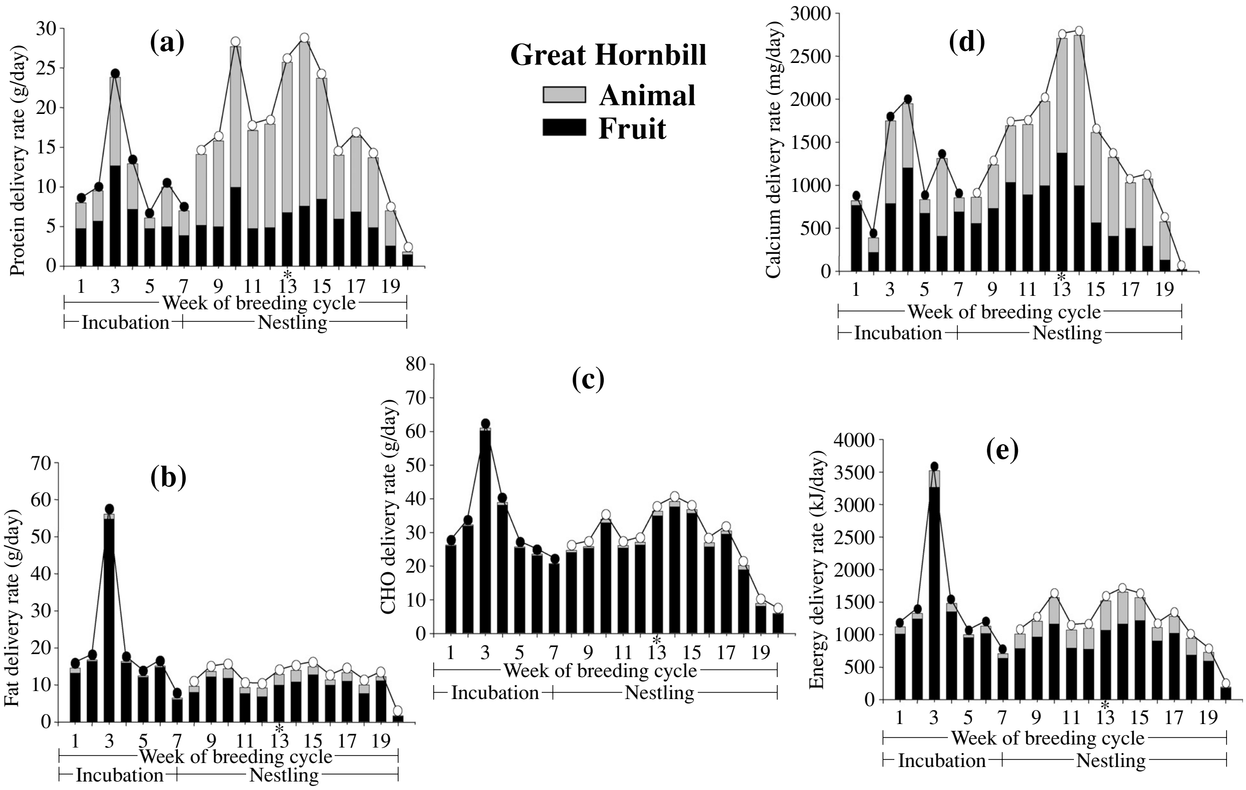

Fig. 2. Estimated mean daily delivery rates of nutrients derived from fruit and animal food by wet weight, including protein (a), fat (b), carbohydrate (c), calcium (d) and energy (e) to nest inmates of Great Hornbill and a total of nutrient delivery daily during each week of the incubation (solid circles) and nestling (open circles) phases. * time of female emergence.

Protein

Both fruits and animals were important protein sources for nesting Great Hornbill (Fig. 2a) and their delivery rates did not significantly differ. In contrast, fruits were the major source of protein in the diet of the Wreathed Hornbill, with a significantly higher delivery rate than for animals ($T=586.0$, $N_1=20$, $N_2=20$, $P<0.001$; Fig. 3a), both before and after hatching ($T=77.0$, $N_1=7$, $N_2=7$, $P=0.002$ and $T=250.5$, $N_1=13$, $N_2=13$, $P<0.001$, respectively).

Animal food was the major source of protein in the diet of White-throated Brown and Oriental Pied Hornbills, since delivery rates from fruits were significantly lower ($T=121.0$, $N_1=15$, $N_2=15$, $P<0.001$ and $T=152.0$, $N_1=14$, $N_2=14$, $P=0.02$, respectively; Figs. 4a and 5a).

