

## AN ASSESSMENT OF FOOD OVERLAP BETWEEN GIBBONS AND HORNBILLS

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**ABSTRACT.** – Hornbills and gibbons are considered to be potential competitors for food. They show considerable overlap in their frugivorous diet, foraging site (outer part of tree crowns), and reproductive period. However, the extent and nature of such overlaps have never been measured. Here we characterize the dietary overlap of the Great Hornbill, Wreathed Hornbill, Oriental Pied Hornbill, White-throated Brown Hornbill and White-handed Gibbon based on a long-term data on their feeding ecology at Khao Yai National Park, Thailand. Results from a Correspondence Analysis showed a slight overlap between the diets of the hornbills and gibbon, which may be attributed primarily on the dietary consumptions of *Ficus* spp. and, to a lesser extent, *Polyalthia viridis*. Due to the large crown size of *Ficus* and the overall low nutritional quality of its fruits, we hypothesized that a dietary overlap between the hornbills and gibbon for *Ficus* is energetically inconsequential for either groups. In contrast, *P. viridis* has comparatively small crowns, is present in the site in low densities, and produces fruits high in protein. Therefore, the overlap in diet between hornbills and gibbon for *P. viridis* may create the basis for competition, which in any event will be limited to pseudo-interference.

**KEY WORDS.** – Food overlap; Resources exploitation; Khao Yai National Park; Thailand.

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### INTRODUCTION

The coexistence of two different animal species using overlapping niches, defined by the full range of ecological conditions and resources under which they can survive, is linked to their capacity for sharing such niches and their resources, in a way that allows both of them to survive and reproduce optimally (Edgerly et al., 1998; Park et al., 1998; Cross & Benke, 2002; Elmberg et al., 2003).

Overlap in the use of niches and their resources may cause competition that result in separation of the two species into specific parts of their original niche (Terborgh & Diamond, 1970). However, competition will not arise when two coexisting species that share resources are limited to different resources (Tilman, 1977) or to one unlimited resource (Camillo & Garofalo, 1989; Geoffrey, 1998; Krasnov et al., 2005).

Feeding overlap may acquire ulterior importance if accentuated during parts of the year when one, or more of the

coexisting species, face increase in energy requirement due to reproduction. In mammals, the physiology of reproduction, regular cycling, gestation, and nursing, place females under substantial energetic pressure, (Lee & Bowman, 1995), and thus access to resources plays an important limitation in regulating overall reproductive success. Similarly, in birds, reproductive success has been related directly to the level of dietary protein available during the nesting period (Beckerton & Middleton, 1982; Wikelski et al., 2000). Those general effects have been so far documented for food overlaps between closely related coexisting species (Luiselli et al., 1999; Neale & Sacks, 2001; Mitchell & Bank, 2005), and not closely related coexisting species (Morin, 1999; Brown et al., 1997).

Two separate long-term ecological research projects have been conducted for more than two decades at Khao Yai National Park, Thailand, on the White-handed Gibbon (*Hylobates lar*) (Brockelman et al., 1998) and four sympatric species of hornbill, *Buceros bicornis* (Great Hornbill), *Aceros undulatus* (Wreathed Hornbill), *Anthracoceros albirostris*

(Oriental Pied Hornbill) and *Anorrhinus austeni* (White-throated Brown Hornbill) (Poonswad et al., 1998a). Both animal groups have been observed to feed on the outer part of the forest canopy and share the same niche (Carpenter, 1967; Kemp, 1995), where they select primarily ripe, sugar-rich, juicy fruits (Leighton, 1998; Poonswad et al., 1998a) with bright colors (Suryadi et al., 1994; Kanwatanakid, 2000). Moreover, a recent investigation of gibbon reproduction has also highlighted significant overlap with hornbills during that period of the year when they have a strong dependence on resources (Poonswad, 1993; Savini et al., 2008). The objective of this study was to characterize the dietary overlap between the White-handed Gibbon and the four sympatric hornbill species, as suggested by Kemp (1995), specifically during the first half of the year when both animal groups face strong feeding pressure due to their reproductive energetic demands (Poonswad, 1993; Savini et al., 2008).

## MATERIALS AND METHODS

**Study site and species** – The study was conducted between May 2001 and Dec. 2005 at Khao Yai National Park, Thailand (2,168 km<sup>2</sup>; 14°26'N 101°22'E), in slightly hilly terrain at about 600–890 m above sea level. The study area (Fig. 1) covered approximately 60 km<sup>2</sup> and was inhabited by a large population of four sympatric hornbill species that have been studied in detail for the past twenty years (Poonswad, 1993; 1995; 1998a). The area was also inhabited by a large population of White-handed Gibbon, which has been studied since the late 1970s (see Raemaekers & Raemaekers, 1985; Reichard, 2003; Bartlett, 2003; Brockelman et al., 1998). Khao Yai supports mainly a seasonally wet, evergreen forest (Kitamura et al., 2005), which experiences a distinct dry season (November–April) and wet season (May–October). The mean annual rainfall from 1993–2002 was 2,360 mm (Kitamura et al., 2005). Average daily temperature varied annually between 18.7 to 28.3°C and mean humidity ranged from 64.6% to 77.1% during the dry and wet season. Although figs (*Ficus* spp.) produce syconia through out the year (Poonswad et al., 1998b), the diversity and abundance of non-fig fruiting species are relatively high only in the rainy season and beginning of the dry season (Bartlett, 2003; Savini et al., 2008).

**Diet composition** – During the breeding season, the female hornbill imprisons herself in the nest site, a cavity in a tree trunk, and is fed by the male during the entire period of her egg incubation and chick development. The male moves constantly between the nest and the selected feeding sources (Kemp & Poonswad, 1993). We studied characteristics of food items consumed by hornbills in the field by using direct observations of feeding behaviour at nests by continuous observation of the visiting male (Altman, 1974). At least six nests of each hornbill species were monitored each breeding season, for a total of 24 nests over a period of two breeding seasons (2004 and 2005). The first author, with the help of research assistants, made feeding observations at each nest during four days per month for 10 hours per day (between 0500–1700 hrs). We scored each feeding visit by the male

from the moment when the female in the nest began to take food from the male until all food items had been passed to the female. We identified and characterized every plant and animal food item that was consumed.

We defined gibbon diet using direct observations of five well-habituated gibbon groups. For a period of two and a half years (May 2001 to Sep. 2003), two trained field assistants observed each group for a minimum of 5 days per month. Data on feeding activities were collected by continuous observations during the time between leaving and re-entering a night-tree (cf. Martin & Bateson, 1993), alternating every hour between males and females. Food sources were known by the observers or were identified later from collected plant samples (for details see Savini et al., 2008).

