FOOD OVERLAP AND FRUIT SELECTION AMONG FOUR SYMPATRIC HORNBILL SPECIES DURING DIFFERENT PHASES OF THEIR ANNUAL CYCLE

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Thesis
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FOOD OVERLAP AND FRUIT SELECTION AMONG FOUR SYMPATRIC HORNBILL SPECIES DURING DIFFERENT PHASES OF THEIR ANNUAL CYCLE

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ABSTRACT

The study was conducted at Khao Yai National Park, Thailand, where close sympatry is observed between four hornbill species, namely: Great hornbills (*Buceros bicornis*), Wreathed Hornbills (*Aceros undulatus*), Oriental Pied Hornbills (*Anthracoceros albirostris)* and White-throated Brown Hornbills *(Anorrhinus austeni)*. The main objective was to determine important factors in fruit selection by hornbills and identify food overlaps of morphology and chemistry of fruits included in hornbill diet. Fruit morphology and their chemical components of food and non-food of hornbill were studied. Figs are important species in the diet during the entire year. Red and black fruits and syconium with pulp that can be detached from the seed easily are preferred. Moreover, consuming fruits with pulp easily detachedable from the seed detached easily from seed is easier for regurgitation and the extraction of the pulp can be done without gut passage. Hornbills tend to choose lipid-rich fruit with high calcium. Fruit types with high lipid were found to be capsule, drupe, berry and syconium respectively. The mean levels of calcium were significantly higher in syconium and fruits with a detached pulp of orange color. My results show that eaten fruits have relatively lower moisture content compared to non-eaten ones it meaning that hornbills prefer dry fruits. The low level of moisture in the birds' diet is explained as a strategy to avoid the carrying around of large volumes of water, which would make it difficult to fly. The model of fruit selection for future management, defined by Logistic Regression analysis, helps describe the relabeing eaten by hornbills. The model can predict which fruit characteristics (fruit type, detachment of pulp, fruit weight, fruit length and color) increase the chance of the fruit being eaten and which characteristics lessen the chance of the fruit being eaten. There was no food limitation so fruit selection was not the consequence of food availability in the forest**.** Schoener's Overlap Index and CCA showed low dietary overlap between the four hornbill species suggests that there is a limited food competition for fruits.

KEY WORDS: HORNBILLS / FOOD OVERLAP / FOOD SELECTION

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การซ้อนทับกันของอาหารและการเลือกกินผลไม้ของนกเงือกสี่ชนิด ที่อาศัยในพื้นที่เดียวกันของช่วงชีวิตต่างๆ ในรอบปี (FOOD OVERLAP AND FRUIT SELECTION AMONG FOUR SYMPATRIC HORNBILL SPECIES DURING DIFFERENT PHASES OF THEIR ANNUAL CYCLE)

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บทคัดย่อ

การศึกษาวิจัยนี้ได้มีขึ้น ณ อุทยานแห่งชาติเขาใหญ่ ประเทศไทย ซึ่งเป็นพื้นที่ที่มีนกเงือกสี่ชนิดอาศัยอยู่ร่วมกันคือนกกก (*Buceros bicornis*) นกเงือกกรามช้าง (*Aceros undulatus*) นกแก๊ก (*Anthracoceros albirostris*) และนกเงือกสีน้ำตาลคอขาว (*Anorrhinus austeni*) จุดประสงค์ของงานวิจัยเพื่อศึกษาปัจจัยที่มีผลต่อการเลือกกินอาหารนกเงือก และเพื่อศึกษาถึงการซ้อนทับกันของการกินอาหารของนกเงือกทั้ง 4 ชนิดและศึกษาองค์ประกอบทางเคมีในอาหารและลักษณะทางสัณฐานวิทยาของพืชอาหาร จากการศึกษาสัณฐานวิทยาและสารอาหารของผลไม้ของพืชที่เป็นอาหารและไม่เป็นอาหารของนกเงือก

ผลการศึกษาพบว่าไทรเป็นพืชอาหารที่มีความสำคัญตลอดปี ในขณะที่ผลไม้ที่ไม่ใช่ไทรมีการเปลี่ยนชนิดที่มีความสำคัญกับนกเงือกในแต่ละเดือนขึ้น อยู่กับสารอาหารและความต้องการสารอาหารนั้นๆ ในแต่ละช่วงฤดูสืบพันธุ์ต่างๆกันของนกเงือก ลักษณะของพืชอาหารในฤดูสืบพันธุ์และนอกฤดูสืบพันธุ์มีความคล้ายคลึงกัน ผลไม้สีแดงและดำแบบซิลโคเนียม (syconium) และมีเนื้อหลุดจากเมล็ดได้ง่ายถูกเลือกกินมากที่สุด เนื่องจากนกมีสายตาที่มีโคนเซลล์ 4 ชิ้น (trichromatic) และความสามารถในการสะท้อนแสงอุลตราไวโอเลตได้ ทำให้สามารถตรวจพบผลไม้ที่มีสีแดงและดำได้ง่ายกว่าสีอื่นที่อยู่บนพื้นใบไม้สีเขียว และสีดังกล่าวเป็นสีที่บอกถึงความสุกของผลไม้ด้วย นอกจากนี้การกินผลไม้ที่มีเนื้อหลุดจากเมล็ดได้ง่ายจะช่วยในการขย้อนเมล็ดออกมาและเนื้อจะหลุดออกได้ง่าย โดยไม่ต้องผ่านการย่อยของลำไส้ นกเงือกเลือกที่มีไขมันและแคลเซียมสูง โดยผลไม้ที่มีไขมันสูงที่พบมากที่สุดคือผลไม้ที่มีผลแบบแคปซูล ตามด้วยแบบ ดรูป (drupe) เบอรี่ (berry) และ syconium ค่าของแคลเซียมมีสูงในผลไม้ที่มีผลแบบ syconium มีเนื้อหลุดจากเมล็ดได้ง่ายและมีสีส้ม ผลการศึกษาพบว่าพืชที่เป็นอาหารนกเงือกมีค่าความชื้นต่ำ เมื่อเทียบกับพืชที่ไม่เป็นอาหาร นั่นคือนกเงือกเลือกผลไม้ที่เป็นผลลักษณะแห้ง อาจเพื่อเป็นการหลีกเลี่ยงการนำพาผลไม้ที่มีน้ำหนักมาก และทำให้ต้องใช้พลังงานมากในการบิน นอกจากนี้แบบจำลอง (model) ที่ได้เพื่อการจัดการสัตว์ป่าในอนาคตที่ได้จากการวิเคราะห์ Logistic Regression ช่วยในการอธิบายความสัมพันธ์ของพืชที่เป็นอาหารและไม่เป็นอาหารของนกเงือก โดยทำนายค่าความเป็นไปได้อย่างมีนัยสำคัญของผลไม้ชนิดนั้นๆ ว่ามีความน่าจะเป็นในการเป็นพืชอาหารของนกเงือกหรือไม่และมีระดับความน่าจะเป็นเท่าไร นอกจากนี้พบว่าปริมาณของอาหารที่มีในป่ามีไม่จำกัด ฉะนั้นพืชที่มีอยู่ในป่าไม่มีผลต่อการเลือกกินอาหารของนกเงือก Schoener’s Overlap Index and CCA แสดงระดับการซ้อนทับของอาหารระหว่างนกเงือกทั้งสี่ชนิดที่ต่ำ จึงคาดว่าน่าจะมีข้อจำกัดของการแก่งแย่งระหว่างนกเงือกในการกินอาหาร

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CHAPTER I

INTRODUCTION

Tropical rain forest ecosystems are characterized by high species diversity and complex relationships among species. Tropical rain forest trees can flower and/or fruit at any time of year, but the reproduction of species and individuals is generally not continuous (Richards, 1952) and often not synchronous. The distribution of resources in these ecosystems is therefore heterogeneous, with patches in time and space that affect patterns of reproduction and food preferences (Whitmore, 1990). The plants within these systems also benefit from a high diversity of seed vectors, which implies that strategies of fruit production, advertisement and nutritional reward should evolve to attract the greatest possible variety of dispersers (Snow, 1971).

Many plants in tropical forest depend on birds and mammals for dispersal of their seeds. The traits of fruits and their frugivores are the product of diffuse coevolution, in which groups of plants interact with groups of animals (Fleming, 1991). Coevolution between plants and their seed dispersers may help therefore to explain some events of plant reproductive biology and animal feeding habits (Krebs, 1985).

Study of food selection is an important tool for understanding animal dispersers and their possible function in relation to future conservation actions (Juilliot, 1996). For example, Thompson and Willson (1978; 1979) suggested that, for birds, fruit selection presumably depends on the behavior, morphology, and nutritional requirements of the species involved, the abundance of alternative food resources, and fruiting characteristics of the plant such as temporal availability, habitat choice, fruit taste, fruit color, and abundance and placement of the parent plants. Fruit colors are often stressed as one of the most important factors that might affect avian color preferences, enhance the conspicousness and ease of detection of the fruit crop, or signal the stage of fruit maturity. (Willson and Whelan, 1990). Interesting studies on feeding ecology and food, using primates as the focal animals, has been done by Guiloton and Dubost (1994). The three major small-bodied primate species in French

Guiana eat smaller and slightly softer fruits and seeds, and greater quantities of invertebrates than larger-bodied species. There were no specific differences depending on fruit hardness, for the smallest monkey, *Colobus apella*, which ate more soft fruits than other monkeys, can also attack and break tough palm nuts (Guiloton and Dubost, 1994). This observation was supported by Juilliot who, studied food choice by Red Howler monkey (*Alouatta seniculus*) in 1996, and suggested that fruit size appeared to be a more determinant characteristics in their fruit choice. Although the consumption of fruits was linked to the resource availability of each species within the habitat, particular fruit species appear to be strongly preferred. Two principle criteria for fruit choice by the monkeys were the colour and size of fruits, where yellow fruits of 5-50 g were preferred (Juilliot, 1996).

Differences in animal morphology might also affect food selection especially with regard to bird species. Zaret (1980) supported this view when he suggested that most fruit-eating birds are "gape-limited", since they typically swallow the whole fruit, even though a few soft fruits, such as *Ficus* spp. may be eaten piecemeal.

However, morphological characteristics of fruits are certainly not the only criteria influencing frugivorous choice. Other characters, such as chemical and nutritional content, presence of secondary compounds, palatability, digestibility and spatial aspects of fruits display must also be taken into account (Coelho et al. 1976; Glander 1978; Milton 1980; Sourd and Gautier-Hion 1986; Janson et al. 1986; Levey and Karasov, 1990).

What is the degree of food competition among sympatric species?

The ecological evidence for food competition between animal species is difficult to determine. Competition can occur via one or more of six distinct mechanisms, consumption, preemption, overgrowth, chemical interaction allopatry, territoriality and encounter competition (Mackenzie et al. 1998) Interspecific competition occurs between two species that use the same limited food resources and one or both experience a shortage. However, if these two species compete in a stable environment two outcomes are possible, one species is excluded or both species coexist (Mackenzie et al. 1998). Simple overlap in resource use is not sufficient evidence to prove that species compete. Species may overlap in resource use without being resource limited, either because resources are not in short supply, or because the species are more limited by some other factor(s). Resource overlap is sometimes considered synonymous with a coefficient of competition, but the logical assumptions required are usually difficult to justify. It seems most difficult in the wild to quantify competition among species that have similar resources and live sympatrically. Where it is possible to measure food availability, degree of food overlap and food selection, these values might distinguish the degree of food competition and partitioning for sympatric species.

Hornbills in and their feeding ecology at Khao Yai National Park: what is still unknown about food competition and selection?

In Khao Yai, there are four hornbill species that live sympatrically, Great Hornbill (*Buceros bicornis*), Wreathed Hornbill (*Aceros undulatus*), Oriental Pied Hornbill (*Anthracoceros albirostris*) and White-throated Brown Hornbill (*Anorrhinus austeni*) (Poonswad et al, 1998). These four species differ insize, with Great Hornbill (body length 107-132 cm) the largest, Wreathed Hornbill (100-110 cm.) the second largest, and Oriental Pied and White-Throated Brown Hornbills (70-80 cm. and 75 cm. respectively) the smallest (Poonswad et al, 1986).

The study on hornbills at Khao Yai National Park was started in 1978 by Prof. Pilai Poonswad. A main goal of the study has been the sustainable conservation of hornbills and their habitat. This ongoing research has been emphasized the breeding biology and ecology of hornbills, including nest and nest site characteristics, food and feeding behavior, nesting behavior, flocking and home ranges. Nest surveys and maintenance are regularly conducted every year, while the roles of hornbill in forest ecology have also been included in the study. Basic information about feeding ecology has been described, but many details remain unclear and need to be magnified, such as the factors influencing selection of a given fruit item over others available in the habitat

Hornbills are known as omnivorous, feeding on a great variety of fruits and animals (Poonswad, et al.). Poonswad et al. (1998) suggested that nature of fruits eaten by the four species of hornbills at Khao Yai be grouped into fleshy pulp with fine seeds, fruit within husks that split when ripe, dry flesh with a single seed-stone or and softjuicy fleshy with a single seed-stone. Great and Oriental Pied Hornbills consumed the greatest diversity of food, showing that they are generalist when compared with Wreathed and White-throated Brown Hornbills. It was hypothesized in the same study that hornbill preferences for fruits were determined by abundance of these fruits, but there were no quantitative data to compare food availability and the amount of food consumed.

However, it is difficult to investigate food selection throughout the year and include the breeding and non- breeding seasons. Most hornbill research has studied only the breeding or the non-breeding season (Poonswad et al. 1998, Suryadi, et al. 1998, Anggraini, et al. 2000, Ouithavon and Poonswad, 2000, Datta, 2003). What influences the selection is also still unclear, even though it is known that fruit was the major source of nutrients, particularly for fat and carbohydrate (Poonswad et al, 2004). Hornbills at Khao Yai consumed lipid-rich fruits, but whether the hornbills selected fruits rich in lipids or the majority of large trees produce fruits rich in lipids remains to be studied (Poonswad et al, 2004). The contribution of different food types in terms of the timing of breeding has not previously been documented, nor has the nutritional requirement during the non-breeding season.

Poonswad and Kemp (1993) suggested that the competition for food in hornbills may be intense, since their main food source was figs. However, it remains unquantified if there is food competition and food overlap among these four species of hornbill that live sympatrically, and whether they really experience competition or actually share their resources. To clarify the factor that influences food selection by hornbills, the following questions, objectives and hypotheses were compiled for this study:

Questions

1. How to define inter-specific overlap in diet among four sympatric hornbill species?
2. Do hornbills select fruit by quantity or by quality?

Objectives

1. Determine important factors in fruit selection by hornbills.
2. Define the main temporal (breeding & non-breeding season), morphological and

chemical factors involved in the fruit diet available to the four hornbill species.

3. Identify overlaps in time, morphology and chemistry of fruits included in the diets of the four hornbill species.

General Hypotheses

1. H_0: food items eaten do overlap among these four hornbill species

H_1: food items eaten do not overlapped among these species

P: Food items overlapconsiderably among these four hornbill species.

Assumption: Hornbills live in sympatry and therefore utilize same food resources

2. H_0: Hornbills select fruits by abundance.

H_1: Hornbills do not select fruits by abundance.

P: Due to cost-benefit considerations, hornbills select fruits by abundance.

Assumption: There is no food limitation for hornbills within study site.

3. H_0: Hornbills select fruits by their morphological characteristics and chemical components.

H_1: Hornbills do not select fruits by their morphological characteristics and chemical components.

P: Due to efficiency and nutritional considerations, hornbills select fruit by morphological characteristics and chemical content.

Assumption: There is a wide diversity available of fruit morphological and chemical characteristics.

The outputs from this study will provide basic knowledge that will be useful for hornbill conservation and management plans for their populations, food sources and forest habitats. It is also be useful for hornbill captive breeding programs. The methodology developed to study fruit selection by hornbills can also be applied for the study of other animals and habitats.

CHAPTER II
LITERATURE REVIEW

1. The four hornbill species at Khao Yai National Park and their biology

Hornbills can be found only in the tropical forests of Asia and Africa. Due to their large body, bill size and monogamous behavior, hornbills are often designated as keystone and/or flagship species in those forests and for ecology and conservation studies.

Asian hornbills live only in tropical forests that provide suitable nest trees and food sources, and thus their forest habitat has to be very healthy (Poonswad and Kemp, 1993).[Once again, be careful how you use this reference] At Khao Yai, there are four sympatric species of hornbills, Great Hornbill (*Buceros bicornis*), Wreathed Hornbill (*Aceros undulatus*), Oriental Pied Hornbill (*Anthracoceros albirostris*) and White-throated Brown Hornbill (*Anorrhinus austeni*) (Poonswad et al, 1998). Great Hornbill (body length 130-150 cm.) and Wreathed Hornbill (114 cm.) are considered to be of large size, while Oriental Pied Hornbill (70-89 cm.) and White-throated Brown Hornbill (75 cm.) are small size hornbills (Poonswad and Kemp, 1993).

They are considered to be one of the most important seed dispersers in their habitat. This is because they generally consume various kinds and sizes of fruits, do not damage the seeds, and can disperse the seed further than most other animal species (Poonswad and Kemp, 1993). These four hornbill species have similar breeding seasons, which start in January and go on until beginning of June, while the non-breeding season is between July to December (Poonswad et al, 1983). The breeding season of Great and Wreathed Hornbills start in January and last until May, while The smaller Oriental Pied and White-throated Brown Hornbills start their breeding seasons later in February but also last until May. The nesting cycle starts when the female is imprisoned and lasts until the chick fledges, taking about 120 days for Great and Wreathed Hornbills, and 92 and 83 days respectively for White-throated Brown and

Oriental Pied Hornbills (Poonswad and Kemp, 1993). The incubation and nestling phases of the larger hornbills, Great and Wreathed Hornbills, extends over weeks 1-7 8-20 respectively. White-throated and Oriental Pied Hornbills, which are smaller, have shorter incubation and nestling phases over weeks 1-5 and 6-14 or 15 respectively (Poonswad, et al., 2004). Oriental Pied Hornbill are known to lay1-3 eggs and White-throated Brown Hornbill 2-3 eggs, but often raise only 1-2 chicks per a nesting cycle. However, the two large hornbill species raise only a single chick per a nesting cycle (Poonswad and Kemp, 1993).

During the non-breeding season, Poonswad and Kemp (1993) suggested that most hornbill species usually form flocks of different size from around July until December. The largest flock size observed at Khao Yai National Park was of the Wreathed Hornbill (up to 1,000 individual) following by Oriental Pied Hornbill (130 individuals), Great Hornbill (70 individuals) and White-throated Brown Hornbill (54 individuals). These results suggested that the number of individuals in the flocks of all species fluctuates, perhaps in relation to the abundance of food.

Poonswad et al (1998) suggested that these hornbills are generally frugivorous, but sometimes they are omnivorous in the breeding season. Sympatric hornbill species also consume relatively similar food, indicating that they forage for and at similar food sources (Poonswad and Kemp 1993). Studies of food preference during the breeding season have also shown that fruit abundance rather than fruit nutritional value is of importance in fruit selection. They also found that, among the 12 highest ranked of the non-fig fruit species, *Polyalthia viridis* and *Strombosia* sp. were the most preferred, while among animals food, centipede and cicada were the most preferred (Poonswad et al, 1998). Food selection of hornbill species during the non-breeding season has been studied partly in the Sulawesi Red-knobbed Hornbill *Aceros cassidix* (Suryadi et al., 1994). They found that hornbills preferred red and purple fruits to other colors, and that they preferred large, heavy fruits over smaller fruits. Moreover, fig species were the most important component of the diet. Poonswad et al. (2004) confirmed the importance of fruits in sympatric hornbill species, with the proportion of fat of particular importance, while the importance on animal protein was linked to breeding success. However, factors influencing food selection by hornbills still need to be clarified. There are many other possibilities that might be able to explain why hornbills consumed certain kinds of food and these possibilities may also explain how they can live sympatrically in the same forest.

2. Food overlap and food competition

Competition is an interaction among individuals that utilize a limiting resource, resulting in reduced fitness in the competing individuals and so competition between species may occur whenever the availability of shared food resources is limited. Wein (1989) pointed out that, in order to show that interspecific competition occur, one must demonstrate that the species involved overlap in resource use and that competitive overlap in resources has negative effects, and Morin (1999) stressed that overlap in resource use alone is not sufficient evidence to prove that species compete. However, the first step in examining the potential for competition is to assess the extent of food overlap (Gorchov, et al. 1995). Species may overlap in resource use without being resource limited, because resources are not in short supply or species are limited by other factors such as predation. It is especially difficult to measure resource utilization, overlap and breadth for a large number of species, although one pattern to study resource partitioning was summarized by Schoener (1974). During the periods when fruit is scarce and only certain foods sustain frugivores, these have been called “keystone resources” (Gautier-Hion and Michaloud, 1989). Specialized birds are those that consume a specific kind of fruit, and Howe and Stephen (1979) suggested that competition among potential dispersers for a limited and highly nutritious food resource has led to facultative specialization by frugivore species.

Competition for food reduces food availability and it reduces forager encounter rates with prey. Competition theory suggested that when competitors reduce prey availability, competitors should respond by altering their attack probabilities for example, foragers might avoid attacking preys that are the preferred prey of competitor (MacArthur and Lavin, 1967).

Competition occurs both between species utilizing shared resources (interspecific competition) and among individual members of a species (intraspecific competition). The niche of an individual or species (the conditions under which it is found, the resources it utilizes and the time it occurs there) is critical in determining the degree of competition with other species or individuals. Large niche overlap generally results in intense competition. If two species compete in a stable environment, there are two possible outcomes: (i) one species is excluded, or (ii) both species coexist. The competitive exclusion principle states that coexistence can only occur in stable environment if the species' niches are differentiated. (Mackenzie et al., 1998). Sometimes the niche requirements of animals can be changed to avoid food competition (Wegner and Hansson, 1998). For example, in a study of food competition and niche separation between fish and the Red-necked Grebe *Podiceps grisegena*, the presence of a high fish density in ponds did not exclude Red-necked Grebe from breeding. Instead these birds shifted their habitat from relatively open areas, with scattered emergent vegetation, high fish and low invertebrate abundance, to very shallow littoral areas with dense vegetation, low fish and high invertebrate abundance (Wegner and Hansson, 1998). However, besides changing the niche requirement, food competition can change behavior as well. For example, a study on competition for food items within the nest found that the begging behavior of nestling birds exhibits evidence of adaptive learning and behavioral adjustment in response to experiences of the competitive environment (Budden and Wright, 2005).

Korpimaki (1987) studied the niche relationships between Long-eared Owls (*Asio otus*) and *Microtus* voles in the breeding season. He found that interspecific competetition for food seemed to be an important factor that affects the niche of these species. In a study of Crested Lark scientific name? and Allenby's gerbil scientific name?, competition explained the mechanism of co-existence in that, when a lark leaves a food patch the patch remains a valuable feeding opportunity for a gerbil, while in contrast, when a gerbil leaves a food patch the patch must experience considerable resource renewal before it provided a profitable foraging opportunity for a Crested Lark (Brown, 1997). However, food competition can sometimes cause mortality of juvenile birds, such as for pigeons that were poor competitors with adults (Sol, 1998). Juvenile pigeons foraged less rapidly and so were more vulnerable to exploitation competition, and juveniles were also subordinate to adults within a despotic social system, so they also suffered more from contest competition.

For species that appear to live sympatrically, taxa that occur together in the same geographical area, the populations may occupy either the same habitat (biotic sympatry) or different habitats (neighboring sympatry) within the same geographical area (Lincoln et al, 1998), but they must have resource partitioning between them (Emmon, 1980). This was supported by the study of nine species of sympatric tree squirrels in the field and captivity in rain forest habitat at Makoukou, Gabon. Resource partitioning among them included (1) two species that were restricted to special habitat types, while the other seven commonly co-occur in mature rain forest and represent a maximum of taxonomic diversity, (2) differential use of the vertical vegetation divided four essentially arboreal species from three ground foraging forms, and (3) the species that shared a given foraging level or habitat differed in body size by approximately Hutchinson’s ratio (Emmons, 1980). Another example of resource partitioning was presented by a study of sympatric hornbill species, Great, Wreathed and Oriental Pied Hornbills, during the non-breeding season in Arunachal Pradesh, northeast India, where food resources were partitioned by varying the relative contribution of figs and non-fig fruits in the diet (Datta 2003). Some primate studies also showed interspecific differences in food selection for primary and secondary plant chemicals, which explained the mechanisms that allow several primate species to coexist in sympatry (Ganzhorn, 1988).

3. Food selection

Most animals are predators of one sort or another, even if only on plant material or immobile seeds. Any animal that has to harvest food from the environment faces broadly similar problems, such as having to decide where to feed, what sort of food items to take, and when to move to a new feeding area. The decision that an animal makes in each case is likely to be shaped by natural selection. Food selection is an important issue in understanding relationships between frugivorous animals and fruiting plants, because their interactions are also important in the maintenance and regeneration of the flora (Janzen, 1970).

One of the goals of research in behavioral ecology is to find out whether animals make decisions and follow rules that maximize foraging efficiency, and whether they forage optimally (Stephen and Krebs, 1986). Researchers usually assume that what is being maximized is the net rate of energy intake, which is express as the intake per unit time. There are certain energy costs in obtaining food, mainly in the search for and pursuit, handling and eating of each item, and these must be subtracted from the benefit which, in this case, is the energy in the food. A rate of energy intake is obtained by dividing the net energy gain by the time taken to acquire than gain:

$$\text{Net rate of energy intake} = \frac{\text{energy from food}}{\text{search time}}$$

The basis for the theory of diet selection in animals can be described as "the animal that chooses the most efficient or optimal solution will have the highest fitness" where fitness is the ability to pass on the genotype to the next generation (Hedrick, 1984). Day-to-day decisions about the organization of foraging are compounded to determine the animal's long-term chance of surviving to reproduce. (Stephen and Krebs, 1986). Wild animals must frequently compromise rather than optimize on food selection because they often have to focus on more than one goal that might maximize their fitness. Most feeding problems in the wild are complex and it is therefore difficult to define optimal foraging (Zach and Smith, 1981).

1. Choosing where to forage (Bernard, 1983)

As it moves through its environment, an animal encounters a range of food patches, some of which have a higher utility (net value in terms of food availability) than others. If it is to feed efficiently, the predator should select the patch with the optimal or highest utility. Therefore, in order to select the best patch, the animal may first have to sample a range of patches. If the animal spends too long exploring different patches before exploiting what it considers the most profitable, its net rate of food intake will be reduced

2. Choosing what to eat (Stephen and Krebs, 1986).

Predators are likely to face with a choice between several different types of prey. For an *optimal diet selection*, *p*redators will choose food items so as maximize their rate of food intake during a foraging bout, and they should be sensitive to the various costs and benefits of taking different types of food. Their *benefit* may be measured in many ways, such as the energy value of an item, its nutrient quality or the tract elements it contains. Their *cost* for taking different items falls into two main categories, search costs that refer to the time, energy and risk involve in seeking prey, and handling costs, that take into account the time and energy spent and the risk of predation, aggression, and competition between the moments an items is picked up until it is swallowed. Handling costs will be increased when it is necessary to remove indigestible integument, kill struggling prey or pulling resisting prey out of the ground. Other factors that affect the benefit: cost ratio is the *prey recognition time, which can increase or* reduce searching costs, and *competition, where* territorial and sympatric species are subject to intrusion by neighbors.

3. Foraging mechanisms

One way in which predators may be able to increase the efficiency is by *area-restricted searching*, where they exploit patchily-distributed food supplies by altering their pattern of movement after finding prey. Another way is by developing a *search image*, where a predator can focus its attention on one particular prey type when presented with a mixture. This ability has the advantage of allowing a predator to concentrate on more profitable prey types and avoid unprofitable or noxious items. Generalist predators acquire their required nutrition through varying the range of prey that they capture, although changes in selection may involve changes in learning and perception.

Birds may be generalized or specialized frugivore within a habitat. Large frugivores are considered to be especially important seed dispersers for many tropical plant species (Kitamura et. al, 2002), and large frugivores may be found higher up within forest than small frugivores, partly due to their choice of large fruit sizes.

Factors that influence food selection or food preference

Fleming (1991) suggested ecological patterns that influence food selection.

1. Patterns in space

Latitude is a factor in the succession and spatial availability of fleshy fruit. It may cause different morphology of fruit as adaptations for their dispersal. Most plant species in different areas also have different characteristics, such as presence of spines, shape of fruits or size of leaves.

2. Patterns in time

The temporal availability of fruit also varies latitudinally, affecting such factors as abundance, diversity, peak fruit abundance, and food availability. In some animal species, patterns in time, such as habitat structure, abundance and plant distribution of fruit resources, have been shown to strongly influence their distribution and food selection.

3. Morphological/nutritional patterns

Other factors that can influence food choice are breeding season, competition among frugivores, and unpredictable locations of food (see later).

Patterns affecting fruit consumption

The details of fruit consumption by vertebrate dispersers have the advantage that fruit traits have been selected so that they enhance detectability by frugivores (Herrera and Pellmyr, 2002). The ripe fruits of vertebrate-dispersed plant are characterized by distinctive odors, conspicuous coloration or some combination of these.

Chemical signals

The ecological correlates of chemical signaling by wild ripe fruits are still unknown. Fruit volatiles may mediate the relationship of fruits not only with dispersers, but also with fruit- and seed-predators (Herrera and Pellmyr, 2002).

Visual signal

In the spectrum visible to humans, ripe fruits vary in color from reds, blacks and blues to greens and browns. A partial dichotomy between bright and dull ripe fruits has probably been selected for by contrasting sensory capacities of bird and mammals (Janson, 1983). The visual conspicuousness of fruits may be further enhanced by the juxtaposition of two or more bright colors. Factors unrelated to consumption by dispersers may also have influence the evolution of fruit color in bird-dispersed plants. Fruit colors may be adaptive in defending fruit against consumers that damage the fruit because of the deterrent properties in the pigments themselves. Fruit color may also be an evolutionary by- product of selection, acting on some correlated character (Herrera and Pellmyr, 2002).

Fruit size

Size is an important attribute of fruits, because its sets limits to ingestion by small sized dispersers that swallow fruits whole. However, fruit size is less important in relation to consumption by large vertebrates or by small frugivores that mandibulate or chew off pieces of fruit. Fruit species with large seed sizes, such as *Aglaia* *spectabilis*, were also consumed and dispersed by hornbills (Kitamura et al. 2004)

Pulp composition

Fruit pulp is the reward offered by plants to dispersers and its nutritional value is a critical element in the plant-disperser interaction. Most fruit pulp has high water and carbohydrate content and low protein and lipid content, features that are considered as the food resource for animals.

Nutrients such as carotenoids, amino acids, and minerals are generated by fruit pulp. The nutritional characteristics of fruits are often related to the season of ripening, and seasonal variation can sometimes match the dispersers' dietary requirements. Secondary metabolites in fruits, some of them detrimental to frugivores, generally decline during ripening, but ripe fruits of many species still contain important amounts of phenolics, alkaloids or saponins in pulp. Some species produce poisonous secondary metabolites that can harm humans.

There are many studies that focus on diet selection and seed dispersal syndromes in animals. Jordano (1995) suggested that avian frugivores may use foraging cues based on "extrinsic" plant characteristics, such as type of surrounding habitat, number of neighbors or proximity of forest edges, when discriminating among fruit crops. Individual seeds might also face strong selection if frugivores use within crop foraging cues based on "intrinsic" fruit traits, such as color, seed size and overall size (Jordano, 1995).

Birds use many foraging locations, such as in the air, under the ground, or on trunks, branches, twigs and leaves. Many bird species have overlapping foraging niches and this might be important in mixed species flocks for enhancing their foraging efficiency (Eguchi, 1991). For example, Snow buntings (*Plectrophenax nivalis*) have some opportunity to choose both the size of the flock to forage and where to feed within a flock and the leading bird might have first access to places it thinks are the best patches (Smith, 1997).

Morphology and nutritional value patterns: attractiveness

In the tropics frugivorous birds have coevolved with fruiting plants. Originally, fruits may have been typically small, since unspecialized frugivores are mostly medium-sized or small birds, with watery flesh containing mainly carbohydrate, and with small seeds (Snow, 1981). Later, some fruits evolved to a larger size with high nutritional value, attracting specialized birds so that seedlings will have a chance to establish on the forest floor.

O' Dowd and Gill (1986) studied seed dispersal syndromes in Australian *Acacia*. They concluded that many dispersal agents, such as birds, ants and mammals, chose brightly colored arils. Bird syndrome species had high dispersal investments, such as higher aril mass and lipid content than ant-dispersed species

Birds may be generalized or specialized frugivores in some habitats. Hornbills are good examples of generalized frugivores. Poonswad et al. (1988) studied food and feeding ecology of sympatric hornbills and found that the main foods were fig fruits, non-figs fruits and animals. Among non fig-fruit, Wreathed Hornbill consumed a great quantity of the fruit of *Polyalthia viridis* in the breeding season. It was different from White-throated Brown Hornbills that consumed mainly animal food, followed by fig and non-fig fruits. However, Helmeted Hornbills [*Buceros* (*Rhinoplax*) *vigil*] fed mostly on fig fruits, in spite of their relatively low energy yield, since figs were available in all months (Poonswad, 1998). Thus, diet selection in hornbills may involve food abundance, regardless of nutritional value. Stiles (1980) found that generalized birds in the eastern deciduous forest of North America ate mainly fruits with large seeds and high lipid content.

A similar study by Snow (1981) suggested that families of greatest importance for specialized bird frugivores are Lauraceae, Burseraceae and Palmae. Their fruits have a large size, with relatively large seeds, and have high protein and fat content. Howe and Estabrook (1977) suggested that specialist feeders may require particular vitamins or minerals from certain fruits which opportunists obtain from alternate sources of food such as insects.

Fruit preferences may be related primarily to the size and color of fruits. Color likely provides the cue to ripeness, while bigger, heavier fruits may be harvest more efficiently. Kitamura et al. (2002) found that hornbills at Khao Yai National Park consumed mostly fruits with black, red and yellow colors. Hornbill flock size and staying time is also related to the large size of the fruit, but also to a large fruit crop. Large crops of large fruit may be harvested efficiently over a longer time period, reducing the search time required to meet daily energetic time budgets (Howe and

Estabrook, 1977). There are no reports of specialist frugivores feeding on unripe fruit. This might be because of the secondary compounds in unripe fruit that will cause toxicity in animals. This is supported by the study of glycoalkaloids in *Solonum* sp. and the food choice by vertebrates that suggested that these glycoalkaloid are toxic (Cipollin and Levey 1997, So the secondary metabolites of ripe fleshy fruits are an important determinant of fruit use by frugivores.

Suryadi et al (1994) found that *Rhyticeros cassidix* is a ripe-fruit specialist during both the non-breeding and breeding season. It fed mainly on figs, which are a highly dependable food resource and the fruits of some fig species are high in sugars and digestible protein. Fruit size and weight were also critical in fruit choice and feeding behavior.In some bird species, like *R. cassidix*, may prefer large fruits because their long bill is poorly suited for handling small fruits, so while color likely provides the cue to ripeness, bigger and heavier fruits may be harvest more efficiently (Suryadi et al, 1994). However, this conclusion about bill size is not similar to the result of other studies, such as Poonswad et al. (1988) found that Great Hornbill consume small ripe fruit in Khao Yai National Park.

Other variations of animal morphology and physiology are also factors that can influence food selection, such as body size and morphology (Whiten, 1982). The study of Morioka (1992) on the smallflowerpeckers (Dicaeidae) showed clearly how morphology influenced feeding habits. A study on fruit size, gape width and the diet of birds also found the relationship, revealing that fruit-eating birds with broad gapes consumed more lauraceous fruit species, and with a large mean and maximum size of fruit overall, than narrow-gaped birds (Wheelwright, 1985). Thus, animal structure may be used as an indication of their food choice, such as non-split tongue for primarily berry and seed feeders.

Nutritional value

Optimal foraging theory explores the choices many animals make while collecting their food. They might select between alternative feeding methods and prey types, and between different places and times of day in which to feed. The theory also states that they will make choices that maximize the net rate of intake when foraging of some particular component of the food (Goss-Custard, 1981).

Adequate nutrition during embryonic life is an important component of an environment that will permit full expression of a genotype. Many examples may be cited of adverse affects on survival, growth and normal development when the nutrient supply is inadequate in one or more components. These may include amino acids, fatty acids, minerals and vitamins.

Food for the laying female

The amount of food that a female bird needs for the production of a clutch varies from species to species and normally depends on two factors, the size of the bird and the size of number of eggs it lays. In general small birds tend to produce both relatively large eggs and large clutches compared with large birds. Consequently, they required relatively larger amount of energy for egg production than large birds (Perrins, 1983).

Birds and other animals eat to satisfy two basic needs: first, the physiological demands of the body and second, a food volume and need to reach satiety. If satiety is fulfilled through bulkiness of the diet before the physiological needs are satisfied, the animal will stop eating before it has acquired its full nutrient requirements. (Fisher and Weiss, 1956). Nutritional values for birds are categorized as follows:

Protein requirements

Protein and amino acids are used for the growth of an animal. The amount of dietary protein, and the type of fat and carbohydrate, has been shown to influence the onset and severity of atherosclerosis in birds (Fisher et al, 1959). Protein reserves must be accumulated during the period of cessation in egg production, while the domestic hen consumes an adequate amount of diet (Fisher, 1967). Amino acids are also used by the chicks for their molting process. The efficiency of utilization of dietary nutrients for egg formation is dependent upon the rate of egg production (Whittow 1965). The energetic, as well as the protein efficiency, for the domestic hen results in relatively good egg production of about 300 eggs per year (Bolton, 1958). Lack of adequate dietary protein can affect reproductive performance (Krapu and Swanson, 1975), while Grau (1968) found that the reducing the dietary levels in individual essential amino acids or total protein may reduce egg size and egg numbers, or may stop egg production entirely.

Carbohydrates

The energetic cost of flight may represent an important fraction of total caloric expenditure, beingabout 3-15 times higher than standard metabolic rate, but depending exactly on the type of bird, kind of flight and flight conditions (Farner, 1970).

Starches, stored mainly in grains and other seeds, are the major carbohydrate energy source for birds. Griminger and Fisher (1963) showed that glucose and sucrose are well utilized by domestic chickens, while lactose and galactose are not. The domestic chicken does not digest cellulose and lignin, and cellulose is not digested by most species of birds. Fiber content, which may be explainable on the basis of the chemical analyses of the materials considered part of the crude fiber content of the diet, may also be important (Bolton, 1955).

Study of the domestic chicken showed that arginine or protein is essential during all stages of development and, qualitatively, it is almost at the top of the list of essential requirements (Allison and Fitzpatrick, 1960), while the growing chick normally requires glycine or serine for optimal growth (Baker et al, 1968).

Fats

The utilization of fats depends primarily upon the absorption of the fatty acid from the digestive tract (Fisher, 1967), but few studies have been made of the role of lipids in development. (Menge et al., 1968) were able to obtain strong evidence of the need for polyunsaturated fatty acids for fertility and hatchability of chicken eggs, although no characteristic abnormalities were noted in deficient embryos. The information presently available about lipids and development had been obtained primarily from analyses of embryos, membranes, and residual yolk at various stages, mostly in the second half of the incubation period (Grau, 1968).

Stored fat can be used as a buffer against fluctuation in food availability (King, 1972), but the size of the fat reserve is expected to be determined by a trade-off between benefit (reduced probability of starvation) and cost (increase risk of predation). It can be predicted that specialists, and species of stable environments, should deposit smaller fat reserved than generalists and species of variable environment (Grau, 1968)

Water requirements for maintenance

Bartholomew and Cade (1963) have summarized data on the water consumption of terrestrial birds in the absence of temperature stress. They noted that water intake was inversely related to body size. Sources of water which birds and animals can acquire, particularly arboreal species, may be found in juicy or fleshy fruit. Schmidt-Nielson (1964) suggested that there was little evidence that birds that live in areas of low water accessibility or desert regions have developed special mechanism that permit them to survive on reduce water intake.

Mineral requirements

It is difficult to estimate accurately the utilization of minerals because of re-use and secretion into the digestive tract for purposes of elimination. There are many factors known to influence the utilization of minerals by bird as well as mammals (Fisher, 1967).

Scott et al. (1969) suggested that in young growing birds the dietary ratio of calcium to phosphorus was optimal at or near 2:1, while in the adult the ratio is reversed, with phosphorus representing a higher requirement than calcium (Mitchell, 1962). Examples of food that provide these minerals (Ca, Ph) and vitamin are common vegetables, such as lettuce, onion and pepper, while in general wild birds can find minerals from plant sources.

The diet of the domestic hen has been shown to influence some of the minerals necessary for the developing embryo, including phosphorus (Rourke, 1954), manganese (Lyon, 1934) and zinc (Kienholz, 1961), but most mineral deficiencies result in cessation of egg laying rather than in production of eggs that are deficient in minerals. Sodium, potassium and chloride ions are required by embryo to balance the osmotic pressure, while yolk sac perfusion studies have shown the importance of potassium and the lesser need for Sodium in the yolk. They found that yolk sac perfusion media needed to be low in calcium to permit good survival, possible because of sensitivity to calcium ions not bound to protein. When embryos are given inadequate amounts of yolk, the amniotic concentration of sodium falls and potassium rises (Grau, 1968).

Co-nutrients or secondary metabolites

The word "co-nutrient" was defined by Mitchell (1964) as the many chemical compounds in food products that may exert a favorable or unfavorable effect upon nutrient requirements, nutritive status and nutrient utilization. Bird species and domestic chickens were studied for co-nutrients including toxins, enzymes-antienzymes, antivitamins, saponins, tannins and fluorine.

Eltayeb and Roddick (1984) suggested that it was generally accepted that the primary function of secondary metabolites in green (immature) fruits was to defend them from all types of potential consumers. It was also broadly assumed that all these important secondary chemicals were lost during ripening. However, the secondary metabolites in ripe fruit represent a trade-off between defense against pest/pathogens and palatability for dispersal agents (Cipollinian and Levey, 1997). The evolution of these secondary metabolites in fleshy fruits is therefore the result of selection for multifunctionality. Since secondary metabolites may be expensive to produce, selection pressures lead to economical solutions for retaining different sets of chemicals that have different functions or purposes.