Fat

The main source of fat delivered by all four hornbill species was lipid-rich fruits, as shown by the significantly higher delivery rate for fruits than animals (Great Hornbill $T=602.5$, $N_1=20$, $N_2=20$, $P<0.001$; Wreathed Hornbill $T=610.0$, $N_1=20$, $N_2=20$, $P<0.001$; White-throated Brown Hornbill $T=345.0$, $N_1=15$, $N_2=15$, $P<0.001$; Oriental Pied Hornbill: $T=301.0$, $N_1=14$, $N_2=14$, $P<0.001$; Figs. 2b, 3b, 4b, and 5b). This was especially evident for the two larger species, Great and the Wreathed Hornbills, where the delivery rate of fat from fruits was 8.9 times and 25.2 times higher respectively than from animals (Figs. 2b and 3b). Delivery rates of fats from fruits and animals were both higher after than before hatching for Great Hornbill ($T=77.0$, $N_1=7$, $N_2=7$, $P<0.001$ and $T=252.5$, $N_1=13$, $N_2=13$, $P<0.001$, respectively).

Carbohydrate

Fruits were the main source of carbohydrate for all four species (Figs. 2c, 3c, 4c, and 5c), with a significantly higher delivery rate than from animals (Great Hornbill $T=610.0$, $N_1=20$, $N_2=20$, $P<0.001$; Wreathed Hornbill $T=610.0$, $N_1=20$, $N_2=20$, $P<0.001$; White-throated Brown Hornbill $T=345.0$, $N_1=15$, $N_2=15$, $P<0.001$; Oriental Pied Hornbill

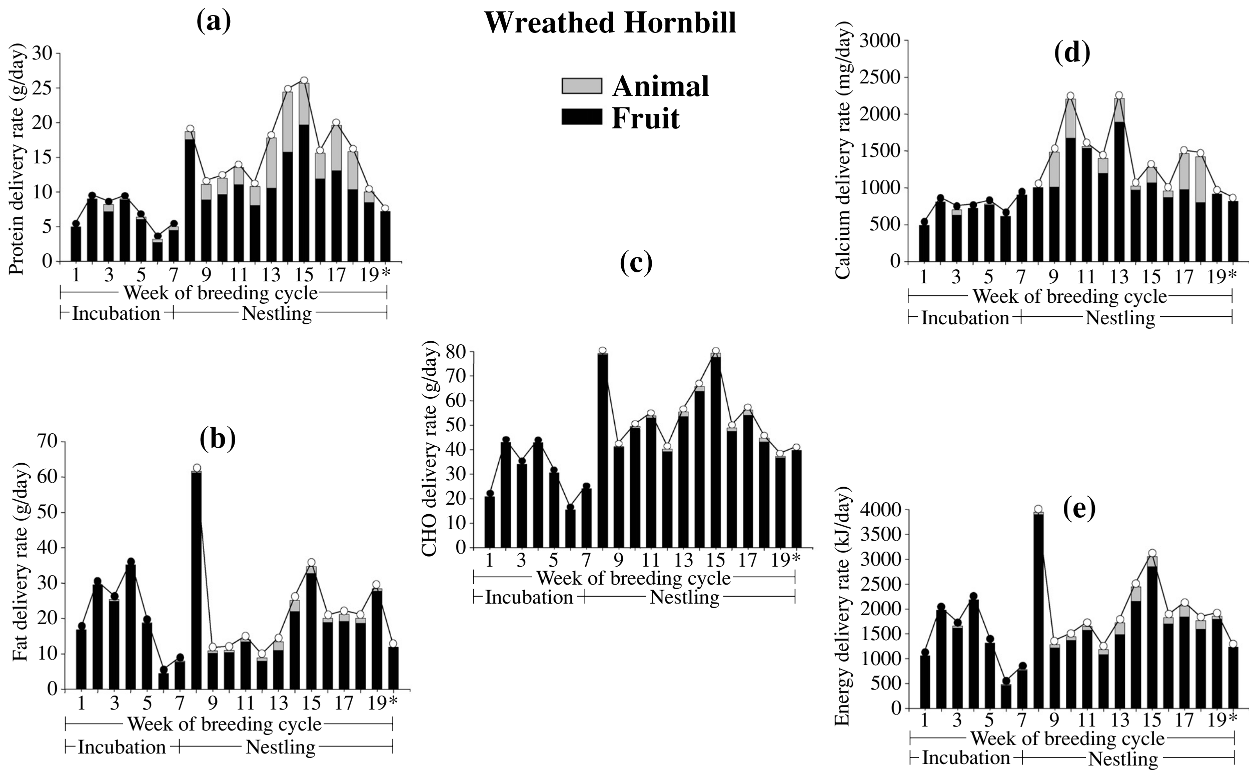

Fig. 3. Estimated mean daily delivery rates of nutrients derived from fruit and animal food by wet weight, including protein (a), fat (b), carbohydrate (c), calcium (d) and energy (e) to nest inmates of Wreathed Hornbill and a total of nutrient delivery daily during each week of the incubation (solid circles) and nestling (open circles) phases. * time of female emergence.