**Resource abundance** – The spatial distribution of plant resources was measured in order to quantify their abundance in the area by using 13 north–south transects (total length 19.4 km, range 620–2,100 m) located within the gibbon study area of 39.8 ha (0.398 km<sup>2</sup>). Along each transect, trees larger than 10 cm diameter at breast height (DBH) were marked, measured, and identified to species, so that a total of 19,524 individual trees were included in our analyses. We calculated the amount of resources as the percentage of the total tree sample, based on both stem number and basal area.

**Statistical analysis** – Correspondence Analysis (CA) using Minitab 15 (Minitab Inc.) was employed to compare feeding assemblages between White-handed Gibbons and the four hornbill species, following Ter Braak (1986) whereby data points are projected on a two-dimensional space that maximizes the correspondence between categories on the rows and columns (Poulsen et al., 2002). CA also helps to

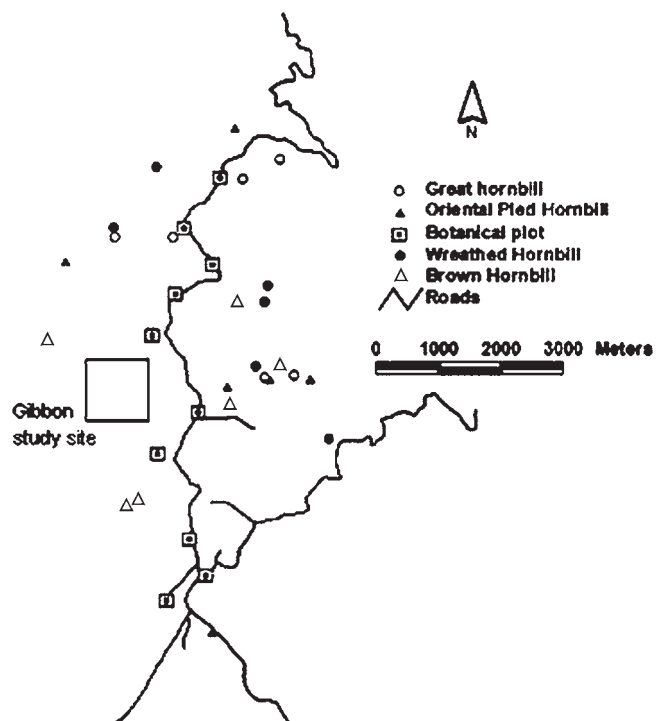


Fig. 1. Hornbill and gibbon study site.

find the best simultaneous representation of the diet records (Gorchov et al., 1995), with frugivorous species as column and fruit species as rows. Species showing similar diets will appear positioned close to each other. To determine which food items generated overlaps, we removed targeted plant species and re-ran the CA analysis. We included in the CA all plant species and animals consumed per hour by gibbon and hornbills based on direct observation. We used the Shannon-Wiener diversity index to define the diversity of each species' diet.

## RESULTS

**Diet composition** – The general composition of the diet during the breeding and/or nesting season in the first half of the year (January to June), for both hornbill and gibbon species had a higher component of fig and animal matter in the diet of hornbills, while the gibbon diet had a higher proportion of non-fig fruits (Fig. 2; see Table 1 for species details). Diet diversity, measured using the Shannon-Wiener diversity index, was: Gibbon (GB) = 2.1, Great Hornbill (GH) = 1.2, Wreathed Hornbill (WH) = 1.6, Oriental Pied Hornbill (PH) = 1.7 and White-throated Brown Hornbill (BH) = 1.8; where higher numbers show a higher diet diversity. The mean estimate for hornbill Shannon-Wiener diversity index was 1.575 with a 95% confidence interval of  $\pm 0.515$  with the Gibbon value falling just above the interval.

**Food overlap** – Fig. 3a shows the results for CA calculated by including all plant species ( $n = 58$ ) consumed by gibbons and hornbills. The two components account for 84% of the variance (variance for Component 1 was 66% and Component 2 was 18%), separating BH and PH from WH and GH, among hornbills, and from GB, which are isolated from the hornbills. After excluding from the analysis *Ficus* sp. and *P. viridis* (Fig. 3b), we observed a clear separation between GB and the four hornbill species, which appeared grouped, with the two components accounting for 88% of the variance (variance for Component 1 was 69% and Component 2 was 19%). To isolate the cause of this overlap, we analyzed the importance of the genus *Ficus* and of *P. viridis* separately. When removing only *P. viridis* from the analysis, we saw no obvious change from what was observed in Fig. 3a, with the separation of the five species along the two component accounting for 85% of the variance (variance for Component 1 was 67% and Component 2 was 18%; Fig. 3c). After removing only the genus *Ficus* from the analysis, we obtained a result similar to as when *Ficus* sp. and *P. viridis* was excluded, where the grouping along the two components accounted for 87% of the variance (variance for Component 1 was 68% and Component 2 was 19%; Fig. 3d). These results suggest that the main component in the overlap was represented by species of the genus *Ficus*, with a smaller proportion represented by *P. viridis*.

A similar pattern was observed when CA considered all the individual nests observed for hornbill and each group observed for gibbons (Fig. 4). Note that the two clusters observed in all hornbill species are the consequence of two years nest

observation where some plant species were not fruiting each year. More in detail were the two components that accounted for 35% of the variance (variance for Component 1 was 21% and Component 2 was 14%) when all plant species were considered (Fig. 4a). After excluding *Ficus* sp. and *P. viridis* from the analysis (Fig. 4b), we observed that both components accounted for 33% of the variance (variance for Component 1 was 19% and Component 2 was 14%). When only *P. viridis* was removed from the analysis (Fig. 4c), both components accounted for 35% of the variance (variance for Component 1 was 21% and Component 2 was 14%). After removing only the genus *Ficus* from the analysis, our result was similar to removing both *Ficus* sp. and *P. viridis* from the analysis, where the grouping along the two components accounted for 33% of the variance (variance for Component 1 was 19% and Component 2 was 14%; Fig. 4d).

**Resource abundance** - Sample percentages of individual species of diet trees that overlapped did not vary much between the five species (Table 2). However, the proportion of trees included in the non-overlapping portion of the diet showed a distinct difference between the gibbon and the four hornbill species, with the gibbons having a much higher proportion of their diet non-overlapping. This suggests that gibbons feed on a much larger set of resources that they do not share with hornbills.