Understanding the nature of secondary metabolites in fruits and their effects on various fruit consumers will help to resolve as apparent evolutionary paradox. Glycoalkaloids are an example which suggests that seed predators and seed dispersers avoid *Solanum* fruit species when they are ripe because the effects of glycoalkaloid were so strong. Animals try to avoid these fruit even though the pulp is highly rewarding. Glycoalkaloids are known to be toxic and act as feeding deterrent for generalist invertebrate herbivores (Mckee, 1959), with one of the first symptoms of these secondary metabolites being irritation of the gut lining and diarrhea (Van Gelder, 1990). Moreover, secondary compounds can affect levels of other minerals in herbivores, such as the sodium balance in birds (Morton, 1978).

Environmental factors and food abundance

Food availability

Optimal food selection depends upon food availability and the time it takes to find the most profitable items. Birds feeding in an unselective manner will spend relatively little time searching for food but will have a relatively low rate of energy intake. For example, Sumatran hornbills showed a positive relationship between the temporal variability in hornbill numbers and the availability of ripe fruits (Anggrani et. al. 2000). These data supported Leighton (1983), Poonswad and Tsuji (1994) and Kemp (1998) who suggested that highly frugivorous hornbills require larger home range than more carnivorous hornbills of comparable body size. These movements may be in response to variation in food availability, as ripe fruit increases in the canopy, so that birds are only attracted to areas for several weeks at a time.

Availability of different foods within the environment has further implications for how hornbills will respond on a given day, and when they will undertake elements of their annual cycle, such as partial migrations and breeding (Poonswad and Kemp, 1993).

Density, abundance and distribution of food

Frugivores depend on a type of food that is patchy in space and time and displays high sensitively to fragmentation and isolation of their habitat (Laurance and Yensen, 1991). Arengo and Baldassarre (1995), who studied the effect of food density on the behavior and distribution of American Flamingo in Yucatan, Mexico, found that the coefficients of variation around sample means reflected high variability within locations. Such variation suggests a patchy distribution, which is the type of circumstances in which flocking will occur. Flocks provide information about the location of food and patch quality (Clark and Mangel, 1984), and therefore flocks usually concentrated initially in areas where food was most abundant.

The theory of Central Place Foraging (CPF) predicted that depletion of nearby patches would lead to exploitation of patches distant from the home base (Bernard, 1983). However, if nearby patches are depleted before CPF has gathered an optimal load, the efficiency of subsequently searching even further away, and/or of the return trip, is reduced. Thus CPF should start with foraging at a distant patch and then work back towards the home base, so that by the time the optimal load is gathered, the return trip will have been considerable shorten.

Plant-frugivore coevolution

Coevolution is the simultaneous evolution of ecologically interacting populations (Howe and Wesley, 1988). Some of the most highly developed modifications for dispersal are adaptations by fruits for consumption by fruit eating birds and mammals [birds are also animals?!] (Howe and Wesley, 1988), and Janson (1983) also suggested that the fruit morphology of plant species is frequently adapted to the general characteristics of the animals that eat them. Plants may adapt in size, color and morphology, even among different species within the same genera, implying that natural selection has produced the divergence in fruit form in association with bird and mammal fruit-eating. Plants might also evolve secondary compounds that only a few species of their insect enemies can detoxify (Howe, 1988), but Bernays (1998), in her studies of the role of secondary plant compounds, found that toxins in the leaves and fruits may deter feeding by seed-dispersing animals. Constitutive secondary compounds included phenolics, such as tannins and lignins, as well as alkaloids, terpenoids and saponins. Induced secondary compounds, that are formed or released only after damage or consumption, may include phytoelexins, phenolic glycosides, cardenolides and cyanogenic glycosides (Cipollini and Levey, 1997), but specialized plant eaters are often capable of detoxifying secondary compounds in their livers and in consequence gain access to food supplies that are poisonous to other species (Terborgh, 1992).

Pair-wise coevolution, in which two species adapt specifically to each other, is not the only possible or likely outcome of ecological interaction. Diffuse coevolution may occur when two sets of species interact, but each set only influences the other more or less equally (Howe, 1988). Snow (1971) reported that in evolutionary aspects of fruit-eating by birds, there are two important developments attributed to differences in food supply. The strategies adopted by fruits for dispersal by birds result in the production of abundant food supplies, which are then easy to access and exploitable by many species of birds (Snow, 1971). There are also some examples from studying the evolution of foraging strategies in shorebirds (Barbosa and Mareno, 1999), where change in bill length was related to changes in foraging strategies from visual hunting to tactile hunting.

In conclusion, there are several factors that influence food choice in animals and, more specifically, in birds. Animal feeding behavior can be explained partly by food selection theory, in which animals are supposed to find the optimal solution that will provide them the highest fitness. However, what is still unclear is which food characteristics each animal species will bring to bear on its fitness. Food choice can be clarified partly by investigating what are the physiological requirements of a given species and how does its diet can relate and respond to them.

CHAPTER III

MATERIALS AND METHODS

Study area

This study was conducted at Khao Yai National Park, Thailand. The Park was established in 1962 (Smitinand, 1977), lies between 14-^{o} 05’ and 14^{o} 15 N’, and 101^{o} 05’ and 101^{o} 50’ E and covers an area of 2,168 km^{2}. It is located approximately 200 km northeast of Bangkok and incorporated the areas of four provinces, Nakhon Ratchasima, Saraburi, Prachinburi and Nakhon Nayok. The park contains a large mountainous area of undisturbed primary tropical evergreen forest,part of the Phanom Dongrak range, which lies between 250 m and 1,351 m above sea level (Smitinand, 1977).

The vegetation is classified into six communities, namely, moist evergreen, hill evergreen, mixed deciduous and dry evergreen forests, savanna and secondary growth forests. The mean annual rainfall was 2,326 mm for the period 1993-2001 (Kitamura et al, 2002) and the rainy season usually runs from May through October and the dry season from November until April. The mean monthly temperature ranges from 21 ºC to 32 ºC.

The study site was located in the core area around the Park headquarters and covers approximately 60 km^{2} (Figure 1). Here elevation ranges from 700 m to 800 m a. s. l. for nest locations, and it is up to 1,300 m a. s. l. for roosting sites. This is the site for a long-term hornbill study, from which some essential information was provided for my present study, including nest locations, identified food plant species, nutritional values of some food plants, and locations of flocking/roosting sites.

In the Park, there are four hornbill species that live in sympatry, Great Hornbill (GH*, Buceros bicornis*), Wreathed Hornbill (WH, *Aceros undulatus*), White-throated Brown Hornbill (BH*, Anorrhinus austeni*) and Oriental Pied Hornbill (PH, *Anthracoceros albirostris*) (Poonswad et al, 1998).

1. Annual cycle of hornbills

The breeding or nesting season, defined as the period from after a female has completed sealing the nest entrance until the chicks (s) fledge, usually starts in January and ends in June. Six nests of each hornbill species were located. These study nests had been monitored for a long-term study by the Thailand Hornbill Project, and therefore greatly facilitated the choice of nests for observations of feeding and breeding success. Each nest was attended for one day per week over the two breeding seasons of 2004 and 2005, regardless of whether or not the same pair reused such nests.

The non-breeding season, defined as the period after chicks fledge until the next breeding season, normally starts in July and ends in December (Poonswad, 1993). Two roosting sites of Great and Wreathed Hornbills, and one of Oriental Pied Hornbill were also selected, based on the previous data of Thailand Hornbill Project. The roosting sites were marked by GPS (Garmin 12 XL) and mapped. From July to December, in 2004 and 2005, each site was visited for about 25 days per month, except for the distant ones that required an overnight visit and such sites were visited only twice per month. Species and number of individuals in each flock that came to each site were recorded between 1500-1900 hours. Since there no regular roosting site of White-throated Brown Hornbill was found, any flocks were followed and the number of individuals counted.

2. Fruit availability and abundance

The fruit availability study was conducted on ten 1-hectare botanical plots, with transects set perpendicular (west-east) to the main north-south Thanarat Road where all the hornbill nests were located (Figure 2). Ten line transects, 500 m long and 20 m wide, and spaced at 1 km intervals, were conducted in both breeding and non-breeding seasons. All trees with DBH ≥ 10 cm were tagged, identified to species or genus and measured, so that average tree height, basal area/ ha, canopy coverage, and density of trees could be calculated. Tree height was measured by Clinometer (SUUNTO Code: PM-5/1520) estimation of fruit abundance was obtained from monthly phenological studies. Fruit abundance was determined as four classes in relation to the canopy coverage 4 (100%), 3 (75%), 2(50%), 1(25%) and 0(0%).

Classes of abundance were determined based on the presence or absence of ripe and unripe fruit, where this differentiation was based primarily on color changes indicating ripeness.

2.1 Abundance of hornbill fruits

Abundance of hornbill fruits for food was calculated from phenological data (Laurence et al, 1998), based on 10 trees per species that were observed every month in 2005. Characteristics of known food and non-food fruits were based on a former study by Poonswad et al. (1998). Linear regression analysis was used to describe the relationship between a categorical response variable of eaten and non-eaten fruits and a set of explanatory variables.

To determine monthly diversity and relative abundance of fruiting trees, all fruiting trees, including food and non-food species, that were sighted on phenology-study transects were noted.

A food abundance index *[FAI]* was used to estimate food abundance as measured monthly for each fruiting species (Andersen et al, 2002, Mitani et al, 2002).

$$FAI \text{ (per fruiting species)} = Dk * Bk * Pkm$$

- Dk is the density of species k in the home range (stems per hectare)
- Bk is the mean basal area of species k in each home range (cm^2 per hectare)
- Pkm is the percentage of observed trees of species k that produce ripe fruit in a given month.

3. Fruit overlap

Since these four hornbill species live in sympatry, overlap in fruit food was expected, but to what extent?

3.1 Diet composition and quantity of food types

Data on food diversity and composition of these four hornbill species were collected at the nests (6 nests/species) during the breeding season (January-June) and at five roosting sites in non-breeding season (July-December) for two years (2004-2005).

3.1.1 Breeding season

A total of 24 nests were selected, based on ease of access and the lesser sensitivity of the breeding male and/or nest helpers. At each nest, observations were conducted weekly between 0700-1700 hours. To obtain complete data on food fed to the brood throughout the breeding season, where nesting had failed, a new nest(s) replaced the original with an assumption that the same species feeds on similar species of food. The locations of these study nests were marked by GPS (Garmin 12 XL) (Figure 1).

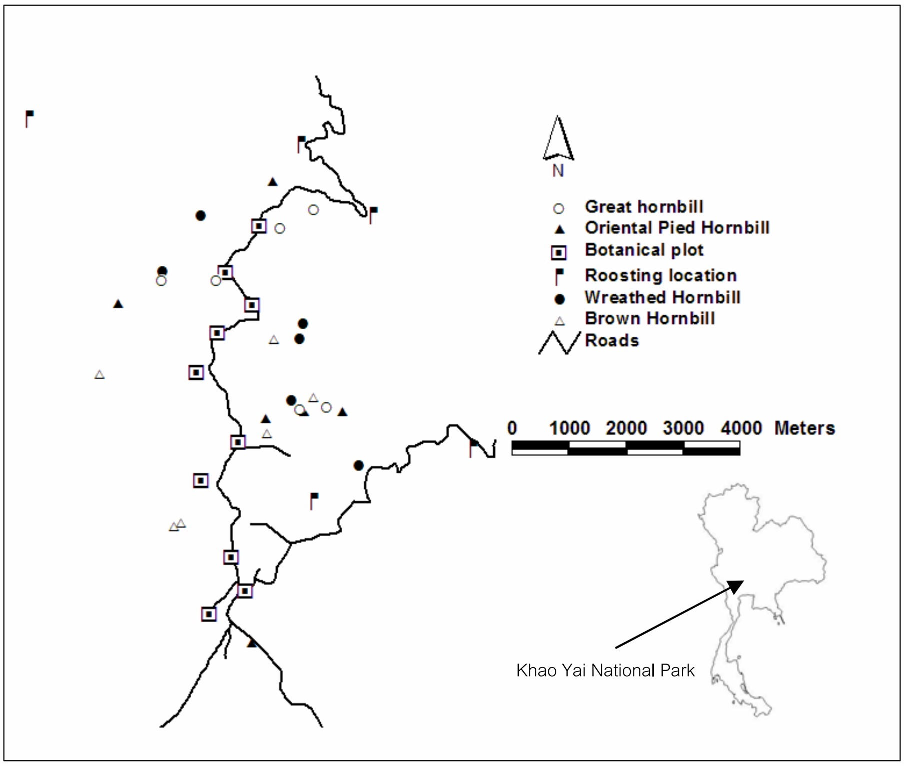


Figure 1. Locations of 24 hornbill nests, roosting sites and botanical plots.

At each nest site, fruits and animal items brought by males, or females (in the case of Great Hornbill where the female emerges after the chick is about 4-6 weeks old), or nest helpers (in the case of cooperative breeding White-throated Brown Hornbill) were characterized, counted and identified into species or genus, and family. Species identification was done by experienced observers using a spotting scope or binoculars, or by study later of samples in the Herbarium at the Department of National Park, Wildlife and Plant Conservation. Measurement of fruits and seeds was done following Kitamura (2002). But detailed study on fruit characteristics was only done later (see fruit characteristics). The daily consumption rate for each fruit species by each hornbill species was calculated as the weight in grams of pulp delivered per feeding bout per hour, divided into the breeding phases ofthe incubation and nestling periods (following Poonswad, et al, 2004; Figure 2).

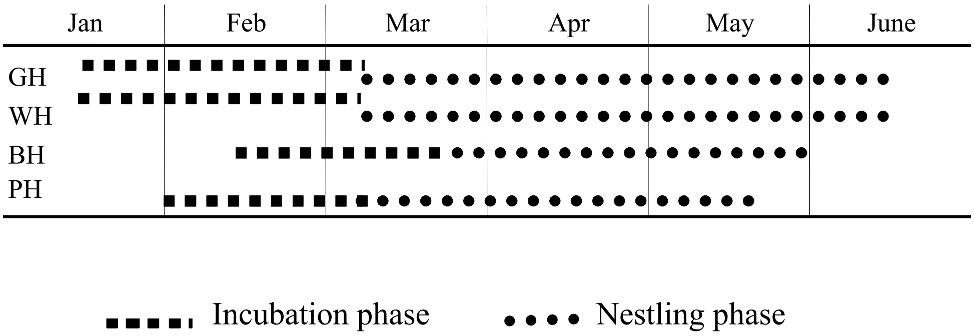


Figure 2. Duration of the breeding phases of the incubation and nestling periods (following Poonswad et al., 2004, and the present study).

3.1.2 Non-breeding season

A total of 25 seed traps (funnel shaped with an opening of 1m^2 surface area) were set randomly under two roosting sites of Great and Wreathed Hornbill and one of Oriental Pied Hornbill. Since no regular roosting sites of White-throated Brown Hornbill were found, flocks were followed to collect any seeds they dropped.

Seed traps were checked every three days for the close roost sites and every two weeks for the distance ones. Seeds were counted, taken from the traps, and then identified into species/genus and measured.

3.1.3 To quantify the importance of fruit species in the hornbill diet

The amount and types of fruits delivered to the brood in each feeding bout in the breeding season, and the amount of seeds in the traps in the non-breeding season was calculated and identified. Plant species consumed were ranked from highest to lowest in terms of their contribution to the total amount of food delivered. To obtain a monthly list and number of important species, once the top ranked species was derived, the second highest ranked species was added, then the third, and so on until the cumulative proportion accounted for 80% of the total hornbill feeding bouts [or amount of food delivered?] (Savini, et al., in press). The highest monthly rank of a fruit species, or top species, was determined by the proportion that such a species contributed to the total diet of each hornbill species in the breeding season. Fruit species that appeared on the list were considered as important food species in the hornbills' diet.

3.1.4 Shannon-Wiener Index

Diversity of hornbill food in both breeding and non-breeding seasons was determined from the Shannon-Wiener Index and evaluated the number of species fruiting each month (Sourd & Gautier-Hion, 1986).

Diversity: $h' = - \sum(pi \ln pi)$

Wherein, pi = proportion of records of each species in the sample

3.2 Food overlap

The data was analyzed for similarity of food consumption among hornbill species by using the Index of Similarity (Poulsen 2002). The index of similarity for each food category was defined by Schoener's overlap (Schoener, 1974). Schoener's overlap was then used to define the dietary overlap between months among species (Poulsen, 2002).

$$R_O = 1 - \frac{1}{2} \sum_{i=1}^{n} |p_{ij} - p_{ik}|$$

R^0 is resource overlap

P_{ij} and P_{ik} are the proportions of observations in which the ith resource is consumed by the jth and kth species.

This index generates a value ranging from 0-1, with 0 representing no overlap and 1 representing complete overlap (Poulsen, 2002).

Canonical Correspondence Analysis (CCA) was used to consider feeding assemblages among the four hornbill species (Ter Braak, 1986; using the PC-ORD software).

4. Food selection

Test for an index of selectivity for each food species

Selectivity was measured by using the Jacobs index (Jacobs, 1974), as adapted by Suryadi et al. (1994). This index was used to rank fruit selection in each of the four species. The Jacob's index compares the frequency with which fruit species are eaten over the availability of the given species in the area.

$$\textit{Jacob's Index [D]} = \frac{(R_x / R_y - P_x / P_y)}{R_x / R_y + P_x / P_y - 2(R_x / R_y)(P_x / P_y)}$$

Where:

Rx is the number of feeding observation on species x

Ry is the total number of feeding observations

Px is the abundance of fruiting trees of species x

Py is the abundance of all fruiting trees

The ranges of D-value are between -1 to +1. The relative difference of D from -1 to 0 was for negative selection from 0 to +1 for positive selection.

4.1 Fruit morphological characteristics

Characteristics of fruits consumed (from under the nests and from seed traps under the roost sites) and non-consumed fruits (from the 10 ha of botanical plots) were studied and measured. Categories of characteristic parameters, as given below, were studied.

4.1.1 Life form: tree, small tree, shrub, climber

4.1.2 Physiognomic category: fruit categories: fruit type; dehiscence, indehiscence, detachment of pulp and fruit skin.

4.1.3 Color: color of edible part. The colors recorded were compared with the color chart that refers to different shades e.g. of yellow, red, green color

Fruit size: fruits were weighed using a TANITA digital pocket scale 1475 (for large fruits, up to 1,000g), 1476 for (medium sized fruits, up to 100g) and a Fine-mini (for small fruits, up to 10g), and measured in three dimensions to the nearest 0.1 mm with an Absolute Solar Digimatic caliper MITUTOYO 500-454. [write out numbers 1-9 in full, use digits for ≥10)

4.1.4 Seed number: seed number and seed size (n = 30) per fruit was counted and measured for average values.

4.1.5 Seed and fruit volume: fruit and seed volume was estimated by using three different flask sizes, i e. length, width (of two dimensions) and volume.

4.1.6 UV reflection: UV reflection of fruit the skin/aril was studied using an Atto: HP-8BL and compared with the visible color from the color chart.

4.1.7 Taste: fruits were tasted and divided into seven categories by five observers.

4.2 Chemical characteristics

Seventy species of fruits eaten (selected) and non-eaten (non-selected) by hornbills were sent for analysis of nutritional value to the Nutritional Laboratory, at the Department of Animal Science, Faculty of Agriculture, Kasetsart University. Due to budget limitations, the nutritional analysis was not done for all fruit species. The macro and micronutrient values that were analyzed, including protein, carbohydrate, fat, water content, minerals, fiber, NDF (Neutral Detergent Fiber: which is composed of hemi-cellulose, cellulose, and acid detergent lignin), ADF (Acid Detergent Fiber), calcium, phosphorus, NaCl, calories and sugar. Anti-feeders or a secondary compound, tannin, was analyzed as well.

Twelve methods, used for analyzing chemical composition in percentages, are shown below.

Moisture	Drying Method
Protein	Semiautomated Method
Fat	Indirect Method
Ash	Official Final Method
Fiber	Asbestos- Free Method
Calcium	Official Final Action Method
Phosphorus	Photometric Method
NDF	Jurens, M. H. 1980

ADF	Jurens, M. H. 1980
Sodium Chloride	Titration Method
Calorie	Analytical Methods for Oxygen Bomps
Tannin	Burns (1971)

For carbohydrate content, as the value for some fruit species are very small, it did not directly measure carbohydrates (i.e., starch and free sugar). Normally, carbohydrate content is derived from the sum of the percentages of crude ash, crude protein, crude fat and NDF, and subtract from 100. Technically, this gives the amount (percentage) of carbohydrates, and the organic rest. Since the organic rest was very small, one can take this as synonymous to the carbohydrate content.

The results of these analyses were incorporated in the selectivity analysis for each species to determine if any of nutritional parameters influences the fruit selection by different hornbill species.

Data analysis

Analysis of fruit morphological characters was done for fruit characteristics and chemical components combined. To analyze which variables were significantly different between eaten and non-eaten fruit, logistic regression was used to predict which fruits would be eaten and not eaten by hornbills (Kinnear and Gray, 2000)
The general formula of the logistic regression is

$$P = \frac{\exp(\beta_0 + \beta_1 X_1 + \beta_2 X_2 + ... + \beta_i X_i)}{1 + \exp(\beta_0 + \beta_1 X_1 + \beta_2 X_2 + ... + \beta_i X_i)}$$

where

P is the probability of the condition being true (i.e., the probability that Y = "Eaten" given the different values of $X_{1...i}$),

exp is the exponential function and is written as exp(x) or $e^{(x)}$ (where "*e*" is the base of the natural logarithm and is approximately equal to 2.7183),

β_0 is the intercept,

$\beta_{1...i}$ are the coefficients of the independent explanatory X-variables, and

$X_{1...i}$ are the values of the independent explanatory X-variables.

Using field observations of the fruits available and used by hornbills, eleven non-correlated, explanatory X-variables were used to develop a set of candidate logistic regression equations or “models”. Variables were input into the logistic regression procedure with forward selection, backward elimination, and stepwise selection. For all selection analyses, a significance level of $\alpha = 0.05$ was used to determine if each explanatory X-variable should enter or remain in the logistic equation.

Simple statistical tests were used to analyze the differences between breeding and non-breeding data and compare differences among the four hornbill species. Where the values of studied parameters of these four hornbill species and two study years were not different, then the data were combined for each statistical test. Multivariate analysis was used to analyze all variables as to whether they were significantly different between eaten and non-eaten food. All basic and some multivariate statistic tests were analyzed by the SPSS program version 13.0.

Food selection experiment

To obtain the degree of selection for various characteristic categories, additional experiments were conducted on captive hornbills at Dusit Zoo.

Experiments on captive hornbills: testing for color and shape selection

To facilitate the experiments on food selection of hornbills, various categories of fruit morphology were fed to captive hornbills. Sixteen hornbills of the four studied species were used to conduct these food selection experiments (Appendix A). The experiments were conducted as the last step of the present study, to determine if the results were similar between captive and wild hornbills. To test if colors influence food selection, artificial food provided by the zoo was dyed with edible dyes of four different colors, black, red, orange, green. Fruits of *Elaeagnus latifolia, Dysoxylum cryptobotryum, Canarium euphyllum and Livistona speciosa* were used for testing fruit shapes. Five visits of three replications were made for each experiment. A Chi-squared test was used to analyze if there were significant differences between different fruit color and shape selection.

Morphology of hornbill; gape size

Correlation between fruit and seed measurements, and gape size for each hornbill species, was also studied. The gape width was obtained and recorded from hornbill specimens in the museums (Lua and Nakkuntod, 1998) and from database of the Thailand Hornbill Project. The method was adapted from the study of fruit size, gape size and the diets of fruit-eating birds (Wheelwright, 1985). Pearson correlation analysis was used to compare the relationships between fruit size and gape size of hornbills.

CHAPTER IV

RESULTS

1. Breeding and flocking

1.1 Breeding season and nesting success

Great Hornbill (GH) was the first species to start nesting, in late January, followed by Wreathed Hornbill (WH) in early February, White-throated Brown Hornbill (BH) in mid February and Oriental Pied Hornbill (PH) in late February. Chicks of all species fledged between May and June. The entire breeding cycle normally includes pre-laying, laying, incubating and nestling periods. However, the present study did not attempt to determine such details, simply divided the breeding cycle into an incubation, counted from after the female was completely imprisoned, and nestling phase, counted from after the chick(s) hatched. The mean periods for the incubation and nestling periods, and for the entire breeding cycle of these four species were: GH, 52.8±1.2, 89.0±3.4, and 141.8±3.7 days; WH, 39.6±2.3, 92.8±3.7, 132.4±3.3 days; BH, 35.8±3.0, 119.2±4.2 days and PH, 32.8±1.5, 78.3±2.4, 111.1±2.1 days, respectively (Appendix B). Great and Wreathed Hornbills raised one chick per pair per year. White-throated Brown Hornbill 2-3 chicks per pair per year (mean = 2.4±0.5, n = 7), and Oriental Pied Hornbill 2-3 chicks per pair per year (mean 2.3±0.43, n = 4) (Appendix B). While the female Wreathed Hornbill emerged at the same time as her chick, the female Great Hornbill emerged by mid April, approximately 88 days after becoming imprisoned and 53 days before the chick fledged.

Over two-year study period (2004 – 2005), I observed a total of 60 pairs, 28 in 2004 and 32 in 2005. Eighteen nests were available for each year of observations, even if the same nesting pairs were not involved. A total of 8,100 hours, 4,030 hours in 2004 and 4,060 in 2005, was spent on nest observations (Table 1). Overall, the average breeding success for all hornbill species in both breeding seasons was 75.0 %

(43 out of 60 pairs). Breeding failure was due to predation (3.3%), human disturbance (5.0%) and unknown causes (16.7%). In 2004, the breeding success was slightly higher (78.5% of total 28 nests observed) than in 2005 (71.9% of 32 nests) (Table 1). Among these four hornbill species, breeding success of the White-throated Brown Hornbill was highest (90.0%), whereas that of the Wreathed Hornbill was lowest (66.7%) (Table 1).

Table 1 Hornbill nest numbers, number of observation hours per nest and breeding status (S = Success, F = Failure, * replaced nest)

2004			2005			Average Success (%)
Nest no.	Observation time (hr)	Breeding Status	Nest no.	Observation time (hr)	Breeding Status	
GH8	160	S	GH8	160	S	
GH12	160	S	GH12	150	S	
GH53	130	F	GH53	140	F	
GH47	160	S	GH47	150	S	
GH52	140	F	GH52	150	F	
GH49	160	S	GH49	150	S	
GH31*	50	S	GH29*	50	F	
GH48*	90	S	GH38*	25	F	
GH9*	80	S	GH33*	40	S	
			GH41*	42	S	
			GH58*	40	S	
Total	1130			1097		
Success (%)		(77.8) 7/9			(63.6) 7/11	(70.0) 14/20
WH27	160	S	WH27	160	S	
WH32	170	S	WH32	140	F	
WH38	160	S	WH38	150	S	
WH40	170	S	WH40	130	F	
WH39	160	F	WH23	160	S	
WH35	170	S	W28	55	F	
WH41*	120	F	WH41*	93	S	
			WH80*	90	S	
Total	1110			978		
Success (%)		(71.4) 5/7			(62.5) 5/8	(66.7) 10/15
BH16	190	S	BH16	150	S	
BH18	200	S	BH18	160	S	
BH20	200	S	BH20	165	S	
BH23	210	S	BH23	160	S	
			BH22	150	F	
			BH17	220	S	
Total	800			1005		
Success (%)		(100) 4/4			(83.33) 5/6	(90.0) 9/10
PH45	160	S	PH45	160	S	
PH80	160	S	PH80	160	S	
PH61	150	S	PH88	180	S	
PH88	80	F	PH92	140	S	
PH42	150	S	PH85	90	F	
PH39	150	S	PH95	160	S	
PH87*	50	F	PH100*	90	S	
PH49*	90	S				
Total	990			980		
Success (%)		(75.0) 6/8			(85.71) 6/7	(80.0) 12/15
All species						
Success (%)		**(78.5) 22/28**			**(71.9) 23/32**	**(75.0) 45/60**
Grand total	**4030**			**4060**		

1.2 Non- breeding season; flocking

Flocking was observed from the end of June, immediately after the end of the breeding season, until the end of December, just before the starting of the next breeding season). During the two non-breeding seasons of 2004 and 2005, I spent a total 680 days over 12 months counting the maximum number of individuals in flocks at roost sites (Figures 1 and 3). When I compared the median flock size of Great Hornbill at two roosting sites over two years, there was no significant difference (Kruskal-Wallis One Way Analysis; H =5.052, df = 3, $p = 0.168$; Figure 3), and it was the same for Wreathed Hornbill, (H = 4.953, df = 3, $p = 0.175$) and White-throated Brown Hornbill (Mann-Whitney Rank Sum Test; U = 14.5, n (small) = 6, n (big) = 6, $p = 0.0589$; Figure 3). In contrast, median flock size of Oriental Pied Hornbill over two different years was significantly different (Mann-Whitney Rank Sum Test; U = 3.0, n (small) = 6, n (big) = 6, $p = 0.015$; Figure 3). The overall flock sizes for each of these four hornbill species were also significantly different (Kruskal-Wallis One Way Analysis; H=23.848, df = 3, $p= 0.001$; medians: GH = 5.5, WH = 61.5, BH = 0, PH = 65.5; Figure3).

Among these four species, Great and Wreathed Hornbills seemed to have the most regular pattern of flocking, Great Hornbill flock size peaking in August in both years (82 individuals in 2004 and 161 in 2005), while Wreathed Hornbill gathered in its biggest flocks in September (590 in 2004 and 207 in 2005**;** Figure 3). Flocking by Oriental Pied Hornbill was not as regular as the former species, but flocking peaked just after the breeding season had finished, in July in 2004 (331 individuals), but in September in 2005 (118 individuals; Figure 3).

However, for White-throated Brown Hornbill, no regular roost site was known. White-throated Brown Hornbill lives in small flocks of 8- 54 individuals (33.5 ± 15.5, n = 20) (Poonswad, 1993). In July 2004, a flock of 35 individuals was found at Khao Sam Yod, just after the breeding season, but then disappeared. They reappeared again in the area in November, with their numbers to 10 individuals, and again in December (12 individuals). In 2005, a flock was found at the same site as in 2004, but only in November (21 individuals) and by December it was reduced to 10 individuals. The re-appearance of this species at the same site each suggested that this was abreeding area and not a regular feeding ground as well. At least 3 nests of White-throated

Brown Hornbill are being monitored at this site (Thailand Hornbill Project, 2004 and 2005)

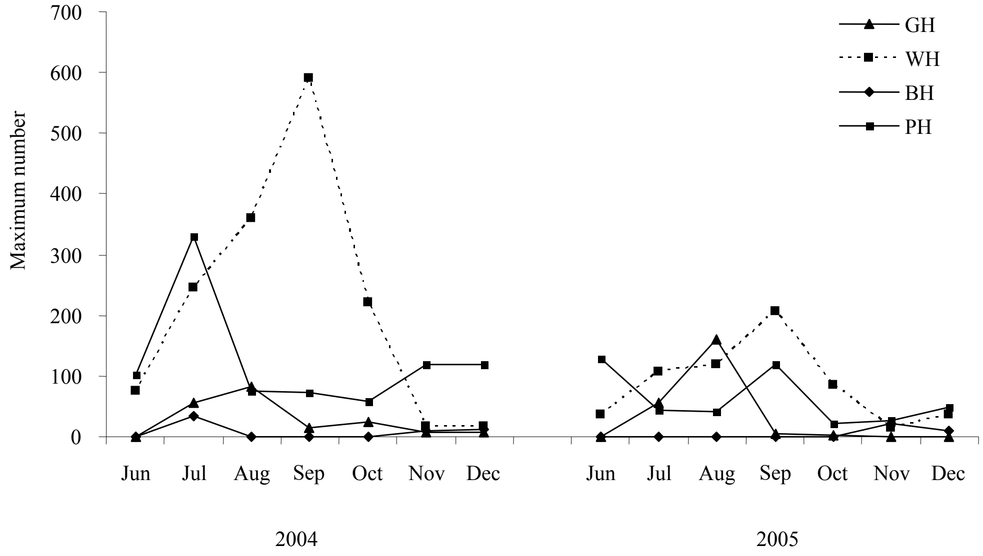


Figure 3 Maximum monthly flock sizes for four hornbill species in 2004 and 2005.

2. Abundance of fruiting trees (FAI-Total)

2.1 General physiognomy and phenology of plants

In the 10 1-hectare plots I recorded phenology, density, basal area and height for a total of 167 plant species from 139 genera and 68 families (Appendix C). Mean tree height was 19.2±6.5 m, while basal area per hectare varied greatly (mean, 115.5±210.3 cm2/ha, or median 32.7 cm2/ha) (Appendix C). There was no statistical difference in the means of either basal area (BA) or tree height (TH) for all trees or for hornbill food trees (Mann-Whitney Rank Sum Test; U (BA) = 4173.00, n (small) = 60, n (big) = 150, p = 0.412; t-test; t (TH) = 1.207, df = 206, p = 0.229) (Appendix C). Of the total of 167 tree species, 80 species (47.9 %; 55 genera in 32 families) were known to be food plants of hornbills, while the rest were not recognized as food plants (52.1%; 87 species of 84 genera in 68 families) (Appendix C).

In 2005, fruiting phenology showed that there was a total of 112 tree species that bore ripe fruits, and among these 57 species (50.1 %) were hornbill food species.

Of these 57 food species, 49 species (86.0 %) had ripe fruit in the breeding season and 28 species (49.1 %) in the non-breeding season (Appendix C)**.** Twenty species bore ripe fruit in both the breeding and non-breeding seasons (Appendix C). The periods of availability of ripe fruit, on trees of hornbill-food species, lasted 1-12 months (mean = 3.3±2.2 months, n = 57) (Appendix C).

In the breeding season, the monthly number of fruiting species with hornbill food did not vary much and peaked in May (42 species), while in the non-breeding season the number of fruiting species gradually decreased toward the end of the season (Figure 4). The pattern of monthly totals of fruiting species from February to May was relatively stable, and then then began gradually to decrease from June until November, except in September. The pattern of fruit availability was similar for hornbill-food species to that of all species combined (Figure 4). The monthly number of fruiting species in the breeding and non-breeding seasons was significantly different (t-test; t = 4.475, df = 10, *p* = 0.001) (Figure 4). Neither the total number of fruiting species or of hornbill-food species correlationed significantly with rainfall (Spearman Rank Order Correlation; r (total) = 0.0140, *p* = 0.956, n = 12; r (hornbill-food) = -0.0879, *p* = 0.766, n = 12) (Figure 4)

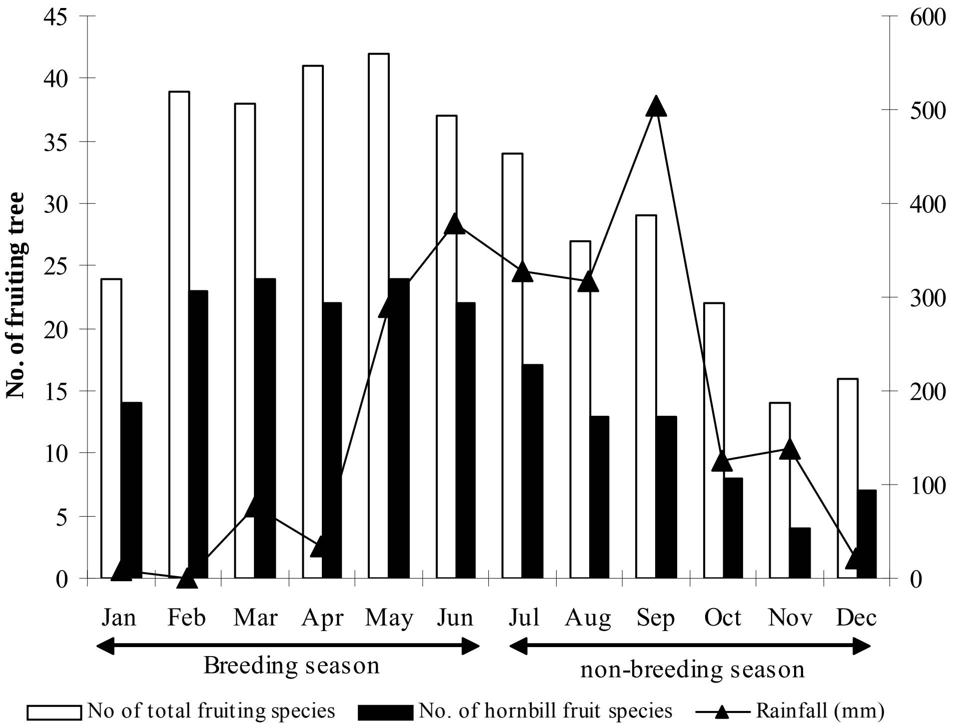


Figure 4 Monthly relationships between number of fruiting species and rainfall.

2.2 Abundance of hornbill fruit foods [(FAI-Hornbill)

In contrast to Figure 4 monthly FAI-Total varied particularly in the non-breeding season (Figure 5a). Hence, the number of fruiting species did not influence FAI-Total (Figures 4 and 5a). Mean FAI-Total, including hornbill food and non-food for all months, was 343.58 ± 300.36, (means: 230.05 ±137.58 in breeding and 457.12 ± 385.51 in non-breeding seasons). FAI-Total in the breeding season reached a peak in February and declined to May, while in the non-breeding season it reached a peak in July and declined during November-December (Figure 5a).

There was a similar pattern for FAI-Hornbill to that of FAI-Total (Figure 5a). The overall mean for FAI-Hornbill throughout the year was slightly lower than that for FAI-Total (means 103.38±69.09 in breeding and 228.9±225.15 in non-breeding seasons; Figure 5a**)**. Similar to the patterns for FAI-Total, FAI-Hornbill peaked in

February and declined towards May-June in breeding season, and in non-breeding season peaked in August, which was slightly different from FAI-Total, and declined towards December (Figure 5a). Surprisingly, monthly means for FAI-Hornbill were markedly low during the nestling period (Figures 2 and 5a). Unfortunately, there was no study to determine if the abundance of animal food was a substitute for fruit resources as food during such a period. There was a significant correlation between FAI–Total and FAI-Hornbill (Spearman Rank Correlation, $r = 0.75$, $p = 0.002$, $n = 12$) (Figure 5a). However, when compare FAI-Total and FAI-Hornbill in both seasons, there was no significant difference (Kruskal-Wallis One Way Analysis; $H = 5.340$, $df = 3$, $p = 0.0149$) (Figure 5a).

Throughout the year, the monthly percentages of FAI-Hornbill as a proportion of FAI-Total fluctuated from 6.6–99.5%. On average, the abundance of hornbill-food fruits was comparatively high, at about 50% of the total fruiting trees (FAI-Hornbill: 50.9±29.2 %, $n = 12$) (Figure 5b).

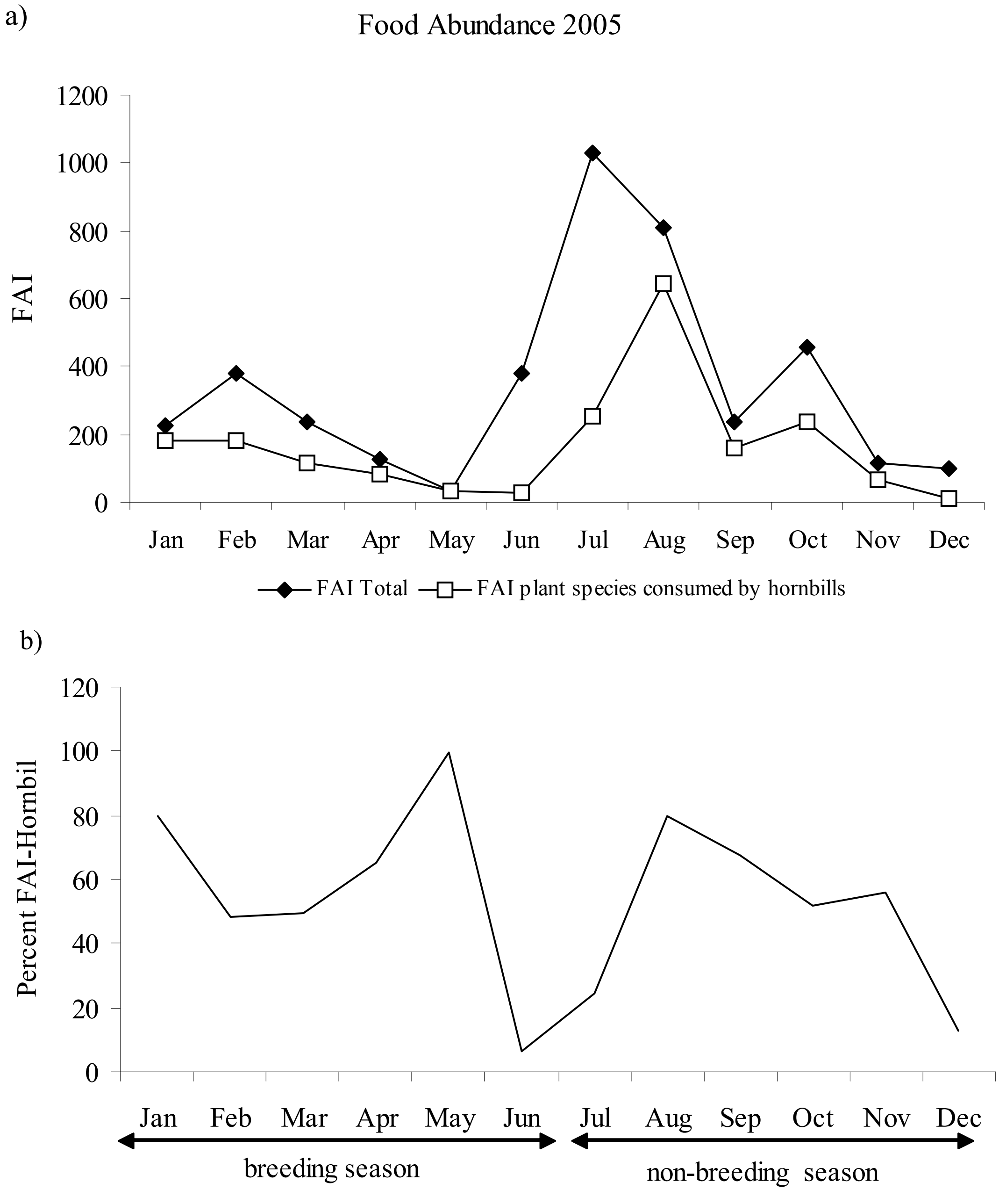


Figure 5 Relationship between the FAI of total fruiting trees (FAI-Total) and of hornbill food trees (FAI-Hornbill), (a) as recorded in the breeding and non-breeding seasons of 2005, and (b) as the monthly percentage that FAI-Hornbill forms of FAI-Total in the breeding and non-breeding seasons of 2005.