$T=299.0$, $N_1=14$, $N_2=14$, $P<0.001$, and this difference occurred both before and after hatching for Wreathed Hornbill ($T=77.0$, $N_1=7$, $N_2=7$, $P<0.001$ and $T=260.0$, $N_1=13$, $N_2=13$, $P<0.001$, respectively).

Calcium

The main source of calcium depended on hornbill species (Figs. 2d, 3d, 4d and 5d). Wreathed Hornbill acquired significantly more calcium from fruits than from animals ($T=607.0$, $N_1=20$, $N_2=20$, $P<0.001$; Fig. 3d), whereas White-throated Brown Hornbill acquired most calcium from animals ($T=167.5$, $N_1=15$, $N_2=15$, $P=0.008$; Fig. 4d). Both Great and Oriental Pied Hornbills acquired calcium about equally from fruits and animals, with no significant differences (Figs. 2d and 5d). Delivery rates of calcium from fruits were higher both before and after hatching for Wreathed Hornbill ($T=77.0$, $N_1=7$, $N_2=7$, $P<0.001$ and $T=260.0$, $N_1=13$, $N_2=13$, $P<0.001$, respectively; Fig. 3d).

Energy

Energy can be derived from proteins, fats, carbohydrates or a combination of these nutrients in fruits and animal foods. Fruits were the main overall source of energy and were delivered significantly more than animals by all four species (Great Hornbill, $T=598.0$, $N_1=20$, $N_2=20$, $P<0.001$; Wreathed Hornbill, $T=610.0$, $N_1=20$, $N_2=20$, $P<0.001$; White-throated Brown Hornbill, $T=330.0$, $N_1=15$, $N_2=15$, $P<0.001$; Oriental Pied Hornbill, $T=300.0$, $N_1=14$, $N_2=14$, $P<0.001$), particularly the Wreathed Hornbill (Figs. 2e, 3e, 4e, and 5e). However, energy delivery from animals significantly increased for all species after hatching, Great ($T=249.0$, $N_1=13$, $N_2=13$, $P<0.001$), Wreathed ($T=260.0$, $N_1=13$, $N_2=13$, $P<0.001$), White-throated Brown ($T=144.0$, $N_1=10$, $N_2=10$, $P=0.004$), and Oriental Pied Hornbills ($T=126.0$, $N_1=9$, $N_2=9$, $P<0.001$) (Figs. 2e, 3e, 4e, and 5e).

For Great and Wreathed Hornbills, fat and carbohydrate were equally important sources of energy by mass, although not necessarily by calorific value per