A comparison of the density and basal area between *Ficus* spp. and *P. viridis*, the two species composing most of the diet overlap, indicated there was a larger amount of figs available, mainly as a low number of individuals but of a large size. Conversely, *P. viridis* was present in the area as a large number of individual trees but of much smaller size (Table 1).

## DISCUSSION

From a general dietary perspective, hornbills were less frugivorous, fed on a smaller number of plant species, and fed more on insects, small mammals and birds than gibbons. Based on the correspondence analyses, overall we detected only a moderate degree of overlap between gibbons and the two larger species of hornbill (Great hornbill and Wreathed hornbill), while the two smaller hornbill species (Oriental pied hornbill and White-throated Brown hornbill) appear more clearly separated. Even this moderate degree of overlap fell away once trees of the genus *Ficus* and, in a lower proportion, of the species *P. viridis*, were removed from the calculation. As a consequence of the relatively low nutritional quality (O'Brien et al., 1998) and the abundant distribution of the genus *Ficus*, we assumed a low importance for any such overlap to both animal groups.

Overall, both hornbills and gibbons persist in habitats of similar forest structure. Hornbills, as well as other large birds are able to observe the forest during flight and so detect fruits in the upper strata of the canopy (Kemp, 1995). This differs from most primate species, which are more likely to detect fruits in the middle strata of the canopy while

traveling through the forest (Poulsen et al., 2002). However, gibbons show the peculiar capacity to forage mainly on the outer part of tree canopy, a consequence of their specialized morphology and physiology (Carpenter, 1967).

We observed an overlap in the reproductive season between hornbills and gibbons at the study site during the first half of the year, when dependence on resources was higher

(Poonswad, 1993; Savini et al., 2008). For the gibbon, this period coincides with the pre-conception period when females must acquire a certain amount of body reserves in order to start cycling regularly and therefore conceive successfully (Savini et al., 2008). For the hornbills, as for other bird species, the nesting period is considered the period of the year where high costs are faced by both the reproductive male and female (Poonswad et al., 2004).

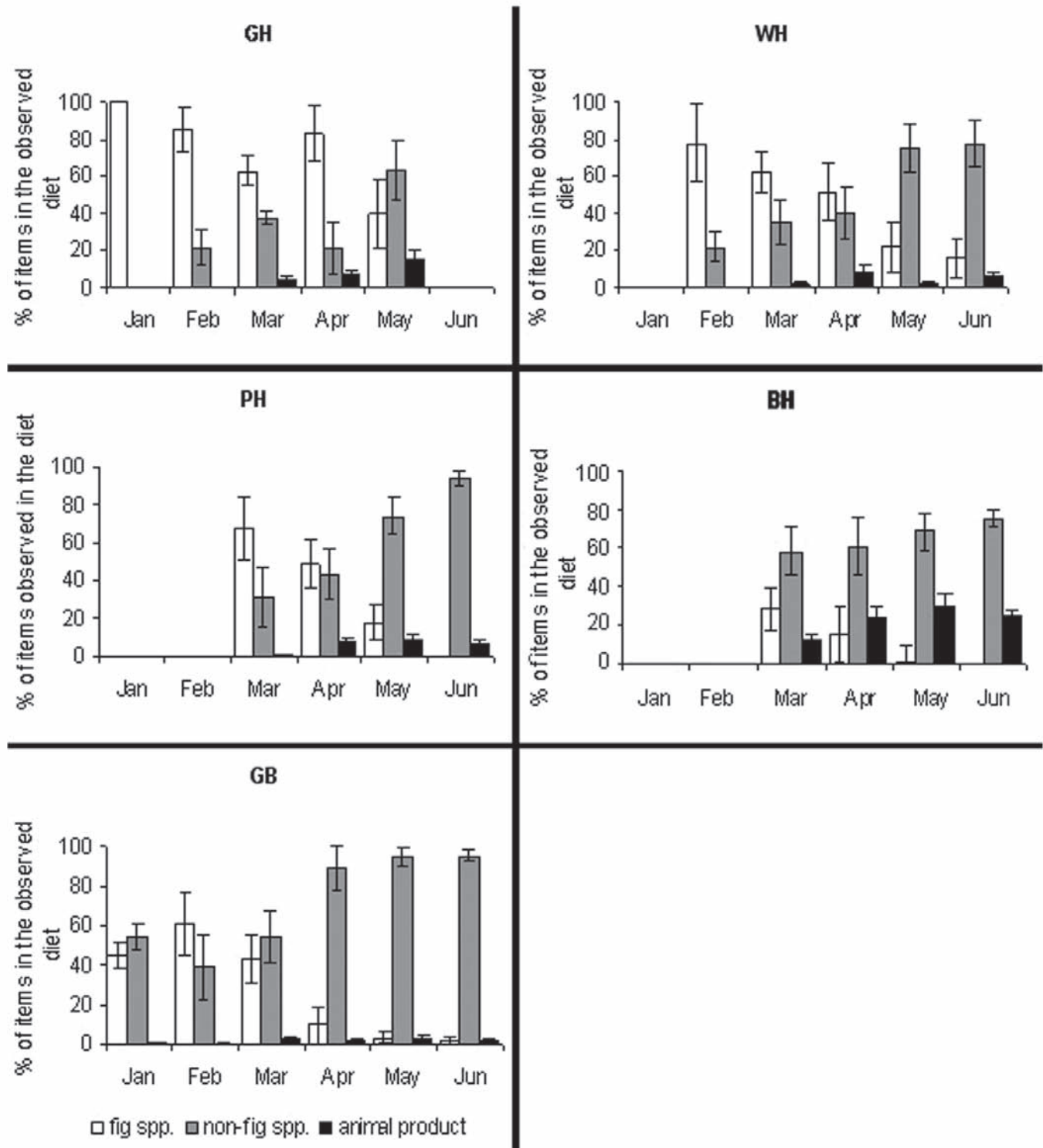


Fig. 2. Diet composition variation, during breeding season, between hornbill species [Great Hornbill (GH), Wreathed Hornbill (WH), Oriental Pied Hornbill (PH), and White-throated Brown Hornbill (BH)] and White-handed Gibbons (GB).

Table 1. Species list in the diet of the four hornbill species hornbill species [Great Hornbill (GH), Wreathed Hornbill (WH), Oriental Pied Hornbill (PH), and White-throated Brown Hornbill (BH)] and White-handed Gibbons (GB).