When the overall FAI-Hornbill was broken down into monthly FAI values for each individual hornbill species, this showed that all species experienced the same abundance of food sources (Figure 6). The FAI-Hornbill of each species peaked during January-February and declined towards May-June, while in non-breeding season, FAI-Hornbill for each species peaked in August and declined towards December. These results provide further evidence that these four hornbill species share food resources especially in the breeding season (Figure 6**)**.

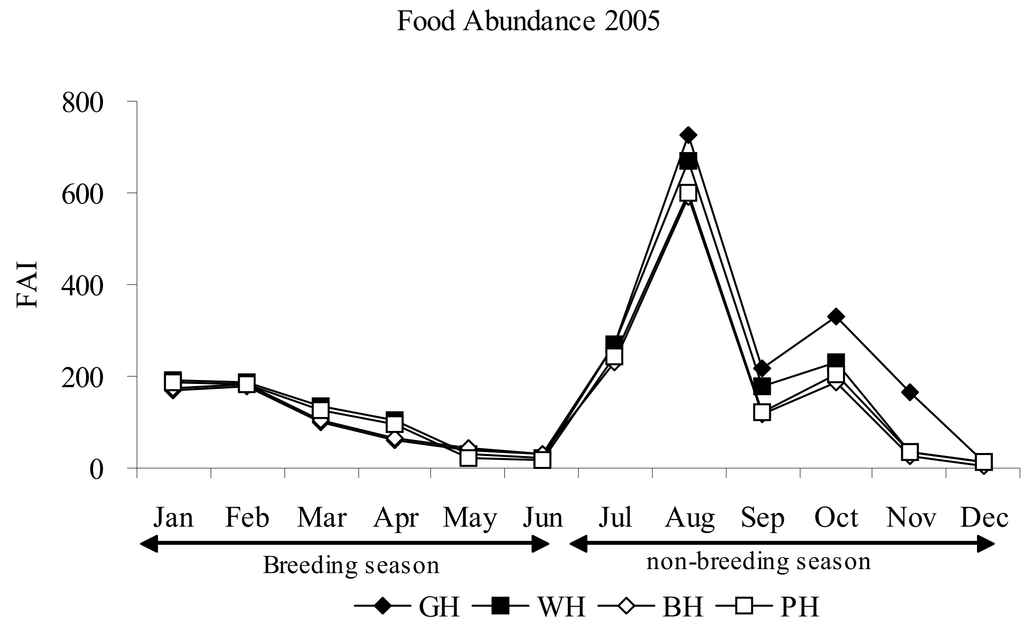


Figure 6 Monthly FAI-Hornbill values of four hornbill species in breeding and non-breeding seasons of 2005.

2.2.1 FAI-Hornbill and flocking

There was no significant correlation between the FAI for the fruit foods of each hornbill species and flock size (Spearman Rank Correlation; GH, r = 0.812, n = 12, p = 0.058; WH, r = 0.600, n = 12, p = 0.242; BH, r = -0.778, n = 12, p = 0.058; PH, r = -0.257, n =12, p = 0.658; Figure 7).

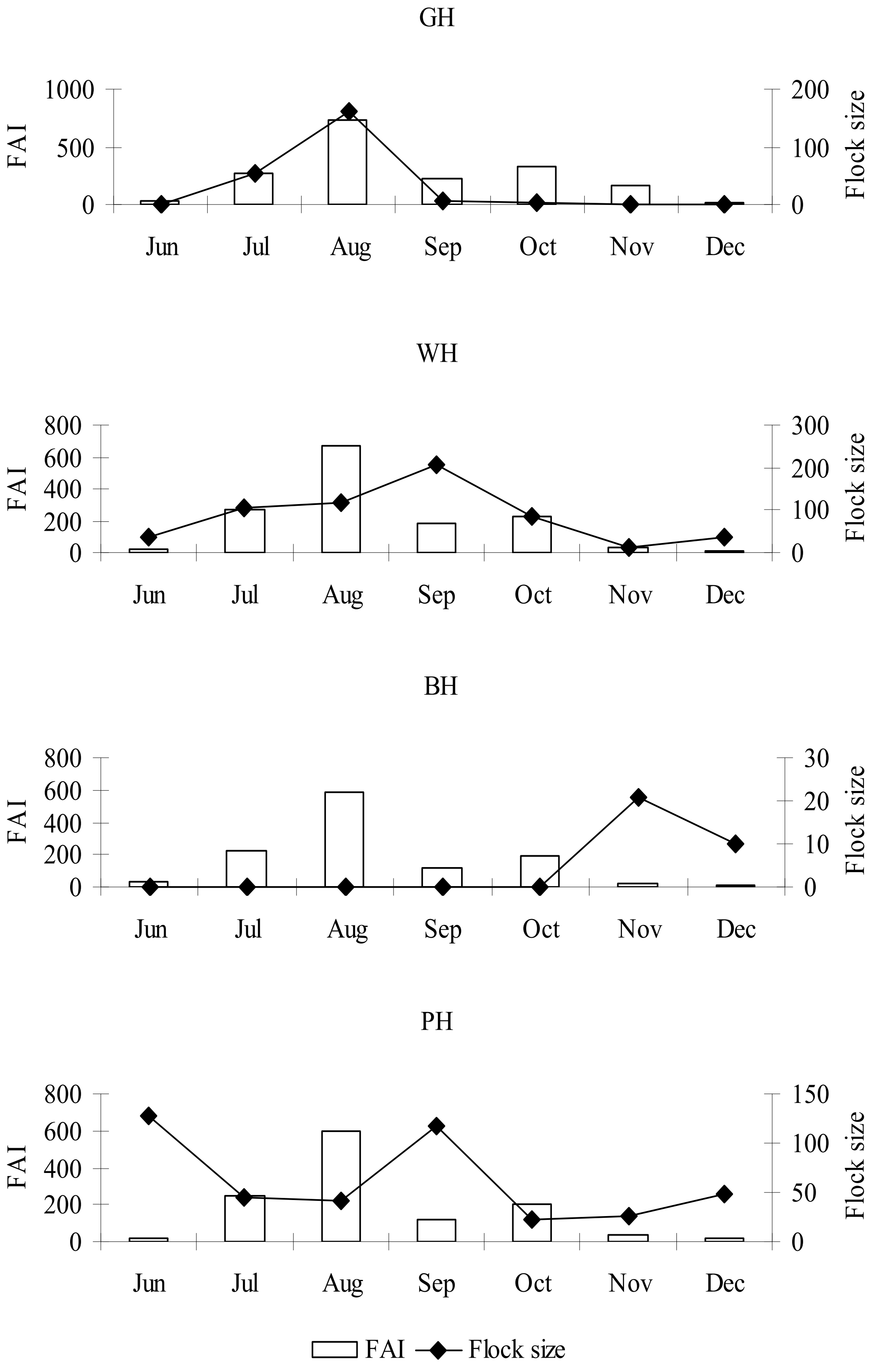


Figure 7 Relationship between FAI-Hornbill and flock size for each hornbill species.

3. Fruit overlap

3.1 Breeding season

3.1.1 Diet composition and quantity of food type

All four hornbill species were omnivorous, feeding on both fruits and animals, and a diversity of fruit and animal species was food consumed by these hornbills (Tables 2 and 3). There was a significantly difference between the diversity of food plant species consumed in both the incubation and nestling phases in 2004 and 2005 (Equal Variance Test; F = 9.306, df = 15, *p* = 0.002). The food diversity consumed was highest during the nestling phase of 2005 (mean = 2.73±0.19) and lowest during the incubation phase of 2004 (1.00±0.44; Table 2). Different animal groups also comprise different percentages of the diet (Table 3).

Table 2 Plant diversity in hornbill diet in different phases and Shannon-Weiner Index

Hornbill species	2004			2005		
	Incubation	Nestling	non-breeding	Incubation	Nestling	non-breeding
GH						
No. of plant species	3	20	6	6	18	7
H'	0.3	1.4	1.4	1.9	2.8	0.8
WH						
No. of species	16	13	12	13	17	17
H'	1.2	1.7	1.5	1.1	2.9	1.0
BH						
No. of species	7	19	-	9	15	3.0
H'	1.5	2.2	-	2.1	2.8	0.4
PH						
No. of species	9	19	9	13	18	8
H'	1.0	1.9	2.0	2.7	2.4	0.7
Total						
Mean	1.00	1.80	1.63	1.95	2.73	0.73
SD	0.44	0.29	0.26	0.57	0.19	0.22

Table 3 Animal consumption during the breeding season of 2004 and 2005

Year	Hornbill	Phase	Feeding (g/hr)	% of animal diet			
				Insect	Mollusc	Reptile	Mam/Bird
2004	GH	Incubation	0.0	0	0.0	0.0	0.0
		Nestling	3.3	38.3	13.7	9.5	38.5
		Total	3.3	38.3	13.7	9.5	38.5
	WH	Incubation	1.4	14.9	85.1	0.0	0.0
		Nestling	4.9	62.4	16.7	8.1	12.8
		Total	6.3	38.7	50.9	4.0	6.4
	BH	Incubation	0.9	16.5	0.0	2.1	81.3
		Nestling	5.7	61.7	24.6	5.5	8.2
		Total	6.5	39.1	12.3	3.8	44.8
	PH	Incubation	0.1	61.2	38.8	0.0	0.0
		Nestling	3.2	56.3	21.4	1.8	20.5
		Total	3.3	58.7	30.1	0.9	10.3
2005	GH	Incubation	0.8	15.1	12.7	7.4	64.9
		Nestling	2.7	70.7	14.0	2.3	12.6
		Total	3.5	42.9	13.3	4.8	38.7
	WH	Incubation	0.3	89.2	10.8	0.0	0.0
		Nestling	4.8	89.6	10.1	0.0	0.0
		Total	5.0	89.4	10.5	0.0	0.0
	BH	Incubation	0.3	86.3	4.4	9.3	0.0
		Nestling	4.9	82.7	12.2	2.2	2.8
		Total	5.3	84.5	8.3	5.7	1.4
	PH	Incubation	1.1	60.1	17.7	0.0	11.5
		Nestling	3.5	73.6	23.3	0.4	1.7
		Total	4.5	133.7	40.9	0.4	13.2
Average	GH	Incubation	0.4	7.6	6.3	3.7	32.4
		Nestling	3.0	54.5	13.9	5.9	25.5
		Total	3.4	40.6	13.5	7.2	38.6
	WH	Incubation	0.8	52.1	47.9	0.0	0.0
		Nestling	4.9	76.0	13.4	4.0	6.4
		Total	5.7	64.0	30.7	2.0	3.2
	BH	Incubation	0.6	51.4	2.2	5.7	40.7
		Nestling	5.3	72.2	18.4	3.8	5.5
		Total	5.9	61.8	10.3	4.8	23.1
	PH	Incubation	0.6	60.6	28.2	0.0	5.7
		Nestling	3.3	64.9	22.3	1.1	11.1
		Total	3.9	96.2	35.5	0.7	11.7

It was difficult to compare the quantity of food consumed by each hornbill species, since these four hornbill species differ in body mass, breeding strategy, number of chicks produced and/ or brood size. Date on food delivery to the brood are presented as the quantity of food seen to be delivered, regardless of number of individuals per brood and calculated per observation hour.

To simplify my analysis of food delivered to the brood, I categorized food into three types, fig, non-fig and animal (with the latter divided further into vertebrate and invertebrate; Table 4). There was variation among food types consumed by hornbills in the two different breeding seasons (Table 4). It appeared that overall feeding rate in the 2004 breeding season was higher for all hornbill species than in 2005 (Table 4). On average, between the large species, the total feeding rate of Great Hornbill was much less than that of Wreathed Hornbill while, between the smaller species, White-throated Brown Hornbill was lower than for Oriental Pied Hornbill (Table 4). Among the three main types of food, the feeding rate of figs by all hornbill species was lower than for non-fig fruits (Table 4), and the feeding rate for figs was highest for Great Hornbill (19.4 g/hr) (Table 4). Unfortunately, I did not study the abundance of or derive an FAI for individual fig species, due to identification difficulties, and only decribed the fruiting phenology for all species combined. All hornbill species, except for White-throated Brown Hornbill, consumed animal foods at a relatively similar rate (Table 4). The total feeding rate for the incubation and nestling phases was also similar for all hornbill species, except that Wreathed Hornbill [again had the lowest rates? (33.5 and 77.7 g/hr, respectively; Table 4).

There was a significant correlation between total consumption of fig and non-fig fruits for Great Hornbill (Spearman Rank Order Correlation; r (GH) = -0.976, n = 10, p < 0.001; r (WH) = -0.976, n = 10, p < 0.001), but not for Oriental Pied Hornbill (Spearman Rank Order Correlation; r = -0.238, n = 8, p = 0.570) (Table 4). White-throated Brown Hornbill consumed animal foods at the highest rate of all hornbill species, particularly in 2004, but there was also an increase on non-fig consumption in 2005 (Table 4).

Table 4 Food categories consumed in different breeding phases

Year	HB species	Breeding phase	Feeding rate (g/hr)				% of food types		
			Fig	non-fig	Animals	Total	Fig	non-fig	Animals
2004	GH	Incubation	18.2	7.4	0.0	5.6	90.0	10.1	0
		Nestling	8.9	31.9	4.9	45.7	55.1	36.9	8.0
		Total	**27.1**	**39.3**	**4.9**	**71.3**	**38.0**	**55.1**	**6.9**
	WH	Incubation	12.1	17.5	3.1	32.7	80.5	18.5	1.1
		Nestling	7.8	75.0	4.6	87.4	29.8	64.5	5.7
		Total	**19.9**	**92.5**	**7.7**	**120.1**	**16.6**	**77.0**	**6.4**
	BH	Incubation	1.2	7.9	14.0	23.1	28.6	58.7	12.6
		Nestling	1.3	29.5	11.8	42.6	5.4	68.0	26.7
		Total	**2.5**	**37.4**	**25.8**	**65.7**	**3.7**	**57.0**	**39.3**
	PH	Incubation	5.9	11.8	3.8	21.5	67.2	31.9	0.9
		Nestling	5.5	46.8	4.2	56.5	21.9	70.8	7.4
		Total	**11.4**	**58.6**	**8.1**	**78.0**	**14.5**	**75.1**	**10.4**
2005	GH	Incubation	7.5	2.5	0.8	10.9	57.1	42.0	0.9
		Nestling	4.2	24.9	17.2	46.3	32.7	60.7	6.6
		Total	**11.7**	**27.5**	**18.1**	**57.2**	**20.4**	**48.0**	**31.6**
	WH	Incubation	5.0	27.2	2.1	34.3	28.2	70.0	1.8
		Nestling	5.3	56.4	6.2	67.9	32.1	61.5	6.4
		Total	**10.3**	**83.6**	**8.3**	**102.2**	**10.1**	**81.8**	**8.1**
	BH	Incubation	0.9	4.4	1.6	6.9	4.7	84.9	10.5
		Nestling	1.1	12.5	10.0	23.6	7.0	57.2	35.8
		Total	**2.0**	**16.9**	**11.6**	**30.5**	**6.4**	**55.5**	**38.1**
	PH	Incubation	2.2	11.8	2.3	16.3	21.3	74.5	4.3
		Nestling	2.4	13.2	7.0	22.7	18.5	48.4	33.0
		Total	**4.6**	**25.0**	**9.3**	**39.0**	**11.8**	**64.3**	**23.9**
Average	GH	Incubation	12.9	5.0	0.4	18.2	70.8	27.2	2.2
		Nestling	6.5	28.4	11.1	46.0	14.2	61.8	24.1
		Total	**19.4**	**33.4**	**11.5**	**64.3**	**30.2**	**51.9**	**17.9**
	WH	Incubation	8.5	22.4	2.6	33.5	25.5	66.8	7.7
		Nestling	6.5	65.7	5.4	77.7	8.4	84.6	7.0
		Total	**15.1**	**88.1**	**8.0**	**111.2**	**13.6**	**79.3**	**7.2**
	BH	Incubation	1.1	6.2	7.8	15.0	7.0	41.1	52.0
		Nestling	1.2	21.0	10.9	33.1	3.5	63.6	33.1
		Total	**2.2**	**27.2**	**18.7**	**48.1**	**4.6**	**56.5**	**38.9**
	PH	Incubation	4.0	11.8	3.1	18.9	21.3	62.5	16.2
		Nestling	4.0	30.0	5.6	39.6	10.0	75.7	14.3
		Total	**8.0**	**41.8**	**8.7**	**58.5**	**13.7**	**71.4**	**14.8**

3.1.2 Important species

The number of important plant species consumed by each hornbill species in the breeding and non-breeding seasons, and the most and least important hornbill food and non-food plant species in 2004-2005 are listed (Table 5 & Appendix D). The number of important plant species for all hornbill species in breeding season was similar, as well as the number in non-breeding season (Table 6). It appeared that *Polyalthia* spp., *Bhesa robusta, Dysoxylum cyrtobotryum* and *Horsfiedia glabra* were important to all hornbill species in the breeding season of both years, while *Cryptocaya impressa* and *Syzygium* sp. were important in the breeding season of 2004, and *Desmos chinensis, Elaeagnus latifolia* and *Cinnamomum subavenium* were important in the breeding season of 2005 (Table 5).

Among the total of 167 tree species recorded, 19% were food plants for Great, 13% for Wreathed, 13% for White-throated Brown and 14% for Oriental Pied Hornbills in at least one breeding phase (Appendix D).

Table 5 Number of important plant species in the diet of hornbills as recorded in the breeding and non-breeding seasons of 2004 and 2005 (with rank in brackets)

Family/ species	2004								2005							
	Breeding season				Non-breeding season				Breeding season				Non-breeding season			
	GH	WH	BH	PH	GH	WH	BH	PH	GH	WH	BH	PH	GH	WH	BH	PH
ANNONACEAE																
Alphonsea boniana							ND							0.38 (3)		
Cyathostemma micranthum						0.02 (1)	ND	0.91 (1)								
Desmos chinensis	7.98 (8)		11.73 (5)				ND		11.43 (6)	0.18 (10)	3.18 (8)	0.77 (1)				
Miliusa lineata							ND							0.15 (2)		0.19 (2)
Polyalthia jucunda							ND		11.04 (5)	23.73 (2)	8.16 (7)	8.74 (6)	0.74 (3)	1.21 (6)		
Polyalthia viridis	35.93 (1)	20.12 (10)	17.01 (11)	14.83 (12)		0.09 (2)	ND	6.89 (3)	16.56 (7)		14.15 (5)	7.22 (5)				
BIGNONIACEAE																
Canarium euphyllum					35.57 (6)	20.85 (10)	ND	8.25 (4)					8.83 (5)			0.05 (1)
CELASTRACEAE																
Bhesa robusta	6.90 (11)	7.02 (1)	10.12 (3)	8.72 (6)			ND		0.10 (1)	4.50 (8)	18.88 (4)	2.85 (3)				
COMBRETACEAE																
Combretum acuminatum	7.27 (9)			6.22 (1)			ND									
CORNACEAE																
Mastixia pentandra					4.47 (2)	49.27 (11)	ND	2.59 (2)					0.56 (2)	0.85 (5)		
ELAEGNACEAE																
Elaeagnus latifolia							ND		8.22 (4)	6.58 (7)	2.69 (10)	2.15 (2)				
FLACOURTIACEAE																
Caseasia grewiawfolia						1.20 (5)	ND	9.84 (5)								
Gnetum montanum				8.60 (5)		0.66 (4)	ND	21.10 (8)						75.42 (12)		79.26 (8)
ICACINACEAE																
Platea latifolia			14.67 (9)	9.37 (9)	13.96 (4)	4.40 (7)	ND	13.49 (6)					10.97 (6)			0.20 (3)
LAURACEAE																
Beichemiedia balansae					11.06 (3)	0.51 (3)	ND									
LAURACEAE																
Cinnamamum ilicioides							ND									
Cinnamomum glaucescens						15.28 (9)	ND	22.88 (9)								
Cinnamomum subavenium							ND		33.29 (9)	13.58 (5)	45.88 (2)	14.95 (8)	1.61 (4)	9.90 (11)	7.04 (2)	13.72 (7)
Cryptocarya impressa	5.28 (12)	12.99 (7)	6.14 (1)	6.47 (2)			ND									
MAGNOLIACEAE																
Michelia baillonii							ND							1.35 (7)	2.30(3)	3.62 (6)
MELIACEAE																
Aglaia lawii							ND			2.89 (9)	2.47 (11)	5.64 (4)				
Aglaia spectabillis							ND		55.39 (11)	59.80 (1)		14.46 (7)				0.32 (4)
Aphanamixis polystachya							ND			23.71 (3)	2.93 (9)					
Dysoxylum cyrtobotryum	9.06 (7)	16.73 (8)	6.72 (2)	7.14 (4)			ND		47.04 (10)	23.53 (4)	60.19 (1)	16.83 (9)				
Dysoxylum densiflorum			13.54 (7)	14.63 (11)			ND									

Table 5 Number of important plant species in the diet of hornbills as recorded in the breeding and non-breeding seasons of 2004 and 2005 (with rank in brackets) (Continued).

Family/ species	2004								2005							
	Breeding season				Non-breeding season				Breeding season				Non-breeding season			
	GH	**WH**	**BH**	**PH**	**GH**	**WH**	**BH**	**PH**	**GH**	**WH**	**BH**	**PH**	**GH**	**WH**	**BH**	**PH**
MYRISTICACEAE																
Horsfieldia glabra	10.51 (6)	9.49 (2)	13.49 (6)	9.00 (8)		1.46 (6)	ND		18.31 (8)	8.73 (6)	41.89 (3)	52.87 (11)		0.84 (4)		
Knema lauriana		18.25 (9)	14.10 (8)	6.84 (3)			ND									
Syzygium sp.	12.78 (4)	21.79 (11)	16.47 (10)	10.93 (10)			ND		7.70 (3)			52.66 (10)				
Syzygium sp.1							ND	14.05 (7)								
OLACACEAE																
Chionanthus ramiflorus							ND							7.86 (10)	90.69 (1)	2.64 (5)
PALMAE																
Levistona speciosa	33.94 (2)	11.11 (3)			34.08 (5)		ND						77.07 (7)	0.01 (1)		
POLEMONIACEAE																
Phoebe cathia					0.86 (1)	5.89 (8)	ND									
ROSACEAE																
Canthium glabrum	7.10 (10)			8.97 (7)			ND		0.98 (2)	(11)	12.55 (6)					
Prunus arboria																
Prunus javanicus		12.05 (5)					ND									
THEACEAE																
Ternstroemia wallichiana	13.26 (3)	11.86 (4)	10.89 (4)				ND									
ULMACEAE																
Celtis tetrandra							ND							1.63 (8)		
Gironniera nervosa							ND						0.22 (1)			
No. of species	**12**	**11**	**11**	**13**	**6**	**12**	**0**	**9**	**11**	**10**	**11**	**11**	**6**	**11**	**3**	**8**
No. of genus	**12**	**10**	**10**	**12**	**6**	**11**	**0**	**9**	**10**	**9**	**10**	**10**	**6**	**10**	**3**	**8**
No. of family	**11**	**9**	**8**	**10**	**6**	**8**	**0**	**7**	**8**	**6**	**7**	**7**	**6**	**9**	**3**	

3.1.3 FAI-Hornbill and feeding rate

In breeding season, the overall FAI-Hornbill declined towards May-June (Figures 4 and 8), but the abundance of food was not significantly correlaed with the feeding rate during the breeding season for any of the hornbill species (Spearman Rank Order Correlation; $r = 0.0431$, $n = 12$, $p = 0.441$; Figure 8). This non-correlation between FAI-Hornbill and feeding rate suggests that abundance of fruit food did not influence the amount of fruit fed to the brood. However, the analysis of monthly FAI-Hornbill was derived from combining data of the abundance of all fruiting food species occurred monthly and feeding rate of all fruit food. If those with low Abundance Index were highly exceeded those with high Abundance Index, they could obscure the fewer species with high abundance.

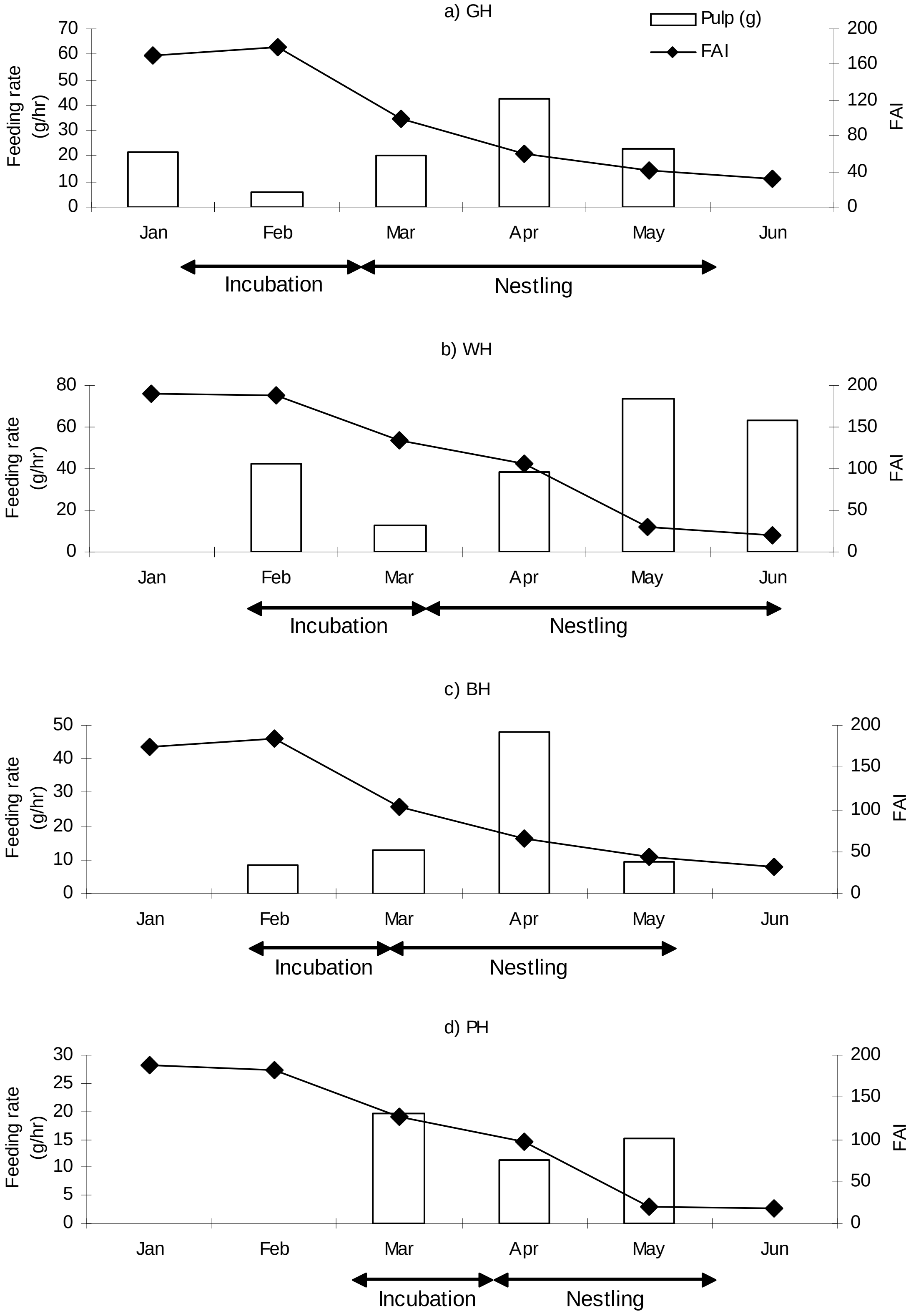


Figure 8 Correlation between FAI and feeding rate (g/hr) in the breeding diet of each of four studied hornbill species during 2005.

There was also no significant correlation between the FAI for each individual hornbill species and the frequency of food delivery in the breeding season (Spearman Rank Order Correlation; GH, r = -0.153, n = 6, *p* = 0.773; WH, r = -0.429 n = 6 *p* = 0.397; BH, r = 0.203 n = 6, *p* = 0.700; PH, r = -0.278 n = 6 p = 0.594; Figure 9).

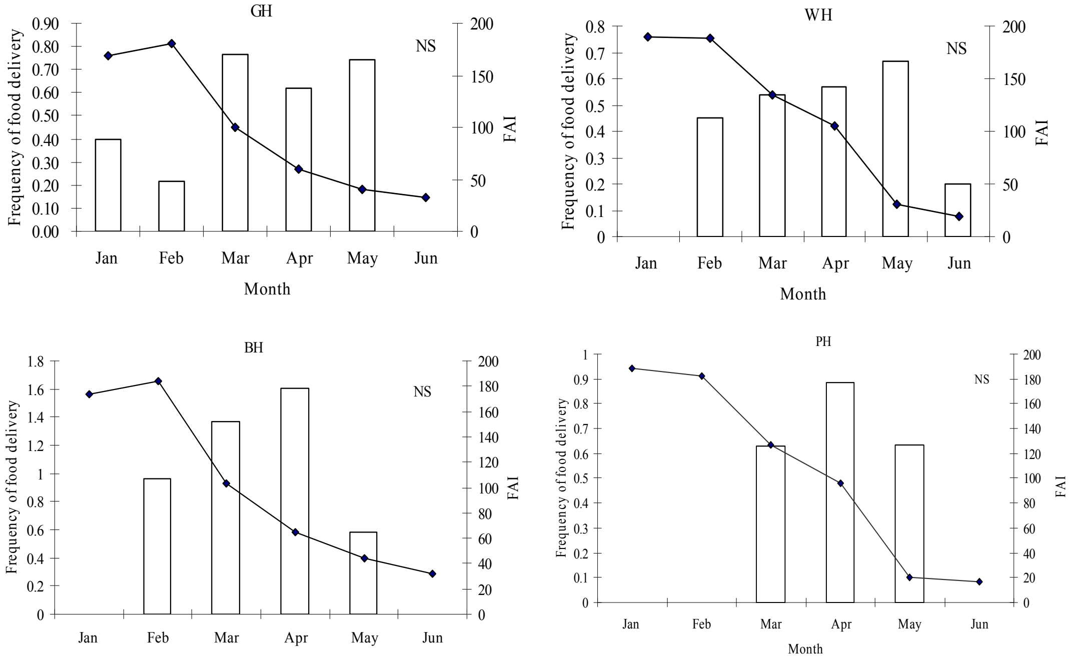


Figure 9 Frequency of food delivery (per hour) compared with FAI of 4 hornbill species (NS = No significant correlation).

3.2 Non-breeding (flocking) season

3.2.1 Important species

The species and importance of fruits in the non-breeding season was determined from seeds collected in traps from under five roost sites (Appendix E). Seeds of *Ficus* were found below every roosting site, but the numbers involved were considered uncountable. Seed of ten plant species (excluded figs) were found under Great Hornbill roosting sites, of which *Beilchemiedia balansae*, *Levistona speciosa* and *Platia latifolia* were the most important. Seeds of 33 species were recorded under the roosting sites of Wreathed Hornbill, of which *Mastixia pentandra* and *Canarium euphyllum* were the most important. White-throated Brown Hornbill. Seeds of 17 species recorded from under the roosting site of Oriental Pied Hornbill, of which *Canarium euphyllum*, *Cinnamomum glaucescens*, *Gnetum montanum*, *Michellia ballonii* and *Persea gamblei* were the most important (Appendix E).

3.3 Food overlap

3.3.1 Schoener Overlap Index (SOI)

Overlap indices of food species, including fruits and animals, varied among hornbill species in both years of study (Table 6). In the breeding season, Great Hornbill overlapped with Oriental Pied Hornbill in both 2004 and 2005 (SOI = 0.62 and 0.75, respectively) and Wreathed Hornbill with Oriental Pied Hornbill (SOI = 0.77 and 0.66, respectively; Table 6).

In the non-breeding season, there was less overlap among these four hornbill species (Table 6), while the overlap in important fruit species between these hornbill species has been shown previously (Table 6).

Table 6 Schoener Overlap Indices (Schoener's 1974) for food species consumed by four hornbill species

Year	Breeding season					
	GH-WH	GH-PH	GH-BH	WH-PH	WH-BH	PH-BH
2004	0.45	0.62	0.18	0.77	0.29	0.46
2005	0.49	0.75	0.57	0.66	0.55	0.51
Year	Non-breeding season					
	GH-WH	GH-PH	GH-BH	WH-PH	WH-BH	PH-BH
2004	0.16	0.02	-	0.14	-	-
2005	0.10	0.17	0.05	0.45	0.33	0.22

3.3.2 Canonical Correspondence Analysis (CCA)

Canonical Correspondence Analysis for four hornbill species was derived from data of food species, including fruits and animals, which were collected in the two breeding seasons of 2004 and 2005. When grouping hornbill species by food similarity in 2004, Axis1 accounted for 92.7% of the variance and clearly separated the group of Great and White-throated Brown Hornbills from Wreathed and Oriental Pied Hornbills

(Figure 10a). Axis2 accounted for 5.2% of the variance and showed little separation between species. In 2005, Axis1 accounted for 75.1% of the variance and showed separation of the same hornbill groups as in 2004, while Axis2 accounted for 19.6% and showed stronger separation of species than in 2004 (Figure 10b).

During the non-breeding season of 2004, Axis1 accounted 63.1% of the variance and showed separation of the same hornbill groups as in the breeding season, while Axis2 accounted for 36.8% of the variance and showed lower separation between Great, Oriental Pied and Wreathed Hornbills (Figure 11a). In 2005, Axis1 accounted for 75.4% of the variance and showed clear separation between Great Hornbill and the other three species, while Axis2 accounted 63.2% of variance) also shows strong separation of group between Great Hornbill and the other three species (Figure 11b).

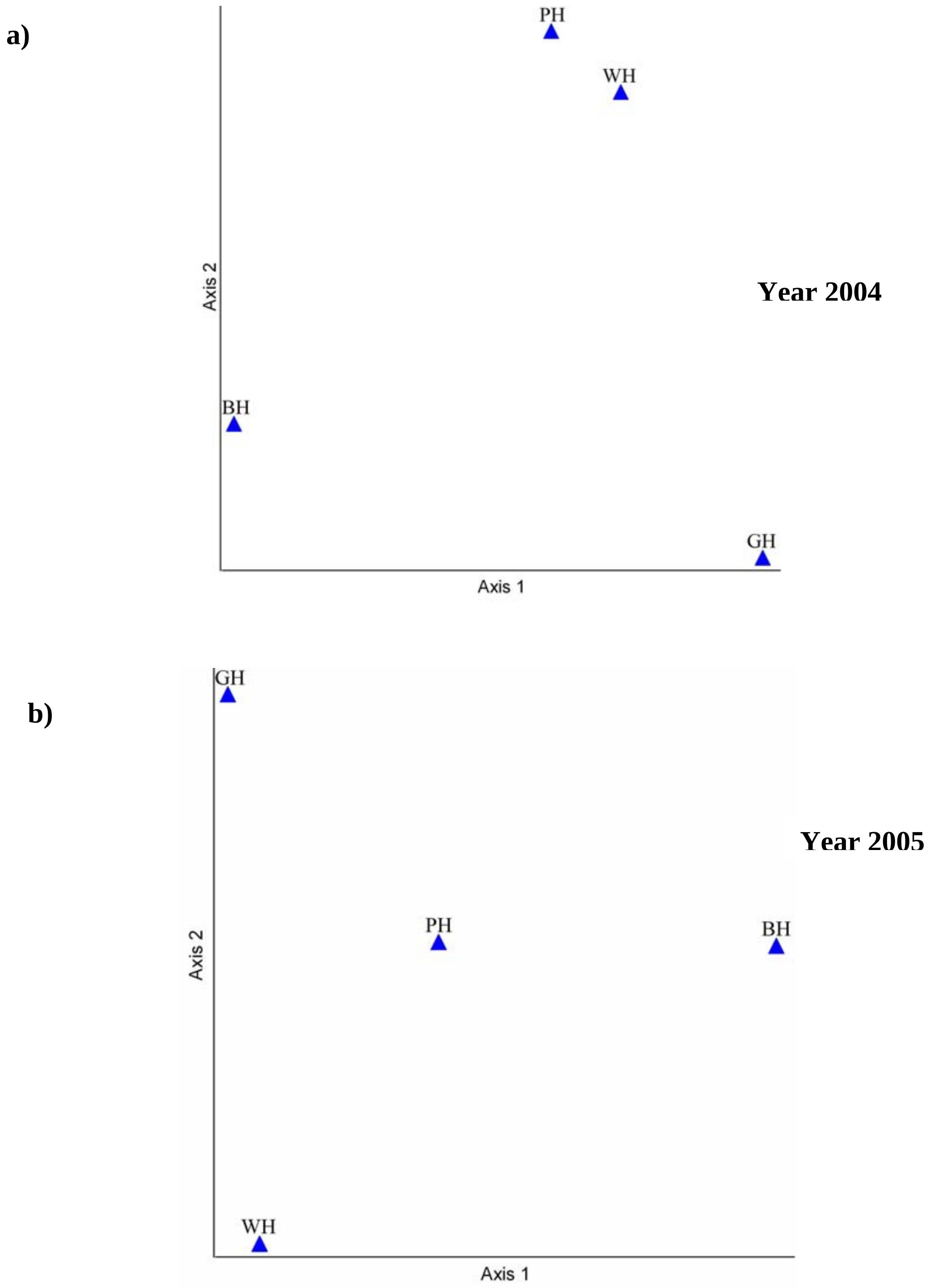
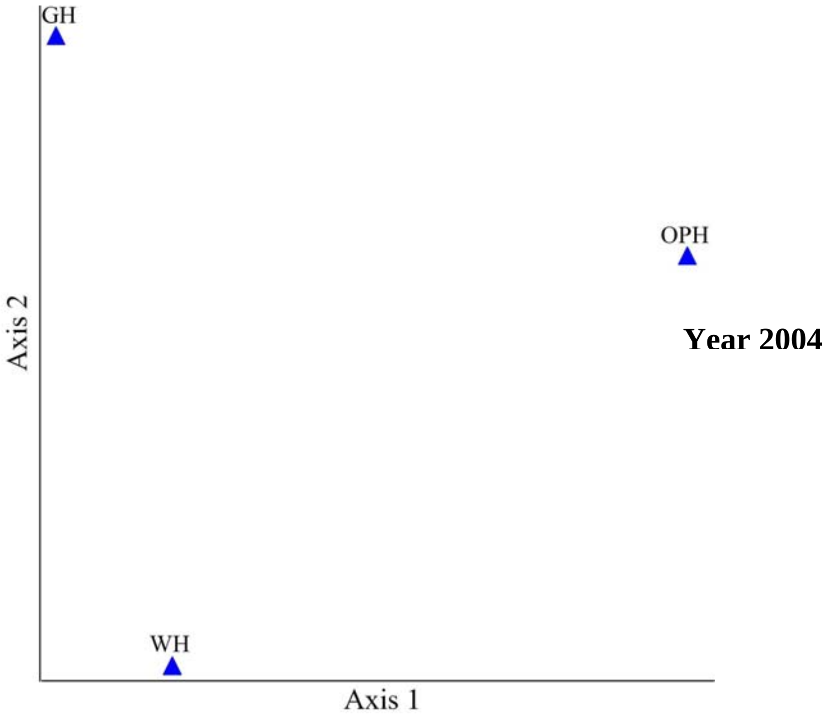


Figure 10 Canonical Correspondence Analysis (CCA) for food species eaten by four hornbill species in the breeding seasons of 2004 and 2005.

a)



b)

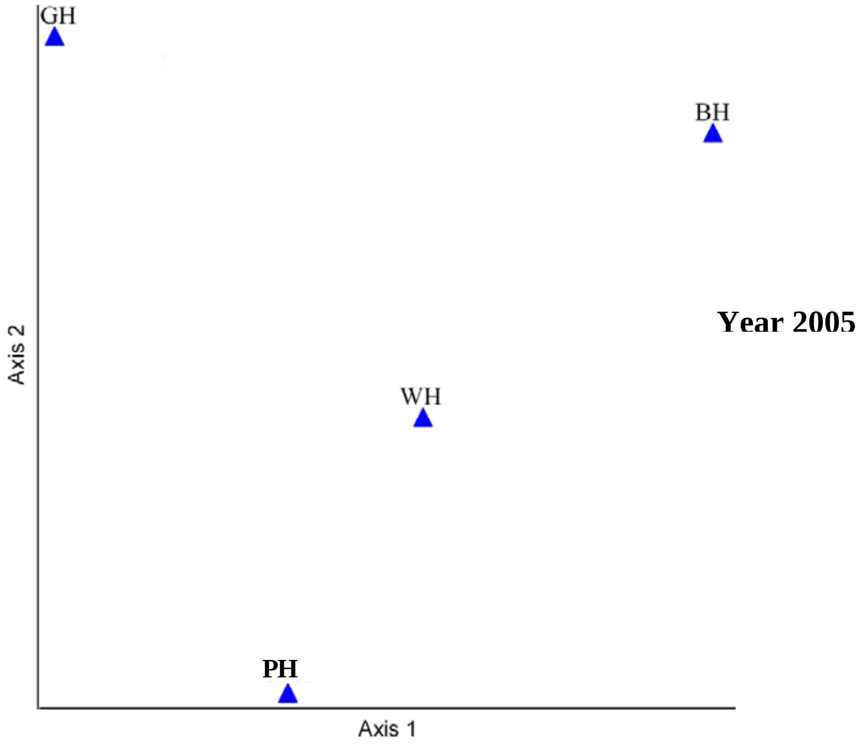


Figure 11 Canonical Correspondence Analysis (CCA) for food species eaten by four hornbill species in the non-breeding seasons of 2004 and 2005.