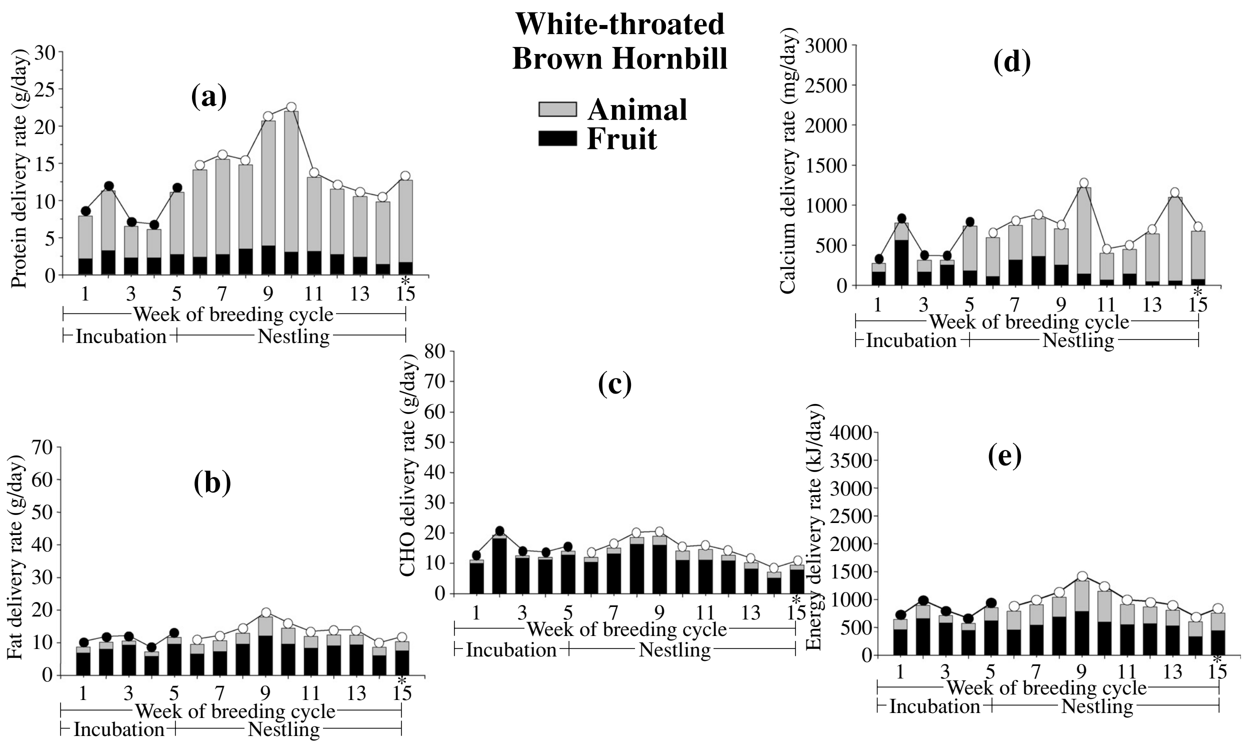

Fig. 4. Estimated mean daily delivery rates of nutrients derived from fruit and animal food by wet weight, including protein (a), fat (b), carbohydrate (c), calcium (d) and energy (e) to nest inmates of White-throated Brown Hornbill and a total of nutrient delivery daily during each week of the incubation (solid circles) and nestling (open circles) phases. * time of female emergence.

unit weight. Mean delivery rates of both nutrition classes were significantly higher than the delivery rate of protein ($H=19.5$, $df=2$, $P<0.001$ and $H=33.7$, $df=2$, $P<0.001$, respectively; Table 4). For the White-throated Brown and Oriental Pied Hornbills, fat was the major source of energy ($F=33.8$, $df=2$, $P<0.001$ and $F=23.7$, $df=2$, $P<0.001$, respectively).

4) Inter-specific comparisons of patterns of nutrient delivery

Comparisons between species of the quantities of food and nutrients delivered to nest inmates is complicated by inter-specific differences in body, clutch and brood sizes, and in the duration of the nesting cycle and its phases (Table 1). Results of the calibrated means are shown for each of the nutrients (Table 5) and for the quantities of nutrients and total energy (Table 6) even though protein and energy requirements are proportional to body-mass$^{0.75}$ (Kleiber's rule; Kleiber 1961). No statistical test of any differences between species was considered appropriate, but adjustment of the means did reduce variance between the species (cf. Table 3), suggesting more equivalent comparisons.

Protein delivery rates adjusted for brood mass for all species were similar to that of the Oriental Pied Hornbill during the incubation phase, except for being lower for the Wreathed Hornbill (Table 5). During the nestling phase, adjusted delivery rates were higher than during the incubation phase for all species, especially the Oriental Pied Hornbill. Adjusted fat delivery rates were low during incubation for White-throated Brown Hornbill and high for Great Hornbill, but were highest for nestling Oriental Pied Hornbill and lowest for Great Hornbill (Table 5). Adjusted carbohydrate delivery rates were most varied among species, lowest for White-throated Brown Hornbill during both incubation and nestling phases, but highest for incubating Great Hornbill and nestling Wreathed Hornbill (Table 5). Adjusted calcium delivery rates were lower during the incubation than the nestling phase for all species, but with the greatest increase for nestlings of Oriental Pied Hornbill (Table 5). Adjusted energy delivery rates to the female during incubation were lowest for White-