	Plant Density	Chemical Composition				Percentage in the Diet				
	Basal area / hectare	Protein g%	Fat g%	Calory kal/g	Ca+ g%	GH	WH	BH	PH	GB
Animal	-	-	-	-	-	3.57	4.42	16.97	8.18	0.30
<i>Acacia megaladena</i>	-	-	-	-	-	-	-	-	-	2.99
<i>Adinadra integerrima</i>	20.9	-	-	-	-	-	-	-	-	0.37
<i>Aglaia elaeagnoidea</i>	37.8	7.72	-	4259.77	0.46	-	-	-	-	0.30
<i>Aglaia lawii</i>	120.9	10.32	48.47	6493.3	0.59	0.64	0.48	0.67	0.76	-
<i>Aglaia spectabilis</i>	-	3.67	6.39	2200.77	0.31	0.93	2.46	0.26	0.20	-
<i>Alphonsea boniana</i>	36.3	-	-	-	-	-	-	-	-	0.18
<i>Anthocephalus chinensis</i>	-	-	-	-	-	-	-	-	-	0.08
<i>Antiaris toxicaria</i>	7.2	12.18	11.84	4670.6	0.4	0.03	-	-	-	-
<i>Aphanamixis polystachya</i>	66.8	8.01	-	6489.79	0.44	-	0.97	0.04	-	-
<i>Aquilaria crassna</i>	218	-	-	-	-	-	-	-	-	7.26
<i>Arthocarpus lakoocha</i>	-	5.27	9.83	4113.76	0.4	0.10	-	-	-	-
<i>Baccaurea ramiflora</i>	125.1	-	-	-	-	-	-	-	-	1.33
<i>Balakata baccata</i>	586.2	4.04	1.63	3877.47	-	-	-	-	-	3.51
<i>Beilschmiedia balansae</i>	-	4.65	6.93	2675.51	0.45	0.09	0.43	0.58	0.11	0.10
<i>Beilschmiedia glabra</i>	69.9	8.34	32.84	5969.97	0.17	0.00	0.07	0.29	0.02	-
<i>Beilschmiedia maingayi</i>	70.02	9.92	-	4842.06	0.68	0.31	0.83	1.97	0.80	0.14
<i>Beilschmiedia sp.</i>	-	-	-	-	-	0.06	0.01	0.04	0.03	-
<i>Bhesa robusta</i>	12.2	12.75	-	6195.61	0.78	2.40	2.28	7.06	2.06	-
<i>Canthium glabrum</i>	-	-	-	-	-	0.71	-	0.32	0.73	-
<i>Carallia brachiata</i>	68.8	-	-	-	-	-	-	-	0.62	-
<i>Cinnamomum subavenium</i>	395.3	5.71	31.92	6390.68	0.3	19.12	12.84	37.06	15.57	2.89
<i>Cleistocalyx opercolatus</i>	768.9	5.83	-	-	-	-	-	-	-	4.41
<i>Combretum acuminatum</i>	-	-	-	-	-	0.29	-	-	4.57	-
<i>Cryptocarya impressa</i>	-	12.73	26.69	6512.13	0.52	0.16	2.81	1.50	1.20	-
<i>Desmos chinensis</i>	climber	5.38	1.87	4465.84	0.63	0.90	0.05	0.43	0.11	4.58
<i>Dipterocarpus gracilis</i>	873.7	-	-	-	-	-	-	-	-	0.07
<i>Duabanga grandiflora</i>	-	-	-	-	-	-	-	-	-	2.51
<i>Dysoxylum cyrtobotryum</i>	143.3	7.4	16.33	4653.66	0.52	0.38	0.10	5.08	3.18	-
<i>Dysoxylum densiflorum</i>	-	11.84	-	6355.67	0.63	1.11	2.09	3.27	1.57	-
<i>Elaeagnus latifolia</i>	climber	4.81	0.12	1500.27	0.29	0.17	0.35	0.04	0.07	2.44
<i>Ericybe elliptilimba</i>	climber	-	-	-	-	-	-	-	-	4.90
<i>Ficus sp.</i>	108.2	4.84	5.07	3093.59	1.57	57.56	44.15	9.84	38.12	33.59
<i>Gironniera nervosa</i>	348.8	-	-	-	-	-	-	-	-	1.71
<i>Gnetum montanum</i>	climber	13.2	2.33	4655.83	0.45	-	-	-	0.46	1.35
<i>Horsfieldia glabra</i>	6.6	3.56	41.61	6939.2	0.32	1.27	1.36	3.15	3.33	-
<i>Knema elegans</i>	132.5	5.93	18.2	4955.44	0.68	0.00	0.59	0.12	0.23	0.74
<i>Livistona speciosa</i>	-	4.16	30.61	5472.85	0.26	1.99	3.40	-	-	-
<i>Mangifera sp.</i>	21.3	-	-	-	-	-	-	-	-	0.07
<i>Nauclea orientalis</i>	205.5	-	-	-	-	-	-	-	-	0.01
<i>Nephelium melliferum</i>	250.4	5.8	11.61	3996.05	0.34	-	-	-	-	8.02
<i>Peninsular sp.</i>	-	-	-	-	-	-	-	-	-	0.79
<i>Platea latifolia</i>	63.3	3.24	-	2062.74	0.66	-	-	0.11	0.28	0.04
<i>Polyalthia jucunda</i>	-	11.59	6.36	4723.72	0.57	1.27	3.13	1.17	0.95	-
<i>Polyalthia viridis</i>	56.1	9.9	12.78	4939.84	0.6	5.03	14.73	2.08	5.10	5.36
<i>Prunus arborea</i>	12.4	-	-	-	-	-	0.08	-	-	-
<i>Prunus javanicus</i>	22.5	-	-	-	-	0.25	1.06	0.58	0.66	1.35
<i>Ratan sp.</i>	ground vegetation	-	-	-	-	-	-	-	-	1.25
<i>Sabia limoniacea</i>	-	-	-	-	-	-	-	-	-	0.73
<i>Salacia chinensis</i>	climber	-	-	-	-	-	-	-	-	0.31
<i>Sarcosperma arboreum</i>	206.9	-	-	-	-	-	0.05	1.28	-	-
<i>Symplocos cochinchinensis</i>	764.5	-	-	-	-	-	-	-	-	3.22
<i>Sterculia balanghas</i>	-	-	-	-	-	-	0.05	-	-	-
<i>Sterculia sp.</i>	-	-	-	-	-	0.14	1.11	0.11	0.20	-
<i>Syzygium sp.</i>	-	2.03	-	4453.14	0.05	0.71	-	5.58	10.86	0.01
<i>Ternstroemia wallichiana</i>	8.7	-	-	-	-	0.80	0.13	0.39	-	-
<i>Walsura robusta</i>	79.1	4.6	4.74	3654.17	0.42	-	-	-	-	2.15
<i>Ziziphus attopoensis</i>	-	-	-	-	-	-	-	-	0.04	0.94