4. Food selection

The monthly index of selectivity for fruits of each plant species showed that *Ficus* spp. were highly selected by all hornbill species throughout the breeding cycle, except for the White-throated Brown Hornbill which had a high selectivity index only in April (part of nestling period) (Table 7). *Cinnamomum subavenium* was another highly selected species by all four hornbill species, even though the period for which it was availability was not as long or as continuous as for *Ficus* spp, whereas *Bhesa robusta* was highly selected only by White-throated Brown Hornbill, and only during a short period of the incubation phase. However, it should be noted that the dominance of *Ficus* spp was biassed and obscured the importance of *C. subavenium*, since analysis of the selectivity index for figs was derived from combined data for at least five species of *Ficus* due to uncertainty of identification which fig species were fed to the brood. Therefore, the remainder of this section will focus on selection of non-fig fruit species. When figs were excluded from the analysis, in the breeding season of 2005, *C. subavenium* appeared as highest selected species by all four hornbill species, and *Aphanamixis polystachya*, *Polyalthia jucunda* and *P. viridis* were also highly selected by Wreathed Hornbill during both the incubation and nestling phases (Table 7).

When considering the percentage of fruit pulp delivered to the brood (excluded figs), for Great Hornbill in 2004 breeding season, among 21 fruit species that appeared on the list of important species, *Livistona speciosa* and *P. viridis* were the most important species during the incubation phase (Appendix Fa). For Wreathed Hornbill, among 18 fruit species, *Dysoxylum densiflorum, Knema lauriana, P. viridis* and *Syzygium sp.* were important species in both breeding phases, different from Great Hornbill. For White-throated Brown Hornbill, among 17 fruit species, *Ternstroemia wallichiana* was important, as well as the rest of the species that were also important for Wreathed Hornbill (Appendix Fa). For Oriental Pied Hornbill, among 18 fruit species, important species were similar to Wreathed Hornbill, wih *D. densiflorum, P. viridis*, *Syzygium* sp and *Prunus javanicus* the most important species (Appendix Fa).

Table 7 Selectivity Index of four hornbill species during the breeding season in year 2005 (bold is important species)

Plant species	GH						WH						BH						PH					
	Incubation		Nestling				Incubation		Nestling				Incubation		Nestling				Incubation		Nestling			
	Jan	Feb	Mar	Apr	May	Jun	Jan	Feb	Mar	Apr	May	Jun	Jan	Feb	Mar	Apr	May	Jun	Jan	Feb	Mar	Apr	May	Jun
Agaia lawii										-0.61					-0.84						-0.37	-0.97		
Aglaia spectabillis			-0.98	-0.86	-0.88			-0.73	-0.87	-0.97	-0.80	0.10											-0.97	
Aphanamixis polystachya				-1.00				**0.90**						-0.38										
Beilschmiedia glabra									-0.99		-0.96					-0.94	-0.41					-0.99		
Beilschmiedia maingayi										-0.82						-0.73								
Bhesa robusta								-0.31						**0.83**										
Cinnamomum subavenium	-0.59	**0.67**	**0.90**	**0.85**				0.27	**0.83**	**0.83**				**0.77**	**0.94**	**0.94**					**0.85**	**0.91**		
Dysoxylum cyrtobotryum										-0.99														
Dysoxylun densiflorum			-0.77					-0.98		-0.88				-0.99	-0.96									
Ficus *spp.*	**0.95**	**0.71**	**0.65**	**0.89**	**0.97**			**0.77**	**0.91**	**0.68**	**0.89**	**0.97**		0.12	-0.22	**0.66**	0.35				**0.65**	**0.88**	**0.63**	
Horsfiedia glabra				0.50	-0.22				0.06		-0.07				-0.88	0.51	**0.60**					0.42	**0.78**	
Knema elegans									-0.41	-0.98						-0.88								
Polyalthai jucunda			0.18	0.59					**0.78**	**0.72**	-0.17				-0.05	0.08					-0.11	0.17	0.17	
Polyalthia viridis				0.10	0.44			-0.26	0.02	-0.60	**0.77**				-0.96	-0.86	0.55				-0.97	-0.52	0.00	

In 2005 breeding season, for Great Hornbill, fruit species that were important differed from those for 2004. Among 17 fruit species that appeared on the list of important species (Appendix Fb), *C. subavenium,* which was not fruiting in 2004, was highly important during the incubation phase, while *Aglaia spectabillis and D. densiflorum* were important during nestling phase. For Wreathed Hornbill, among 20 fruit species, *A. spectabillis* was highly important species throughout the breeding cycle, with *P. jucunda* and *P. viridis* less important (Appendix Fb). For White-throated Brown Hornbill, among 20 fruit species, the most important species was *C. subavenium* during both breeding phases, like Great Hornbill, while *D. densiflorum* and *Horsfeidia glabra* were important during the nestling phase (Appendix Fb).

4.1 Fruit characteristics

The categories of fruit characteristics and percentage availability of total fruit foods and non-foods are summarized (Appendices G and H), and those percentages for fruit eaten by each hornbill species presented (Table 8). The majority of life forms for the plants studied plants are trees and, of these, hornbill food species accounted for 95.7 % of a total 70 species and non-foods for 98.2 % of a total 56 species (Appendix G). Among all categories of fruit characteristics, the percentages of availability of both hornbill-food and non-food plants were similar to those for fruits presented at the nests, where fruits with orange and black colors contrasted with the remainder of the categories (Appendix G).

During both the breeding and non-breeding seasons, hornbills appeared to eat slightly more fruits that were present in clusters rather than singly, except for White-throated Brown Hornbill (overall proportion of Single: Clustered fruits available = 1:1.5, and for each hornbill species, GH = 1:1.3, WH =.1:1.7, BH = 1:0.7, PH = 1:1.05; Table 8). Hornbills ate berry and drupe fruit types, but not legume, nut or samara types. Fruits with shiny skin, including *Aglaia* spp, *Beilchemiedia maingayi* and *C. subavenium*, may have attracted hornbills or were most visible, particularly for White-throated Brown Hornbill (overall proportion Dull : Shiny available = 1:0.98, and for each hornbill species, GH = 1:1.8, WH = 1:1.8, BH = 1:2.4, PH = 1:1.8; Table 8). All hornbills obviously ate fruits with pulp that was easily detached from the seed, such as *D. cryptobotryum* and *Casearia grewiaefolia* and *Livistona speciosa* (overall proportion Detached: Non- detached available = 1:0.7, for each hornbill species, GH = 1:0.1, WH = 1: 0.2, BH = 1:0.1, PH = 1:0.1; Table 8). Non-dehiscent fruits, including *Alangium kurzii*, *B. maingayi* and *H. glabra*, were highly selected, which may have been influenced by the dominance of such fruit types in the sample (overall proportion Dehiscent: Non-dehiscent available = 1:3.8, for each hornbill species, GH = 1:3.8, WH = 1:2.9, BH = 1:3.5, PH = 1:2.2; Table 8). Fruits eaten by hornbills were of various colors, including, yellow, orange, red green and black. Hornbills ate mostly dark fruits, with black or dark purple colors, such as *C. subavefnium* and *B. maingayi*, followed by orange colors, such as, *B. robusta* and *Elaeagnus latifolia*, with green fruit eaten least, and this corresponded with the abundance of species with such fruit colors (Table 8). Fruits eaten by hornbills were both UV-reflective and non-UV-reflective, but availability of fruit species with UV reflection was lower than that of non-UV-reflective species (36.1 % and 63.9 %, respectively or 1.8:1). It appeared that hornbills ate almost as much fruit with UV-reflection, for instance *Mastixia pentandra*, *C. euphyllum* and *P. viridis*, fruit with non-UV-reflection (overall UV-reflection : Non-UV-reflection available = 1:1.8, for each hornbill species, GH = 1 : 1.5, WH = 1 : 1.3, BH = 1 : 1.1, P = 1 : 0.9; Table 8), and fruits with UV-reflection may enhance their detection of birds. Fruit with a single seed were most abundant in the diet (51.7 % of total) and were eaten more by most hornbill species (GH = 60 %, WH = 58.5 %, BH = 48.8 %, PH = 62.7 %; Table 8). Among the diversity of tastes selected, fruit without taste (tasteless) was eaten most, followed by fruits with astringent flavors (Table 8).

Table 8 Percentage of characteristic categories of fruit-food species eaten by four hornbill species in breeding and non-breeding seasons (n = number of fruit species eaten)

		% species Availabity (n = 70)	%			
			GH n = 45	WH n = 53	BH n = 41	PH n = 51
Lifeform	Climber	3.1	4.4	3.8	4.9	3.9
	Tree	96.9	95.6	96.2	95.1	96.1
Fruit presentation	Single fruit	39.4	43.2	36.4	56.3	48.8
	Cluster	60.6	56.8	63.6	43.8	51.2
Fruit type	Berry	34.7	35.6	41.5	24.4	35.3
	Capsule	18.5	13.3	13.2	24.4	17.6
	Drupe	31.5	33.3	30.2	31.7	31.4
	Legume	4.0	0.0	0.0	0.0	0.0
	Nut	2.4	0.0	0.0	0.0	0.0
	Samara	1.6	0.0	0.0	0.0	0.0
	Syconium	7.3	17.8	15.1	19.5	15.7
Fruit skin	Dull	50.4	35.6	35.8	29.3	35.3
	Shiny	49.6	64.4	64.2	70.7	64.7
Detachment of pulp from seed	Detached	57.9	88.9	81.1	87.8	86.3
	Non-detached	42.1	11.1	18.9	12.2	13.7
Dehiscence	Dehiscent	21.0	20.8	25.5	22.2	31.7
	Non-dehiscent	79.0	79.2	74.5	77.8	68.3
Color	Yellow	12.7	6.7	7.5	2.4	3.9
	Orange	22.2	33.3	41.5	41.5	37.3
	Red	19.1	6.7	5.7	9.8	13.7
	Green	6.3	0.0	0.0	0.0	0.0
	Black	39.7	53.3	45.3	46.3	45.1
UV - Reflection	Reflection	36.1	40.5	44.4	47.1	52.3
	Non-reflect	63.9	59.5	55.6	52.9	47.7
Seed number per fruit	1 seed	51.7	60.0	58.5	48.8	62.7
	2-10 seeds	25	22.2	22.6	24.4	17.6
	11-50 seeds	11.2	15.6	0.0	7.3	5.9
	>50 seeds	12.1	2.2	18.9	19.5	13.7
Taste	Sweet	10.5	6.3	9.5	0.0	11.1
	Sweet and sour	2.6	0.0	4.8	0.0	0.0
	Sour	26.3	0.0	14.3	8.3	5.6
	Bitter	5.3	0.0	0.0	0.0	0.0
	Astringent	21.1	31.3	23.8	25.0	27.8
	Sweet and astringent	21.1	12.5	9.5	0.0	11.1
	Tasteless	13.2	50.0	38.1	66.7	44.4

Fruit and seed sizes varied greatly but tended to be correlated (Table 9). Fruit and seed weights and lengths were significantly correlation (Spearman Rank Correlation, r = 0.670, n = 104, $p < 0.001$ and r = 0.589, N = 103, $p < 0.001$, respectively; Table 9). Among hornbill food species, *Platymitra macrocarpa* (family Annonaceae) and *Michelia baillonii* (Magnoliaceae) were the two species that had the largest fruits, i. e. 140.5 mm (with 2-10 seeds per fruit) and 116.3 mm in length (> 50 seeds per fruit), respectively, and were fruiting in both the breeding and non-breeding seasons (Appendix H).

Table 9 Fruit and seed measurement of plant species found in different season consumed by four hornbill species (**FW** = Fruit weight (g); **FL** = Fruit length (mm); **FW1** = Fruit greatest width (mm); **FW2** = Fruit least width (mm); **Fvol** = Fruit volume (mm^3); **Sflesh** = Fruit pulp (g); **SW** = Seed weight (g); **SL** = Seed length (mm); **SW1** = Seed greatest width (mm); **SW2** = Seed least width (mm); **Svol** = Seed volume (mm^3); ***** = could not be measured)

Variable	Breeding season		Non-breeding season		All year	
	Median	Range	Median	Range	Median	Range
FW	4.65	0.33-140.45	3.65	0.14-116.29	0.65	0.15-3.26
FL	28.27	6.43-73.37	21.77	5.23-89.83	9.82	8.40-21.00
FW1	16.30	6.45-58.04	15.64	5.49-48.72	10.62	6.48-16.92
FW2	16.95	6.45-56.36	15.63	5.41-46.36	12.35	5.23-16.85
Fvol	4.53	0.50-134-33	1.25	0.06-110.90	0.69	0.14-3.67
Sflesh	1.09	0.19-9.08	0.91	0.16-7.74	0.13	*
SW	0.91	0.08-5.89	0.23	0.00-6.43	0.02	*
SL	14.81	4.12-37.28	9.02	1.68-32.16	4.06	*
SW1	10.32	4.02-18.98	6.49	1.04-20.12	4.02	*
SW2	9.30	4.42-16.60	5.83	0.84-19.19	2.59	*
Svol	1.05	0.11-5.39	0.24	0.00-5.73	0.06	*

Multivariate analysis of fruit characteristics for all fruits consummed by hornbills were conducted by PCA and Discriminant Analysis to help explain which variables were important and how much they differed in importance. For a total of 22 morphological and nutritional variables (fruit type, fruit skin, life form, detachment of pulp dehiscence, fruit weight, color, UV detection, seed weight, seed number per fruit, moisture, protein, fat, ash, calcium, phosphorus, NDF, ADF, NaCl, tannin, height, basal area per ha), the correlation between them was extracted and then reduced to 11 morphological variables (fruit type, fruit skin, life form, detachment of pulp, dehiscence, fruit weight, color, UV detection, seed weight, seed number per fruit) to ensure multi-colinearality. The results from PCA, for 24 variables and fruit characteristics of plant species eaten by hornbills, showed that color, fruit type, number of seed per fruit and detachable pulp appeared to be the most important variables (Figure 12), even though the PCA results for fruit species in different seasons also showed the similar characteristics of fruit (Figure 13). There was some overlap of fruit characteristics for fruits eaten in the breeding or non-breeding seasons, but fruit food species found all year round had a different morphology (64.3 % of original of cases correctly classified; Figure 14).

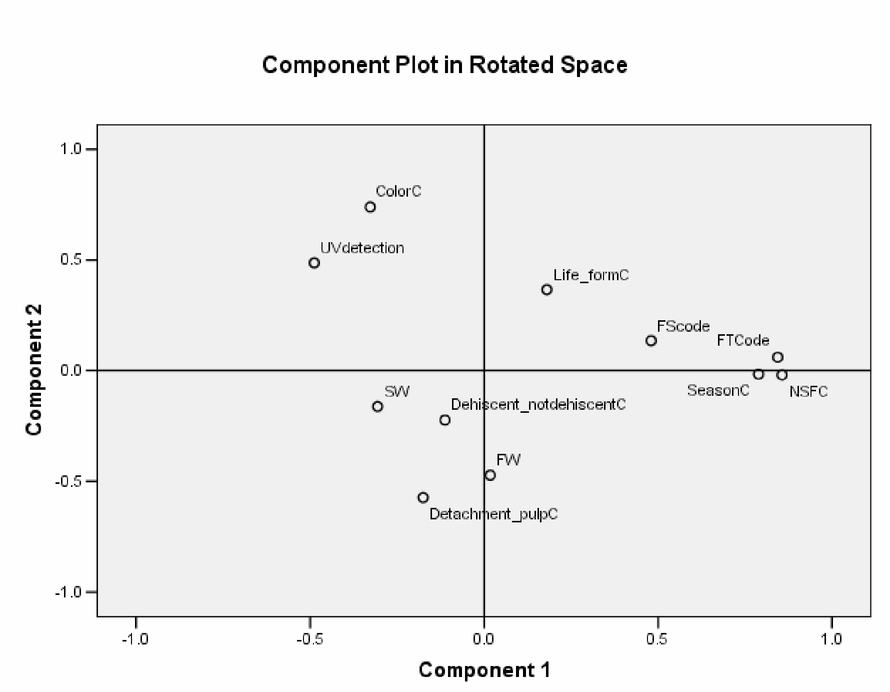


Figure 12 Morphological Variables of 2 components from Principle Component Analysis.

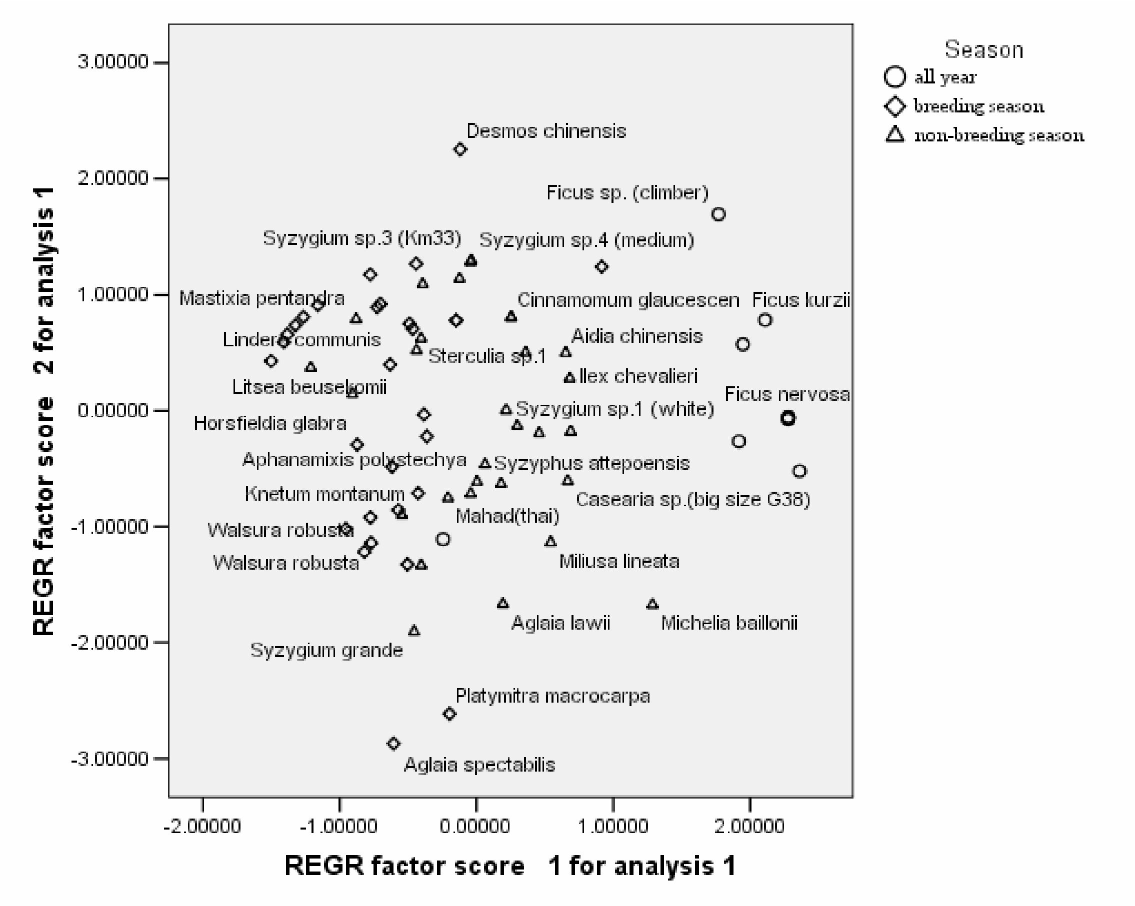
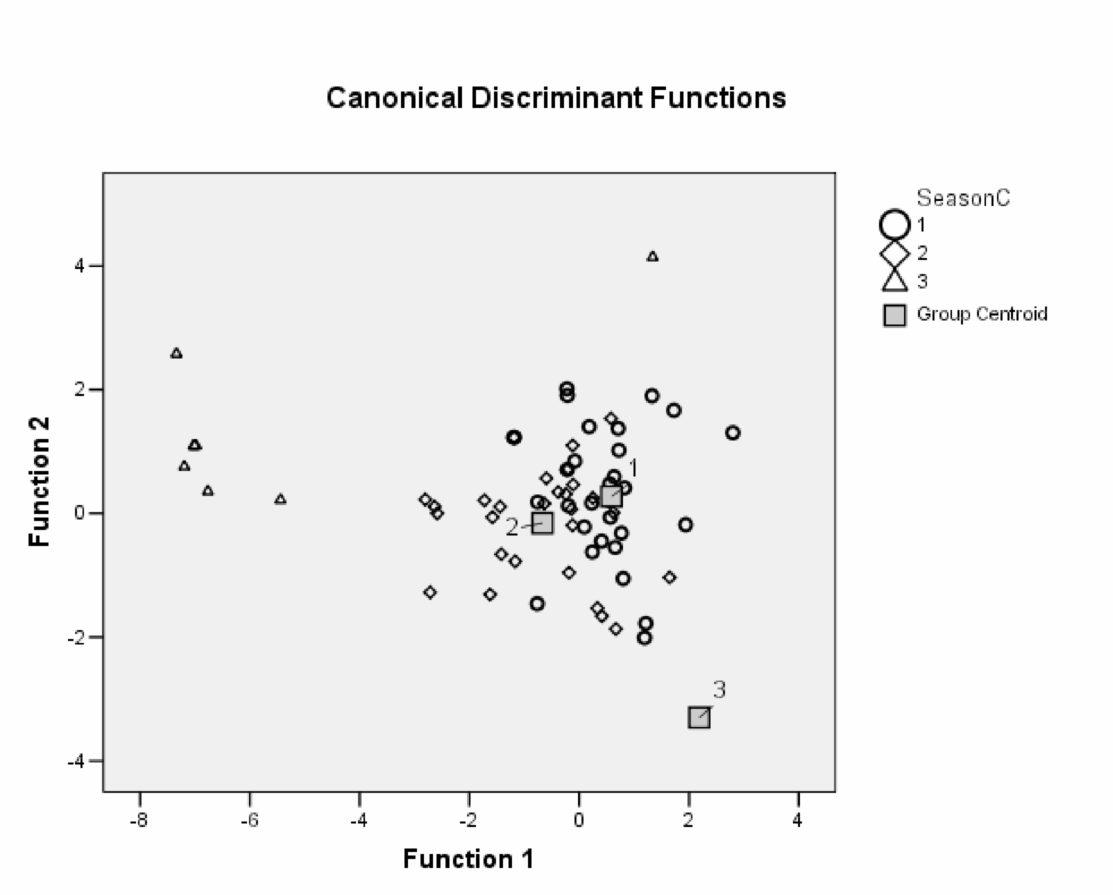


Figure 13 Plant species consumed by hornbills found in different seasons.

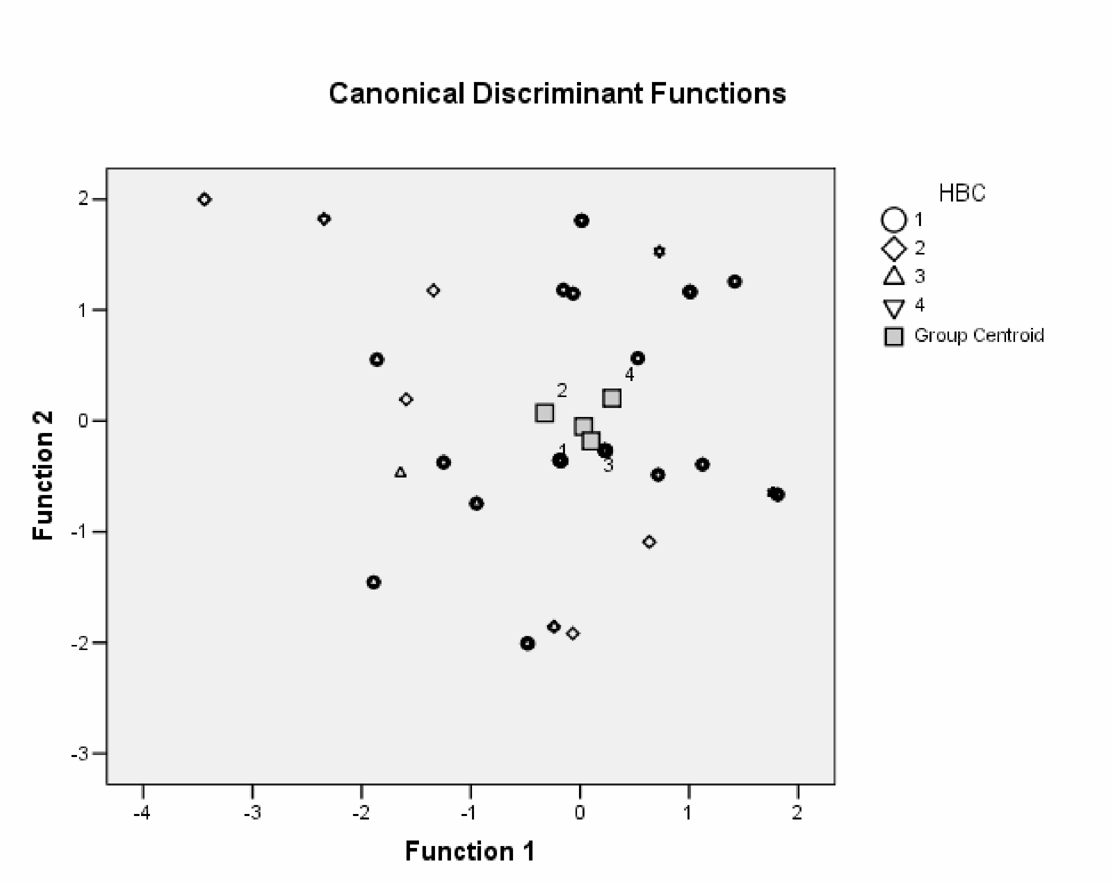


1=breeding, 2= non-breeding, 3= all year

Figure 14 Output from Discriminant Analysis presented groups of plant species consumed by hornbill in different season.

A comparison of the mean from Discriminant analysis (100% accuracy) showed that selection of eaten fruit species favoured a berry that was heavier but with a lower fruit length (smaller), with pulp detached from the seed, and with a black and/or red color.

Fruit characteristics selected among four different hornbill species were analyzed by multivariate analysis, with the Canonical Discriminant function showing the fruit characteristics that were similar among the four hornbill species (Figure 15).



1 = GH, 2 = WH, 3 = PH, 4 = BH

Figure 15 Discriminant Analysis output presented the similarity of fruit characteristics in different hornbill species.

Experiments on selection of fruit color in captive hornbills

When wild fruit species were provided to captive hornbills, none of birds fed on any of the fruits. However, the conditions of the fruit were poor, due to duration since picked, handling and freshness. Instead, dyed pellets of their regular food in five colors (black, red, orange, yellow and green) were fed to 16 hornbills of four species in captivity, and this revealed that there were differences in color selection (Chi-Square test; $X^2 = 3.105$, n= 154, $p < 0.001$). Black was picked first, although not consumed immediately, followed by red, orange, green and yellow in that order, which was slightly different from what had been observed in the wild (Table 8).

Relationship between fruit size and gape size

Descriptive statistics were compiled for variables of fruit and gape size (Table 10). Great Hornbill had the longest gape length (maximun280 mm, mean 236.75 ± 30.6 mm, n = 28) then Wreathed Hornbill (235 mm, 193.54 ± 28.79 mm, n = 26), then Oriental Pied Hornbill (142 mm, 122.21 ± 11.28 mm, n = 26) with White-throated Brown Hornbill the shortest (120 mm, 110.83 ± 7.04 mm, n = 8). Gape size of the four hornbill species was not correlated with any of the variables for fruit size (Spearman Rank Correlation; rGH = 0.137, n = 20, $p = 0.559$, rWH = -0.291, n = 16, $p = 0.267$, rBH = 0.200, n = 5, $p = 0.783$, rPH = 0.268, n = 15, $p = 0.325$; Table 10).

Table 10 Fruit size parameters and gape sizes of four hornbill species **Gape** = gape width (mm); **FW** =Fruit weight (g); **FL** = Fruit length (mm); **FW1** = Fruit greatest width (mm); **FW2** = Fruit least width (mm); **FV** = Fruit volume (mm^3)

	GH						WH						PH						BH					
	Gape	FW	FL	FW1	FW2	FV	Gape	FW	FL	FW1	FW2	FV	Gape	FW	FL	FW1	FW2	FV	Gape	FW	FL	FW1	FW2	FV
N	28	37	37	37	37	25	26	46	46	46	31	44	26	44	44	44	28	34	8	34	34	34	22	46
Minimum	120.4	0.2	7.1	6.5	5.2	0.1	137.0	0.3	6.0	6.5	0.3	0.3	105.2	6.4	6.4	6.4	0.2	0.3	104.0	8.8	6.5	6.5	0.3	6.5
Maximum	280.0	71.7	71.2	51.7	48.1	69.5	235.1	116.3	89.8	51.7	110.9	116.3	142.0	89.8	51.7	48.1	110.9	71.7	120.4	71.2	51.7	48.1	69.5	48.1
Mean	236.8	6.3	24.8	17.5	16.7	6.5	193.5	8.6	25.5	18.0	9.7	9.1	122.2	25.8	18.0	17.4	10.0	8.0	110.8	27.4	19.3	18.5	7.0	17.4
SD	30.7	11.8	14.7	9.4	8.3	13.6	28.8	19.5	16.9	9.9	22.5	20.3	11.3	17.4	10.4	9.5	23.6	13.1	7.0	14.6	9.5	8.5	14.3	9.0

4.2 Nutritional components in fruits

Thirteen chemical components were analyzed for 50 species of fruits eaten by hornbills and 15 uneaten species (Appendix I, summary in Table 11). There was no significant difference between the nutrional components of foods and non-foods, except for moisture, calcium and fat (Mann-Whitey Rank Order Test/ t-test; t Moisture = 2.253, df = 64, $p = 0.028$, U Calcium = -2.381, n = 50, $p = 0.017$, U Fat = 322.00, n (small) = 11, n (big) = 39, $p = 0.012$,) (Table 11). Although, not significant, tannin content in fruits eaten by hornbills was relatively higher than that in non-food fruits (Table 11).

Tests of the nutrient value of fruits found during the breeding and non-breeding seasons (Appendix I) found significant differences in Moisture (Mann-Whitney test, Z = -4.906, $p < 0.001$), Fat (Mann-Whitney test, Z = -3.842, $p = 0.001$), Ash (Mann-Whitney test, Z = -1.566, $p < 0.001$), Fiber (Mann-Whitney test, Z = -2.140, $p = 0.030$, Calcium (Mann-Whitney test, Z = -5.425, $p < 0.001$) Phosphorus (Mann-Whitney test, Z = -4.094, $p = 0.001$), and Calories (Mann-Whitney test, Z = -4.148, $p < 0.001$).

Table 11 Summary and comparison of nutrional values of fruit food and non-food (CHO = carbohydrate, * = significant difference)

	Calory (kal/g)	Moisture* (g%)	Protein (g%)	Fat* (g%)	CHO (g%)	Ash (g%)	Fiber (g%)	Ca* (g%)	P (g%)	NDF (g%)	ADF (g%)	Tannin (g%)
Food												
N	50	51	51	39	39	50	42	50	50	27	28	41
Minimum	570.8	8.87	0.61	0.07	21.11	0.37	0.69	0.03	0.00	1.51	0.01	0.10
Maximum	6939.2	86.85	15.24	48.47	95.42	12.67	60.47	4.01	4.63	71.56	58.59	11.00
Mean	4412.6	65.39	6.53	13.86	59.45	3.84	15.51	0.65	0.12	28.59	24.94	2.42
SD	1723.1	15.14	3.76	14.31	20.87	2.35	15.17	0.62	0.65	18.94	15.57	2.77
Non-food												
N	14	15	15	11	10	14	11	13	13	5	5	13
Minimum	2920.0	29.20	1.84	0.29	44.92	1.42	1.80	0.07	0.002	13.91	11.72	0.10
Maximum	6168.4	88.25	10.90	23.85	80.77	13.33	36.54	0.75	0.100	55.33	54.24	7.17
Mean	4204.8	75.32	6.08	5.27	69.21	5.55	15.84	0.42	0.025	31.84	27.35	1.52
SD	701.8	14.54	2.39	7.39	14.27	3.23	12.13	0.19	0.029	15.26	16.84	1.84

Important plant species, with respect to nutritional values, which contributed to monthly consumption by four hornbill species during the breeding season of 2004 and 2005 are shown in Appendix Fa and Fb. Important species changed between these two years and differed among the four hornbill species. *Polyalthia viridis* was most consumed and yielded high nutrients for all hornbill species. In 2005, in particular, *C. subavenium* was an important source for protein, fat or both, and also calories and tannin (Appendix Fb). For Great Hornbill, figs were the most important fruits that provided high nutritional values of protein, fat, calcium, ADF, calories, and tannin from January to May. For Great Hornbill, *Livistona speciosa* and *P. viridis* were the most important species in January, during the incubation phase. High nutrient contents for protein, fat, calcium ADF and tannin were obtained from figs, while the highest calories were from *L. speciosa.* For White-throated Brown Hornbill, *T. wallichiana* and *Polyalthia viridis* were consumed most and provided high nutritional values of protein, fat, calcium, ADF, calories and tannin. Oriental Pied Hornbill consumed high proportion of *P.viridis*, *Prunus javanicus* and fig species, but figs contributed high nutritional values April and May.

In the 2004 breeding season, among four dominant nutritional obtained from fruits, i. e. moisture, fat, protein and calcium, the monthly patterns of consumption for Wreathed Hornbill was highest and fluctuated most, but was similar to that of Great Hornbills in that all components increased towards the end of the breeding season. White-throated Brown and Oriental Pied Hornbills had similar pattern, but differed from the former two species for fat and calcium that decreased at the end of the breeding season (Figure 16).

In the 2005 breeding season, among all four hornbill speciesWreathed Hornbill consumed all nutritional components at the highest rates, while, intraspecifically, Wreathed Hornbill consumed higher rates in the 2005 breeding season than in 2004. The patterns of consumption for these nutritional components of Wreathed Hornbill increased gradually initially but then sharply increased toward the end of the breeding season. The patterns, however, clearly differed from those in 2004, and also differed from the rest of the hornbill species, whose consumption patterns were similar in certain components, with Great and White-throated Brown Hornbills showing similar patterns for all nutrients (Figure 16).

In the 2005 breeding season, among all four hornbill speciesWreathed Hornbill consumed all chemical components at the highest rates, while, intraspecifically, Wreathed Hornbill consumed higher rates in the 2005 breeding season than in 2004. The patterns of consumption for these nutritional components of Wreathed Hornbill increased gradually initially but then sharply increased toward the end of the breeding season. The patterns, however, clearly differed from those in 2004, and also differed from the rest of the hornbill species, whose consumption patterns were similar in certain components, with Great and White-throated brown Hornbills showing similar patterns for all nutrients (Figure 16).

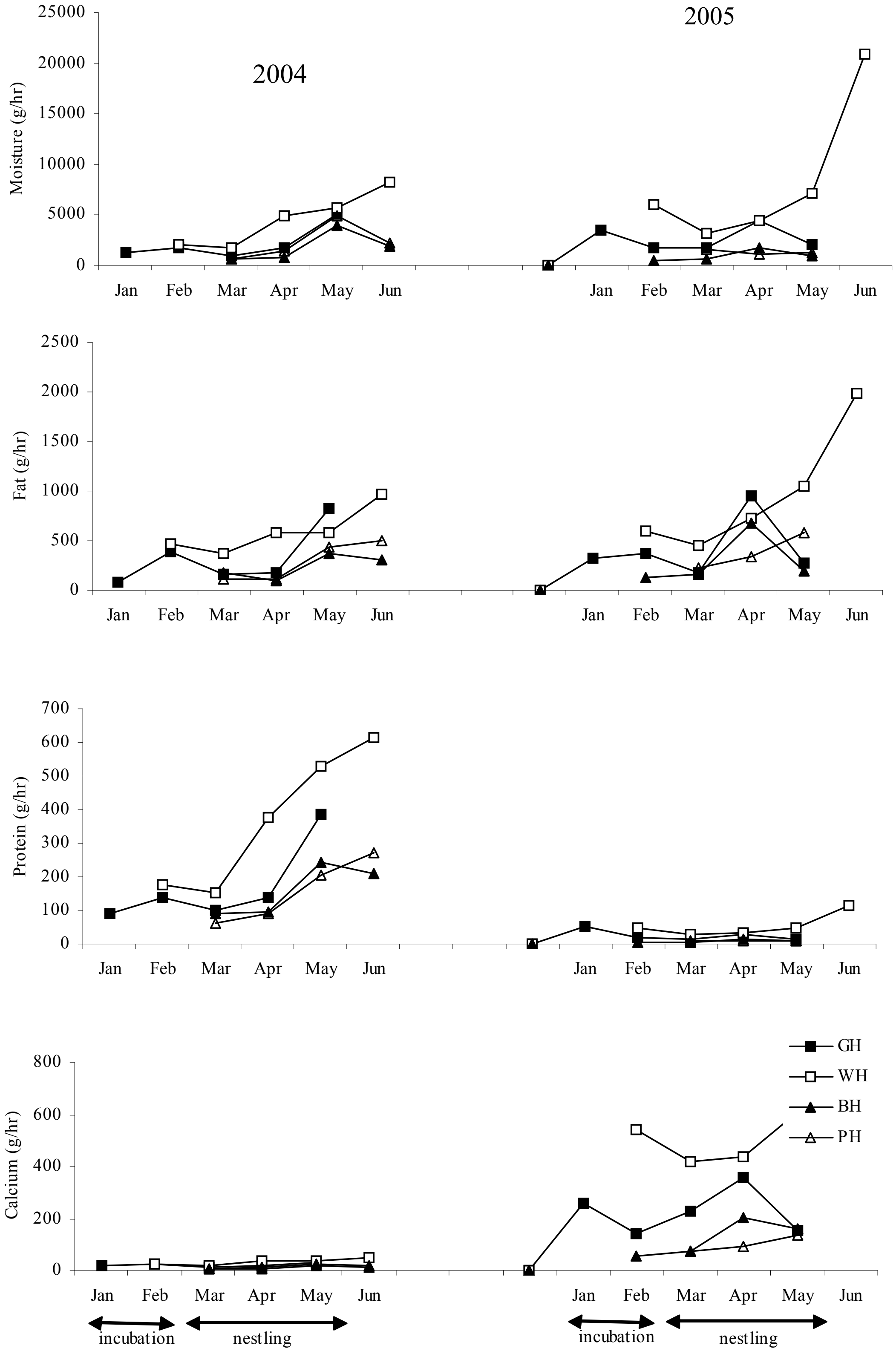


Figure 16 Rate of moisture, fat, protein and calcium consumption by four hornbill species during the breeding season of 2004-2005.

There were significant differences between consumtion of nutritional components by Wreathed and White-throated Brown Hornbills, such as protein (Mann-Whitney Rank Sum Test; U = 342.00, n (small) = 30, n (big) = 31, *p* = 0.012), fat (U = 293.10, n (small) = 36, n (big) = 39, *p* = 0.034), calcium (U = 366.00, n (small) = 36, n (big) = 39, *p* = 0.006), calorie (U = 329.80, n (small) = 37, n (big) = 39, *p* = 0.016), and between Wreathed Hornbill and Oriental Pied Hornbill, such as protein (U = 335.40, n (small) = 35, n (big) = 44, *p* = 0.014), fat (U = 254.8, n (small) = 26, n (big) = 33, *p* = 0.070), calcium (U = 308.70, n (small) = 34, n (big) = 42, *p* = 0.025), calories (U = 321.90, n (small) = 42, n (big) = 43, *p* = 0.019).(Figure 17).

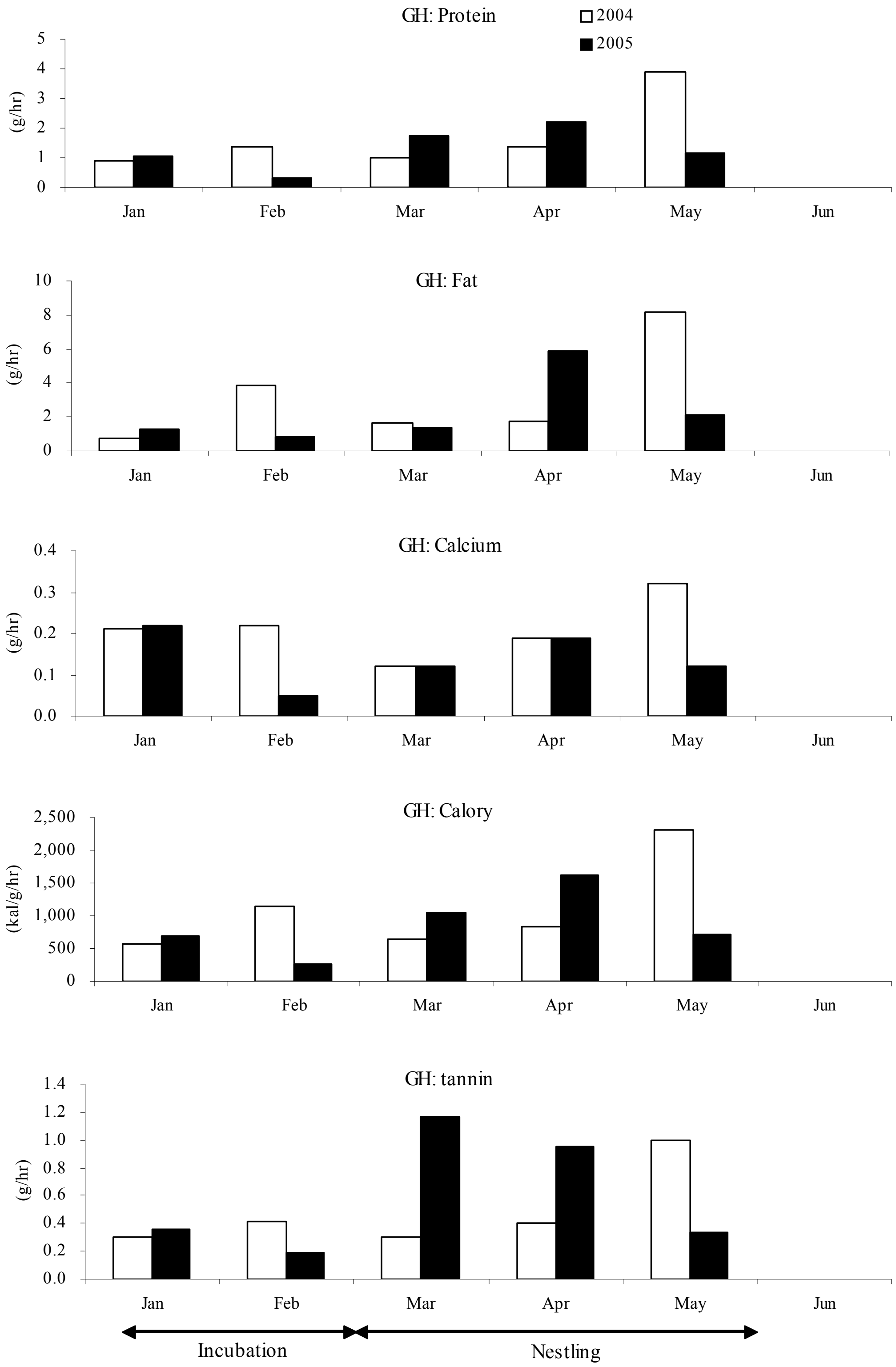


Figure 17 Comparison between nutrient consumption by four hournbill species during breeding seasons of 2004 and 2005.