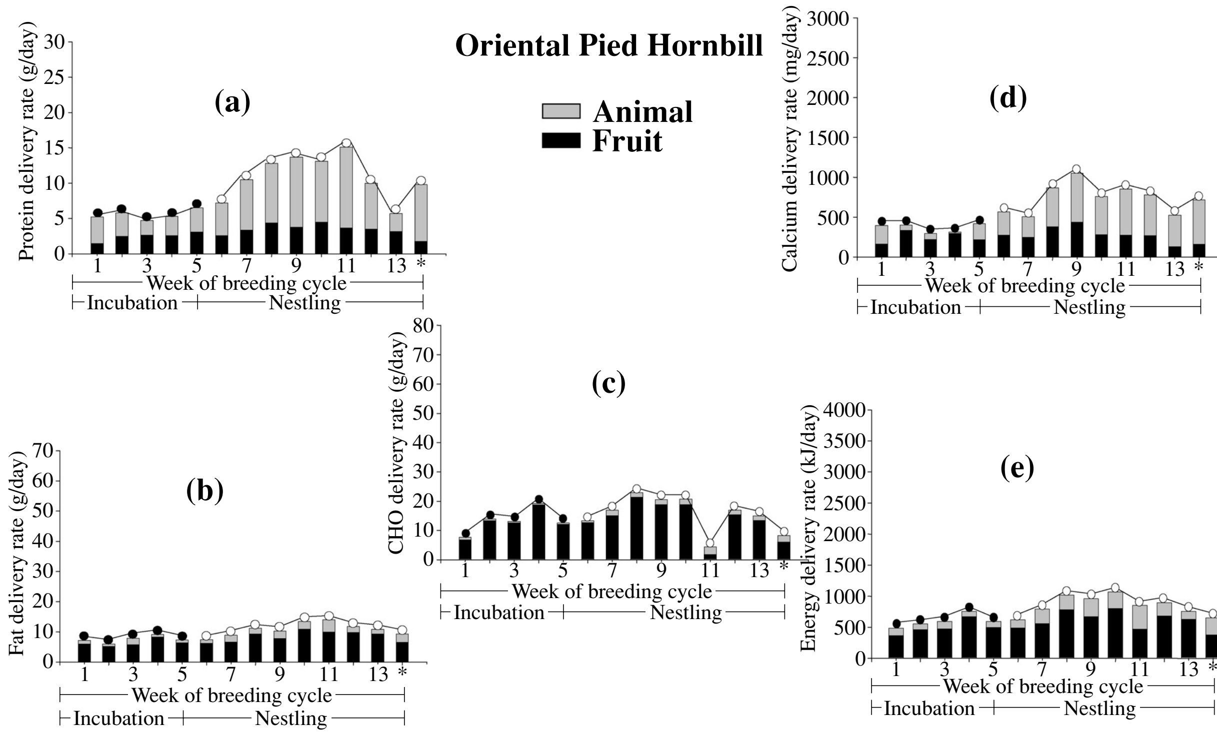

Fig. 5. Estimated mean daily delivery rates of nutrients derived from fruit and animal food by wet weight, including protein (a), fat (b), carbohydrate (c), calcium (d) and energy (e) to nest inmates of Oriental Pied Hornbill and a total of nutrient delivery daily during each week of the incubation (solid circles) and nestling (open circles) phases. * time of female emergence.

throated Brown Hornbill, but rose during the nestling phase for all species except Great Hornbill where the incubating female received more energy than the nestling (Table 5).

Delivery rates for nutrients and total energy, once adjusted for the duration of the nesting cycle, reduced considerably the overall differences between species (Table 5 cf. Table 4). Adjusted protein delivery rates were especially important to Great and White-throated Brown Hornbills, and more important in the nestling than the incubation phases for all species. Adjusted fat delivery rates were important during incubation for the larger species, Great and Wreathed Hornbills, but especially during the nestling phase for the smaller species-pair of White-throated Brown and Oriental Pied Hornbills, although about equal in both phases for Wreathed Hornbill. Adjusted carbohydrate delivery rates were especially important to both larger species during incubation, particularly for Great Hornbill, and markedly increased during the nestling phase for Wreathed Hornbill, but varied least in both phases for the smaller species. Adjusted delivery rates for total energy were only highest during the incubation phase for Great Hornbill, being similar and higher during the nestling phase for all the other species, particularly for Wreathed Hornbill.

The percentages of nutrients delivered to the nestlings also needs to be adjusted by the brood mass (Table 6), especially for any comparisons with fledging success. The adjusted percentages of nutrients and energy for the Oriental Pied Hornbill were 1.05 for protein, 1.17 for fat, 1.85 for carbohydrate, and 92.38 for energy (Table 6) while the other three species had relatively lower protein intakes, especially the Wreathed Hornbill during the incubation phase (Table 3). The Oriental Pied Hornbill had the highest breeding success (95.8%) and the Wreathed Hornbill the lowest (66.7%, Table 6).

DISCUSSION

1) Food delivery pattern

The overall pattern of food delivery to nest inmates was similar for all four hornbill species, despite differences in size, duration of nesting cycle and breeding strategy. There was a rise in the mass of food de-

Table 5. Mean delivery rates of nutrients to the nest inmates by wet weight during the incubation and nestling phases (from Table 2), adjusted for body and brood mass (BM) and nesting cycle (NC) of each hornbill species (from Table 1, see text), in Khao Yai National Park, Thailand. GH=Great Hornbill, WH=Wreathed Hornbill, BH=White-throated Brown Hornbill, PH=Oriental Pied Hornbill.