For several reasons, this small overlap in resources might affect hornbills more than gibbons. The gibbon's diet appears to be more diverse than that of hornbills. Overall, Asian primates are known among all primate species for their high diversity in diet (Kappeler & Heymann, 1996). However, the higher diversity of primate diet versus hornbill diet has also been observed in lowland rainforest of south-central Cameroon (Poulsen et al., 2002). In more detail, the diversity of the gibbon's diet is a consequence of both lower selectivity by gibbons, in terms of fruit morphology, and their travel mode, which allows them to move through the canopy by brachiating at relatively low energetic cost (Usherwood & Bertram, 2003). From the point of view of fruit morphology, Kanwatanakid & Brockelman (2005)

suggested that the structure of fruits might influence their selection by gibbons, which prefer ripe fruits with juicy pulp in bright colors (red, orange and yellow) and with one large generally well-protected seed. White-handed gibbons are also generalized frugivores, consuming various morphological types of fruits because of the advantage of hands for manipulation and long digestive tracts that allow consumption of fruit species with hard covers and flesh attached to seeds (e.g. *Choerospondias axillaris*, *Sandoricum koetjape* and *Garcinia xanthochymus*) (Kanwatanakid, 2000). Conversely, hornbills do not consume these fruit species because their feeding adaptations are restricted by their bill morphology, which significantly reduces their capability to manipulate and extract food. Hornbills tend to select the

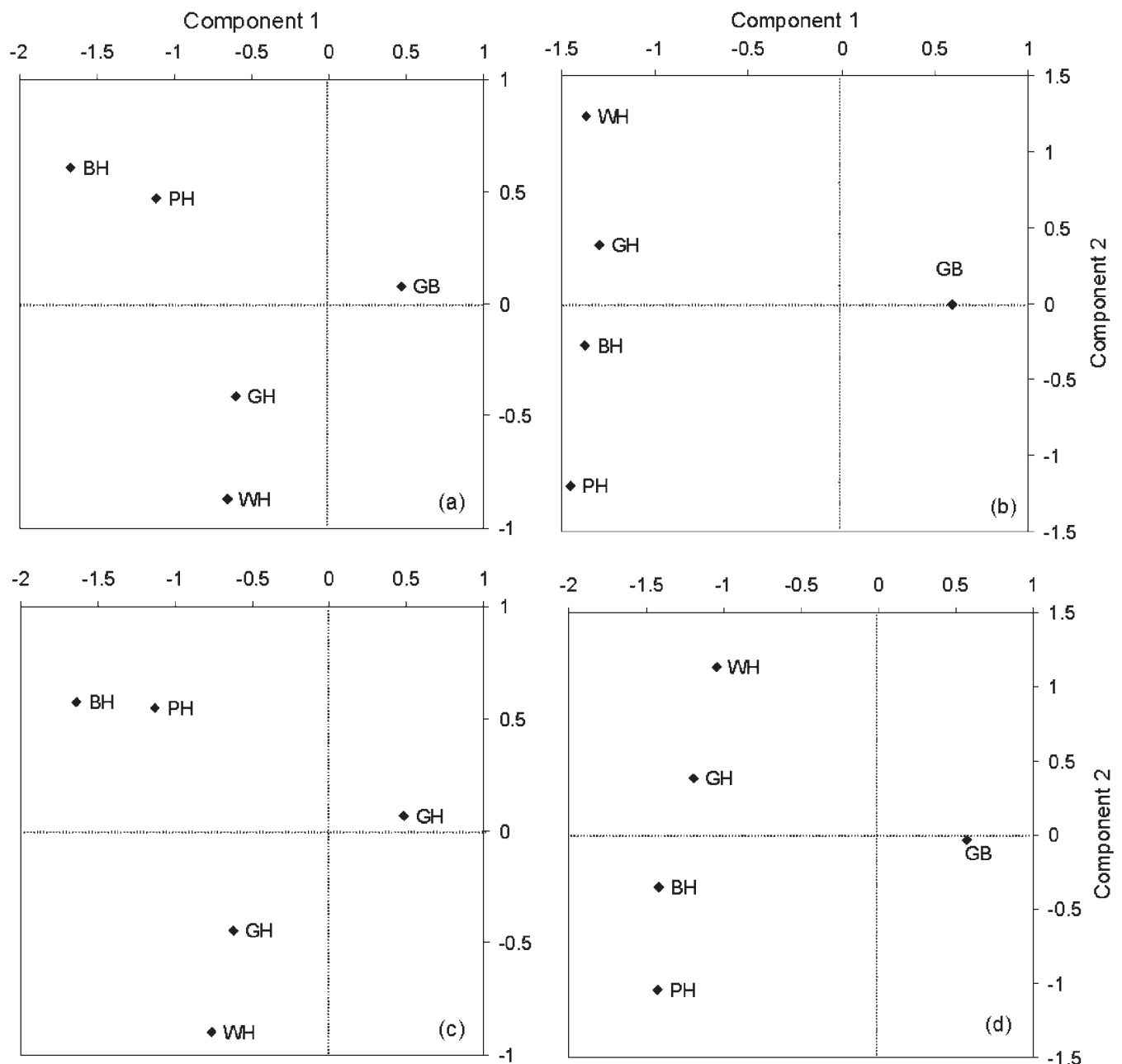


Fig. 3. Correspondence Analysis per animal species: a, with all plant species included (n = 58); b, with the genus *Ficus* and *P. viridis* excluded; c, with only *P. viridis* excluded; d, with only the genus *Ficus* excluded. Hornbill species [Great Hornbill (GH), Wreathed Hornbill (WH), Oriental Pied Hornbill (PH), and White-throated Brown Hornbill (BH)] and White-handed Gibbons (GB).

Table 2. Amount of individual trees belonging to overlapping and non-overlapping diet species (data expressed in % over total tree population measured in the 40 hectare botanical plot). Hornbill species [Great Hornbill (GH), Wreathed Hornbill (WH), Oriental Pied Hornbill (PH), and White-throated Brown Hornbill (BH)] and White-handed Gibbons (GB).