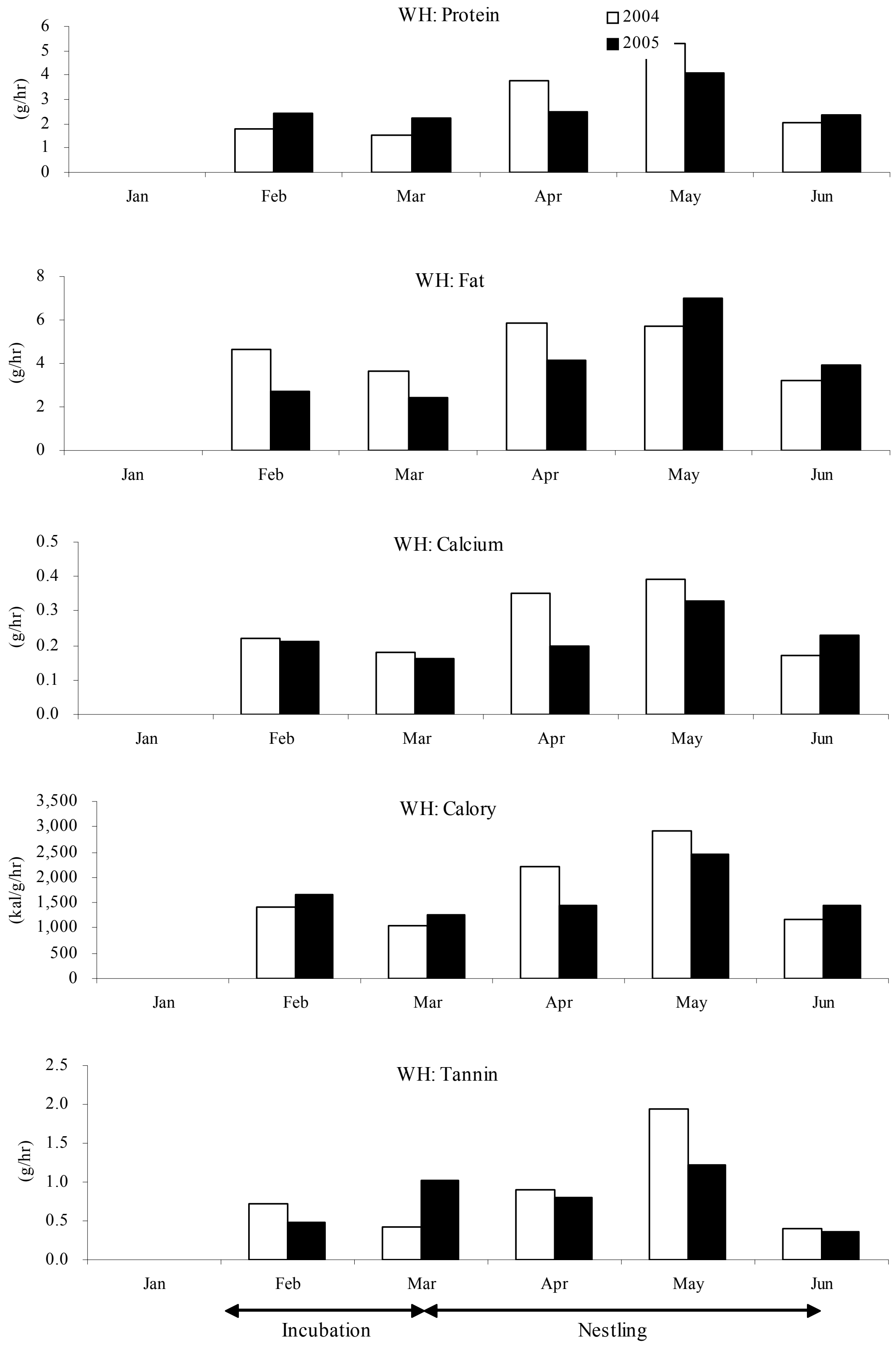


Figure 17 Comparison between nutrient consumption by four hournbill species during breeding seasons of 2004 and 2005 (Continued).

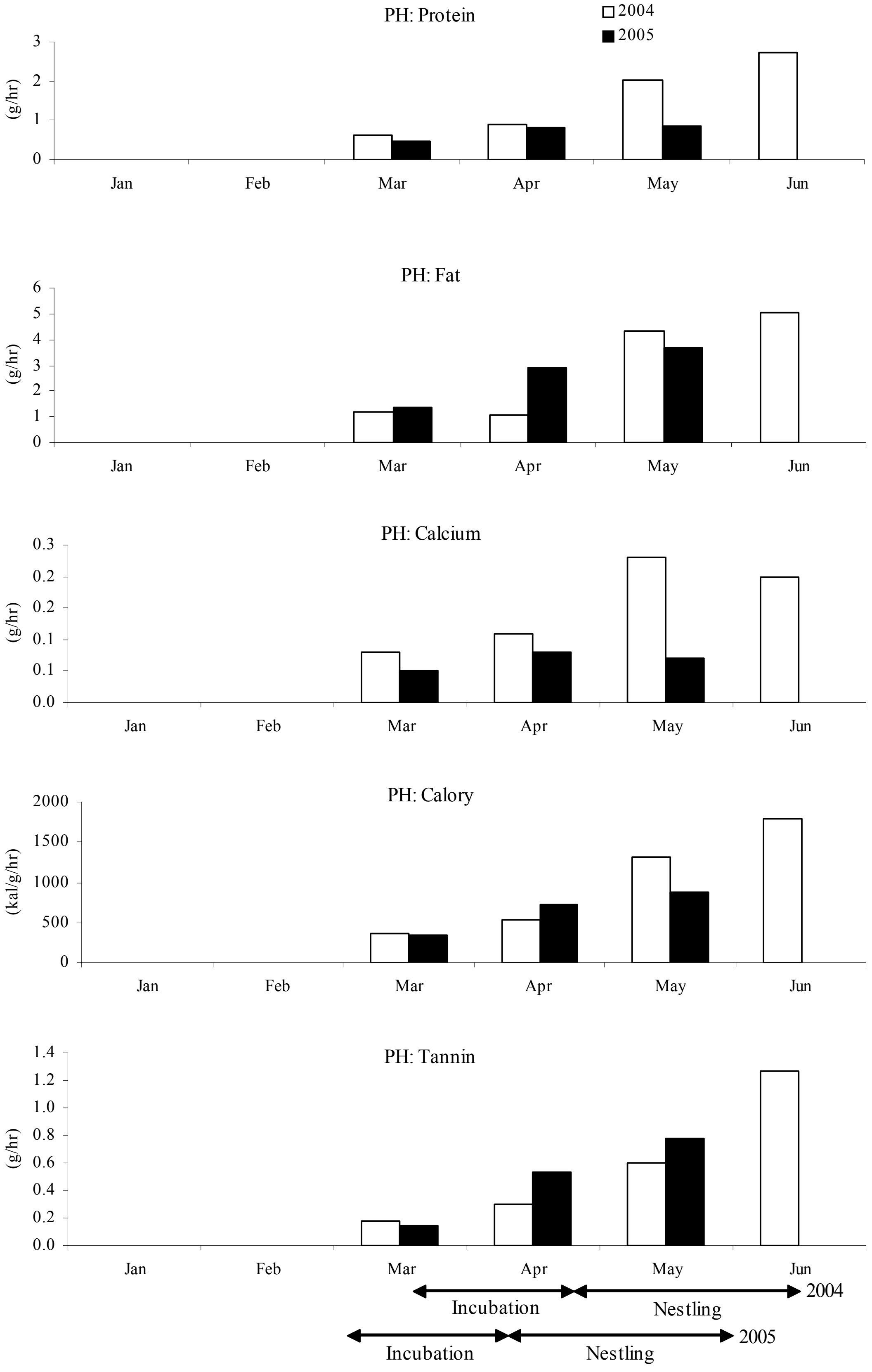


Figure 17 Comparison between nutrient consumption by four hournbill species during breeding seasons of 2004 and 2005 (Continued).

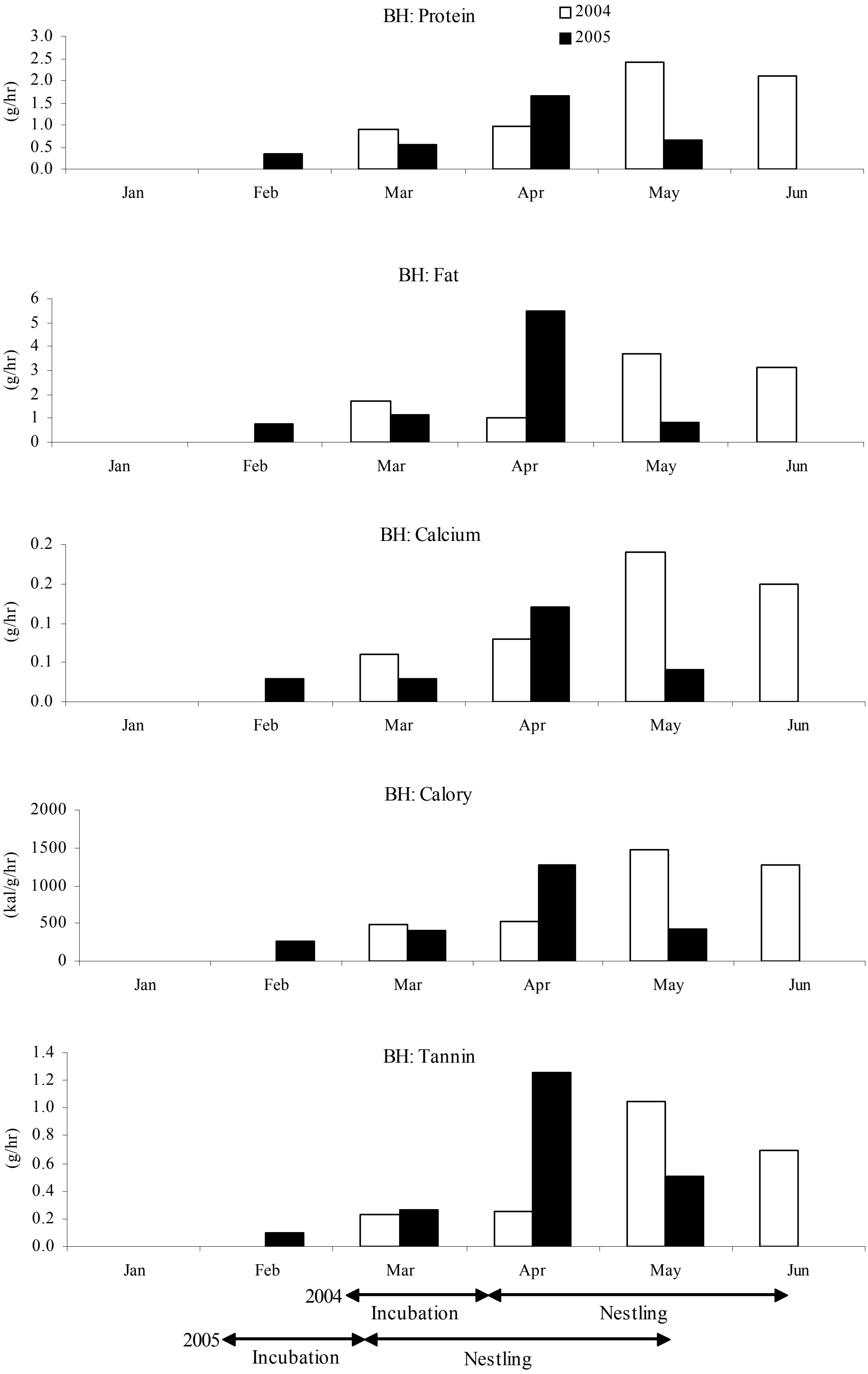


Figure 17 Comparison between nutrient consumption by four hournbill species during breeding seasons of 2004 and 2005 (Continued).

When considering fruit species that contributed important nutritional components during the 2004 breeding season for Great Hornbill, these were *A. lawii* and *A. spectabilis* for fat and calcium, *L. speciosa* for fat and *P. viridis* for protein (Appendix Fa). For Wreathed Hornbill, similar to Great Hornbill, *A. spectabilis* was important for protein, fat and calcium, *L. speciosa* for fat and *P. viridis* for protein, fat, calcium and ADF (Appendix Fa). For White-throated Brown Hornbill, *A. lawii* was important for fat, *D. cyrtobotryum* and *D. densiflorum* for protein and fat, and *P. viridis* for protein, fat calcium and ADF (Appendix Fa). For Oriental Pied Hornbill, similar to White-throated Brown Hornbill, *A. lawii* was important for protein and fat, *D. cyrtobotryum* and *D. densiflorum* for protein, fat and calcium, *P. viridis* for protein and fat, and *Syzygium* sp. for fat and calcium (Appendix Fa).

In the 2005 breeding season, the important species for Great Hornbill changed slightly and were *A. spectabilis* for protein, fat and calcium, *C. subavenium* for protein and particularly for fat, *H. glabra* for fat and *P. viridis* for protein and fat (Figure ?Fb). For Wreathed Hornbill, the important species were *A. spectabilis* for protein, fat, calcium and ADF, *A. polystachya* for protein and calcium, *C. subavenium* for fat and ADF, *D. densiflorum* for protein and calcium, *P. jucunda* for protein and calcium, and *P. viridis* for protein fat and calcium (Appendix Fb). For White-throated Brown Hornbill, the important species were *B. robusta* for protein and calcium, *C. subavenium* for protein, fat, calcium and ADF, *D. densiflorum* for protein and calcium, and *H. glabra* for fat and calcium (Appendix Fb). For Oriental Pied Hornbill, the important species were *C. subavenium* for fat and ADF, *H. glabra* for protein, fat and calcium, and *P. viridis* for fat (Appendix Fb).

Multivariate analysis was not possible using Discriminant Analysis as there were many missing values. However, by using PCA, it was showed that moisture, calories, fat and calcium were important variables (Figure 18). Mann-Whitney U test showed that significant variables the between breeding and non-breeding season were moisture (Z = -2.768*, p* =0.018) and calcium (Z = -1.402*, p* = 0.017).

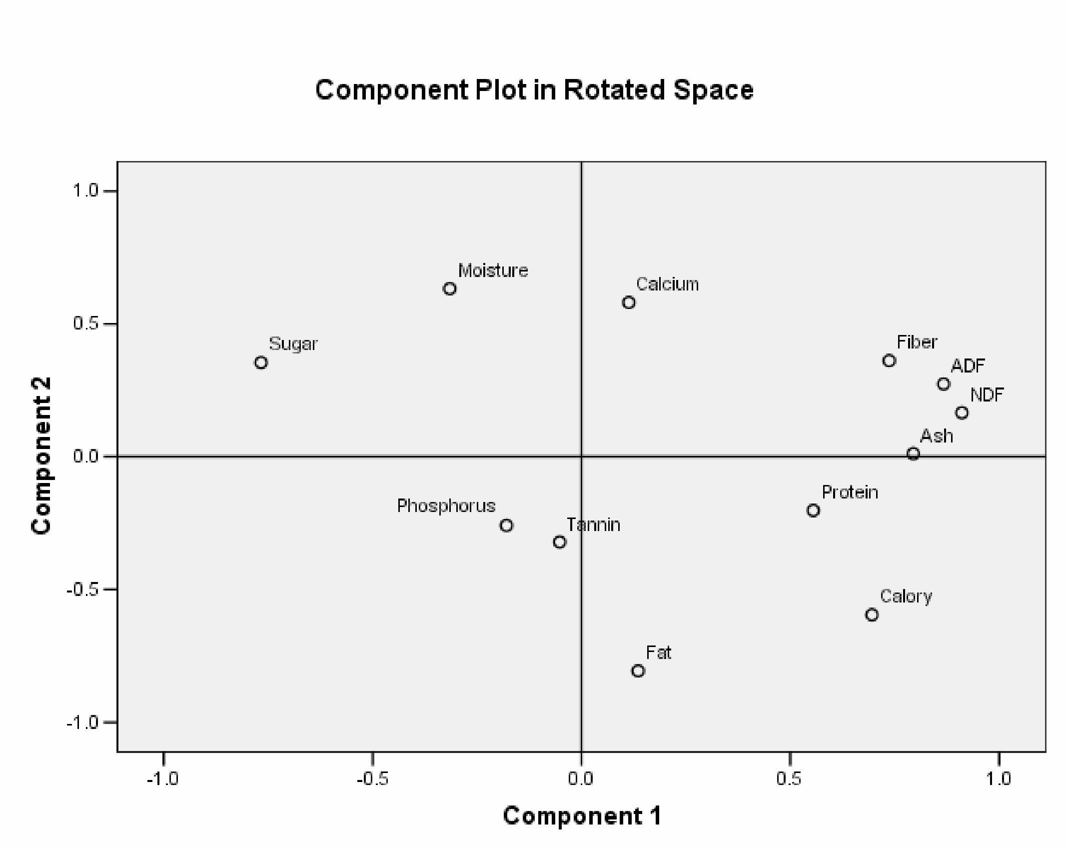


Figure 18 Nutritional variables of plant consumed by hornbill species as separated by PCA.

Most tannin was consumed at the beginning of the nestling phase in 2005. Fruits that contain tannin (*Dysoxylum densiflorum* and *Polyalthia viridis*) were clearly selected by Wreathed Hornbill in May, and for the other three hornbill species there were similar changes (Appendix F). The amount of tannin in the fruit was not significantly correlated with its color (Mann Whitney U test, N = 10, *p* = 0.189) (Figure 19).

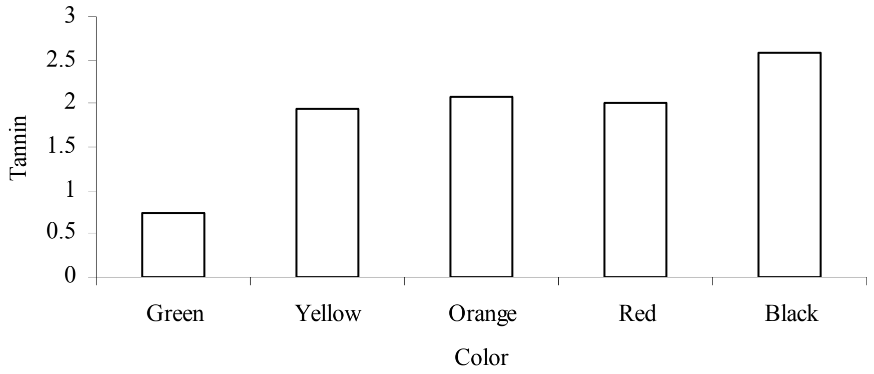


Figure 19 Tannin content in different fruit colors.

This chapter will attempt to link and explain what factors influence the bigger picture of food selection by hornbills. Logistic regression was used to test whether there were any variables that showed significant differences between food that was eaten and not eaten by hornbills.

The results showed that there was significant differences only for some morphological factors that could explain and fit the proposed model of selection, but that chemical and abundance variables were not be able to explain the model.

Fruit characteristics and abundance were combined for analyze with PC[A stands for analysis] and Discriminant Function Analyses. The result showed low values for communality (Table 12), which suggests that the analyses only slightly explain the variation in all variables.

Table 12 Communalitiy values from PCA, between values for morphology and abundance of fruit species

Variable	Initial	Extraction
Fruit Type Code	1	0.51
Fruit Sskin code	1	0.35
Life form Code	1	0.24
Detachment pulp Code	1	0.18
Dehiscent notdehiscent Code	1	0.03
Fruit weight	1	0.36
Color Code	1	0.00
UVdetection	1	0.36
Seed Weight	1	0.09
Number of seed per fruit	1	0.55
Height average	1	0.58
Basal area per ha	1	0.25

Logistic Regression explained the most about food selection, often with high accuracy and confidence limits (> 80%). Anaylsis of independent variables with logistic regression predicted certain probabilities of a fruit being eaten by a hornbill (Table 13), and these are discussed below. The detachment of pulp, color and number of seed per fruit showed significant differences between fruits that were eaten and not eaten.

Table 13 Tests of Equality for group means from Discriminant Function Analysis between values for morphology and abundance of fruit species

Variable	Wilks' Lambda	F	df1	df2	Sig.
Life form Code	0.99	0.71	1.00	70.00	0.40
Detachment pulp Code	0.82	15.65	1.00	70.00	0.00
Dehiscent notdehiscent Code	1.00	0.04	1.00	70.00	0.85
Fruit weight	0.98	1.13	1.00	70.00	0.29
Color Code	0.95	4.02	1.00	70.00	0.05
UVdetection	0.94	4.61	1.00	70.00	0.04
Seed weight	0.99	0.40	1.00	70.00	0.53
Number of seed per fruit	0.94	4.50	1.00	70.00	0.04
Basal area per ha	1.00	0.33	1.00	70.00	0.57

Selection on fruit characteristics

Statistical values that predict the probability of fruits being eaten by hornbills, for different combinations of the independent explanatory X-variables, can be analyzed from the logistic regression equations. The Hosmer and Lemeshow Goodness-of-Fit Test tests have the null hypothesis that there is no difference between the observed and model-predicted values of the dependent Y-variable. The non-significant results from both of these tests (i.e., $p > 0.05$) suggested that all four models fitted the data well (Table 14).

Table 14 Statistical significance of the logistic regression equations (see also text)

Model	Independent X-variables in the model	No.of Observations		Hosmer and Lemeshow Goodness-of-Fit		
		Eaten	Not Eaten	$\chi2$	*df*	*P*-value
1 (Global Model)	Fruit type, season, Fruit skin, Detachment of pulp, Dehiscence, Fruit weight, Fruit length, color, UV, Seed weight, Seed length	55	46	9.24	8	0.32
2	Fruit type, Detachment of pulp, color, UV	63	50	10.93	8	0.21
3	Fruit type, Detachment of pulp, Fruit weight, Fruit length, color	63	50	3.97	8	0.86
4	Fruit type, Season, Fruit skin, Detachment of pulp, Dehiscence, Fruit weight, Fruit length, color, UV, Seed weight, Seed length	63	50	7.11	8	0.52

The area under the receiver-operating-characteristic (ROC) curve of these models, *c*, is a measure of the predictive accuracy of the logistic regression equation (e.g., *c* = 1.00 is a model that can predict the value of Y at 100 %). The percent of correct classifications reveals how well the models classified the fruit species as either "Eaten" or "Not Eaten".

Statistics for model selection, that compared models from Table 15, predicted the probability that fruit species would be eaten by hornbills. Model 1-4 showed a high percent for correct classification (> 80%) for comparisons between eaten and non-eaten fruit species. The Akaike's Information Criterion (AIC) reflected the balance between the predictive power of a model and the number of variables used in that model (Table 16). Model 3 had the lowest AIC value and is the model that best fits the data using a minimum number of X-variables (i.e., offers an effective balance of accuracy and parsimony).

Table 15 The area under the receiver-operating-characteristic (ROC) curve as a test of the predictive value of different models.

Model	Area under ROC Curve (*c*)	Correct Classification (%)	
		Eaten	Not Eaten
1	0.91	83.6	82.6
2	0.89	85.7	80
3	0.89	85.7	82
4	0.89	85.7	82

Table 16 The Akaike's Information Criterion (AIC) of each model

Model (i)	AIC$_i$	Δ_i	Akaike Weight (w_i)	Evidence Ratio (wmax/wi)
1	114.9	4.9	0.05	0.64/0.05 = 12.8
2	111.6	1.5	0.29	0.64/0.29 = 2.2
3	110	lowest	0.64	0.64/0.64 = 1/1
4	117.3	7.2	0.02	0.64/0.02 = 32

The estimated values for each X-variable represent the coefficient (i.e., β_i values) for that X-variable in the logistic regression equations showed in Table 17. The odds ratio for interval data (i.e., fruit weight and fruit length) indicated that for every unit change in the X-variable measurement, the probability of a fruit being "eaten" will change by the amount of the odds ratio. The Odds Ratio Estimates for the logistic regression (Table 18) indicated the influence that an X-variable had on the outcome of the logistic regression relative for the reference category, and by comparing all the fruit characteristics listed in Table 18 one can determine the probability of a fruit being eaten:

For fruit type, the order is;

Syconium (highest probability) > berry > drupe > capsule > other (lowest probability)

For detachment of pulp, the order is

Detachment > *not detachment*

For color, the order is

Orange > *red* > *black* > *yellow* > *green*

Fruit weight and fruit length have only a minor influence on the probability of a fruit being eaten because the Odds Ratio Estimates are very close to 1.0 (i. e., 0.968 g for weight and 1.065 mm for length). This actually means that the probability of heavier fruits being eaten will go down slightly because multiplying the probability by an odds ratio that is less than 1 will lower that probability (Table 18).

The logistic regression equation that best describes the probability that a fruit will be eaten or not eaten by hornbills in Thailand is the following:

$$P = \frac{\exp\left(-2.546+0.525X_1+(-0.665)X_2+(-31.855)X_3+13.100X_4+1.764X_5+(-0.032)X_6+0.063X_7+0.883X_8+(-13.050)X_9+2.068X_{10}+0.929X_{11}\right)}{1+\exp\left(-2.546+0.525X_1+(-0.665)X_2+(-31.855)X_3+13.100X_4+1.764X_5+(-0.032)X_6+0.063X_7+0.883X_8+(-13.050)X_9+2.068X_{10}+0.929X_{11}\right)}$$

where

P is the probability that a fruit will be eaten (i.e., Y= "Eaten") given the data for X_1 to X_{11} as described below,

exp is the exponential function and is written as exp(x) or $e^{(x)}$ (where "*e*" is the base of the natural logarithm and is approximately equal to 2.7183),

X_1 = 1 if fruit form = "berry" and X_1 = 0 for all other fruit forms including "drupe",

X_2 = 1 if fruit form = "capsule" and X_2 = 0 for all other fruit forms including "drupe",

X_3 = 1 if fruit form = "other" and X_3 = 0 for all other fruit forms including "drupe",

X_4 = 1 if fruit form = "syconium" and X_4 = 0 for all other fruit forms including "drupe",

X_5 = 1 if pulp detached = "detached" and X_5 = 0 for "not detached",

X_6 = the actual fruit weight in g,

X_7 = the actual fruit length in cm,

X_8 = 1 if fruit color = "black" and X_8 = 0 for all other fruit colors including "yellow",

X_9 = 1 if fruit color = "green" and X_9 = 0 for all other fruit colors including "yellow",

X_{10} = 1 if fruit color = “orange” and X_{10} = 0 for all other fruit colors including “yellow”,

X_{11} = 1 if fruit color = “red” and X_{11} = 0 for all other fruit colors including “yellow

Example Calculation of Logistic Regression Model

For example, the logistic regression predicts that a black berry that has a detached pulp, weighs 0.4 g and is 7.1 cm long will have a probability = 0.743 of being eaten, as calculated below.

Generic Model 3 calculated by the logistic regression analysis:

$$P=\frac{\exp\left(-2.546+0.525X_1+(-0.665)X_2+(-31.855)X_3+13.100X_4+1.764X_5+(-0.032)X_6+0.063X_7+0.883X_8+(-13.050)X_9+2.068X_{10}+0.929X_{11}\right)}{1+\exp\left(-2.546+0.525X_1+(-0.665)X_2+(-31.855)X_3+13.100X_4+1.764X_5+(-0.032)X_6+0.063X_7+0.883X_8+(-13.050)X_9+2.068X_{10}+0.929X_{11}\right)}$$

Model 3 with example for a black berry with a detached pulp that is 0.4 g and 7.1 cm:

X-variable		X_i	Example field data for X_i in Model 3	β_i values from Table 5
Intercept		-		-2.546
Fruit type	Berry	X_1	1	0.525
Fruit type	Capsule	X_2	0	-0.665
Fruit type	Other	X_3	0	-31.855
Fruit type	Syconium	X_4	0	13.100
Detachment of pulp	Detach	X_5	1	1.764
Fruit weight		X_6	0.4 g	-0.032
Fruit length		X_7	7.1 cm	0.063
Color	Black	X_8	1	0.883
Color	Green	X_9	0	-13.050
Color	Orange	X_{10}	0	2.068
Color	Red	X_{11}	0	0.929

$$P = \frac{\exp(-2.546+0.525(1)+(-0.665)(0)+(-31.855)(0)+13.100(0)+1.764(1)+(-0.032)(0.4)+0.063(7.1)+0.883(1)+(-13.050)(0)+2.068(0)+0.929(0))}{1+\exp(-2.546+0.525(1)+(-0.665)(0)+(-31.855)(0)+13.100(0)+1.764(1)+(-0.032)(0.4)+0.063(7.1)+0.883(1)+(-13.050)(0)+2.068(0)+0.929(0))}$$

$$P = \frac{\exp(-2.546+0.525+1.764-0.0128+0.4473+0.883)}{1+\exp(-2.546+0.525+1.764-0.0128+0.4473+0.883)}$$

$$P = \frac{\exp(1.0605)}{1+\exp(1.0605)}$$

$$P = \frac{2.887815}{1+(2.887815)}$$

$$P = \frac{2.887815}{3.887815}$$

$$P = 0.743$$

There is a 74.3% probability that a black berry with a detached pulp that weighs 0.4 g and is 7.1 cm long will be eaten by hornbillsat Khao Yai.

Table 17 The estimated values for each X-variable that represent the coefficient (i.e., β_i values) for that X-variable in the logistic regression equation

X-variable		*df*	Estimate	*Wald* χ^2	*Pr* > χ^2
Intercept		1	-2.546	5.09	0.02
Fruit type	berry	1	0.525	0.57	0.45
Fruit type	capsule	1	-0.665	0.85	0.36
Fruit type	other	1	-31.855	0.02	0.89
Fruit type	syconium	1	13.1	0	0.97
Pulp	detach	1	1.764	9.59	<0.01
Fruit weight		1	-0.032	2.33	0.13
Fruit length		1	0.063	4.55	0.03
Color	black	1	0.883	1.18	0.28
Color	green	1	-13.05	0	0.97
Color	orange	1	2.068	4.74	0.03
Color	red	1	0.929	1.06	0.3

Table 18 Confidence limits for each variable

Effect	Odds Ratio Estimate	95% Wald Confidence Limits	
Fruit type (berry *vs*. drupe)	1.69	0.43	6.62
Fruit type (capsule *vs*. drupe)	0.514	0.13	2.12
Fruit type (other *vs*. drupe)	<0.001	<0.01	>999.99
Fruit type (syconium *vs*. drupe)	>999.99	<0.01	>999.99
Pulp (detachable *vs*. non-detachable)	5.834	1.91	17.81
Fruit weight	0.968	0.93	1.01
Fruit length	1.065	1.01	1.13
Color (black *vs*. yellow)	2.418	0.49	11.87
Color (green *vs*. yellow)	<0.001	<0.01	>999.99
Color (orange *vs*. yellow)	7.912	1.23	50.95
Color (red *vs*. yellow)	2.532	0.43	14.89

Selection on nutritional composition

Once the Logistic Regression had showed that four characteristics of the fruit, fruit type, color, detachment of pulp and color had a significant probability of being eaten by hornbills, the links between these fruit characteristics were analyzed.

After determining that none of the nutritional variables were correlated [how, where], all nutritional variables were tested separately and three nutritional values had statistically significant ANOVA results: calcium, fat, and moisture. In general, fruits that were eaten by hornbills were higher in calcium, higher in fat, and lower in moisture than fruits that hornbills did not eat (Table 12). The levels for all other nutritional variables were not statistically different between fruits that were eaten and fruits that were not eaten.

Within the three statistically significant nutrition variables, individual Tukey Tests (i.e., means comparison tests) were calculated to determine which levels were grouped within each statistically significant source of variation. For example, Table 20 revealed that there was a significant difference among calcium content. Results from the Tukey Test (Table 21) revealed that there were statistically significant differences in the means due to the sources of variation in fruit form, pulp, and colour. Tables 22, 23, 24, 25 and 26 showed which levels of the sources of variation are grouped together (e.g., Table 22 revealed that syconium fruit are in one group that explained the variation in the mean level of calcium, and that all other fruit forms are in another group that explained the variation in levels of calcium.

The results below explain in detail the links between the three significant nutritional values and fruit characteristics.

Calcium

The main ANOVA for the mean levels of calcium was significantly different in all fruits found in the eaten and not eaten categories (ANOVA, df = 8 $p < 0.0001$; Table 20). Hornbills chose fruits with statistically higher levels of calcium in syconium fruit (*Ficus* spp), that were orange (*Elaeagnus latifolia*) and that had detachable pulp (*Polyalthia viridis*). The Tukey Test also determined that calcium was significantly different in different fruit types and colors (Table 21). Significantly different comparisons of calcium levels were found between syconium and capsule, drupe and berry fruit types, (Table 22) and syconium fruits were in a different group

(Table 22). Calcium was also significantly different between fruits with detachable and non-detachable pulp (Table 23). A Tukey Test to compare calcium content between different fruit colors, orange-yellow, orange-black, and orange-red, were significant differences (Table 24) and that orange was separated from the other colors (Table 25).

Table 19 Main ANOVA for the mean levels of calcium in all categories of eaten and non-eaten fruit

Source	DF	Sum of Squares	Mean Square	F Value	Pr > F
Model	8	5.543	0.693	16.76	<0.0001*
Error	46	1.901	0.041		
Corrected Total	54	7.445			

Table 20 Overall results of the Tukey Tests to determine the importance of fruit characteristics

Source	DF	Anova SS	Mean Square	F Value	P > F
Eaten and Non-eaten	1	0.117	0.117	2.83	0.09
Fruit type	3	3.656	1.219	29.48	<0.0001*
Pulp	1	0.295	0.295	7.13	0.01*
Color	3	1.476	0.492	11.9	<0.0001*

Table 21 Tukey Test to determine the difference of means of calcium content of various fruit types

Comparisons significant at the 0.05 level indicated by ***.

Fruit type comparison	Difference between Means	Simultaneous 95% Confidence Limits		
Syconium - Capsule	0.726	0.424	1.027	***
Syconium - Drupe	0.759	0.524	0.994	***
Syconium - Berry	0.797	0.559	1.035	***
Capsule - Syconium	-0.726	-1.027	-0.424	***
Capsule - Drupe	0.033	-0.217	0.282	
Capsule - Berry	0.071	-0.181	0.323	
Drupe - Syconium	-0.759	-0.994	-0.524	***
Drupe - Capsule	-0.033	-0.282	0.217	
Drup - Berry	0.038	-0.129	0.205	
Berry- Syconium	-0.797	-1.035	-0.559	***
Berry- Capsule	-0.071	-0.323	0.181	
Berry - Drupe	-0.038	-0.205	0.129	

Table 22 Tukey Test to group the statistical difference in means of calcium content by fruit type

Tukey Grouping	Fruit type
A	Syconium
B	Capsule Drupe Berry

Table 23 Tukey Test to group fruit pulp in relation to means of calcium content

Tukey Grouping	Mean	N	Pulp
A	0.599	39	Detach
B	0.438	16	Not-detach

Table 24 Tukey Test to determine the statistical difference in means of calcium content of various fruit colors

Comparisons significant at the 0.05 level indicated by ***.

Color Comparison	Difference between Means	Simultaneous 95% Confidence Limits		
Orange - Yellow	0.276	0.002	0.55	***
Orange - Black	0.356	0.184	0.528	***
Orange - Red	0.358	0.145	0.572	***
Yellow - Orange	-0.276	-0.55	-0.002	***
Yellow - Black	0.079	-0.189	0.348	
Yellow - Red	0.082	-0.215	0.379	
Black - Orange	-0.356	-0.528	-0.184	***
Black - Yellow	-0.079	-0.348	0.189	
Black - Red	0.003	-0.204	0.209	
Red - Orange	-0.358	-0.572	-0.145	***
Red - Yellow	-0.082	-0.379	0.215	
Red - Black	-0.003	-0.209	0.204	

Table 25 Turkey Test to group the statistical difference in means of calcium content by fruit color

Tukey Grouping	Color
A	Orange
B	Black, Red, Yellow

Fat

An ANOVA for the mean levels of fat was significantly higher for eaten than non-eaten fruit (ANOVA, DF = 8 p = 0.04; Table 26), and also that fat content was significantly different in all fruit types (Table 27). The ANOVA results for fat content indicated that the relative order for fat content of different fruit forms was capsule > drupe > berry > syconium. This order is the reverse of the order of fruit forms from the logistic regression that described the probability of a fruit being eaten by hornbills: syconium > berry >capsule > drupe.

Although the logistic regression results indicated that fruit types that have a higher probability of being eaten by hornbills (i.e., syconium > berry >drupe > capsule > drupe) (Table 8) generally have lower content of fat (Appendix I), the ANOVA results indicated that hornbills chose fruits with the highest fat content for a paticular fruit form because the overall mean fat content of individual fruits within a category was higher in fruits that were eaten (13.5 g) than that were not eaten (5.7 g). For example, syconium fruits had the highest probability of being eaten by hornbills, although syconium fruits have the lowest mean fat content. It is likely that hornbills ate more yielded syconium fruits, which yield high fat content (Appendix I). Comparison of different fruit types shoewed the same trend in the mean fat content among fruit types, but not significant (Table 28)

Moisture

ANOVA results for moisture content indicated that there was a significantly difference between eaten and non-eaten fruits (ANOVA, df = 8*, p* = 0.04), and that moisture content was lower in fruits that were eaten compared to fruit that were not eaten by hornbills (Table 29). Overall, Turkey Test showed that moisture content differed between eaten and non-eaten fruits and among fruit types (Table 30).

Table 26 Main ANOVA for the mean levels of fat in all fruit categories

Source	DF	Sum of Squares	Mean Square	F Value	Pr > F
Model	8	2812.9	351.6	2.36	0.04*
Error	37	5521.5	149.2		
Corrected Total	45	8334.4			

Table 27 Tukey Test to determine the statistical difference in means of fat content by various fruit characteristics

Source	DF	Anova SS	Mean Square	F Value	P > F
Eaten and Non-eaten	1	485.3	485.3	3.25	0.08
Fruit type	3	1565.7	521.9	3.5	0.02*
Pulp	1	269.6	269.6	1.81	0.19
Color	3	492.2	164.1	1.1	0.36

Table 28 Tukey Test to determine the statistical difference in means of fat content by fruit type

Comparisons significant at the 0.05 level indicated by ***.

Fruit type comparison	Difference between Means	Simultaneous 95% Confidence Limits	
Capsule - Drupe	7.325	-13.018	27.669
Capsule - Berry	17.035	-3.542	37.611
Capsule - Syconium	18.66	-4.574	41.894
Drupe - Capsule	-7.325	-27.669	13.018
Drupe - Berry	9.709	-1.13	20.549
Drupe - Syconium	11.335	-3.96	26.629
Derry - Capsule	-17.035	-37.611	3.542
Berry - Drupe	-9.709	-20.549	1.13
Berry - Syconium	1.625	-13.978	17.228
Syconium - Capsule	-18.66	-41.894	4.574
Syconium - Drupe	-11.335	-26.629	3.96
Syconium - Berry	-1.625	-17.228	13.978

Table 29 Main ANOVA for the mean levels of moisture content of eaten and non-eaten fruits

Source	DF	Sum of Squares	Mean Square	F Value	Pr > F
Model	8	3746.38436	468.29805	2.22	0.04*
Error	48	10120.10246	210.83547		
Corrected Total	56	13866.48682			

Table 30 Tukey Test to determine the statistical difference in means of moisture content of various furit characteristics

Source	DF	Anova SS	Mean Square	F Value	P > F
Eaten and Non-eaten	1	987.9	987.9	4.69	0.04*
Fruit type	3	1758.6	586.2	2.78	0.05
Pulp	1	428.4	428.4	2.03	0.16
Color	3	571.5	190.5	0.9	0.45

Table 31 Tukey Test to group the statistical difference in means of moisture of eaten and non-eaten fruits

Tukey Grouping	Mean	N	Choice
A	75.2	12	Not Eaten
B	65	45	Eaten

CHAPTER V
DISCUSSION

1. Hornbill reproductive cycle and food

1.1 Breeding season

1.1.1 Nesting

I observed high nesting success, ranging from a minimum of 66.7% for Great Hornbill in 2005 and Pied Hornbill in 2004, to a maximum of 100% for White-throated Brown Hornbill for 2004, even though the sample sizes were small (Table 2). Such high success was similar to that observed for the Malabar Grey Hornbill (*Tockus griseus***)** in the South Western Ghats of India, where 88.9 % of the observed nests were reported to succeed in fledging chicks (Mudappa and Kannan, 1997).