Nutrient	Nesting phase	Hornbill species, adjusted mean delivery rates (g/day, adjustment ratio from Table 1)											
		GH			WH			BH			PH		
		Before adjust	BM (2.1)	NC (1.4)	Before adjust	BM (2.5)	NC (1.4)	Before adjust	BM (1.7)	NC (1.1)	Before adjust	BM (1.0)	NC (1.0)
Protein (g/day)	Incubation	11.0	5.2	7.9	6.5	2.6	4.6	8.6	5.1	7.8	5.5	5.5	5.5
	Nestling	17.3	8.2	12.3	15.6	6.2	11.1	14.5	8.5	13.2	10.9	10.9	10.9
	Total	28.3	13.4	20.2	22.1	8.8	15.8	23.1	13.6	21.0	16.4	16.4	16.4
Fat (g/day)	Incubation	19.7	9.4	14.1	19.7	7.9	14.1	9.6	5.6	8.7	7.5	7.5	7.5
	Nestling	11.3	5.4	8.1	21.6	8.6	15.4	12.1	7.1	11.0	10.8	10.8	10.8
	Total	31.0	14.8	22.1	41.3	16.5	29.5	21.7	12.7	19.7	18.3	18.3	18.3
CHO (g/day)	Incubation	32.6	15.5	23.3	30.1	12.3	21.5	13.8	8.1	12.5	13.3	13.3	13.3
	Nestling	26.3	12.5	18.8	53.2	21.3	38.0	13.3	7.8	12.1	15.5	15.5	15.5
	Total	58.9	28.0	42.1	83.3	33.6	59.5	27.1	15.9	24.6	28.8	28.8	28.8
Ca (g/day)	Incubation	1.13	0.54	0.81	0.72	0.29	0.51	0.48	0.28	0.44	0.36	0.36	0.36
	Nestling	1.43	0.68	1.02	1.32	0.55	0.98	0.73	0.43	0.66	0.74	0.74	0.74
	Total	2.56	1.22	1.83	2.09	0.84	1.49	1.21	0.71	1.10	1.10	1.10	1.10
Energy (kJ/day)	Incubation	1,466.9	698.2	1,049.8	1,350.1	540.1	964.7	733.6	430.5	665.4	595.3	595.3	595.3
	Nestling	1,151.9	548.2	823.2	1,958.9	781.7	1,397.5	918.1	538.6	835.0	845.9	845.9	845.9
	Total	2,618.8	1,246.4	1,873.0	3,309.0	1,321.9	2,362.2	1,651.7	969.1	1,500.4	1,441.2	1,441.2	1,441.2

Table 6. Total delivery rates of nutrients to the nest inmates by wet weight (from Table 5), percentages of nutrients by body and brood mass (BM) and breeding success of each species of hornbills (from Table 1) in Khao Yai National Park, Thailand. GH=Great Hornbill, WH=Wreathed Hornbill, BH=White-throated Brown Hornbill, PH=Oriental Pied Hornbill.

Nutrient	GH (3,316 g)		WH (3,900 g)		BH (2,718 g)		PH (1,560 g)	
	Total nutrient	% by BM	Total nutrient	% by BM	Total nutrient	% by BM	Tota nutrient	% by BM
Protein (g/day)	28.2	0.85	22.1	0.57	23.1	0.85	16.4	1.05
Fat (g/day)	31.0	0.93	41.3	1.06	21.7	0.80	18.3	1.17
CHO (g/day)	58.9	1.78	83.3	2.14	27.1	1.00	28.8	1.85
Ca (g/day)	2.56	0.08	2.09	0.05	1.21	0.04	1.10	0.07
Energy (kJ/day)	2,618.8	78.97	3,309.0	84.85	1,651.7	60.77	1,441.20	92.38
Breeding success (%)	93.8		66.7		92.9		95.8	

livered during the first few weeks after enclosure, a drop towards hatching time, an even higher rise until the chicks attained full size and then a drop until fledging (Fig. 1). The form of diet, whether fruits or animals, and of nutrients, whether protein, fat, carbohydrate, calcium or energy, varied between phases of the nesting cycle. Diet also varied between species and was influenced by inter-specific differences in duration of the nesting cycle and in body, clutch and brood sizes (Table 1). Due to their peculiar breeding strategy as part of which the males feed imprisoned incubating and brooding females, it is difficult to compare hornbills with other birds. However, peaks in food delivery by all four hornbill species during the early weeks of the nesting phase may be associated with the need to supply nutrients for egg production, incubation, and the commencement of molt in Week 2 for smaller species (Fig. 1c & 1d), and the restoration of any reserves used in egg production and in the regeneration of new feathers in Weeks 2–4 for larger species (Figs. 1a & 1b) (Walsberg 1983; Bryant 1997), and/or the establishment of new reserves prior to rearing chicks (Poonswad 1993).