	GB	GH	WH	PH	BH
Overlapping sp.	5.2	5.2	4.4	5.2	1.8
non-overlapping sp.	22.5	4.0	4.1	4.4	5.0

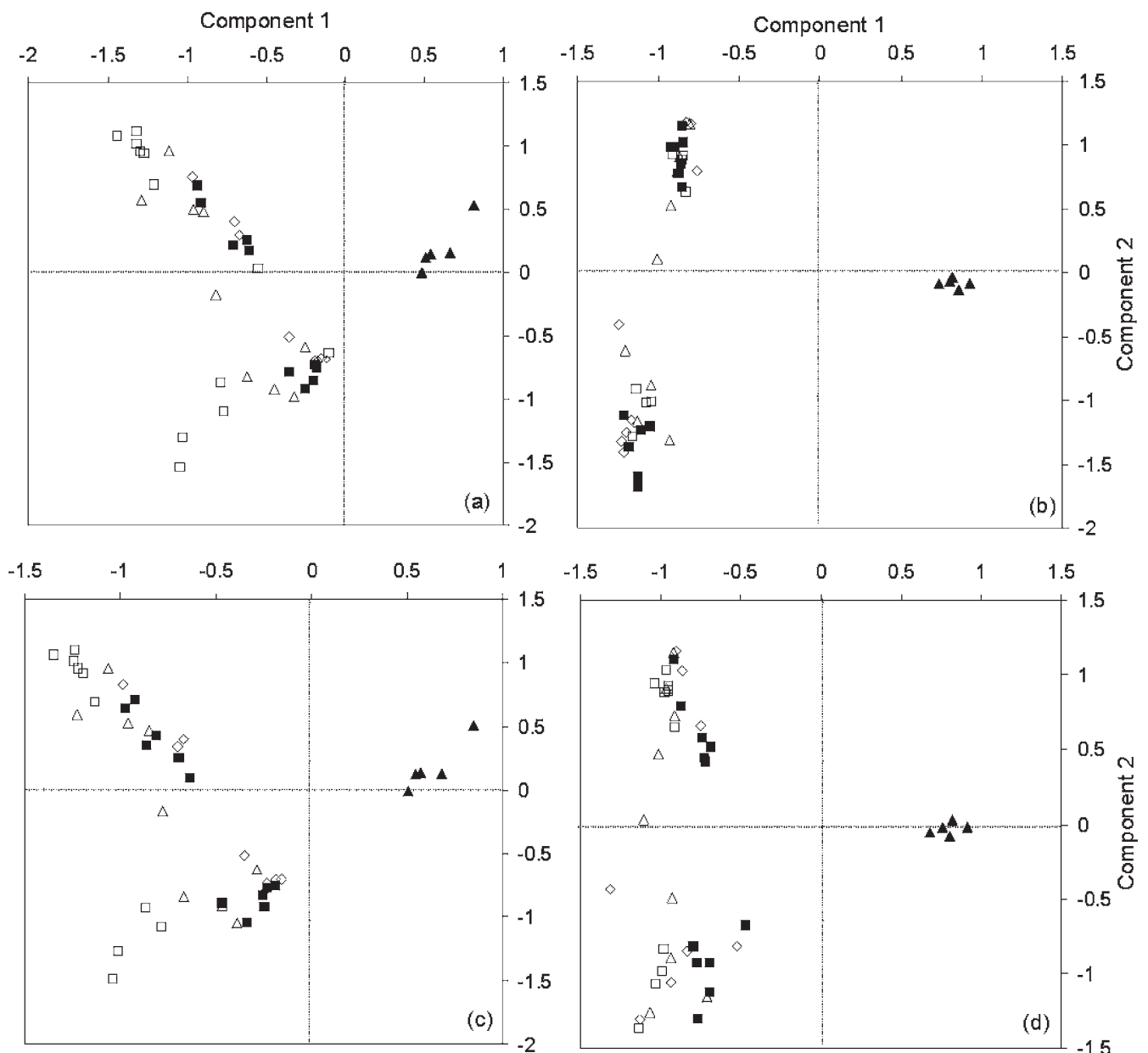


Fig. 4. Correspondence Analysis per hornbill nest and gibbon group: a, with all plant species included ( $n = 58$ ); b, with the genus *Ficus* and *P. viridis* excluded; c, with only *P. viridis* excluded; d, with only the genus *Ficus* excluded. Hornbill species [Great Hornbill  $\diamond$ , Wreathed Hornbill  $\blacksquare$ , Oriental Pied Hornbill  $\triangle$ , and White-throated Brown Hornbill  $\square$ ] and White-handed Gibbons  $\blacktriangle$ .

ripest fruits that show split (dehiscent) husks when ripening and high nutritional value (Poonswad et al., 1998a). During digestion, seeds do not pass through the digestive track and allow complete detachment of the nutritious flesh from the seed. In birds in general, regurgitated seeds spend less time in the digestive track than seeds defecated by other animals (Johnson et al., 1985), to limit body weight and reduce flight costs. An alternative explanation for the low diet diversity in hornbills may be due to their larger home ranges (from 5.9 km<sup>2</sup> for BH to 30.8 km<sup>2</sup> for WH, Poonswad & Tsuji, 1994), compared to gibbon [on average 25 hectares (0.25 km<sup>2</sup>), Savini et al., 2008], which allows hornbills to select only high quality resources that can be found more easily by covering a larger area.

Due to the high cost of flying (Gill, 1989), the selection of foraging sites for birds is affected by the distance from the nesting site and quality of the resources (Drent & Daan, 1980). Hornbills will fly preferentially to larger resources that will provide them with sufficient nutritional rewards. On the other hand, the low cost of brachiation for gibbons (Usherwood & Bertram, 2003) allows them greater mobility, resulting in multiple visits to a larger variety of sources due to the relatively low cost of traveling.

Hornbill diet showed a relatively higher proportion of animal food items, which were absent in the gibbon's diet, with the complete absence of vertebrates reported in the Khao Yai population and insect consumption recorded at less than 1% over the study period (T. Savini, unpublished data). We may assume that the vertebrate component of hornbill's diets may reduce the direct impact of resource overlap with gibbons for protein-rich fruit (e.g. *P. viridis*), and on which gibbons may be more successful foragers. The evolution of the hornbill's diet to include a higher quantity of vertebrates as a source of protein may also have arisen as a result of competition with other frugivorous animals that feed on protein-rich plant parts. Our interpretation was supported partly by observations of Great Hornbill diets in southern of Thailand (Budo Sungai Padi National Park), where the Great Hornbill consumed less than 5% of animal matter during the late nesting period (Chaisuriyanun, 2005). This amount is lower, although not significantly lower, than the 8% observed for the same species during the same nesting period in Khao Yai National Park. One explanation could be the lower gibbon density in the southern study area (WCS Thailand, 2006) reduces competition for plant species with high nutritional value for proteins.