Although based on a small sample size, the results showed no basic difference in nesting success linked to the size of the hornbill species. Both a large and a small species showed lower success, suggesting that adult for each species, not individual body size might not be a deterrent factor for potential predators (Sporadic personal observations) have also shown a strong negative impact from human disturbance, which forced the male to abandon the nest while the female was still incubating or brooding. In this regard, extra care must be taken when researchers approach or leave the observation hide.

Overall, the results on nesting success are higher than the ones recorded for other bird species at the study site. In their long-term work, Round et al. (2007) found the average nesting success for smaller under-story birds to be lower than 25%. The predominant reason for nest failure was to be found predation, generally considered the major cause of nest failure in tropical small birds (Stutchbury and Morton, 2001). The reason for the high nesting success by hornbills may be found in the peculiar nesting habit of the family which, by imprisoning the female in a cavity nest, reduces both detectability of the nest to predators, as well as access to it in the case of detection. However, attacks by large sized predators on hornbill nests have been reported sporadically in the area (Poonswad, 1993). The beginning of the nesting period appeared to be in the middle of the dry season for the Great Hornbill, the first species to start nesting, and extended to the end of the dry season for the Oriental pied Hornbill that started nesting in the period March - April. The beginning and peak of the nesting period for hornbills coincided with the beginning and peak for the majority of the bird community in the area, which appear to be January and April respectively (Round et al, 2007). For the small bird community, the factor that triggered nesting behavior was not clear but was hypothesized to be related to food abundance, both of fruits and insects. The abundance of these foods did not appear to be directly related to precipitation, although nesting synchronicity with precipitation was observed in more temperate areas where a more direct link with food availability was observed (Schluter, 1984).

1.2. Non-breeding season

1.2.1 Flock size

Flock size during the non-breeding season ranged between a maximum observed size of 590 individuals, in September 2004 for Wreathed Hornbills, to a minimum of 5 individuals, in September 2005 for Great Hornbills (Figure 3). The average for Great Hornbill was 41 [individuals], 179 for Wreathed Hornbill, 17 for White-throated Brown Hornbill and 109 for Oriental Pied Hornbill.

Those results differed from what had been observed at other sites for the same species. For Great Hornbill, Yang and Wen (1993) observed a flock of 20 individuals in Yunnan province, China, where resources might be scarcer, due to the higher latitude, and for which stronger seasonal variation might be observed. Other animal species, such as gibbons (*Hylobates concolor*), are found in much lower densities in Yunnan province (Jang et al, 1999) than in Khao Yai National Park (Savini et al, in press).

The population of Wreathed Hornbill at Khao Yai also appears to be larger than that reported in lowland rainforest at Bali Barat, Indonesia, where a flock of 40 individuals has been observed (Holmes et al, 1993). However, his note does not provide details on the overall observation and on how this number was obtained. I can assume it was the result of a sporadic observation and not a combination of repeated systematic observations as Indonesian rainforests are expected to provide plentiful resources, due to the high number of food species that characterize the Sundaican region (Woodruff, 2003).

For White-throated Brown Hornbill, no data were found on flocking at other sites. However, generic data are provided by Hussain (1993) for the closely related species Austen's Brown Hornbill (*Anorrhinus austeni*) where flock sizes of from 8 to 20 individuals were reported in India, although no details on the location were given. This result is similar to the one I recorded for the Khao Yai population.

Finally, Oriental Pied Hornbill also showed a much larger flock size than was observed by Yang and Wen (1993) in Yunnan province, China, with 30 individuals, and by Hussain (1993) in an unknown site in India, with 10 individuals. In both these cases, the more seasonal habitat and different observation methods may explain the lower numbers.

Our results do not show any correlation between flock size and the relative FAI for the forest. Two major explanations can be found for this result. For the breeding season, the lack of a significant correlation might be a consequence of the absence of a lean period during which there is a crunch period for the four hornbill species. This result contrasts partially with what Hussain (1993) observed in India, where there was an increase in flock size for Wreathed Hornbill during period of increased food abundance, and a similar pattern was observed for Indian Grey (*Ocyceros birostris*) and Malabar Grey Hornbills (*Ocyceros griseus*). As pointed our previously, no information was given by the author on the way data on food abundance were collected, the type of habitat where the populations were found and the method used to record flocks size.

Several works in the ecological literature have considered the determinants of animal group size in both mammals (Nudds, 1978; Chapman et al, 1995) and birds (Ekman and Hake, 1988; Saino, 1994). In particular, it is suggested that the amount of available resources plays an important role in determining when animals may or may not group, and on the size that groups can reach before food competition increases above bearable levels (Isbell, 1991).

Flock size in this study could be explained under three major hypotheses, as it is widely agreed that avian communal roosting behavior is unlikely to provide only one type of benefit (Crook 1965; Weatherhead 1983): a) the Information Center hypothesis, for which flock sizes at the roosting site will be higher when food abundance is low (Ward and Zahavi, 1973; Wright et al, 2003); b) individuals gather at one roosting site when resources are limited and the roosting site provides an important clumped food patch (Caccamise and Morrison, 1986); and c) the Anti-predation Hypothesis (Goldman, 1980; Cresswell, 1994) for which larger flock during their resting period, when vigilance is reduced, will limit the predation risk for single individuals.

My results reject one of the predictions for the Information Center hypothesis, as flock size at roosting did not increased when food abundance decreased. The same results also reject the second suggested hypothesis, although in this case I did not have precise data on the distribution and size of food sources around the roosting site as these sites were often not closely accessible. The absence of correlation between FAI and flock size could also be a direct consequence of the absence of a crunch period during the months of reduced fruit productivity. Other work, conducted on hornbills in Sulawesi, has shown that during the non-breeding season the diet appears to be less diverse than during the breeding season, and that flock size was correlated with the abundance of food resources (Suryadi et al, 1994).

Finally, the predation hypothesis could not be confirmed or rejected, as no predation events were observed and predators and predation events are extremely hard to detect in a wild environment.

A similar result on flocking at the roosting site was observed for parrot at Santa Rosa National Park, Costa Rica, where flock size at the roost site was not correlated with food abundance (Chapman et al, 1989). However, Chapman and coauthors (1989) found that daily flock size and party size were linked with resources whose availability may have been influenced by foraging efficiency. I am currently unable to answer questions related to daily flock size, as data on this subject are not yet available for my population.

In conclusion, at night, several factors may determine the number of individuals that attend a roost, but at dawn the roost may function to reduce potential feeding competition by dispersing foragers (Chapman et al, 1989). In this regard, hornbills during the non-breeding season might be considered as a fission and fusion society, with a large group that gathers at the end of the daily activity period and then splits into smaller groups or parties during the daily activity period (Dunbar, 1988). For chimpanzees (*Pan troglodytes*) party size has been proved to be the consequence of both food abundance and the number of receptive females within the large party that is observed when food is abundant and/or a high number of receptive females is present (Anderson et al, 2002; Mitani et al, 2002). In my study, no females were receptive during the flocking period, which is also the non-breeding season, I can predict that party size will be related mainly to food abundance.

Flock size was reported to be, only in part, related to weather conditions (Powell, 1979), where a parameter like rainfall has been considered, on a long term basis, as a good indicator for food productivity (Savini et al, in press). The results did not show any clear correlation between the two factors, with the exception of Wreathed Hornbill where a trend was recorded of larger flocks in periods of high rainfall.

1.3 Food overlap

The results on diet overlap between the four species of hornbill, as defined by using the Schoener's Overlap Index (SOI), showed a high overlap only between Wreathed and Pied Hornbills, which showed overall a more frugivorous diet, while for the other species the overlap was minimum (Table 6). This result was confirmed when I reanalyze the data using Canonical Correspondence Analyzes (CCA) (Figures 10 and 11). CCA is more precise than SOI, as the four species were analyzed together simultaneously and not by pairwise cross analyses.

This generally low food overlap for plant species might be the consequence of the high proportion of animals in the diet during the breeding season, especially for White-throated Brown Hornbill that appeared distinctively from the other three hornbill species in this respect (Figures 10). Their particular diet might also explain their complex social structure and cooperative breeding and their need of helpers during the breeding season.

During the non-breeding season, low food overlap might be the consequence of the exclusion of figs from the analysis, due to difficulties in species quantification. However, the overall difficulties in collecting reliable feeding data during this part of the year may also have resulted in an incomplete definition of the diet for which only limited overlap could be calculated.

The closely related diet between Wreathed and Pied Hornbill might induce competition between the two species, but in this case is kept low by a distinct use of the habitat. While Wreathed Hornbill use mainly the top of the canopy (Personal observation) and cover larger home ranges, Oriental Pied Hornbill tends to forage on the middle to low part of the forest canopy while covering a smaller area.

In conclusion, I suggest that the overall low dietary overlap observed between the four hornbill species and indicates that there is a limited food competition for fruits. Although simple dietary overlap has often been used as a proximate parameter indicating competition (Gorchov et al, 1995), in order to clearly quantify competition, more precise information should be collected on the spatial distribution and depletion of high quality resources.

2. Forest and food availability for hornbill in Khao Yai National Park

2.1 Forest definition

2.1.1 Framing Khao Yai forest

The forest type observed at the Mo Singto study site showed 508 individual trees with a DBH ≥ 10 cm per hectare (N), belonging to 77 species (S). This relatively low species diversity seems to be typical of the Indochinese part of Thailand, as it was also observed in Huai Kha Khaeng Wildlife Sanctuary, another hornbill study site, where the Fisher's α was equal to 21 (Losos & Leight, 2004). Other forest sites that showed a similar low value of species diversity were defined as relatively poor when compared to plots on other evergreen rainforest sites, where the species diversity Fisher's α is above 100 (Gunatilleke *et al.*, 2004).

2.1.2 Adequacy of the sample

Adequate sample size becomes fundamental in order to maximize the accuracy of results (Greig-Smith, 1983), however, the minimum sample size possible may depend on the type of forest (number of individual trees, number of species and species diversity) that is shown in the area one plans to monitor. As suggested by previous work, the minimum coverage necessary may be defined by plotting the cumulative density of species in relation to the percentage of area covered (Greig-Smith, 1983; Malenky *et al.*, 1993).

A previous study has reported that a plot of eight hectares, randomly selected in Khao Yai seasonally wet evergreen forest, will offer a representative sample for all major species, excluding only those species considered to be rare (Savini, 2005).

2.1.3 Food Abundance Index

As already observed in another study conducted in the area, the FAI showed two high and two lean periods over the course of a year (Savini et al, in press). Lean periods appeared to be between May to June and November to December (Figure 6), when the number of important fruiting species was the lowest.

The correlation between the FAI and weather conditions was not significant. The reason for this might be the detail and complexity of the environmental parameters that trigger flowering first and fruiting later in tropical plants, and in this case the weather conditions are only one part of the factors involved.

During the breeding season, the food productivity of species consumed by hornbills show a trend inverse to that observed for the diet of other animal species in the same area, where food abundance increased from January to a peak in April, followed by a rapid decline that ended in June (Savini et al, in press). In our study, food availability appeared to be similar for all four hornbill species, showing a peak in February followed by a slow decline until June where the lowest productivity was observed (Figure 6). The period showing the highest decline coincided with the last part of the breeding season, during which chicks require larger amount of high quality food for the last stage of their development. This decline in selectable plant species may explain in part the strong component of animal products in the diet of each hornbill species (Table 3) that increases relatively in the last part of their nesting periods.

However, a closer look at the variation in nutritional composition of the diet during the months of the nesting season showed a clear increase in the quantity of those plant components that appeared important in the latter stages of chick development, (Figure 17). Although plant productivity was declining in the late nesting period, hornbills appeared to increase their feeding capacity by increasing their selectivity on the few species that could be considered of higher quality from a nutritional point of view.

3. Diet

My results showed an overall decrease in fig consumption during the breeding season and an increase in non-fig consumption, although in detail, fig consumption was actually higher during the incubation phase while non-figs were predominant in the nestling phase in both years of 2004 and 2005 (Table 4). This decline of figs during the nestling period might be a consequence of their low content of protein and fat, which are important dietary components for chick development. When comparing the nutritional composition of the diet, I found that protein and fat were often delivered during the incubation phase, while proteins were not delivered, as a major component, during the nestling phase. This result was similar to what had already observed in the area by Poonswad et al (2004), even though they investigated nutritional components in less detail.

Various studies have shown an overall importance of figs in the diet of tropical frugivorous species, both mammals and birds (Wendeln et al, 2000), and including for hornbills at Khao Yai (Kitamura et al, 2005) and on Sulawezi (Kinnaird et al, 1996). The reasons for the high consumption of figs is to be found in their asynchronous intra-population fruiting patterns, but generally with synchrony of intra-canopy fruiting; their structurally unprotected fruits that are easily ingested and digested' their small seeds that provide little ballast' and their offer of relatively safe foraging, as they are heavily utilized by large numbers of species and individuals (Leighton & Leighton 1983, Kinnaird *et al.* 1996, Shanahan *et al.* 2001). Due to their bright coloration figs are also easily detected by foraging animals that have mixed capacities for chromatic distinction (Dominy et al, 2003). From a nutritional viewpoint, figs tend to provide high sugar and calcium (O' Brien et al., 1998) but are low on lipid and protein (Wendeln et al, 2000). It is the high calcium contents that might explain their high presence in the hornbill's diet in the early stage of incubation, when females need to generate shells for their eggs. Overall, I can explain the selection of figs by hornbills as being due to their large and unprotected crops, not showing any physical barriers to avoid or limit removing their fruits, allowing fast harvesting of calcium and calories, and including seeds with small volume.

The importance of figs in frugivorous diets, due to their peak fruit production during periods when fruiting by other plant species is scarce, has been proved extensively in the Neotropic (Frankie et al, 1974), Africa (Gautier-Hion and Michaloud, 1989; Bleher et al, 2003) and South-east Asia (Raemaeker et al, 1980; Kinnard et al, 1999). Due to their asynchronous fruiting, species of the genus *Ficus* were considered as a keystone plant resource, defined as any reliable food that plays a prominent role in sustaining frugivores through periods of general food scarcity (Terborgh, 1986). However, this prominent role must decline during periods of general food productivity, when other species are fruiting abundantly (Lambert and Marshal, 1991). The results provide evidence that figs in Khao Yai forest are eaten by the hornbill population during the entire breeding seasons and part of the non-breeding season as well (Tables 4). Besides, throughout the breeding season, figs appear to be the most important plant species in the diet in every month and for each hornbill species (Appendix Fa and Fb). These results allow us to exclude their keystone resources role for hornbills in our study site, as the assumption suggested by Lambert and Marshal (1991) is rejected.

Protein demand in bird species is highest during the nestling season due to the high demands of nestling growth during early development (Stile, 1980 and 1995; Poonswad et al, 2004). In our population, the highest rate of protein provisioning to nestling came from animal products, both vertebrate and invertebrate (Table 3). Of particular importance were insects, which appear to be good sources of protein, electrolytes and potassium, (Hiebert and Calder, 1983) but, were generally low in calcium (Des Lauriers, 1994).

When comparing the overall diet of the four study species, I can conclude that Great and Oriental Pied Hornbills are generalist feeders, as they consumed all kinds of food in the similar amounts, while White-throated Brown and Wreathed Hornbills are specialists on animals and non-fig fruits respectively.

The correlation between the FAI and the weight of pulp, expressed in gram that was carried to the nest by each on the four observed hornbill species was not significant. This result could be in part the consequence of a small sample size overall, although there are also several possible ecological explanations.

On a food selection basis, food abundance and availability are not to be considered the same. Items that appear abundant in the overall habitat may not be accessible for several reasons, such as distance from the nest and the resource (Boinski and Garber, 2000), accessibility to the resource (Boinski and Garber, 2000), predator presence around specific resources (Wilson, 1983; Downes, 2001) and/or high energy demand to harvest and process the items (Zach, 1979; Maire and Ervynck, 1986). As hornbills are reported to fly long distances and cover large home ranges (Poonswad and Tsuji, 1994), I can exclude distance as a barrier to access of any available resources. Accessibility to resources may also be excluded, as all four hornbill species have been observed foraging at every canopy level (personal observations), and fruiting crops in the study site do not provide evident barriers to block the access of foraging hornbills. As hornbills are particularly large animals, the number of predators in the study is that might treat them as prey is limited, so I can then exclude the limited access to resources by presence of potential predators in the area. Some of the observed fruit in the study area were not selected by hornbills but were selected by other frugivorous species with higher manipulation capacity, such as primates (*Hilobates lar* and *Macaca nemestrina*; Kanwatanakid and Brockelman, 2005; Savini, 2005). Overall, however, this type of limitation appeared to affect only a small number of fruiting species. Finally, the FAI does not include a variable that refers to the presence, absence or biomass consumed by competitors for food sources.

The lack of significance observed between correlations of the FAI and amount of fruit pulp carried to the nest can be explained with the absence of a crunch period for hornbill in the study habitat. In other words, the seasonal variations in FAI values do not reflect a limitation on the resident hornbill population that would limit the amount of food they carry to the nest. The absence of a crunch period for a species during most, if not all of the year, is expected to trigger selective behavior for better quality resources (McConkey, 2002). Unfortunately, no information is so far available on the effects of lean periods on the body fitness of hornbills. Such information will be difficult to collect if normally there are no lean periods during the year but, to test if lean periods do affect hornbill body condition, marked animals would have to be weighted at regular intervals, with the prediction that reduction in body weight would relate to a reduction of food availability. I cannot conclude without considering the important part represented in the hornbill's diet by animals, both vertebrate and invertebrate (Table 3). The increase of animal in the diet may be considered as an evolutionary pattern that developed as a response to an overall reduction in available resources.

Diversity of the diet, as expressed by the Shannon H' Index, showed a significant difference between 2004 and 2005, but not between hornbill species within the same year (Table 2). This result was explained by the different number of plant species that fruited each year. My data clearly showed that *Prunus javanica*, an important species in 2004, was not consumed in 2005 as it did not fruit, but was substituted for by *Cinnamomum subavenium*, which had itself not fruited in 2004.

An index of selectivity, following the one suggested by Jacobs and used in a similar study by Suryadi et al. (1994), showed t high selectivity on certain plant species that were then considered as important species.

However, such an index showed the major problem of being explained by "two variables". The results were actually the direct consequence not only of the level at which a given plant species was selected by hornbills, but also of the relative abundance at which the same species inhabited the forest (Jacobs, 1974). The meaning of the selectivity index drops, therefore, when food abundance is unequal and the spatial distribution of resources was not controlled for.

How to choose an optimal food item?

Food selection by the four hornbill species found in our study site was the major question of my work.

3.1 Morphological characteristics of fruits

My results on confidence limits for the effects of each morphological variable on the selection of eaten and non-eaten fruits (Table 18) showed high predictive values for fruit color (red and black were highly selected), fruit type (syconium was highly selected over berry, drupe and capsule), capacity of the pulp to detach easily from the seed, and fruit size, this last one appearing overall less valuable. These variables all showed a significant difference between selection of eaten and non-eaten fruit items within our hornbill population.

The strong selection for bright colors was supported by experiments on color selection conducted in a captive population. Once again, when all other factors were controlled for, hornbills tended to select more for black, orange and red fruits.

3.1.1. Color

Overall, the predominance of selection for red and black fruits over dull-colored ones (yellow and green) that I observed is similar to what was observed for other tropical frugivorous birds (Willson and Whelan, 1990) and mammals (Sourd and Gautier-Hion, 1986), as well as for vertebrates consuming fleshy fruits in temperate regions (Willson et al. 1989). In general, color, above other morphological and nutritional traits of fruits, reflects the major selection exerted by frugivorous (Voigt, et al., 2004), as a change in color is linked to a signal of nutritional quality that indicates the mature status of the fruits (Dominy and Lucus, 2004). Besides, for animals with trichromatic vision, for which red is highly visible (Bowmaker, 1998), bright colors facilitate the detection of fruit crops in forest, where they are especially conspicuous against a background of green leaves (Willson and Melampy, 1983; Willson and Whelan, 1990). In contrast, dull-colored fleshy fruits have been reported to possess a relatively low nutritive value and high concentration of fibers (Gautier-Hion et al, 1985). Moreover, Sourd and Gautier-Hion, (1986) found that brightly colored fruit, as consumed by Moustached Guenon (*Cercopithecus cephus*), possessed either a succulent pulp rich in water or arillated seeds high in protein and fatty acids.

In the wild, the most common colors for ripe fruits are dark purple and red (Janson 1983, Wheelwright and Janson 1985), colors that are coevolved by plants to increase their success in the dispersion of their seeds by birds (Janson, 1983;, Wheelwright and Janson, 1985; Willson el al, 1989; Voigt, et al, 2004), and fruit colors have been suggested to have evolved together with color vision of birds (Osorio and Vorobyev, 1996). This dispersal pressure on plants has been one of the predicted reasons for the evolution of red color, especially for pseudo fruits, and at least one pseudo fruit was observed in large amounts in the diet of the studied hornbill population. *Aglaia spectabilis* was consumed as an important species (Appendix F), and it was regurgitated when of large size. In this regard, hornbills may learn to associate food with particular colors more quickly than with other color, as for honey bees (Menzel et al., 1974). Social learning, sampling behavior, and hunger-driven consumption of alternative fruits should allow foraging birds to associate colors of initially non-preferred fruits with the fruit's rewards (Willson and Whelan, 1990).

Bright colors are the co-occurrence of different kinds of pigments, such as carotenoids, flavonoids and betalains (Goodwin and Mercer, 1983). Selecting brightly colored fruits, with their high carotenoid content, might also reflect in an increase of those substances that cannot be synthesized by vertebrates but need to be ingested with the diet.

Finally, when compared to other hornbill species, our results are similar to what was observed for Red-knobbed Hornbill in North Sulawesi, Indonesia, where it was observed to prefer large fruit with purple and red colors. Such selection was reported as an important indicator for the maturity level of the fruit items (Suryadi et al, 1994).

3.1.2. Ultraviolet vision in birds

Although UV deflection by fruits in this study was not found to be significantly different in eaten versus non-eaten fruits, there was a significant correlation with fruit color. I decided to discuss this parameter as it might offer further understanding of the visual mechanism in hornbills. Avian vision is one of the most richly endowed among vertebrates (Goldsmith, 1991), as birds can distinguish wavelengths within the UV range (between 320 nm to 400 nm) thanks to a complex system of four cone types (tetrachromatism), with oil droplets in addition to visual pigments, which filter the light entering their retina (Bowmaker, 1991; Bennett and Cuthill, 1994). In contrast to mammals, which are supposed to be UV blind, with an electromagnetic spectrum ranging between 400 nm and 700 nm (Bennett and Cuthill, 1994), the detection of UV light range might appear as an important factor in food choice by birds (Emmerton and Delius, 1980; Goldsmith et al, 1981). However, there is still no information in this regard for hornbill, other than that I can assume that they have tetrachromatic vision (Corlett RT, personal communication).

In this context, it has been proved that not only is detection by the color of the fruit itself important but also the detection of fruit by its color contrast against the foliage background (Burkhardt, 1982; Burns and Dalen, 2002). Burns and Dalen (2002) confirm that red is more visible when imposed over a green background than when alone and so, vision within the UV range may be an explanation for learning the pre-ripening signs of fruits by birds.

3.1.3 Fruit type

My results show a predominance of a syconium as the selected fruit type. As the syconium type of fruit is only represented by figs at the study site, this result might show a prevalenc for the choice of fig in general. Beside figs being consumed in large quanities, especially in the first part of the breeding season (Table 4, Appendix F), they are also quite diverse in the study site, with 20 species divided in structure between trees, hemi-epiphytes, shrubs, stranglers and climbers (Savini T, unpublished data). After the syconium the second most selected fruit type was a berry, which shares with the synconium small-sized seeds available in large amounts. Those two types were followed in selection by a drupe showing only one large seed. This selection by hornbills contrasts with what was observed for primates by Gautier-Hion and coauthors (1985), where drupes were selected over berries. The selection of fruit types showing small seed size might be a consequence of reticence by birds to ingest large seeds and so reduce gut volume for optimal flight efficiency.

3.1.4 Pulp detachment

For similar reasons, the selection by hornbills for fruit with flesh that is easily detached from the seeds may also be to maintain a low stomach content. Hornbills tend to select fruit such as *Polyaltia viridis*, where the seed can be easily regurgitated and the extraction of the pulp can be done without passage through the gut. This is not what happens for mammals at the study site where, for example, white-handed gibbon “*Hylobates lar*” consume large amounts of fruit, such as *Choerospondia axillaries* and

Nepheliu mellifera, where the pulp can only be extracted after passage through the gut (Kanwatanakid and Brockelman, 2005).

3.1.5. Fruit size.

Although my work suggests that the size of fruit appears to be a less important factor in fruit selection, it has been suggested as one of the selected factors for Red-knobbed Hornbill in North Sulawesi, Indonesia, where crops with larger fruits are harvested more efficiently (Suryadi et al, 1994). Fruit size was also the most important physical factor for other frugivorous, such as lemurs in Madagascar (Bollen, et al., 2003), and in general for fruits dispersed by vertebrates, where larger fruits were preferred over smaller one (Gautier-Hion et al, 1985). As a general rule, it was suggested that trends of selection by fruit characteristics were consistent in South East Asia, where small fruits, and large soft fruits with many small seeds, are consumed by large frugivorous species, while larger fruits, with a single large seed, are consumed by relatively few potential dispersers (Kitamura et al., 2002).

To explain fruit size selection by hornbills, I investigated the gape size and found no significant correlation with fruit size selected, even though gape size is critical for birds that swallow whole fruit (Leighton and Leighton, 1983) as the size of the bill must be considered as setting the first physical limit to the size of the fruit that can be selected (Stapanian, 1982). Hornbills, due to their large gape size, do not appear limited to any fruit as consequence of their size. Moreover, particular large fruit, such as *Platimitra* sp., selected by a couple of species, were eaten by detaching part and so not swallowing the entire fruit. The only limitation for hornbills was found in fruits with thick husks, as observed for other bird species (Voigt, et al., 2004). Our result confirm a suggested coevolutionary pattern, for which maximum fruit size and maximum gape size evolve on a parallel way to optimize access to resources, from a bird's point of view, and access a disperser, from the plant's point of view. Only the gape size of frugivorous birds limits the maximum seed diameter of fruit that they can swallow (Kitamura et al., 2002; Bollen et al. 2003), while this concept does not apply to mammals that, thanks to their teeth, can access fruits and seeds larger than their mouth size (Corlett, 2002).

3.2 Logistic Regression Model

The model of fruit selection derived from Logistic Regression helped describe the relationship between eaten and non-eaten food and predicted the probability of eaten and non-eaten fruit species being selected by hornbills. It also predicted which fruit characteristics (fruit type, detachment of pulp, fruit weight, fruit length and color) were eaten (at 82.7 % correct) and which were not eaten (at 82% correct). These are very high predictive values, particularly for ecological studies, and so the results are very powerful. These predictions can be tested with many other models and it will be found [it is likely] that my model is robust. This model can represent food selection for all species of hornbill at Khao Yai National Park as, if one enters values for fruit type, pulp, weight, length and color, this logistic regression equation will calculate the probability that this particular fruit will be eaten by hornbills, expressed as the percentage probability of the condition being true for a fruit eaten by hornbills.

3.3 Nutrition

Nutritional and morphological attributes of fruits were linked to explain food selection by hornbills. Three nutritional values had statistically significant ANOVA results for the differences in calcium, fat and moisture content between eaten and non-eaten fruit species. Fruits that were eaten by hornbills were higher in calcium and fat, and lower in moisture, than fruits that hornbills did not eat (Table 11).

3.3.1. Fat (Lipids)

My results indicate that hornbills tend to choose lipid-rich fruits. For fruit types, high lipid content was found in capsule, drupe, berry and syconium fruits. Overall the mean lipid content of fruits was higher in fruits that were eaten by hornbills than fruits that were not eaten. When combining our results, I detected that fruit types with a higher probability of being eaten by hornbills (syconium) had lower levels of fat, while fruit forms with the lowest probability of being eaten (drupe and capsule) had the highest levels of fat. Perhaps, hornbills select fruits to gain other nutrient, like calcium, and they eat other food, such as animals, to obtain the energy they need from fat. However, a threshold might be observed when comparing costs with benefits, where, up to a certain level, a lipid rich fruit that requires a high hydration cost, to start the assimilation process, may exceed the benefit obtained by the high level of lipid that it contains (Place et al, 1989). Moreover, birds, as well as mammals, tend to assimilate only 50% of ingested lipids (Clifford et al, 1986), with exception of a few highly specialized birds that show high assimilation levels (>80%), such as Yellow-rumped Warbler (*Dendroica coronata*) (Place and Stiles, 1992).

Overall, birds have been observed to favor lipid-rich fruit while mammals seem to avoid them. (Bolen et al, 2003). The need for large amounts of lipids in birds is, in part, a consequence their fast rate of molt and feather regeneration that requires a large amount of well-balance amino acids (Namara, 2006). However, our results contrast with what has been observed in smaller birds, such as American Robins (*Turdus migratorius*), where sugar-rich fruit are preferred over lipid-rich fruits, because their simple and fast rate of digestion enables higher rates of energy gain (Lepczyk et al., 2000) and where, in the field, fruits of low-lipid species were removed more quickly than fruits of high-lipid species (Borowicz and Stephenson, 1985).

3.3.2 Calcium

I observed a high association of calcium with the selection of fruits by hornbills. The mean levels of calcium were significantly higher in fruits with a syconium, detached pulp and orange color. All those three fruit characteristics had the highest Odd Ratio estimates (Table 18)

Of those three parameters, two are typical of figs, fruits that are ingested in large amounts during most of the year. The syconium is the typical fruit form of figs, their flesh is detachable, and some turn orange when ripe, besides which fig syconia have been considered as particularly high in calcium (O'Brien et al, 1998). In animals,calcium is of major importance in many metabolic processes, such as construction of muscles, clotting of blood, permeability of membranes, activity of enzymes, the metabolism of bones and the production of eggs (Zwart, 2000). It is especially important in the production of egg shells, and this was suggested as the primary cause for calcium consumption in hornbills during their nesting period (Poonswad, at al 2004). It has been proved in captive studies that newborn animals need double the amount of calcium content in their diet than what is required by adults

(Kass et al, 1982), and this explains the importance of figs, as a good source of calcium, during the breeding period.

3.3.3. Protein

No significant difference was found in the protein contents of eaten versus non-eaten fruits, and I assumed that most of the protein in the diet was provided by animal products (Stile, 1980; Poonswad et al., 2004; McNamara, 2006). In general fruits are poor source of protein, but they usually contain carbohydrates, fats, vitamins and minerals (McNamara, 2006).

Protein consumption has been reported, in previous study conducted in Khao Yai National Park, to correlate with breeding success in hornbills. Oriental Pied Hornbill was reported to show the highest breeding success (96%) while receiving the highest amount of protein (1.05% of brood mass per day), whereas Wreathed Hornbills, that received the lowest amount of protein (0.57%), had only 67% breeding success (Poonswad et al., 2004).

3.3.4. Tannin

There was no significantly difference in tannin content between eaten and non-eaten fruit in this study. Unfortunately, this result might be, in part, the consequence of the lack of tannin analysis in this study due to the low sample amount collected and budget available. Currently cooperation is planned with other existing projects to increase the amount of samples analyzed by using matching funding.

However, tannin is one of the secondary compounds known to influence animal feeding behavior (Arnold and Hill, 1972) as it affects the choice of foods, although in a way that it is difficult to assess (Hagerman, et al., 1992). A concentration higher than 0.02% in food will cause a reduction in feeding, if not a refusal to eat (Oates, et al. 1977). It is difficult to explain the effects of tannin on an animal as its diverse effects on digestion are partly the consequence of differences in the physiological capabilities of animals to process tannins and partly the consequences of differences in the nutritional reactivity of various types of tannins (Hargerman, et al. 1992). However, our negative results on the importance of tannins might be a consequence of hornbill preferences for ripe and very ripe fruits, in which tannin levels are low, or at least lower than folivorous and herbivorous animals. The reduction of tannin in ripe fruits has been widely explained as an evolutionary strategy by plants to regulate the ingestion of fruits by dispersers until the seed is ready for dispersal and will not be destroyed by digestion (Sherburne, 1972; Stevens and De Bont, 1980; Corlett, 1998).

3.3.5. Moisture

My results showed that eaten fruits had a relatively lower moisture content compared to non-eaten fruits. The low level of moisture in a birds' diet was explained as a strategy to avoid carrying around the large volumes of water that would make it difficult to fly and, as a consequence of this, birds developed concentrated urine in which a high content of uric acid is eliminated (McNamara, 2006).

3.3.6. Carbohydrate

No significant difference in the carbohydrate content was observed between eaten and non-eaten fruit species. Adult birds require a source of quick energy during the breeding season, particularly when foraging for insects for nestlings, so there would be selection for those plants that fruit during the bird's breeding season to have fleshy fruits with energy in the form of soluble carbohydrates or sugars (Stapanian, 1982). Carbohydrates and lipids are digested though very different pathways and require a multi-step biochemical process of emulsification, hydrolysis and absorption (Griminger, 1986).

3.3.7. Taste

When discussing results of taste tests, I have to be aware that animals perceive tastes at different intensities to what human do (Glaser and Hobi, 1985; Simmen and Hladik, 1988; Hladik and Simmen, 1997), and this is important when taste detection of animal-eaten items is dome by humans. For this reason, I might think that birds may not care much about mild sourness and bitterness, as they regular eat fruits that have those traits, but they might be more sensitive to sugar detection, with the results that mild sourness and/or bitterness, as tested by humans, appear sweet for birds.

However, fruits taste also provides information on their chemical components. The best example is for extreme bitterness, which is often associated with a high level of tannins and is typical of immature fruits (Willson and Whelan, 1990), and that may have the role of excluding some potential fruit consumers (Goldstein and Swain, 1963; Janson, 1978; Herrara 1982).

3. 4. Edibility

Finally, it was suggested that the choice for a given fruiting species was not only related to morphological characteristics and/or nutritious quality of fruits but also depends on easy access to its edible parts (Laferriere, 1999). A positive relationship between temporal variability in hornbill numbers and the availability of ripe fruits was observed in Sumatran hornbills (Anggraini et al., 2000).

CHAPTER VI
CONCLUSION

Over 20 year research on food selection of hornbills is summarized and concluded completely in this work. Figs are important species in the diet during the entire year while important non-fig species changed monthly due to their nutritional content and the nutrient requirement of hornbill during different breeding phases. Fruit characteristics of plants consumed by the four hornbill species are similar during the breeding and non-breeding season. Red and black fruits, syconium with pulp that easily detachable from the seed are preferred. It is because of hornbill’s trichromatic vision and UV detection capacity red and black fruits are detected better than other colors on green leave background, and besides that these colors showed the sign of maturity of fruits. Moreover, consuming fruits with pulp detached easily from seed are easier for regurgitation and the extraction of the pulp can be done without gut passage. Hornbills tend to choose lipid-rich fruit with high calcium. The need of high amount of lipids in birds is a consequence of fast rate of molting with all feather regeneration, requiring a large amount of energy and well-balance amino acid. It is especially the production of egg shell that was suggested as the primary cause for calcium consumption in hornbills during their nesting period. For what is concerning fruit type high lipid was found in capsule, drupe, berry and syconium respectively. The mean content of calcium were significantly higher in syconium and fruits with a detached pulp of orange color. My results show that eaten fruits have relatively lower moisture content compared to non-eaten one. It means that hornbill preferred dry fruits. The low content of moisture in birds’ diet was explained as a strategy to avoid the carrying around large volumes of water which would make it difficult to fly. The model of fruit selection for future management, defined from Logistic Regression analysis, helps describe the relationship between eaten and non-eaten food predicting the probability for a given fruit of been eaten by hornbills. The model can predict which fruit characteristics (fruit type, detachment of pulp, fruit weight, fruit length and color) are selected (at 82.7 % correct) and which fruit characteristics that are not selected (at 82 % correct).

The study revealed that the limitation in the fruit size consumed by hornbills was not the consequence of their gape size. There was no food limitation in the forest, therefore fruit selection was not influenced by food availability. Schoener’s Overlap Index showed overlap only between Wreathed and Oriental Pied Hornbills, which showed similar degree of frugivorous diet, while for the other species overlap was low. However, CCA showed low dietary overlap among these four hornbill species suggesting that there is low food competition for fruits.