2) Breeding cycle and nutrients

We realize that our methods for estimating nutrient delivery to nest inmates can only be applied in broad terms. We are also conscious of errors that may arise from assuming that food delivered and the nutrients analyzed match those absorbed by the female and/or chicks, especially for carbohydrates that included indigestible crude fiber (Bolton 1955) and for fruits (Levey & Matínez del Rio 2001; Pryor et al. 2001).

In terms of nutrients and energy, breeding and molt are the most demanding processes within the annual cycle of any non-migratory bird species (Payne 1972; Walsberg 1983). In hornbills, the incubation and nestling phases may be more demanding for male hornbills than for any other birds (Klaasen et al. 2003). Among the four hornbill species studied in Thailand, only the female Great Hornbill emerges midway through the nestling phase to feed herself and so reduces the workload of her mate and helps provide food for the large chick. In the White-throated Brown Hornbill, the male is assisted by non-breeding helpers, which reduced the male's workload throughout nesting by 40% (Table 1; Poonswad 1993).

We noted that delivery rates for protein by all four hornbill species rose to a peak during Weeks 2–4 of incubation (Fig. 1), as might be expected to replace resources used in egg-laying and commencement of molt. We also recorded levels for delivery of energy during incubation that were as high as during chick rearing, which may relate to the costs of female molt.

Formation of eggs requires extra quantities of protein to form albumen, fat to form yolk, protein and fat to provide energy, and calcium to form eggshells (Meijer & Drent 1999). Due to the relatively high demands of clutch production versus female maintenance in various large bird species (Meijer & Drent 1999), deposition of body reserves prior to laying would be expected in hornbills rather than an increase in food delivery.

The coincidence of nesting and complete molt of all flight feathers is uncommon in birds, but total dependence on the male hornbill for delivery suggests that food availability is high, at least for the breeding female since the breeding male only molts after nesting (Poonswad 1993). In the Great Hornbill, where the female emerges earlier in the nesting cycle than other species (Table 1), high delivery rates of protein may also contribute to the regeneration of new feathers within a more restricted time frame. Video recordings from inside a Great Hornbill nest have shown that flight feather molt commences during Week 2 and is virtually complete by Week 10 (P. Poonswad, unpublished).

It should be noted that the most important sources of energy were fat and/or carbohydrate depending on species (Table 4). Non-significant differences in fat or carbohydrate delivery rates indicated that both were the main source of energy during the incubation and nestling phases for each species (Table 3), but from significant differences between them it seems that the amount of protein delivered was important in determining breeding success (Table 6), particularly during the seven-day pre-laying phase for production of quality eggs (Gill 1990).

Differences in nutrient delivery during the nestling phase probably reflected changes in requirements of the growing chick(s), such as for skeleton formation and feather growth (Gill 1990). In all four species there was a general increase in delivery rates during the nesting cycle, rising to a peak until chicks were expected to have completed their body growth midway through the nestling phase, followed by a drop until fledging (Fig. 1). However, this pattern did not hold for all nutrients and the exact amounts varied between species.

For example, lower fat delivery rates during the nestling phase in the Great Hornbill indicated the importance of fat for the incubating female, whereas fat was important to nestling Oriental Pied Hornbills as an energy source, possibly as a reserve to insure against poor food delivery by parents during the days just after fledging (Gill 1990).

Calcium delivery rates to incubating female Great and White-throated Brown Hornbills were as high as during the nestling phase, even though these species have different parental care strategies and brood sizes (Poonswad 1993; Table 1). Both species lay up to four eggs, thus high calcium delivery may replace that lost during egg production. Increased calcium may also help the female Great Hornbill to prepare for early emergence in Week 13, and the female White-throated Brown Hornbill to share reserves with its large brood of up to four chicks. In contrast, female Wreathed and Oriental Pied Hornbills, with similar modes of parental care but different brood sizes (Poonswad 1993, Table 1), have the whole nesting cycle to replace lost calcium, yet enjoy a significant increase in calcium delivery when the chick(s) are growing. Calcium was derived from both fruits and animal foods, the latter were especially common in the nestling diets of White-throated Brown and Oriental Pied Hornbills with their larger broods, but some fruits, especially figs, are also known to contain calcium (Poonswad 1993; O'Brien et al. 1998), and were important in the diet of the Wreathed Hornbill throughout breeding (Poonswad et al. 1987).

3) Source of nutrients

The overall proportion of fruits and animals in the diet had been recorded for nesting hornbills (Poonswad et al. 1987), but the respective nutritional contributions of these foods were not estimated from the food types delivered.