Overall, our results show limited resource overlap between gibbons and hornbills, mainly based on figs that are of low quality generally, except for their calcium content (O'Brien et al., 1998), but were relatively abundant at the study site. The recorded overlap might assume importance for the second species involved, *P. viridis*, because it shows a high value in protein, which appears important during the breeding of both hornbills and gibbons, and was represented at the study site by small crops. If the overlap of such a species can generate competition between the two animal groups, then we can consider it as a simple exploitation of one or

more resources (Milinski & Parker, 1991), also referred to as pseudo-interference (Free et al., 1977). We do not exclude the presence of aggressive behaviour, but we expect the limit of such events to be sporadic. From our study, we can classify gibbons as "depleting competitors", the species that is more efficient in reaching and depleting a food resource, and hornbills as "unsuccessful competitors" that may suffer from the exploitation effects (Milinski & Parker, 1991).

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## LITERATURE CITED

- Altman, J., 1974. Observational study of behaviour: sampling methods. *Behaviour*, **49**: 227–267.
- Bartlett, T. Q., 2003. Intragroup and intergroup social interactions in white-handed gibbons. *International Journal of Primatology*, **24**: 239–259.
- Beckerton, P. R., & A. L. A. Middleton, 1982. Effects of dietary protein levels on ruffed grouse reproduction. *Journal of Wildlife Management*, **46**: 569–579.
- Brockelman, W. Y., U. Reichards, U. Treesucon & J. J. Raemaekers, 1998. Dispersal, pair formation and social structure in gibbons (*Hylobates lar*). *Behavioural Ecology and Sociobiology*, **42**: 329–339.
- Brown, J. S., B. T. Kotler & W. A. Mitchell, 1997. Competition between birds and mammals: A comparison of giving up densities between crested lark and gerbils. *Evolutionary Ecology* **11**: 757–771.
- Camillo, E. & C. A. Garofalo, 1989. Analysis of niche of two sympatric species of *Bombus* (*Hymenoptera Apidae*) in South eastern Brazil. *Journal of Tropical Ecology*, **5**: 81–92.

- Carpenter, C. R., 1967. *A field study in Siam of the behavior and social relations of the gibbon (Hylobates lar)*. New York: The John Hopkins Press.
- Chaisuriyanun, S., 2005. A Comparative study of diets of Great hornbill (*Buceros bicornis*) and Rhinoceros hornbill (*Buceros rhinoceros*) during the breeding season in Budo Su-Ngai Padi National Park Southern Thailand. [M.Sc. thesis in the Natural Resource Management]. Bangkok. School of Bioresources and Technology. King Mongkut's University of Technology Thonburi.
- Cross, W. F. & A. C. Benke, 2002. Intra-and interspecific competition among coexisting lotic snails. *Oikos*, **96**: 251–264.
- Drent, R. & S. Daan, 1980. The prudent parent: energetic adjustments in avian breeding. *Ardea*, **68**: 225–252.
- Edgerly, J. S., M. McFarland, P. Morgan & T. Livdahl, 1998. The seasonal shift in egg-laying behavior in response to cues of future competition in a tree hole mosquito. *Journal of Animal Ecology*, **67**: 805–818.
- Elmberg, J., P. Nummi, H. Poysa & K. Sjöberg, 2003. Breeding success of sympatric dabbling ducks in relations to population density and food resources. *Oikos*, **100**: 333–341.
- Free C. A., J. R. Beddington & J. H. Lawton, 1977. On the inadequacy of simple models of mutual interference for parasitism and predation. *Journal of Animal Ecology*, **46**: 543–554.
- Gill, F. B., 1989. *Ornithology*. W. H. Freeman and Company. New York. 660 pp.
- Geoffrey, M. W., 1998. Diet and habitat overlap in two sympatric primates species, the Tana crested mangabey *Cercocebus galertus* and yellow baboon *Papio cynocephalus*. *African Journal of Ecology*, **36**: 159–173.
- Gorchov, D. L., F. Carnejo, C. F. Ascorra, & J. Jaramillo, 1995. Dietary overlap between frugivorous birds and bats in Peruvian Amazon. *Oikos* **74**: 235–250.
- Johnson, R. A., M. F. Willson, J. N. Thompson & R. I. Berton, 1985. Nutritional values of wild fruits and consumption by migrant frugivorous birds. *Ecology*, **66**: 819–827.
- Kanwatanakid, C. 2000. Characteristics of fruit consumed by the white-handed gibbon (*Hylobates lar*) in Khao Yai National Park, Thailand. [M.Sc. thesis in Environmental Biology] Bangkok. Faculty of Graduate Studies. Mahidol University.
- Kanwatanakid, C. & W. Y. Brockelman, 2005. Characteristics of fruits consumed by the White-handed gibbon (*Hylobates lar*) at Khao Yai National Park, Thailand. In: Lum, S. & P. Poonswad. (eds.) *Proceeding of the third International Hornbill workshop*, Pp. 97–116. Phuket, Thailand.
- Kappeler, P. M. & E. W. Heymann, 1996. Nonconvergence in the evolution of primate life history and socio-ecology. *Biological Journal Linnean Society*, **59**: 297–326.
- Kemp, A. 1995. *The Hornbills: Bucerotiformes*. Oxford University Press. 301 pp.
- Kemp, A. & P. Poonswad, 1993. Life history of Great Hornbill *Buceros bicornis*. In: Poonswad, P. & A. C. Kemp (eds.). *Manual to the Conservation of Asian Hornbills*, Pp. 100–108. Sirivatana Interprint Co. Ltd., Bangkok, Thailand.
- Kitamura, S., T. Yumoto, P. Poonswad, P. Chualua, K. Plongmai, N. Noma, T. Muruhashi & P. Wohandee, 2005. Fruit-frugivore interactions in a moist evergreen forest of Khao Yai National Park in Thailand. *Tropics*, **14**: 345–355.
- Krasnov, B. R., N. V. Burdelova, I. S. Khokhlova, G. I. Shenbrot & A. Degen, 2005. Larval interspecific competition in two flea species parasitics on the same rodent host. *Ecological Entomology*, **30**: 146–155.
- Lee, P. C. & J. E. Bowman, 1995. Influence of ecology and energetic on primate mothers and infants. In: Pryce, C. R., R. D. Martin & D. Skuse (eds.). *Motherhood in human and nonhuman primates*, Karger Press, Basel, Switzerland. Pp. 47–58.
- Leighton, D. R., 1998. Gibbons, Territoriality and Monogamy. In: Smuts, B. B., D. L. Cheney, R. M. Syfarth, R. W. Wrangham & T. T. Struhsaker (eds.). *Primate Societies*, Chicago University Press, Chicago, USA. Pp. 83–97.
- Luiselli, L., G. C. Akani & D. Capizzi, 1999. Is there any interspecific competition between dwarf crocodiles (*Osteolaemus tetraspis*) and Nile monitors (*Varanus niloticusornatus*) in the swamps of central Africa? A study from southeastern Nigeria. *Journal of Zoology London*, **247**: 127–131.
- Martin, P. & P. Bateson, 1993. *Measuring Behavior. An Introductory Guide*, 2<sup>nd</sup> edition. Cambridge: Cambridge University Press.
- Milinski, M. & G. A. Parker, 1991. Competition for resources. In: Krebs, J. R. & N. B. Davies (eds.). *Behavioural Ecology*, Blackwell Scientific Publication. Oxford. UK. Pp. 137–168.
- Mitchell, B. D. & P. B. Bank, 2005. Do wild dogs exclude foxes? Evidence for competition from dietary and spatial overlaps. *Australian Ecology*, **30**: 581–591.
- Morin, P. J. 1999. *Community Ecology*. Blackwell Science, England. 424 pp.
- Neale, J. C. C. & B. N. Sacks, 2001. Resource utilization and interspecific relations of sympatric bobcats and coyotes. *Oikos* **94**: 236–249.
- O'Brien, T. G., M. F. Kinnaird, E. S. Dierenfeld, N. L. Conklin-Brittain, R. W. Wrangham & S. C. Silver, 1998. What's so special about figs? *Nature*, **392**: 668.
- Park, K. J., E. Masters & J. D. Altringham, 1998. Social structure of three sympatric bat species (Vespertilionidae). *Journal of Zoology, London*, **244**: 379–389.
- Poonswad, P., 1993. Aspects of the biology and ecology of some Asian Hornbills. In: Poonswad, P. & A. C. Kemp (eds). *Manual to the Conservation of Asian Hornbills*, Sirivatana Interprint Co. Ltd., Bangkok, Thailand. Pp. 76–97.
- Poonswad, P., 1995. Nest site characteristics of four sympatric species of hornbills in Khao Yai National Park, Thailand. *Ibis*, **137**: 183–193.
- Poonswad, P. & A. Tsuji, 1994. Ranges of males of the Great Hornbill *Buceros bicornis*, Brown Hornbill *Ptilonaemus tickelli* and Wreathed Hornbill *Rhyticeros undulatus* in Khao Yai National Park, Thailand. *Ibis*, **136**: 79–86.
- Poonswad, P., A. Tsuji, N. Jirawatkavi & V. Chimchome, 1998a. Some aspects of food and feeding ecology of sympatric hornbills in Khao Yai National Park, Thailand. In: Poonswad, P. (ed.). *The Asian Hornbill Ecology and Conservation*, The studies in Biodiversity No. 2, National Center for Genetic Engineering and Biotechnology (Biotec), National Science and Technology Development Agency (NSTDA), Bangkok, Thailand. Pp. 137–158.
- Poonswad, P., P. Chuailua, K. Plongmai & S. Nakkuntod, 1998b. Phenology of some *Ficus* species and utilization of *Ficus* resources in Khao Yai National Park, Thailand. In: Poonswad, P. (ed.). *The Asian Hornbill Ecology and Conservation*, The studies in Biodiversity No. 2, National Center for Genetic Engineering and Biotechnology (Biotec), National Science