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APPENDIX

Appendix A Sixteen Hornbills from Dusit zoo used for conducting captive experiment

Number	Hornbill species	Sex	Code
1	WH	M	WA1
2	WH	F	WB1
3	WH	M	WA2
4	WH	F	WB2
5	BH	M	BA1
6	BH	F	BB1
7	BH	M	BA2
8	BH	F	BB2
9	OPH	M	PA1
10	OPH	F	PB1
11	OPH	M	PA2
12	OPH	F	PB2
13	GH	M	GA1
14	GH	F	GB1
15	GH	M	GA2
16	GH	F	GB2

Appendix B Length of various phases in breeding cycle of four sympatric hornbill species recorded in 2004 and 2005 (ND = No data)

Great Hornbill				
Nest no.	Incubation	Nestling	Total	No. chick
G8	51	90	141	1
G12	54	95	149	1
G47	53	88	141	1
G8	53	89	142	1
G12	52	87	139	1
G47	54	85	139	1
Mean	52.83	89.00	141.83	1
SD	1.17	3.41	3.71	0
Median	53.00	88.50	141.00	1
N =	6	6	6	6

Wreathed Hornbill				
Nest no.	Incubation	Nestling	Total	No. chick
W27	43	92	135	1
W32	38	98	136	1
W38	40	90	130	1
W40	39	95	134	1
W35	39	90	129	1
W27	38	89	127	1
W38	37	98	135	1
W23	43	90	133	1
Mean	39.63	92.75	132.38	1
SD	2.26	3.73	3.29	0
Median	39.00	91.00	132.69	1
N =	8	8	8	8

White-throated Brown Hornbill				
Nest no.	Incubation	Nestling	Total	No. chick
B16	39	85	124	2
B18	39	84	123	3
B20	38	83	121	2
B23	38	82	120	3
B17	30	88	118	2
B16	35	81	116	ND
B18	35	89	124	ND
B20	34	80	114	2
B23	34	79	113	3
Mean	35.78	83.44	119.22	2.4
SD	2.99	3.43	4.21	0.53
Median	35.00	83.00	120.00	2.00
N =	9	9	9	7

Oriental Pied Hornbill				
Nest no.	Incubation	Nestling	Total	No. chick
P45	33	75	108	2
P80	34	80	114	2
P61	32	81	113	ND
P42	35	78	113	ND
P39	30	79	109	ND
P45	34	77	111	ND
P80	31	83	114	ND
P92	33	76	109	2
P88	32	78	110	3
P95	34	76	110	ND
Mean	32.80	78.30	111.10	2.25
SD	1.47	2.37	2.12	0.43
Median	33.00	78.00	110.50	2.00
N =	10	10	10	4

Appendix C Phenology (ripe fruiting = grey shade), density (D) of known hornbill food (F) and plant species found in plot

Family	Species	F	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	D	Basal Area per ha	Tree hight
ALANGIACEAE	*Alangium*	*							▨	▨	▨				0.7	27.8	15.92
ANACARDIACEAE	*Choerospondias axillaris*							▨	▨						6.8	775.2	19.58
	Rhus chinensis	*	▨	▨											1.1	89.8	24.30
ANNONACEAE	*Alphonsea boniana*	*					▨	▨							0.6	36.3	21.19
	Desmos Chinensis	*		▨	▨	▨											
	Miliusa lineata	*					▨	▨	▨						3.7	101.1	20.11
	Platymitra macrocarpa	*									▨				0.3	83.5	36.17
	Polyalthia jucunda	*															
	Polyalthia viridis	*		▨	▨	▨	▨	▨							3.3	56.1	16.24
	Pseudovaria														0.7	13.8	11.70
	Uvaria cordata	*													0.1	1.0	
APOCYNACEAE	*Alstonia scholaris*			▨	▨	▨									0.8	23.9	11.41
AQUIFOLIACEAE	*Ilex chevalieri*	*		▨	▨	▨	▨	▨	▨						14.5	342.9	17.70
ARACEAE	*Colocasia esculenta*														2.0	178.1	
ARALIACEAE	*Macropanax dispermus*														4.0	197.3	
BIGNONIACEAE	*Oroxylum indicum*		▨	▨	▨	▨	▨								0.9	40.9	18.33
	Palaquiun garrettii														0.3	4.1	
	Radermachera ignea											▨	▨	▨	0.3	2.7	16.75
	Stereospermum														0.1	7.1	
	Radermachera glandulosa														0.2	31.1	
BURSERACEAE	*Canarium euphyllum*	*															
	Canarium subulatum	*						▨	▨	▨					1.1	79.3	25.18
CAESSALPINNIOIDEAE	*Acrocarpus fraxinifolius*					▨	▨								6.2	163.2	16.44
CAPRIFOLIACEAE	*Viburnum sambucinum*		▨	▨	▨								▨	▨	0.6	7.7	12.20
CELASTRACEAE	*Bhesa robusta*	*													0.4	12.2	14.87
	Euonymous cochinchinensis														0.4	6.8	
	Euonymous sp.														0.4	2.9	12.13
COMBRETACEAE	*Combretum acuminatum*	*				▨	▨										
CORNACEAE	*Mastixia euonymides*	*								▨	▨	▨			2.4	63.9	21.50
CORNACEAE	*Mastixia pentandra*	*													18.8	735.2	23.81
DIPTEROCARPACEAE	*Dipterocarpus gracilis*														11.9	873.7	25.46
EBENACEAE	*Diospyros glandulosa*									▨	▨	▨			1.7	51.5	23.84
ELAEGNACEAE	*Elaeagnus latifolia*	*		▨	▨												
ELAEOCARPACEAE	*Elaeocarpus floribundus*														0.9	20.6	17.50
	Eleaocarpus robustus														3.5	198.3	17.89
	Sloanea sigun	*													5.1	314.1	19.62
ELAEOCARPACEAE	*Vitex peduncularis*														0.1	12.0	
EUPHORBIACEAE	*Alchornea rugosa*			▨											0.5	4.0	14.11
	Aporusa octandra																14.00
	Aporusa planchoniana														1.6	65.9	12.50
	Aporusa wallichii																24.00
	Baccaurea ramiflora						▨	▨	▨						2.9	125.1	11.48
	Balacata baccata	*	▨	▨	▨	▨	▨	▨	▨						1.6	586.2	30.68
	Bridelia retusa										▨	▨	▨		3.7	121.6	17.95
	Excoecaria oppositifolia		▨												8.4	226.0	16.56
	Glochidion lanceolarium														0.7	9.8	10.33
	Macaranga gigantea								▨	▨	▨	▨			0.7	109.3	25.75
	Mallotus philippensis	*	▨	▨	▨										0.3	8.3	14.63
FAGACEAE	*Castanopsis acuminatissima*										▨	▨			7.7	664.8	29.01
	Lithocarpus pattaniensis								▨	▨	▨				0.7	23.3	24.41
	Lithocarpus aggregatus		▨	▨										▨	2.8	117.2	21.62
	Lithocarpus thomsonii				▨	▨	▨	▨							3.6	136.7	21.83

Appendix C Phenology (ripe fruiting = grey shade), density (D) of known hornbill food (F) and plant species found in plot (Continued)

Family	Species	F	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	D	Basal Area per ha	Tree hight
FLACOURTIACEAE	*Casearia grewiaefolia*	*						▨	▨						1.9	56.0	23.89
	Hydnocarpus ilicifolius														1.8	27.9	13.35
GNETACEAE	*Gnetum montanum*	*				▨											
GUTTIFERAE	*Garcinia speciosa*									▨	▨	▨			0.6	8.4	21.07
	Mangifera cochinchinensis														0.5	21.3	17.56
	Mangifera longipetiolata									▨					0.3	7.3	18.67
HAMAMELIDACEAE	*Altingia excelsa*		▨	▨		▨		▨			▨	▨		▨	3.2	330.5	31.39
HYPERICACEAE	*Cratoxylum cochinchinense*					▨	▨								4.4	62.5	11.41
ICACINACEAE	*Apodytes dimidiana*	*									▨	▨					26.78
	Platea latifolia	*													2.0	63.3	20.03
	Gonocaryum lobbianum														6.5	79.7	15.05
IRVINGIACEAE	*Irvingia malayana*								▨	▨	▨	▨			0.1	62.3	
JUGLANDACEAE	*Engelhardtia spicata*			▨	▨	▨									1.2	18.7	18.23
LAURACEAE	*Beilschemiedia balansae*	*	▨	▨	▨	▨	▨										
	Beilshmiedia glauca	*	▨												4.7	69.9	15.20
	Beilschmiedia maingayi	*	▨	▨											1.8	70.2	22.42
	Beilshmiedia villosa	*															
	Cinnamomum glacescen	*					▨	▨							0.4	9.9	39.67
	Cinnamomum ilicioides	*		▨	▨										1.9	136.3	17.60
	Cinnamomum iners					▨	▨								1.5	25.5	14.96
	Cinnamomum subavenium	*	▨	▨	▨									▨	8.0	395.3	22.42
	Cryptocarya impressa	*			▨	▨	▨										
	Litsea beusekomii	*					▨	▨							0.4	11.3	21.69
	Litsea monopetala	*						▨	▨	▨					1.3	69.3	16.28
	Litsea sp.1														26.2	780.1	19.22
	Litsea sp.2														0.2	2.1	
	Litsea sp.3														0.2	4.6	
	Litsea tomentosa				▨										0.3	2.6	
	Litsea verticillata	*													0.1	4.2	22.32
	Neolitsea sp.	*						▨	▨	▨	▨				0.1	0.5	21.60
LEGUMINOSAE	*Cassia bakerina*		▨								▨	▨	▨	▨	0.2	2.8	9.76
	Erithrina subumbrans			▨	▨	▨	▨	▨	▨	▨					0.2	62.8	17.85
	Erithrina teysmanii														0.1	94.0	44.00
	Ormosia sumatrana														0.2	3.7	26.00
LYTHRACEAE	*Lagerstroemia balansae*											▨	▨		0.6	15.5	5.28
MAGNOLIACEAE	*Michelia baillonii*	*					▨	▨	▨	▨					2.6	398.2	22.94
MALVACEAE	*unk* (Malvaceae)																
	Hibiscus macrophyllus		▨									▨	▨	▨	1.0	34.4	19.85
MELASTOMATACEAE	*Memecylon edule*	*													0.6	8.8	18.65
	Memecylon geddesianum	*									▨	▨			0.1	0.6	14.50
MELIACEAE	*Aglaia elaeagnoidea*	*		▨	▨	▨	▨	▨							2.6	37.8	14.85
	Aglaia lawii	*		▨	▨	▨	▨								2.3	120.9	21.90
	Aglaia odoratissima	*					▨	▨	▨	▨					1.1	14.5	14.66
	Aglaia spectabilis	*			▨	▨	▨										
	Aphanamixis polystachya	*	▨	▨	▨	▨	▨	▨	▨					▨	4.1	66.8	18.25
	Dysoxylum cyrtobotryum	*		▨	▨	▨	▨								7.6	143.3	16.83
	Dysoxylum densiflorum	*		▨	▨												12.33
	Melia azedarach					▨	▨								0.2	6.8	26.50
	Sandoricum koetjape							▨	▨	▨					0.1	11.0	21.85
	Toona microcarpa			▨											1.4	207.2	22.61
	Walsura robusta	*													3.6	79.1	15.09
MORACEAE	*Antiaris toxicaris*	*		▨	▨										0.3	7.2	23.00
	Arthocarpua lakooxha	*				▨											
MORACEAE	*Artocarpus lanceifolius*	*													0.2	13.7	18.40
	Ficus spp.	*	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	1.7	108.2	23.48
	Broussonetia kurzii														0.1	0.6	
MYRSINACEAE	*Ardisia colorata*	*	▨								▨	▨	▨	▨	0.5	3.3	17.03
	Ardisia nervosa	*								▨	▨	▨					20.75
MYRISTICACEAE	*Knema laurina*	*				▨	▨	▨	▨						5.0	132.5	10.48

Appendix C Phenology (ripe fruiting = grey shade), density (D) of known hornbill food (F) and plant species found in plot (Continued)

Family	Species	F	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	D	Basal Area per ha	Tree hight
MYRTACEAE	*Horsfieldia glabra*	*		▨	▨	▨	▨								0.5	6.6	30.71
	Cleistocalyx operculatus	*						▨	▨	▨	▨				19.2	768.9	25.94
	Decaspermum fruticosum														0.1	0.7	9.50
	Syzygium cinereum	*													0.1	4.3	
	Syzygium cratum	*													0.4	8.9	13.50
	Syzygium cuminii	*													0.7	7.4	10.10
	Syzygium grande	*		▨											1.8	122.7	19.18
	Syzygium siamensis	*													2.7	38.1	15.46
	Syzygium syzygioides	*													1.2	23.5	21.39
OLEACEAE	*Chionanthus ramifeorus*		▨	▨									▨	▨	1.9	103.7	19.28
	Fraxinus floribunda						▨	▨	▨						3.3	129.5	24.56
	Gomphandra tetrandra				▨	▨	▨	▨	▨						0.6	7.9	16.70
PALMAE	*Levistona speciosa*	*	▨	▨	▨	▨											24.59
PATISCACEAE	*Tetrameles nudiflora*					▨	▨								0.7	77.0	23.60
PODOCARPACEAE	*Podocarpus neriifolius*	*									▨	▨			0.1	3.7	35.00
POLEMONIACEAE	*Phoebe lanceolata*	*	▨											▨	2.3	49.1	12.83
	Phoebe paniculata	*													1.8	25.0	11.44
PROTEACEAE	*Helicia excelsa*														4.6	137.9	17.04
	Helicia formosana														2.3	39.5	17.10
	Helicia nilagirica		▨	▨	▨	▨							▨	▨	1.0	15.5	15.85
RHAMNACEAE	*Zizyplus attopoensis*	*				▨											
RHIZOPHORACEA	*Carallia brachiata*	*					▨	▨							1.1	68.8	22.53
ROSACEAE	*Canthium glabrum*	*	▨	▨	▨								▨	▨			
	Prunus arborea	*													0.6	12.4	26.36
	Prunus javanica	*													0.6	22.5	21.29
RUBIACEAE	*Aidia cochinchinensis*	*								▨	▨				2.6	51.7	15.10
	Neolarmarkia cadamba														2.0	741.1	34.00
	Neonauclea excelsa														6.4	205.5	16.25
	Randia ecodom			▨	▨	▨	▨	▨	▨	▨	▨				2.8	27.0	12.40
	Acronychia pedunculata								▨	▨	▨	▨			2.1	21.4	12.01
	Clausena excavata	*					▨	▨	▨	▨							3.97
	Zanthoxylum rhetsa										▨	▨			0.3	11.1	
SABIACEAE	*Meliosma pinnata*				▨						▨				0.1	13.3	18.00
SANTALACEAE	*Scleropyrum wallichianum*										▨	▨	▨		0.2	1.1	24.00
SAPINDACEAE	*Dimocarpus longon*								▨	▨	▨				0.1	10.2	9.75
	Lepisanthes sp.														0.1	2.3	
	Lepisanthes tetraphylla			▨	▨	▨									1.8	49.2	20.68
	Nephelium melliferum														7.0	250.4	16.28
SAPOTACEAE	*Sarcosperma arboreum*	*				▨	▨	▨	▨						4.1	206.9	24.47
SIMAROUBACEAE	*Ailanthus triphysa*				▨	▨									0.2	4.1	13.73
SONNERATIACEAE	*Duabanga grandiflora*					▨	▨	▨							0.7	148.8	30.06
STAPHYLEACEAE	*Turpinia montana*							▨	▨	▨					0.7	20.7	10.95
STERCULIACEAE	*Pterospermium cinnamomeum*						▨	▨	▨						2.6	199.2	21.43
	Sterculia balanghas	*			▨	▨											
	Symplocos cochinchinensis	*			▨										34.3	764.5	20.06
	Symplocos sumuntia	*													3.3	88.4	12.70
THEACEAE	*Adinandra integerrima*								▨						1.6	20.9	11.04
THEACEAE	*Aglaia edulis*	*													0.8	15.7	13.81
	Eurya nitida														2.9	21.9	12.73
	Schima wallichii		▨	▨									▨	▨	34.8	1293.2	21.57
	Ternstroemia wallichiana						▨	▨							0.6	8.7	20.67
THYMELAEACEAE	*Aquillaria crassna*								▨	▨	▨				6.1	218.0	20.07
ULMACEAE	*Aphananthe cuspidata*	*															25.00
	Gironniera nervosa	*	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	7.9	348.8	20.73
	Trema orientalis					▨	▨	▨							0.2	19.1	21.75
XANTHOPYLLACEAE	*Xanthophyllum virens*			▨			▨	▨	▨	▨					0.2	8.2	29.20
Hornbill food plant																	
	Number of species	**80**															
Mean															**3.3**	**119.9**	**20.02**
SD															**5.6**	**186.5**	**6.27**
Median															**1.7**	**56.1**	**20.11**
Total plant species																	
	Number of species	**167**															
Mean															**2.9**	**118.1**	**19.3**
SD															**5.5**	**212.1**	**6.5**
Median															**1.2**	**32.7**	**18.4**

Appendix D List of important and least consumed of food and non-food plant species in different breeding phases of four hornbill species "-" no data Abbreviation: W = Pulp weight (g), Incub = Incubation, Nesl = Nestling, F = Food or non-food: 0 = non-eaten, 1 = eaten, IM = Important species or least consumed: 1 = Important, 0 = Less consumed

Family	Species	GH							WH							BH							PH						
		W	Total		Incub.		Nestl.		W	Total		Incub.		Nestl.		W	Total		Incub.		Nestl.		W	Total		Incub.		Nestl.	
		(g)	F	IM	F	IM	F	IM	(g)	F	IM	F	IM	F	IM	(g)	F	IM	F	IM	F	IM	(g)	F	IM	F	IM	F	IM
ALANGIACEAE	*Alangium*		0	-	0	-	0	-		0	-	0	-	0	-		0	-	0	-	0	-		0	-	0	-	0	-
ANACARDIACEAE	*Choerospondias axillaris*		0	-	0	-	0	-		0	-	0	-	0	-		0	-	0	-	0	-		0	-	0	-	0	-
	Rhus chinensis		0	-	0	-	0	-		0	-	0	-	0	-		0	-	0	-	0	-		0	-	0	-	0	-
ANNONACEAE	*Alphonsea boniana*		0	-	0	-	0	-		0	-	0	-	0	-		0	-	0	-	0	-		0	-	0	-	0	-
	Desmos Chinensis	869	1	1	1	2	1	1	287	1	1	1	2	1	1	596	1	1	1	1	1	1	22	1	2	0	-	1	2
	Miliusa lineata		0	-	0	-	0	-		0	-	0	-	0	-		0	-	0	-	0	-		0	-	0	-	0	-
	Platymitra macrocarpa		0	-	0	-	0	-		0	-	0	-	0	-		0	-	0	-	0	-		0	-	0	-	0	-
	Polyalthia jucunda	1134	1	1	0	-	1	1	3174	1	1	1	1	1	1	483	1	1	0	-	1	1	407	1	1	1	2	1	1
	Polyalthia viridis	3119	1	1	1	1	1	1	8995	1	1	1	1	1	1	1319	1	1	1	1	1	1	1926	1	1	1	1	1	1
	Pseudovaria		0	-	0	-	0	-		0	-	0	-	0	-		0	-	0	-	0	-		0	-	0	-	0	-
	Uvaria cordata		0	-	0	-	0	-		0	-	0	-	0	-		0	-	0	-	0	-		0	-	0	-	0	-
APOCYNACEAE	*Alstonia scholaris*		0	-	0	-	0	-		0	-	0	-	0	-		0	-	0	-	0	-		0	-	0	-	0	-
AQUIFOLIACEAE	*Ilex chevalieri*		0	-	0	-	0	-		0	-	0	-	0	-		0	-	0	-	0	-		0	-	0	-	0	-
ARACEAE	*Colocasia esculenta*		0	-	0	-	0	-		0	-	0	-	0	-		0	-	0	-	0	-		0	-	0	-	0	-
ARALIACEAE	*Macropanax dispermus*		0	-	0	-	0	-		0	-	0	-	0	-		0	-	0	-	0	-		0	-	0	-	0	-
BIGNONIACEAE	*Canarium euphyllum*		0	-	0	-	0	-		0	-	0	-	0	-		0	-	0	-	0	-		0	-	0	-	0	-
	Canarium subulatum		0	-	0	-	0	-		0	-	0	-	0	-		0	-	0	-	0	-		0	-	0	-	0	-
	Oroxylum indicum		0	-	0	-	0	-		0	-	0	-	0	-		0	-	0	-	0	-		0	-	0	-	0	-
	Palaquiun garrettii		0	-	0	-	0	-		0	-	0	-	0	-		0	-	0	-	0	-		0	-	0	-	0	-
	Radermachera glandulosa		0	-	0	-	0	-		0	-	0	-	0	-		0	-	0	-	0	-		0	-	0	-	0	-
	Radermachera ignea		0	-	0	-	0	-		0	-	0	-	0	-		0	-	0	-	0	-		0	-	0	-	0	-
	Stereospermum		0	-	0	-	0	-		0	-	0	-	0	-		0	-	0	-	0	-		0	-	0	-	0	-
CAESSALPINNIOIDEAE	*Acrocarpus fraxinifolius*		0	-	0	-	0	-		0	-	0	-	0	-		0	-	0	-	0	-		0	-	0	-	0	-
CAPRIFOLIACEAE	*Viburnum sambucinum*		0	-	0	-	0	-		0	-	0	-	0	-		0	-	0	-	0	-		0	-	0	-	0	-
CELASTRACEAE	*Bhesa robusta*	475	1	1	0	-	1	1	1035	1	1	1	2	1	1	1028	1	1	1	1	1	1	582	1	1	1	1	1	2
	Euonymous cochinchinensis		0	-	0	-	0	-		0	-	0	-	0	-		0	-	0	-	0	-		0	-	0	-	0	-
	Euonymous sp.		0	-	0	-	0	-		0	-	0	-	0	-		0	-	0	-	0	-		0	-	0	-	0	-
COMBRETACEAE	*Combretum acuminatum*	496	1	1	0	-	1	1	-	0	-	0	-	0	-		0	-	0	-	0	-	501	1	1	1	1	1	1
CORNACEAE	*Mastixia euonymides*		0	-	0	-	0	-		0	-	0	-	0	-		0	-	0	-	0	-		0	-	0	-	0	-
	Mastixia pentandra		0	-	0	-	0	-		0	-	0	-	0	-		0	-	0	-	0	-		0	-	0	-	0	-
DIPTEROCARPACEAE	*Dipterocarpus gracilis*		0	-	0	-	0	-		0	-	0	-	0	-		0	-	0	-	0	-		0	-	0	-	0	-
EBENACEAE	*Diospyros glandulosa*		0	-	0	-	0	-		0	-	0	-	0	-		0	-	0	-	0	-		0	-	0	-	0	-
ELAEGNACEAE	*Elaeagnus latifolia*	337	1	1	0	-	1	1	792	1	1	1	1	1	1	35	1	2	1	2	1	2	1587	1	2	1	2	0	-
ELAEOCARPACEAE	*Elaeocarpus floribundus*		0	-	0	-	0	-		0	-	0	-	0	-		0	-	0	-	0	-		0	-	0	-	0	-
	Eleaocarpus robustus		0	-	0	-	0	-		0	-	0	-	0	-		0	-	0	-	0	-		0	-	0	-	0	-

Appendix D List of important and least consumed of food and non-food plant species in different breeding phases of four hornbill species “-” no data Abbreviation: W = Pulp weight (g), Incub = Incubation, Nesl = Nestling, F = Food or non-food: 0 = non-eaten, 1 = eaten, IM = Important species or least consumed: 1 = Important, 0 = Less consumed (Continued)

Family	Species	GH							WH							BH							PH						
		W	Total		Incub.		Nestl.		W	Total		Incub.		Nestl.		W	Total		Incub.		Nestl.		W	Total		Incub.		Nestl.	
		(g)	F	IM	F	IM	F	IM	(g)	F	IM	F	IM	F	IM	(g)	F	IM	F	IM	F	IM	(g)	F	IM	F	IM	F	IM
ELAEOCARPACEAE	*Sloanea sigun*		0	-	0	-	0	-		0	-	0	-	0	-		0	-	0	-	0	-		0	-	0	-	0	-
EUPHORBIACEAE	*Alchornea rugosa*		0	-	0	-	0	-		0	-	0	-	0	-		0	-	0	-	0	-		0	-	0	-	0	-
	Aporusa octandra		0	-	0	-	0	-		0	-	0	-	0	-		0	-	0	-	0	-		0	-	0	-	0	-
	Aporusa planchoniana		0	-	0	-	0	-		0	-	0	-	0	-		0	-	0	-	0	-		0	-	0	-	0	-
	Aporusa wallichii		0	-	0	-	0	-		0	-	0	-	0	-		0	-	0	-	0	-		0	-	0	-	0	-
	Baccaurea ramiflora		0	-	0	-	0	-		0	-	0	-	0	-		0	-	0	-	0	-		0	-	0	-	0	-
	Balacata baccata		0	-	0	-	0	-		0	-	0	-	0	-		0	-	0	-	0	-		0	-	0	-	0	-
	Bridelia retusa		0	-	0	-	0	-		0	-	0	-	0	-		0	-	0	-	0	-		0	-	0	-	0	-
	Excoecaria oppositifolia		0	-	0	-	0	-		0	-	0	-	0	-		0	-	0	-	0	-		0	-	0	-	0	-
	Glochidion lanceolarium		0	-	0	-	0	-		0	-	0	-	0	-		0	-	0	-	0	-		0	-	0	-	0	-
	Macaranga gigantea		0	-	0	-	0	-		0	-	0	-	0	-		0	-	0	-	0	-		0	-	0	-	0	-
	Mallotus philippensis		0	-	0	-	0	-		0	-	0	-	0	-		0	-	0	-	0	-		0	-	0	-	0	-
FAGACEAE	*Castanopsis acuminatissima*		0	-	0	-	0	-		0	-	0	-	0	-		0	-	0	-	0	-		0	-	0	-	0	-
	Lithocarpus pattaniensis		0	-	0	-	0	-		0	-	0	-	0	-		0	-	0	-	0	-		0	-	0	-	0	-
	Lithocarpus aggregatus		0	-	0	-	0	-		0	-	0	-	0	-		0	-	0	-	0	-		0	-	0	-	0	-
	Lithocarpus thomsonii		0	-	0	-	0	-		0	-	0	-	0	-		0	-	0	-	0	-		0	-	0	-	0	-
FLACOURTIACEAE	*Casearia grewiaefolia*		0	-	0	-	0	-		0	-	0	-	0	-		0	-	0	-	0	-		0	-	0	-	0	-
	Hydnocarpus ilicifolius		0	-	0	-	0	-		0	-	0	-	0	-		0	-	0	-	0	-		0	-	0	-	0	-
GNETACEAE	*Gnetum montanum*	-	1	-	0	-	0	-	-	0	-	0	-	0	-	-	0	-	0	-	0	-	350	1	1	1	1	0	-
GUTTIFERAE	*Garcinia speciosa*		0	-	0	-	0	-		0	-	0	-	0	-		0	-	0	-	0	-		0	-	0	-	0	-
	Mangifera cochinchinensis		0	-	0	-	0	-		0	-	0	-	0	-		0	-	0	-	0	-		0	-	0	-	0	-
	Mangifera longipetiolata		0	-	0	-	0	-		0	-	0	-	0	-		0	-	0	-	0	-		0	-	0	-	0	-
HAMAMELIDACEAE	*Altingia excelsa*		0	-	0	-	0	-		0	-	0	-	0	-		0	-	0	-	0	-		0	-	0	-	0	-
HYPERICACEAE	*Cratoxylum cochinchinense*		0	-	0	-	0	-		0	-	0	-	0	-		0	-	0	-	0	-		0	-	0	-	0	-
ICACINACEAE	*Apodytes dimidiana*		0	-	0	-	0	-		0	-	0	-	0	-		0	-	0	-	0	-		0	-	0	-	0	-
	Gonocaryum lobbianum		0	-	0	-	0	-		0	-	0	-	0	-		0	-	0	-	0	-		0	-	0	-	0	-
	Platea latifolia	-	1	-	0	-	0	-	-	0	-	0	-	0	-	384	1	1	0	-	1	1	381	1	1	1	1	0	-
IRVINGIACEAE	*Irvingia malayana*		0	-	0	-	0	-		0	-	0	-	0	-		0	-	0	-	0	-		0	-	0	-	0	-
JUGLANDACEAE	*Engelhardtia spicata*		0	-	0	-	0	-		0	-	0	-	0	-		0	-	0	-	0	-		0	-	0	-	0	-
LABIATAE	*Vitex peduncularis*		0	-	0	-	0	-		0	-	0	-	0	-		0	-	0	-	0	-		0	-	0	-	0	-
LAURACEAE	*Beilschemiedia balansae*	221	1	1	0	-	1	1	469	1	1	1	1	1	2	270	1	1	0	-	1	1	219	1	1	1	1	1	2
	Beilschmiedia maingayi	439	1	1	0	-	1	1	496	1	2	1	2	1	2	470	1	1	0	-	1	1	670	1	1	1	1	1	1
	Beilshmiedia glauca	2	1	2	0	-	1	2	34	1	2	0	-	1	2	59	1	2	0	-	1	2	4	1	2	0	-	1	2
	Beilshmiedia villosa		0	-	0	-	0	-		0	-	0	-	0	-		0	-	0	-	0	-		0	-	0	-	0	-
	Cinnamomum glacescen		0	-	0	-	0	-		0	-	0	-	0	-		0	-	0	-	0	-		0	-	0	-	0	-
	Cinnamomum ilicioides		0	-	0	-	0	-		0	-	0	-	0	-		0	-	0	-	0	-		0	-	0	-	0	-
	Cinnamomum iners		0	-	0	-	0	-		0	-	0	-	0	-		0	-	0	-	0	-		0	-	0	-	0	-

Appendix D List of important and least consumed of food and non-food plant species in different breeding phases of four hornbill species "-" no data Abbreviation: W = Pulp weight (g), Incub = Incubation, Nesl = Nestling, F = Food or non-food: 0 = non-eaten, 1 = eaten, IM = Important species or least consumed: 1 = Important, 0 = Less consumed (Continued)

Family	Species	GH							WH							BH							PH						
		W	Total		Incub.		Nestl.		W	Total		Incub.		Nestl.		W	Total		Incub.		Nestl.		W	Total		Incub.		Nestl.	
		(g)	F	IM	F	IM	F	IM	(g)	F	IM	F	IM	F	IM	(g)	F	IM	F	IM	F	IM	(g)	F	IM	F	IM	F	IM
LAURACEAE	*Cinnamomum subavenium*	1825	1	1	1	1	1	1	1389	1	1	1	1	1	2	1627	1	1	1	1	1	1	711	1	1	1	1	1	1
	Cryptocarya impressa	258	1	1	0	-	1	1	788	1	1	0	-	1	1	509	1	1	0	-	1	1	783	1	1	1	1	1	1
	Litsea beusekomii		0	-	0	-	0	-		0	-	0	-	0	-		0	-	0	-	0	-		0	-	0	-	0	-
	Litsea monopetala		0	-	0	-	0	-		0	-	0	-	0	-		0	-	0	-	0	-		0	-	0	-	0	-
	Litsea sp.1		0	-	0	-	0	-		0	-	0	-	0	-		0	-	0	-	0	-		0	-	0	-	0	-
	Litsea sp.2		0	-	0	-	0	-		0	-	0	-	0	-		0	-	0	-	0	-		0	-	0	-	0	-
	Litsea sp.3		0	-	0	-	0	-		0	-	0	-	0	-		0	-	0	-	0	-		0	-	0	-	0	-
	Litsea tomentosa		0	-	0	-	0	-		0	-	0	-	0	-		0	-	0	-	0	-		0	-	0	-	0	-
	Litsea verticillata		0	-	0	-	0	-		0	-	0	-	0	-		0	-	0	-	0	-		0	-	0	-	0	-
	Neolitsea sp.		0	-	0	-	0	-		0	-	0	-	0	-		0	-	0	-	0	-		0	-	0	-	0	-
LEGUMINOSAE	*Cassia bakerina*		0	-	0	-	0	-		0	-	0	-	0	-		0	-	0	-	0	-		0	-	0	-	0	-
	Erithrina subumbrans		0	-	0	-	0	-		0	-	0	-	0	-		0	-	0	-	0	-		0	-	0	-	0	-
	Erithrina teysmanii		0	-	0	-	0	-		0	-	0	-	0	-		0	-	0	-	0	-		0	-	0	-	0	-
	Ormosia sumatrana		0	-	0	-	0	-		0	-	0	-	0	-		0	-	0	-	0	-		0	-	0	-	0	-
LYTHRACEAE	*Lagerstroemia balansae*		0	-	0	-	0	-		0	-	0	-	0	-		0	-	0	-	0	-		0	-	0	-	0	-
MAGNOLIACEAE	*Michelia baillonii*		0	-	0	-	0	-		0	-	0	-	0	-		0	-	0	-	0	-		0	-	0	-	0	-
MALVACEAE	*Hibiscus macrophyllus*		0	-	0	-	0	-		0	-	0	-	0	-		0	-	0	-	0	-		0	-	0	-	0	-
	unk (Malvaceae)		0	-	0	-	0	-		0	-	0	-	0	-		0	-	0	-	0	-		0	-	0	-	0	-
MELASTOMATACEAE	*Memecylon edule*		0	-	0	-	0	-		0	-	0	-	0	-		0	-	0	-	0	-		0	-	0	-	0	-
	Memecylon geddesianum		0	-	0	-	0	-		0	-	0	-	0	-		0	-	0	-	0	-		0	-	0	-	0	-
MELIACEAE	*Aglaia elaeagnoidea*		0	-	0	-	0	-		0	-	0	-	0	-		0	-	0	-	0	-		0	-	0	-	0	-
	Aglaia lawii	514	1	2	0	-	1	2	729	1	2	1	2	1	2	534	1	1	1	1	1	2	894	1	2	1	2	1	2
	Aglaia odoratissima		0	-	0	-	0	-		0	-	0	-	0	-		0	-	0	-	0	-		0	-	0	-	0	-
	Aglaia spectabilis	4925	1	1	0	-	1	1	19998	1	1	1	1	1	1	559	1	2	0	-	1	2	591	1	1	1	2	1	1
	Antiaris toxicaris	202	1	2	0	-	1	2	-	0	-	0	-	0	-	-	0	-	0	-	0	-	-	0	-	0	-	0	-
	Aphanamixis polystachya	-	1	-	0	-	0	-	1922	1	1	1	1	1	2	587	1	2	1	2	0	-	-	0	-	0	-	0	-
	Arthocarpua lakooxha	310	1	2	0	-	1	2	-	0	-	0	-	0	-	-	0	-	0	-	0	-	-	0	-	0	-	0	-
	Artocarpus lanceifolius		0	-	0	-	0	-		0	-	0	-	0	-		0	-	0	-	0	-		0	-	0	-	0	-
	Broussonetia kurzii		0	-	0	-	0	-		0	-	0	-	0	-		0	-	0	-	0	-		0	-	0	-	0	-
	Dysoxylum cyrtobotryum	285	1	1	0	-	1	1	135	1	2	1	2	0	-	856	1	1	1	2	1	1	573	1	1	1	1	1	1
	Dysoxylum densiflorum	2861	1	1	0	-	1	1	3965	1	1	1	1	1	1	2572	1	1	1	2	1	1	1211	1	1	1	1	1	1
	Melia azedarach		0	-	0	-	0	-		0	-	0	-	0	-		0	-	0	-	0	-		0	-	0	-	0	-
	Sandoricum koetjape		0	-	0	-	0	-		0	-	0	-	0	-		0	-	0	-	0	-		0	-	0	-	0	-
	Toona microcarpa		0	-	0	-	0	-		0	-	0	-	0	-		0	-	0	-	0	-		0	-	0	-	0	-
	Walsura robusta		0	-	0	-	0	-		0	-	0	-	0	-		0	-	0	-	0	-		0	-	0	-	0	-
MORACEAE	*Ficus* sp.	7539	1	1	1	1	1	1	6426	1	1	1	1	1	1	1959	1	1	1	1	1	1	2527	1	1	1	1	1	1
MYRISTICACEAE	*Horsfieldia glabra*	2415	1	1	0	-	1	1	2132	1	1	0	-	1	1	2631	1	1	0	-	1	1	2707	1	1	1	1	1	1

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Family	Species	GH							WH							BH							PH						
		W	Total		Incub.		Nestl.		W	Total		Incub.		Nestl.		W	Total		Incub.		Nestl.		W	Total		Incub.		Nestl.	
		(g)	F	IM	F	IM	F	IM	(g)	F	IM	F	IM	F	IM	(g)	F	IM	F	IM	F	IM	(g)	F	IM	F	IM	F	IM
MYRISTICACEAE	*Knema laurina*	4	1	2	0	-	1	2	1254	1	1	1	1	1	1	762	1	1	0	-	1	1	378	1	1	1	1	1	2
MYRSINACEAE	*Ardisia colorata*		0	-	0	-	0	-		0	-	0	-	0	-		0	-	0	-	0	-		0	-	0	-	0	-
	Ardisia nervosa		0	-	0	-	0	-		0	-	0	-	0	-		0	-	0	-	0	-		0	-	0	-	0	-
MYRTACEAE	*Cleistocalyx operculatus*		0	-	0	-	0	-		0	-	0	-	0	-		0	-	0	-	0	-		0	-	0	-	0	-
	Decaspermum fruticosum		0	-	0	-	0	-		0	-	0	-	0	-		0	-	0	-	0	-		0	-	0	-	0	-
	Syzygium cinereum		0	-	0	-	0	-		0	-	0	-	0	-		0	-	0	-	0	-		0	-	0	-	0	-
	Syzygium cratum		0	-	0	-	0	-		0	-	0	-	0	-		0	-	0	-	0	-		0	-	0	-	0	-
	Syzygium cuminii		0	-	0	-	0	-		0	-	0	-	0	-		0	-	0	-	0	-		0	-	0	-	0	-
	Syzygium grande		0	-	0	-	0	-		0	-	0	-	0	-		0	-	0	-	0	-		0	-	0	-	0	-
	Syzygium siamensis		0	-	0	-	0	-		0	-	0	-	0	-		0	-	0	-	0	-		0	-	0	-	0	-
	Syzygium syzygioides		0	-	0	-	0	-		0	-	0	-	0	-		0	-	0	-	0	-		0	-	0	-	0	-
OLACACEAE	*Chionanthus ramifeorus*		0	-	0	-	0	-		0	-	0	-	0	-		0	-	0	-	0	-		0	-	0	-	0	-
OLEACEAE	*Fraxinus floribunda*		0	-	0	-	0	-		0	-	0	-	0	-		0	-	0	-	0	-		0	-	0	-	0	-
	Gomphandra tetrandra		0	-	0	-	0	-		0	-	0	-	0	-		0	-	0	-	0	-		0	-	0	-	0	-
PALMAE	*Levistona speciosa*	1127	1	1	1	1	1	1	1568	1	1	1	1	1	1	-	0	-	0	-	0	-	-	0	-	0	-	0	-
PATISCACEAE	*Tetrameles nudiflora*		0	-	0	-	0	-		0	-	0	-	0	-		0	-	0	-	0	-		0	-	0	-	0	-
PODOCARPACEAE	*Podocarpus neriifolius*		0	-	0	-	0	-		0	-	0	-	0	-		0	-	0	-	0	-		0	-	0	-	0	-
POLEMONIACEAE	*Phoebe lanceolata*		0	-	0	-	0	-		0	-	0	-	0	-		0	-	0	-	0	-		0	-	0	-	0	-
	Phoebe paniculata		0	-	0	-	0	-		0	-	0	-	0	-		0	-	0	-	0	-		0	-	0	-	0	-
PROTEACEAE	*Helicia excelsa*		0	-	0	-	0	-		0	-	0	-	0	-		0	-	0	-	0	-		0	-	0	-	0	-
	Helicia formosana		0	-	0	-	0	-		0	-	0	-	0	-		0	-	0	-	0	-		0	-	0	-	0	-
	Helicia nilagirica		0	-	0	-	0	-		0	-	0	-	0	-		0	-	0	-	0	-		0	-	0	-	0	-
RHAMNACEAE	*Zizyplus attopoensis*	-	1	-	0	-	0	-	-	0	-	0	-	0	-	-	0	-	0	-	0	-	9	1	2	0	-	1	2
RHIZOPHORACEA	*Carallia brachiata*	-	1	-	0	-	0	-	-	0	-	0	-	0	-	-	0	-	0	-	0	-	17	1	2	1	2	0	-
ROSACEAE	*Canthium glabrum*	265	1	1	1	2	1	1	-	0	-	0	-	0	-	151	1	1	1	1	1	2	489	1	1	1	1	0	-
	Prunus arborea	-	1	-	0	-	0	-	412	0	-	0	-	0	-	-	0	-	0	-	0	-	845	1	1	1	1	0	-
	Prunus javanica	840	1	2	0	-	1	2	1276	1	1	1	1	1	1	832	1	1	0	-	1	1	-	0	-	0	-	0	-
RUBIACEAE	*Acronychia pedunculata*		0	-	0	-	0	-		0	-	0	-	0	-		0	-	0	-	0	-		0	-	0	-	0	-
	Aidia cochinchinensis		0	-	0	-	0	-		0	-	0	-	0	-		0	-	0	-	0	-		0	-	0	-	0	-
	Clausena excavata		0	-	0	-	0	-		0	-	0	-	0	-		0	-	0	-	0	-		0	-	0	-	0	-
	Neolarmarkia cadamba		0	-	0	-	0	-		0	-	0	-	0	-		0	-	0	-	0	-		0	-	0	-	0	-
	Neonauclea excelsa		0	-	0	-	0	-		0	-	0	-	0	-		0	-	0	-	0	-		0	-	0	-	0	-
	Randia ecodom		0	-	0	-	0	-		0	-	0	-	0	-		0	-	0	-	0	-		0	-	0	-	0	-
	Zanthoxylum rhetsa		0	-	0	-	0	-		0	-	0	-	0	-		0	-	0	-	0	-		0	-	0	-	0	-
SABIACEAE	*Meliosma pinnata*		0	-	0	-	0	-		0	-	0	-	0	-		0	-	0	-	0	-		0	-	0	-	0	-
SANTALACEAE	*Scleropyrum wallichianum*		0	-	0	-	0	-		0	-	0	-	0	-		0	-	0	-	0	-		0	-	0	-	0	-
SAPINDACEAE	*Dimocarpus longon*		0	-	0	-	0	-		0	-	0	-	0	-		0	-	0	-	0	-		0	-	0	-	0	-

Appendix D List of important and least consumed of food and non-food plant species in different breeding phases of four hornbill species “-” no data Abbreviation: W = Pulp weight (g), Incub = Incubation, Nesl = Nestling, F = Food or non-food: 0 = non-eaten, 1 = eaten, IM = Important species or least consumed: 1 = Important, 0 = Less consumed (Continued)

Family	Species	GH							WH							BH							PH						
		W	Total		Incub.		Nestl.		W	Total		Incub.		Nestl.		W	Total		Incub.		Nestl.		W	Total		Incub.		Nestl.	
		(g)	F	IM	F	IM	F	IM	(g)	F	IM	F	IM	F	IM	(g)	F	IM	F	IM	F	IM	(g)	F	IM	F	IM	F	IM
	Lepisanthes sp.		0	-	0	-	0	-		0	-	0	-	0	-		0	-	0	-	0	-		0	-	0	-	0	-
	Lepisanthes tetraphylla		0	-	0	-	0	-		0	-	0	-	0	-		0	-	0	-	0	-		0	-	0	-	0	-
	Nephelium melliferum		0	-	0	-	0	-		0	-	0	-	0	-		0	-	0	-	0	-		0	-	0	-	0	-
SAPOTACEAE	*Sarcosperma arboreum*		0	-	0	-	0	-		0	-	0	-	0	-		0	-	0	-	0	-		0	-	0	-	0	-
SIMAROUBACEAE	*Ailanthus triphysa*		0	-	0	-	0	-		0	-	0	-	0	-		0	-	0	-	0	-		0	-	0	-	0	-
SONNERATIACEAE	*Duabanga grandiflora*		0	-	0	-	0	-		0	-	0	-	0	-		0	-	0	-	0	-		0	-	0	-	0	-
STAPHYLEACEAE	*Turpinia montana*		0	-	0	-	0	-		0	-	0	-	0	-		0	-	0	-	0	-		0	-	0	-	0	-
	Pterospermium cinnamomeum		0	-	0	-	0	-		0	-	0	-	0	-		0	-	0	-	0	-		0	-	0	-	0	-
	Sterculia balanghas	156	1	2	0	-	1	2	116	1	2	1	2	0	-	-	0	-	0	-	0	-	-	0	-	0	-	0	-
SYMPLOCACEAE	*Symplocos cochinchinensis*		0	-	0	-	0	-		0	-	0	-	0	-		0	-	0	-	0	-		0	-	0	-	0	-
	Symplocos sumuntia		0	-	0	-	0	-		0	-	0	-	0	-		0	-	0	-	0	-		0	-	0	-	0	-
THEACEAE	*Adinandra integerrima*		0	-	0	-	0	-		0	-	0	-	0	-		0	-	0	-	0	-		0	-	0	-	0	-
	Aglaia edulis		0	-	0	-	0	-		0	-	0	-	0	-		0	-	0	-	0	-		0	-	0	-	0	-
	Eurya nitida		0	-	0	-	0	-		0	-	0	-	0	-		0	-	0	-	0	-		0	-	0	-	0	-
	Schima wallichii		0	-	0	-	0	-		0	-	0	-	0	-		0	-	0	-	0	-		0	-	0	-	0	-
	Ternstroemia wallichiana	454	1	1	0	-	1	1	455	1	1	0	-	1	1	905	1	1	1	1	1	1	-	0	-	0	-	0	-
THYMELAEACEAE	*Aquillaria crassna*		0	-	0	-	0	-		0	-	0	-	0	-		0	-	0	-	0	-		0	-	0	-	0	-
ULMACEAE	*Aphananthe cuspidata*		0	-	0	-	0	-		0	-	0	-	0	-		0	-	0	-	0	-		0	-	0	-	0	-
	Gironniera nervosa		0	-	0	-	0	-		0	-	0	-	0	-		0	-	0	-	0	-		0	-	0	-	0	-
	Trema orientalis		0	-	0	-	0	-		0	-	0	-	0	-		0	-	0	-	0	-		0	-	0	-	0	-
XANTHOPYLLACEAE	*Xanthophyllum virens*		0	-	0	-	0	-		0	-	0	-	0	-		0	-	0	-	0	-		0	-	0	-	0	-
Summary																													
Average		1180							2270							881							763						
SD		1845							4433							776							725						
Median		447							914							587							582						
Number of species			31	25	6	6	25	25		22	22	18	18	20	20		22	22	12	12	21	21		24	24	21	21	18	18
Number of genus			29	23	6	6	23	23		20	20	17	17	18	18		19	20	12	12	19	19		22	22	20	20	16	17
Number of family			15	11	5	5	10	11		11	10	9	9	9	7		10	9	7	7	9	9		12	12	11	11	7	7
Total number of species	167																												
Total number of genus	139																												
Total number of family	68																												

Appendix E Species diversity and values of important species determined during two non-breeding seasons (2004-2005) “*” = uncountable seed number