Generally, fruit was the major source of nutrients, particularly for fat and carbohydrate. Hornbills in Khao Yai consumed as much lipid-rich fruit as those in Borneo (Leighton 1982), but whether hornbills selected lipid-rich fruits or the majority of large trees produce fruits rich in lipids remains to be studied. Differences in nutrient sources among the four Thai hornbill species were related also to feeding niche of each species. Wreathed Hornbill is a fruit specialist whereas White-throated Brown Hornbill is an animal specialist. In contrast, Great and Oriental Pied Hornbills are generalists (Poonswad 1993). Wreathed Hornbill delivers the least protein from animal sources and Oriental Pied Hornbill the most (Table 4, 5, and 6), which may affect breeding success, particularly during egg production and incubation. Wreathed and Great Hornbills feed mainly in tree canopies, but Great Hornbill was frequently observed seeking animal food. White-throated Brown Hornbill occupies the forest under-story and hunts more animal food while Oriental Pied Hornbill forages from the ground up to the canopy and consumes the greatest diversity of food among these four species (Poonswad 1993; Poonswad et al. 1998).

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REFERENCES

Bolton W (1955) The digestibility of the carbohydrate complex by birds of different ages. J Agr Sci 46: 420–424.

Bryant DM (1997) Energy expenditure in wild birds. Proceedings of the Nutrition Society 56: 1025–1039.

Department of Health (1978) *Nutrient composition table of Thailand foods*. Nutrition Division, Department of Health, Ministry of Public Health, Bangkok.

Department of Health (1984) *Nutrient composition table of Thailand foods*. Nutrition Division, Department of Health, Ministry of Public Health, Bangkok.

Gill FB (1990) *Ornithology*. WH Freeman and Company, New York.

Jandel Corporation (1995) *SigmaStat* 2.0. Jandel Corporation, San Rafael.

Kemp AC (1995) *The Hornbills (Bucerotiformes)*. Oxford University Press, Oxford.

Kemp AC (2001) Family Bucerotidae (Hornbills). In: del Hoyo J, Elliott A & Sargatal J (eds) *Handbook of birds of the world*. Vol 6. pp 436–523. Lynx Editions, Barcelona.

Klaasen M, Brenninkmeijer A, Boix-Hinzen C & Mendelsohn J (2003) Fathers with highly demanding partners and offspring in a semidesert environment: energetic aspects of the breeding system of Monteiro's Hornbills (*Tockus monteiri*) in Nambia. Auk 120: 866–873.

Kleiber M (1961) *The fire of life*. John Wiley, New York.

Leighton M (1982) Fruit resources and patterns of feeding, spacing and grouping among sympatric Bornean hornbills (Bucerotidae). PhD thesis, University of California, Ann Arbor.

Levey DJ & Martínez del Rio C (2001) It takes guts (and more) to eat fruit: lessons from avian nutritional ecology. Auk 118: 819–831.

Meijer T & Drent R (1999) Re-examination of the capital and income dichotomy in breeding birds. Ibis 141: 339–414.

O'Brien TG, Kinnaird MF, Dierenfeld ES, Conklin NL, Wrangham RW & Silver SC (1998) What's so special about figs? Nature 392: 668.

Payne RB (1972) Mechanism and control of molt. In: Farner DS & King JR (eds) *Avian biology* II. pp 103–155. Academic Press, New York.

Poonswad P (1993) Comparative ecology of sympatric hornbills (Bucerotidae) in Thailand. D Sc Thesis, Osaka City University, Osaka.

Poonswad P, Tsuji A, Jirawatkavi N & Chimchome V (1998) Some aspects of food and feeding ecology of sympatric hornbill species in Khao Yai National Park, Thailand. In: Poonswad P (ed) *The Asian hornbills: ecology and conservation*. pp 137–157. BIOTEC–NSTDA, Bangkok.

Poonswad P, Tsuji A & Ngampongsai C (1987) A comparative ecological study of four sympatric hornbills (Family Bucerotidae) in Thailand. In: *Acta XIX Congressus Internationalis Ornithologici*. pp 2781–2791.

Pryor GS, Levey DS & Dierenfeld ES (2001) Protein requirements of a specialized frugivore, Pesquet's Parrot (*Psittrichas fulgidus*). Auk 118: 1080–1088.

Puwastien P & Sungpuag P (1983) Nutritive value of unconventional protein sources, insects. J Nutr Assoc Thailand 17: 5–12.

Walsberg GE (1983) Avian ecological energetics. In: Farner JR, King JR & Parkes KC (eds) *Avian biology*. Vol VII. pp 161–220. Academic Press, New York.