- and Technology Development Agency (NSTDA), Bangkok, Thailand. Pp. 227-244.
- Poonswad, P., A. Tsuji & N. Jirawatkavi, 2004. Estimation of nutrients delivered to new inmates by four sympatric species of hornbill in Khao Yai National Park, Thailand. *Ornithological Science*, **3**: 99–112.
- Poulsen, J. R., C. J. Clark, E. F. Connor & T. B. Smith, 2002. Differential resource use by primates and hornbills implications for seed dispersal. *Ecology*, **83**: 228–240
- Raemaekers, J. J. & P. M. Raemaekers, 1985. Field back of loud calls to gibbons (*Hylobates lar*): territorial, sex-specific and species-specific responses. *Animal Behaviour*, **33**: 481–493.
- Reichard, U. H., 2003. Social monogamy in gibbons: the male perspective. In: Reichard, U. H. & C. Boesch (eds.). *Monogamy: mating strategies and partnerships in birds, humans and other mammals*, Cambridge: Cambridge University Press, Cambridge, UK. Pp. 190–213.
- Savini, T., C. Boesch & U. H. Reichard, 2008. Home range characteristics and the influence of seasonality on female reproduction in white-handed gibbons (*Hylobates lar*) at Khao Yai National Park, Thailand. *American Journal of Physical Anthropology*, **135** :1–12.
- Suryadi, S., M. F. Kinnard, T. G. O'Brien, J. Supriatna & S. Somadikarta, 1994. Food preferences of the Sulawesi Red-knobbed hornbill during the non breeding season. *Tropical Biodiversity*, **2**: 377–384.
- Ter Braak, C. J. F., 1986. Canonical correspondence analysis: a new eigenvector technique for multivariate direct gradient analysis. *Ecology*, **67**: 1167–1179.
- Terborgh, J. & J. M. Diamond, 1970. Niche overlap in feeding assemblages of New Guinea birds. *The Wilson Bulletin*, **82**: 29–52.
- Tilman, D. 1977. Resources competition between planktonic algae: an experimental and theoretical approach. *Ecology* **58**: 338–348
- Usherwood, J. R. & J. E. A. Bertram, 2003. Understanding brachiation: insight from a collisional perspective. *Journal of Experimental Biology*, **206**: 1631–1642.
- WCS Thailand, 2006. Conservation of agile gibbon *Hylobates agilis* and siamang *Symphalangus syndactylus* in the Halabala Forest Complex, Southern Thailand. WCS Thailand's final report to USFWS Great Ape Conservation Fund.
- Wikelski, M., M. Hau & J. C. Wingfield, 2000. Seasonality of reproduction in a neotropical rain forest bird. *Ecology* **81**: 2458–2472.