GH: Seed trap		2004			2005		
Family	Species	Number	% Number	% Pulp	Number	% Number	% Pulp
Moraceae	*Ficus* spp.	*	*	*	*	*	*
Lauraceae	*Beichemiedia balansae*	13	**23.6**	*11.1*			
Burseraceae	*Canarium euphyllum*	5	**9.1**	**35.6**	5	*3.3*	*8.8*
Lauraceae	*Cinnamamum ilicioides*				36	**23.5**	*1.6*
Ulmaceae	*Gironniera nervosa*				9	*5.9*	*0.2*
Palmae	*Livistona speciosa*	9	**16.4**	**34.1**	82	**53.6**	**77.1**
Cornaceae	*Mastixia pentandra*	2	**3.6**	*4.5*	1	*0.7*	*0.6*
Lauraceae	*Phoebe cathia*	1	**1.8**	*0.9*			
Icacinaceae	*Platea latifolia*	6	**10.9**	**14.0**	19	**12.4**	**11.0**
Annonaceae	*Polyalthia jucunda*				1	*0.7*	*0.7*
	Unk (1 species)	19	*34.5*	-			
Grand Total		**55**	**100**	**100**	**153**	**100**	**100**

WH: Seed trap		2004			2005		
Family	Species	Number	% Number	% Pulp	Number	% Number	% Pulp
Moraceae	*Ficus* spp.	*	*	*	*	*	*
Meliaceae	*Agaia spectabilis*				1	*0.2*	*0.9*
Alangiaceae	*Alangium kurzii*	29	*1.8*	*0.4*	34	**6.7**	*0.2*
Annonaceae	*Alphonsea boniana*				6	*1.2*	*1.2*
Ulmaceae	*Aphananthe cuspidata*	23	*1.4*	-			
Lauraceae	*Beichemiedia balansae*	19	*1.2*	*0.5*			
Theaceae	*Camelia* sp.	1	*0.1*	-			
Burseraceae	*Canarium euphyllum*	93	**5.7**	**20.8**	84	**16.6**	**9.9**
Flacourtiaceae	*Caseasia grewiawfolia*	9	*0.6*	*1.2*			
Oleaceae	*Chionanthus ramiflorus*				1	*0.2*	*0.0*
Lauraceae	*Cinnamomum glaucescens*	172	10.6	**15.3**			
Lauraceae	*Cinnamomum ilicioides*				4	*0.8*	*0.0*
Rutaceae	*Clausena excavata*				2	*0.4*	*0.0*
Annonaceae	*Cyathostemma micranthum*	1	*0.1*	*0.0*			
Gnetaceae	*Gnetum montanum*	8	*0.5*	*0.7*			
Myristicaceae	*Horsfieldia glabra*	10	*0.6*	*1.5*	5	*1.0*	*0.4*
Palmae	*Livistona speciosa*				26	*5.1*	*1.6*
Euphorbiaceae	*Mallotus phillippensis*				1	*0.2*	*0.0*
Cornaceae	*Mastixia pentandra*	699	**43.1**	**49.3**	212	**41.9**	*7.9*
Magnoliaceae	*Michelia baillonii*				50	**9.9**	**75.4**
Annonaceae	*Miliusa lineata*				10	*2.0*	*0.8*
Lauraceae	*Persea gambeil*	102	**6.3**	-	20	*4.0*	-
Lauraceae	*Phoebe cathia*	217	**13.4**	*5.9*			
Piperaceae	*Piper ribesioides*	2	*0.1*	-			
Icacinaceae	*Platea latifolia*	60	**3.7**	*4.4*	35	**6.9**	*1.3*
Annonaceae	*Polyalthia jucunda*				3	*0.6*	*0.1*
Annonaceae	*Polyalthia viridis*	1	*0.1*	*0.1*	2	*0.4*	*0.1*
Meliaceae	*Walsura robusta*				1	*0.2*	*0.0*
	Unk (6 species)				9	*1.8*	-
Grand Total		**1446**	**89.204195**	**100**	**506**	**100**	**99.999**

Appendix E Species diversity and values of important species determined during two non-breeding seasons (2004-2005) "*" = uncountable seed number (Continued)

PH: Seed trap		2004			2005		
Family	Species	Number	% Number	% Pulp	Number	% Number	% Pulp
Moraceae	*Ficus spp.*	*	*	*	*	*	*
Burseraceae	*Canarium euphyllum*	1	**0.3**	*8.2*	31	**27.7**	**13.7**
Flacourtiaceae	*Caseasia grewiaefolia*	2	**0.6**	**9.8**			
Ulmaceae	*Celtis tetrandra*				6	**5.4**	*0.0*
Oleaceae	*Chionanthus ramiflorus*				2	*1.8*	*0.2*
Lauraceae	*Cinnamomum glaucescens*	7	**2.2**	**22.9**			
Annonaceae	*Cyathostemma micranthum*	1	**0.3**	*0.9*			
Gnetaceae	*Gnetum montanum*	7	**2.2**	**21.1**	2	*1.8*	*0.3*
Cornaceae	*Mastixia pentandra*	1	**0.3**	*2.6*	19	**17.0**	*2.6*
Magnoliaceae	*Michellia ballonii*				14	**12.5**	**79.3**
Lauraceae	*Persea gamblei*	180	**56.1**	-			
Piperaceae	*Piper ribesioides*	3	**0.9**	-			
Icacinaceae	*Platea latifolia*	5	**1.6**	**13.5**	25	**22.3**	*3.6*
Annonaceae	*Polyalthia jucunda*				1	*0.9*	*0.2*
Annonaceae	*Polyalthia viridis*	2	**0.6**	*6.9*			
Myrtaceae	*Syzygium* sp.1	2	**0.6**	**14.0**			
	Unk (2 species)	110	34.3	-			
Grand Total		**321.0**	**100.0**	**100.0**	**100.0**	**89.3**	**100.0**

BH: Seed trap		2004	2005		
Family	Species		Number	% Number	% Pulp
Burseraceae	*Canarium euphyllum*		1	*2.3*	*7.0*
Cornaceae	*Mastixia pentandra*	NO DATA	41	**95.3**	**90.7**
Icacinaceae	*Platea latifolia*		1	*2.3*	*2.3*
Grand Total			**43**	**100**	**100.03**

Appendix Fa Important species (Bold) of food consumed by hornbill and their nutritional values in the breeding season year 2004

GH	Pulp (%)					Protein (%)					Fat (%)				
	Incubation		Nestling			Incubation		Nestling			Incubation		Nestling		
	Jan	Feb	Mar	Apr	May	Jan	Feb	Mar	Apr	May	Jan	Feb	Mar	Apr	May
ANNONACEAE															
Desmos chinensis			**8.0**	**5.6**				*1.0*	*0.0*				*0.2*	*0.0*	
Polyalthia viridis		**35.9**	**11.7**	**8.1**	**11.7**		*10.0*	**22.2**	**28.4**	**12.6**		*4.6*	**17.7**	**29.1**	*7.7*
CELASTORACEAE															
Bhesa robusta			*6.9*	**4.8**				**18.6**	*0.7*				-	-	
COMBRETACEAE															
Combretum acuminatum				**5.1**	**7.3**				-	-				-	-
ICACINACEAE															
Platea latifolia															
LAURACEAE															
Beilschiedia balansae				**4.2**					*0.1*					*0.1*	
Beilschmeidia maingayi				**4.5**	**6.5**				*3.5*	*1.5*				-	-
Cryptocarya impressa				**5.3**					*0.2*					*0.4*	
MELIACEAE															
Aglaia lawii			*5.0*	*3.5*	*5.1*			**10.5**	*0.5*	**18.4**			**30.5**	*1.9*	**41.0**
Aglaia spectabilis				*3.9*	**5.7**				**13.9**	**49.4**				**19.2**	**40.8**
Dysoxylum cyrtobotryum			**9.1**		**8.3**			*5.4*	*4.7*	*5.5*				*5.8*	
Dysoxylum densiflorum				**6.3**	**8.6**					*6.1*			-	-	-
MORACEAE															
Antiaris toxicaria			*5.9*					-	-					-	
Ficus spp.	**100.0**	**30.1**	**9.8**	**6.8**	**9.9**	**100.0**	**60.2**	**34.6**	**44.2**	*5.9*	**100.0**	**17.3**	*17.2*	**28.4**	*2.2*
MYRISTICACEAE															
Horsfieldia glabra				**7.3**	**10.5**				*0.2*	*0.3*				*1.5*	*1.7*
Knema lauriana															
MYRTACEAE															
Syzygium sp.				**8.9**	**12.8**				*0.5*	*0.4*				*1.8*	*0.8*
PALMAE															
Livistona speciosa		**33.9**	**11.0**	**7.7**			**29.8**	*7.6*	*3.0*			**78.1**	**34.5**	**17.6**	
ROSACEAE															
Prunus javanicus			**12.3**	**8.6**				-	-				-	-	
RUBIACEAE															
Cantium glabrum			**7.1**					-						-	
STERCULIACEAE															
Sterculia sp.															
THEACEAE															
Ternstroemia wallichiana			**13.3**					-						-	

Appendix Fa Important species (Bold) of food consumed by hornbill and their nutritional values in the breeding season year 2004 (Continued)

GH	Ca (%)					ADF (%)					Calory (%)					Tannin (%)				
	Incubation		Nestling			Incubation		Nestling			Incubation		Nestling			Incubation		Nestling		
	Jan	Feb	Mar	Apr	May	Jan	Feb	Mar	Apr	May	Jan	Feb	Mar	Apr	May	Jan	Feb	Mar	Apr	May
ANNONACEAE																				
Desmos chinensis			*1.0*	*0.0*				-	-				*1.3*	*0.0*				*6.5*	*0.2*	
Polyalthia viridis		*3.8*	**11.4**	**12.4**	**9.2**		*5.5*	**21.9**	**22.8**	**15.5**		*6.0*	**17.7**	**23.4**	**10.5**		*8.9*	**19.6**	**25.8**	**12.8**
CELASTORACEAE																				
Bhesa robusta			**9.6**	*0.3*				-	-				**14.5**	*0.6*				-	-	
COMBRETACEAE																				
Combretum acuminatum				-	-				-	-				-	-				-	-
ICACINACEAE																				
Platea latifolia																				
LAURACEAE																				
Beilschiedia balansae				*0.1*					*0.1*					*0.1*					-	
Beilschmeidia maingayi				*1.7*	*1.2*				-	-				*2.8*	*1.2*				-	-
Cryptocarya impressa				*0.1*					*0.1*					*0.2*					*0.1*	
MELIACEAE																				
Aglaia lawii			*5.1*	*0.2*	**12.8**			*3.5*	*0.1*	*7.7*			*10.6*	*0.5*	**19.4**			**15.2**	*0.8*	**30.8**
Aglaia spectabilis				*8.5*	**50.6**				*10.7*	**58.8**				**13.7**	**49.7**				*6.6*	**26.2**
Dysoxylum cyrtobotryum				*4.7*					*4.7*					*5.8*					*1.8*	
Dysoxylum densiflorum			*2.4*	*1.8*	*3.9*			-	-	-			*4.6*	*4.2*	*5.5*			**14.4**	**13.1**	**18.9**
MORACEAE																				
Antiaris toxicaria			-						-					-					-	
Ficus spp.	**100.0**	**84.7**	**66.5**	**72.6**	**16.2**	**100.0**	**55.5**	**56.9**	**59.4**	**12.1**	**100**	**46.5**	**35.3**	**46.7**	**6.3**	**100**	**66.8**	**38.1**	**50.1**	*7.5*
MYRISTICACEAE																				
Horsfieldia glabra				*0.1*	*0.3*				-	-				*0.5*	*1.0*				*0.9*	*2.0*
Knema lauriana																				
MYRTACEAE																				
Syzygium sp.				*0.8*	*1.1*				*1.0*	*1.2*				*0.7*	*0.6*				*0.0*	-
PALMAE																				
Livistona speciosa		*11.5*	*4.0*	*1.4*			**39.0**	**17.8**	*5.7*			**47.4**	**16.0**	*6.5*			**24.3**	*6.2*	*2.5*	
ROSACEAE																				

Appendix Fa Important species (Bold) of food consumed by hornbill and their nutritional values in the breeding season year 2004 (Continued)

WH	Pulp (%)					Protein (%)					Fat (%)				
	Incubation		Nestling			Incubation		Nestling			Incubation		Nestling		
	Feb	Mar	Apr	May	Jun	Feb	Mar	Apr	May	Jun	Feb	Mar	Apr	May	Jun
ANNONACEAE															
Desmos chinensis			**7.4**					*0.0*					*0.0*		
Polyalthia viridis	**10.6**	**12.0**	**11.0**	**11.2**	**20.1**	**14.3**	**27.0**	**26.1**	**28.5**	**40.6**	*7.1*	**14.4**	**21.8**	**33.9**	**33.3**
CELASTORACEAE															
Bhesa robusta		*7.0*	**6.5**	**6.6**			*7.6*	*0.1*	*0.1*			-	-	-	
ELAEAGNEACEAE															
Elaeagnus latifolia			**8.3**					*4.7*					*0.0*		
LAURACEAE															
Beilschiedia balansae	**5.5**	*6.1*				*0.5*	*0.4*				*0.3*	*0.2*			
Beilschmeidia maingayi			*6.1*	*6.2*				*4.3*	*2.3*				-	-	
Cryptocarya impressa			**7.1**	**7.1**	**13.0**			*0.4*	*1.5*	*0.7*			*0.6*	*2.9*	*0.9*
MELIACEAE															
Aglaia lawii		*5.2*	*4.8*	*4.9*			**15.0**	*3.0*	*1.0*			**29.1**	*9.0*	*4.5*	
Aglaia spectabilis			*5.4*	*5.5*	*9.8*			**45.0**	**33.3**	**51.2**			**50.6**	**53.5**	**56.6**
Aphanamixis polystachya			*5.3*					*2.3*					-		
Dysoxylum densiflorum	**8.2**	**8.6**	**8.5**	**16.7**		**14.7**	**25.1**	*6.3*	*3.4*		-	-	-	-	
MORACEAE															
Ficus sp	**9.0**	**10.2**	**9.4**	**9.5**	**17.1**	**36.9**	**34.1**	**12.2**	*4.4*	*4.0*	**11.5**	*11.4*	*6.4*	*3.3*	*2.0*
MYRISTICACEAE															
Horsfieldia glabra			**9.5**					*3.9*					**17.7**		
Knema lauriana	**9.6**	**10.9**	**18.2**			*0.6*	*1.1*	*3.2*			*0.7*	*1.4*	*6.2*		
MYRTACEAE															
Syzygium sp.		**13.0**	**12.0**	**12.1**	**21.8**		*1.3*	*0.3*	*0.4*	*0.4*		*2.6*	*0.9*	*1.8*	*1.1*
PALMAE															
Livistona speciosa	**9.9**	**11.1**	**10.3**			**22.1**	**13.5**	*2.3*			**62.7**	**40.9**	**10.8**		
ROSACEAE															
Prunus arboria			**12.0**					-					-		
Prunus javanicus		**12.4**	**11.5**	**11.6**			-	-	-			-	-	-	
THEACEAE															
Ternstroemia wallichiana			**11.9**					-					-		

Appendix Fa Important species (Bold) of food consumed by hornbill and their nutritional values in the breeding season year 2004 (Continued)

WH	Ca (%)					ADF (%)					Calory (%)					Tannin (%)				
	Incubation		Nestling			Incubation		Nestling			Incubation		Nestling			Incubation		Nestling		
	Feb	Mar	Apr	May	Jun	Feb	Mar	Apr	May	Jun	Feb	Mar	Apr	May	Jun	Feb	Mar	Apr	May	Jun
ANNONACEAE																				
Desmos chinensis			*0.1*					-					*0.1*					*0.4*		
Polyalthia viridis	**7.0**	**13.6**	**17.2**	**23.2**	**30.1**	*10.5*	**21.7**	**26.8**	**40.5**	**41.5**	9.0	**19.7**	**22.2**	**25.7**	**35.7**	*9.3*	**25.1**	**28.6**	**20.2**	**53.4**
CELASTORACEAE																				
Bhesa robusta		*3.9*	*0.1*	*0.1*			-	-	-			*5.4*	*0.1*	*0.1*			-	-	-	
ELAEAGNEACEAE																				
Elaeagnus latifolia			*2.3*					*5.7*					*1.8*					*1.9*		
LAURACEAE																				
Beilschiedia balansae	*0.4*	*0.3*				*0.2*	*0.2*				*0.4*	*0.3*				-	-			
Beilschmeidia maingayi			*3.2*	*2.1*				-	-				*3.6*	*2.0*				-	-	
Cryptocarya impressa			*0.2*	*0.8*	*0.3*			*0.3*	*1.3*	*0.4*			*0.4*	*1.4*	*0.6*			*0.3*	*0.7*	*0.6*
MELIACEAE																				
Aglaia lawii		**7.1**	*1.8*	*0.8*			*4.1*	*1.0*	*0.5*			**13.8**	*3.2*	*1.2*			**22.8**	*5.3*	*1.2*	
Aglaia spectabilis			**41.3**	**37.8**	**52.9**			**44.6**	**45.6**	**50.4**			**45.9**	**36.1**	**54.0**			**25.6**	**12.3**	**35.1**
Aphanamixis polystachya			*1.0*					-					*2.4*					*0.3*		
Dysoxylum densiflorum	*6.3*	**12.5**	*3.6*	*7.9*		-	-	-	-		**9.9**	**17.0**	*5.7*	**10.7**		**29.0**	**37.8**	**20.9**	**23.9**	
MORACEAE																				
Ficus spp.	**68.2**	**64.4**	**30.2**	**13.5**	*11.1*	**45.2**	**45.7**	**21.0**	*10.5*	*6.8*	**29.7**	**31.8**	**13.3**	*5.1*	*4.5*	**30.0**	**39.5**	**16.7**	*3.9*	*6.5*
MYRISTICACEAE																				
Horsfieldia glabra			*2.9*					-					**9.6**					**16.0**		
Knema lauriana	*0.6*	*1.1*	*4.4*			-	-	-			*0.6*	*1.3*	*4.6*			*0.4*	*1.1*	*4.4*		
MYRTACEAE																				
Syzygium sp.		*2.7*	*0.8*	*1.4*	*1.1*		*2.7*	*0.8*	*1.5*	*1.0*		*1.8*	*0.5*	*0.7*	*0.6*		-	-	-	-
PALMAE																				
Livistona speciosa	**11.2**	*7.0*	*1.5*			**38.4**	**25.6**	*5.5*			**36.6**	**25.9**	*5.1*			**13.2**	*11.5*	*2.3*		
ROSACEAE																				
Prunus arboria			-					-					-					-		
Prunus javanicus		-	-	-			-	-	-			-	-	-			-	-	-	
THEACEAE																				
Ternstroemia wallichiana			-					-					-					-		

Appendix Fa Important species (Bold) of food consumed by hornbill and their nutritional values in the breeding season year 2004 (Continued)

PH	Pulp (%)				Protein (%)				Fat (%)			
	Incubation		Nestling		Incubation		Nestling		Incubation		Nestling	
	Mar	Apr	May	Jun	Mar	Apr	May	Jun	Mar	Apr	May	Jun
ANNONACEAE												
Polyalthia viridis	**14.83**	**7.45**	**10.07**	**9.93**	*9.49*	**28.41**	**25.85**	**8.72**	*6.35*	**30.56**	**15.70**	*6.05*
CELASTORACEAE												
Bhesa robusta	**8.72**	**4.38**			**13.44**	*1.41*			-	-		
COMBRETACEAE												
Combretum acuminatum		**4.62**	**6.22**			-	-			-		
GNETACEAE												
Gnetum montanum		**8.60**				-				-		
ICACINACEAE												
Platea latifolia		**9.37**				*1.14*				-		
LAURACEAE												
Beilschiedia balansae		**7.62**				*0.11*				*0.09*		
Beilschmeidia maingayi	**8.17**	*4.10*	**5.56**		*2.09*	**6.97**	*1.95*		-	-	-	
Cryptocarya impressa		**4.79**	**6.45**	**6.47**		*0.34*	*0.64*	*0.30*		*0.59*	*0.63*	*0.34*
MELIACEAE												
Aglaia lawii	*6.45*	*3.22*	*4.39*	*4.30*	**30.88**	*3.97*	*8.10*	*3.07*	**75.17**	**15.53**	**17.90**	*7.75*
Aglaia spectabilis		*3.62*	**4.89**			*5.37*	**11.87**			*7.80*	*9.73*	
Dysoxylum cyrtobotryum		**5.28**	**7.14**	**7.06**		*0.49*	**12.30**	**39.13**		*0.90*	**12.77**	**46.47**
Dysoxylum densiflorum	**7.41**	**5.75**	**7.74**	**14.63**	*0.48*	**15.41**	**8.72**	**35.72**	-	-	-	-
MORACEAE												
Ficus spp.	**12.56**	**6.30**	**8.53**	**8.41**	**43.98**	**31.54**	**16.92**	*5.78*	**18.39**	**21.20**	*6.42*	*2.51*
MYRISTICACEAE												
Horsfieldia glabra		**6.67**	**9.00**	**8.90**		*0.07*	*2.24*	*5.66*		*0.65*	**12.34**	**35.63**
Knema lauriana		**6.84**				*0.85*				*2.18*		
MYRTACEAE												
Syzygium sp.		**8.11**	**10.93**	**10.81**		*5.18*	**10.93**	*0.49*		**20.58**	**24.53**	*1.25*
ROSACEAE												
Prunus javanicus	**15.49**	**7.80**			-	-			-	-		
RUBIACEAE												
Cantium glabrum	**8.97**	**4.51**			-	-			-	-		
STERCULIACEAE												
Sterculia sp.		**7.93**				-				-		

Appendix Fa Important species (Bold) of food consumed by hornbill and their nutritional values in the breeding season year 2004 (Continued)

PH	ADF (%)				Calory (%)				Tannin (%)			
	Incubation		Nestling		Incubation		Nestling		Incubation		Nestling	
	Mar	Apr	May	Jun	Mar	Apr	May	Jun	Mar	Apr	May	Jun
ANNONACEAE												
Polyalthia viridis	*10.15*	**27.94**	**24.47**	**17.81**		**24.19**	**20.00**	*14.48*	*8.26*	**22.59**	**22.88**	*4.88*
CELASTORACEAE												
Bhesa robusta	-	-			**10.90**	*1.17*			-	-		
COMBRETACEAE												
Combretum acuminatum		-	-			-	-			-	-	
GNETACEAE												
Gnetum montanum		-				-				-		
ICACINACEAE												
Platea latifolia		*2.77*				*1.09*				*0.08*		
LAURACEAE												
Beilschiedia balansae		*0.08*				*0.11*				-		
Beilschmeidia maingayi	-	-	-		*1.71*	*5.80*	*1.48*		-	-	-	
Cryptocarya impressa		*0.20*	*0.37*	*0.38*		*0.30*	*0.51*	*0.23*		*0.17*	*0.35*	*0.11*
MELIACEAE												
Aglaia lawii	**11.16**	*1.32*	*2.59*	*2.12*	**32.43**	*4.26*	**7.90**	*2.92*	**43.97**	*5.17*	**11.74**	*2.81*
Aglaia spectabilis		*5.09*	**10.84**			*5.50*	**11.04**			*2.23*	*5.47*	
Dysoxylum cyrtobotryum		*0.33*	*7.95*	**54.59**		*0.53*	**11.99**	**37.21**		*0.13*	*3.54*	*7.13*
Dysoxylum densiflorum	-	-	-	-	*0.40*	**14.12**	*7.26*	**29.00**	*1.31*	**37.35**	**23.52**	**60.99**
MORACEAE												
Ficus spp.	**78.61**	**51.83**	**26.78**	**19.73**	**46.95**	**34.43**	**16.78**	*5.59*	**47.77**	**31.32**	**18.70**	*4.04*
MYRISTICACEAE												
Horsfieldia glabra		-	-	-		*0.22*	*6.78*	**16.69**		*0.33*	**12.49**	**19.96**
Knema lauriana		-				*1.22*				*0.72*		
MYRTACEAE												
Syzygium sp.		**13.29**	**27.00**	*2.60*		**8.27**	**15.86**	*0.69*		-	-	-
ROSACEAE												
Prunus javanicus	-	-			-	-			-	-		
RUBIACEAE												
Cantium glabrum	-	-			-	-			-	-		
STERCULIACEAE												
Sterculia sp.		-				-				-		

Appendix Fa Important species (Bold) of food consumed by hornbill and their nutritional values in the breeding season year 2004 (Continued)

BH	Pulp (%)				Protein (%)				Fat (%)				Ca (%)			
	Incubation		Nestling		Incubation		Nestling		Incubation		Nestling		Incubation		Nestling	
	Mar	Apr	May	Jun	Mar	Apr	May	Jun	Mar	Apr	May	Jun	Mar	Apr	May	Jun
ANNONACEAE																
Desmos chinensis	**11.7**	**6.5**			*0.7*	*0.5*			*0.1*	*0.2*			*1.2*	*0.7*		
Polyalthia viridis	**17.0**	**9.4**	**8.9**		**37.9**	**18.6**	*1.5*		**25.2**	**22.7**	*1.2*		**32.5**	**13.9**	*1.1*	
CELASTORACEAE																
Bhesa robusta	**10.1**	**5.6**			**25.3**	*3.8*			-	-			**21.9**	*2.9*		
ICACINACEAE																
Platia latifolia				**14.7**				*0.6*				-				*1.8*
LAURACEAE																
Beilschiedia balansae		**5.0**				*0.1*				*0.1*				*0.1*		
Beilschmeidia maingayi		**5.2**				**27.6**	*3.5*			-				**23.3**	*3.1*	
Cryptocarya impressa		**6.1**				*0.6*	*0.8*			*1.3*	*1.1*			*0.3*		
MELIACEAE																
Aglaia lawii	**7.2**	*3.9*			**29.8**	*9.2*	**8.1**		**72.1**	**40.8**	**24.8**		**24.1**	*6.4*	*6.0*	
Aglaia spectabilis		*4.4*		*7.1*		**14.6**	**6.9**	*7.7*		**24.1**	*7.8*	*8.9*		**15.2**	**7.5**	*9.3*
Dysoxylum cyrtobotryum		**6.7**	**6.4**	*10.7*		*1.7*	**26.3**	**56.1**		*3.5*	**37.9**	**82.8**		*1.5*	**23.9**	**56.5**
Dysoxylum densiflorum		**7.4**	**13.5**	**11.1**		**13.7**	**43.5**	**33.2**		-		-		**8.9**	**29.9**	**25.3**
MORACEAE																
Ficus spp.	**14.2**	**7.8**	**7.4**	**12.3**	*6.3*	**9.6**	*1.8*	*0.8*	*2.6*	*7.3*	*1.0*	*0.4*	**20.4**	**26.8**	*5.4*	*2.5*
MYRISTICACEAE																
Horsfieldia glabra			**8.0**	**13.5**				*0.6*			*4.6*	*4.4*			*0.7*	*0.7*
Knema lauriana			**8.3**	**14.1**				*0.1*			*0.3*	*0.1*				*0.1*
MYRTACEAE																
Syzygium sp.			**9.8**	**16.5**			*6.9*	*1.1*			**21.4**	*3.4*			**21.8**	*3.7*
ROSACEAE																
Prunus javanicus		**10.1**	**9.4**			-				-				-		
STERCULIACEAE																
Sterculia sp.			**9.7**													
THEACEAE																
Ternstroemia wallichiana	**19.7**	**10.9**			-	-			-	-			-	-		

Appendix Fa Important species (Bold) of food consumed by hornbill and their nutritional values in the breeding season year 2004 (Continued)

BH	ADF (%)				Calory (%)				Tannin (%)			
	Incubation		Nestling		Incubation		Nestling		Incubation		Nestling	
	Mar	Apr	May	Jun	Mar	Apr	May	Jun	Mar	Apr	May	Jun
ANNONACEAE												
Desmos chinensis	-	-	-		*1.1*	*0.8*			*5.6*	*3.7*		
Polyalthia viridis	**64.7**	**34.8**	*2.9*		**34.6**	**17.0**	*1.2*		**37.8**	**18.7**	*0.9*	
CELASTORACEAE												
Bhesa robusta	-	-			**22.5**	*3.4*			-	-		
ICACINACEAE												
Platia latifolia				*1.5*				*0.6*				*0.1*
LAURACEAE												
Beilschiedia balansae		*0.1*				*0.1*				-		
Beilschmeidia maingayi		-				**24.8**	*2.8*			-	-	
Cryptocarya impressa		*0.7*	*0.9*			*0.6*				*0.4*	*0.3*	
MELIACEAE												
Aglaia lawii	**17.2**	**5.8**	**5.4**		**34.3**	*10.6*	**8.4**		**48.7**	**15.1**	**8.0**	
Aglaia spectabilis		**26.4**	**13.2**	**14.7**		**16.1**	*6.8*	*7.6*		*7.6*	*2.2*	*3.1*
Dysoxylum cyrtobotryum		*2.2*	**35.7**	**75.9**		*2.0*	**27.2**	**58.1**		*0.6*	*5.2*	**14.3**
Dysoxylum densiflorum		-	-	-		**13.5**	**38.4**	**29.4**		**41.9**	**79.8**	**79.0**
MORACEAE												
Ficus spp.	**18.1**	**30.0**	*6.1*	*2.6*	*7.4*	**11.3**	*1.9*	*0.8*	*7.9*	**12.0**	*1.4*	*0.8*
MYRISTICACEAE												
Horsfieldia glabra				-			*1.9*	*1.8*			*2.3*	*2.7*
Knema lauriana				-				*0.1*			*0.1*	*0.0*
MYRTACEAE												
Syzygium sp.			**35.7**	*5.4*			**10.6**	*1.6*			-	-
ROSACEAE												
Prunus javanicus		-				-				-	-	
STERCULIACEAE												
Sterculia sp.											-	
THEACEAE												
Ternstroemia wallichiana	-	-			-	-			-	-		

Appendix Fb Important species (in bold) of fruit food species consumed by four hornbill species and percentage of pulp and multitional values in 2005 breeding season

GH	Pulp (%)					Protein (%)					Fat (%)				
	Incubation		Nestling			Incubation		Nestling			Incubation		Nestling		
	Jan	Feb	Mar	Apr	May	Jan	Feb	Mar	Apr	May	Jan	Feb	Mar	Apr	May
ANNONACEAE															
Desmos chinensis		*11.4*	*1.8*				*12.1*	*1.1*				*1.7*	*0.5*		
Polyalthai jucunda			*5.8*	**11.0**				*7.8*	**24.7**				*5.4*	*5.1*	
Polyalthia viridis	*1.4*			**11.7**	**16.6**	*2.9*			**22.4**	**33.0**	*3.1*			**11.0**	**23.1**
CELASTORACEAE															
Bhesa robusta			*0.1*					*0.1*					-		
ELAEAGNEACEAE															
Elaeagnus latifolia			**8.2**					*4.6*					*0.1*		
LAURACEAE															
Beilschmiedia balansae				*0.2*					*0.2*					*0.1*	
Beilschmiedia glabra				*0.0*					*0.0*					*0.1*	
Beilschmiedia sp.		-		-			-		-			-		-	
Cinnamomum subavenium	*6.9*	**33.3**	**17.2**	*2.5*		*8.1*	**37.5**	**11.4**	*2.8*		*37.5*	**82.3**	**81.0**	*5.8*	
MELIACEAE															
Dysoxylun densiflorum			**47.0**		*0.6*			**64.8**		*1.5*			-		-
Aglaia spectabillis			*4.8*	**31.5**	**55.4**			*2.1*	**22.3**	**41.0**			*4.6*	**14.7**	**38.7**
MORACEAE															
Arthocarpus lakooxha				*3.8*					*3.9*					*2.7*	
Ficus spp	**91.7**	**54.3**	**14.9**	**11.4**	**20.9**	**89.0**	**50.4**	**8.2**	*10.4*	**19.8**	**59.4**	*16.0*	*8.4*	*3.2*	*8.7*
MYRISTICACEAE															
Horsfiedia glabra				**18.3**	*6.5*				**12.6**	*4.6*				**55.7**	**29.4**
Knema elegans					*0.1*	*0.1*									*0.1*
MYRTACEAE															
Syzygium sp.			*0.2*	*7.7*					*0.9*					*1.6*	
RUBIACEAE															
Canthium glabrum		*1.0*					-					-			
STERCULIACEAE															
Sterculia sp.				*1.8*				-	-				-	-	

Appendix Fb Important species (in bold) of fruit food species consumed by four hornbill species and percentage of pulp and multitional values in 2005 breeding season (Continued)

GH	Ca (%)					ADF (%)					Calory (%)					Tannin (%)				
	Incubation		Nestling			Incubation		Nestling			Incubation		Nestling			Incubation		Nestling		
	Jan	Feb	Mar	Apr	May	Jan	Feb	Mar	Apr	May	Jan	Feb	Mar	Apr	May	Jan	Feb	Mar	Apr	May
ANNONACEAE																				
Desmos chinensis		*9.6*	*1.9*				-	-				*11.9*	*1.5*				**39.2**	*3.3*		
Polyalthai jucunda			*5.6*	**14.1**				-	-				*5.3*	**13.8**				*3.4*	**16.7**	
Polyalthia viridis	*0.8*			**15.8**	**19.1**	*1.8*			**33.1**	**31.3**	*2.1*			**15.4**	**25.9**	*2.2*			**13.7**	**29.3**
CELASTORACEAE																				
Bhesa robusta			*0.1*					-					*0.1*					-		
ELAEAGNEACEAE																				
Elaeagnus latifolia			*4.0*					**19.1**					*2.4*					*1.1*		
LAURACEAE																				
Beilschmiedia balansae				*0.2*					*0.2*					*0.1*					-	
Beilschmiedia glabra				*0.0*					*0.0*					*0.0*					-	
Beilschmiedia sp.		-		-			-		-			-		-			-		-	
Cinnamomum subavenium	*2.0*	**13.3**	**8.7**	*1.7*		*7.3*	**39.6**	**41.9**	*6.0*		*13.5*	**49.8**	**21.4**	*4.2*		*13.1*	**33.9**	**9.5**	*3.6*	
MELIACEAE																				
Dysoxylun densiflorum			**50.1**		*0.8*			-		-			**58.4**		*1.3*			**78.2**		*4.0*
Aglaia spectabillis			*2.5*	**21.9**	**33.1**			*4.9*	**31.7**	**37.4**			*2.1*	**18.4**	**38.6**			*0.4*	*7.1*	**18.9**
MORACEAE																				
Arthocarpus lakooxha				*3.4*					-					*4.1*					*2.9*	
Ficus spp	**97.1**	**77.2**	**27.0**	**27.3**	**43.0**	**90.9**	**60.4**	**34.0**	**25.6**	**31.3**	**84.4**	**38.3**	**8.8**	*9.1*	**19.9**	**84.7**	**26.9**	*4.0*	**7.9**	**21.9**
MYRISTICACEAE																				
Horsfiedia glabra				**13.1**	*4.0*				-	-				**33.7**	*14.2*				**48.2**	**25.8**
Knema elegans					*0.1*					-					*0.1*					*0.1*
MYRTACEAE																				
Syzygium sp.				*2.6*					*3.5*					*1.2*					-	
RUBIACEAE																				
Canthium glabrum		-					-					-					-			
STERCULIACEAE																				
Sterculia sp.			-	-				-	-				-	-				-	-	

Appendix Fb Important species (in bold) of fruit food species consumed by four hornbill species and percentage of pulp and multitional values in 2005 breeding season (Continued)

WH	Pulp (%)					Protein (%)					Fat (%)				
	Incubation		Nestling			Incubation		Nestling			Incubation		Nestling		
	Feb	Mar	Apr	May	Jun	Feb	Mar	Apr	May	Jun	Feb	Mar	Apr	May	Jun
ANNONACEAE															
Desmos chinensis	*0.2*					*0.2*					*0.1*				
Polyalthai jucunda		**22.1**	**23.7**	*1.2*			**29.2**	**42.3**	*2.4*			**14.9**	**14.0**	*0.8*	
Polyalthia viridis	*7.7*	*6.3*	**11.9**	**22.9**		**13.3**	**7.1**	**18.2**	**41.1**		**15.4**	**8.6**	**14.2**	**30.8**	
CELASTORACEAE															
Bhesa robusta	*0.2*	*4.5*				*0.5*	*6.5*				-	-			
ELAEAGNEACEAE															
Elaeagnus latifolia	**6.6**					*5.5*					*0.1*				
LAURACEAE															
Beilschmiedia balansae			*0.8*					*0.6*					*0.5*		
Beilschmiedia glabra			*0.1*	*0.1*				*0.2*	*0.2*				*0.4*	*0.4*	
Beilschmiedia maingayi		*0.7*					*0.8*					-			
Beilschmiedia sp.			-					-					-		
Cinnamomum subavenium	*4.5*	**13.6**	*2.7*			*4.5*	**8.8**	*2.4*			**22.4**	**46.1**	*8.1*		
MALIACEAE															
Dysoxylum cyrtobotryum	*1.7*	*0.2*				*2.2*	*0.1*				*4.4*	*0.3*			
Dysoxylun densiflorum	*1.9*	**23.5**		*3.1*		*4.0*	**31.8**		*6.6*		-	-		-	
Aglaia lawii		*2.9*					*3.4*					**14.9**			
Aglaia spectabillis	**35.5**	**7.0**	**34.5**	**59.8**	**92.8**	**22.6**	*2.9*	**19.5**	**39.8**	**90.9**	**35.4**	*4.7*	**20.5**	**40.1**	**95.6**
Aphanamixis polystachya	**23.7**	*0.1*				**32.9**	*0.1*				-	-			
MORACEAE															
Ficus spp	**15.1**	**16.1**	**14.7**	*7.0*	*7.2*	**12.3**	**8.7**	*10.6*	*6.0*	*9.1*	*8.9*	*6.5*	*5.2*	*2.8*	*4.4*
MYRISTICACEAE															
Horsfiedia glabra			*8.7*	*5.4*				*4.8*	*3.5*				**33.7**	**23.6**	
Knema elegans		*0.2*	*2.1*	*0.0*			*0.1*	*1.0*	*0.0*			*0.2*	*1.8*	*0.0*	
PALMAE															
Livistona speciosa	*2.8*	*1.2*	*0.6*	*0.5*		*2.0*	*0.6*	*0.4*	*0.4*		**13.4**	*3.8*	*1.8*	*1.6*	
SAPOTACEAE															
Sacrosperma arboria			-					-					-		
STERCULIACEAE															
Sterculia balanghas		*1.7*					-					-			

Appendix Fb Important species (in bold) of fruit food species consumed by four hornbill species and percentage of pulp and multitional values in 2005 breeding season (Continued)

WH	Ca (%)					ADF (%)					Calory (%)					Tannin (%)				
	Incubation		Nestling			Incubation		Nestling			Incubation		Nestling			Incubation		Nestling		
	Feb	Mar	Apr	May	Jun	Feb	Mar	Apr	May	Jun	Feb	Mar	Apr	May	Jun	Feb	Mar	Apr	May	Jun
ANNONACEAE																				
Desmos chinensis	*0.2*					-					*0.2*					*1.7*				
Polyalthai jucunda		**20.7**	**26.0**	*1.5*			-	-	-			**21.1**	**29.4**	*1.7*			**18.6**	**37.5**	*2.4*	
Polyalthia viridis	**9.5**	*6.2*	**13.8**	**31.1**		**17.1**	**17.8**	**30.4**	**45.5**		**9.7**	**6.3**	**15.5**	**34.1**		**17.5**	*4.1*	**14.5**	**35.9**	
CELASTORACEAE																				
Bhesa robusta	*0.4*	*5.8*				-	-				*0.4*	*5.6*				-	-			
ELAEAGNEACEAE																				
Elaeagnus latifolia	*3.9*					**11.8**					*2.5*					*4.4*				
LAURACEAE																				
Beilschmiedia balansae			*0.7*					*0.7*					*0.6*					-		
Beilschmiedia glabra			*0.0*	*0.0*				*0.2*	*0.2*				*0.2*	*0.2*				*0.0*	*0.0*	
Beilschmiedia maingayi		*0.8*					-					*0.7*					-			
Beilschmiedia sp.			-					-					-					-		
Cinnamomum subavenium	*2.8*	**6.7**	*1.6*			*8.4*	**32.6**	*5.9*			*7.3*	**17.6**	*4.6*			**12.4**	**10.8**	*4.0*		
MALIACEAE																				
Dysoxylum cyrtobotryum	*1.8*	*0.1*				*1.9*	*0.2*				*2.1*	*0.1*				*1.0*	*0.0*			
Dysoxylun densiflorum	*2.5*	**24.4**		*4.4*		-	-		-		*3.1*	**30.3**		*5.9*		**16.0**	**55.8**		**17.7**	
Aglaia lawii		*2.8*					*2.9*					*3.8*					*3.2*			
Aglaia spectabillis	**22.7**	*3.5*	**20.6**	**41.9**	**78.9**	**28.1**	*7.0*	**31.4**	**42.4**	**85.3**	**19.9**	*3.1*	**19.9**	**39.6**	**90.4**	**15.5**	*0.9*	*8.1*	**18.1**	**80.7**
Aphanamixis polystachya	**21.5**	*0.1*				-	-				**39.2**	*0.1*				*8.7*	*0.0*			
MORACEAE																				
Ficus spp	**33.2**	**28.4**	**30.2**	**16.9**	*21.1*	**26.5**	**36.2**	**29.8**	*11.0*	*14.7*	**11.6**	**9.8**	*11.6*	*6.3*	*9.6*	**20.3**	*6.2*	**10.6**	*6.5*	*19.3*
MYRISTICACEAE																				
Horsfiedia glabra			*5.4*	*3.9*				-	-				**15.9**	**11.3**				**24.1**	**19.1**	
Knema elegans		*0.1*	*1.4*	*0.0*			-	-	-			*0.1*	*1.4*	*0.0*			*0.0*	*0.8*	*0.0*	
PALMAE																				
Livistona speciosa	*1.5*	*0.5*	*0.3*	*0.3*		*6.2*	*3.3*	*1.6*	*1.0*		*3.9*	*1.3*	*0.9*	*0.8*		*2.5*	*0.3*	*0.3*	*0.3*	
SAPOTACEAE																				
Sacrosperma arboria			-					-					-					-		
STERCULIACEAE																				
Sterculia balanghas		-					-					-					-			

Appendix Fb Important species (in bold) of fruit food species consumed by four hornbill species and percentage of pulp and multitional values in 2005 breeding season (Continued)

BH	Pulp (%)				Protein (%)				Fat (%)				Ca (%)		
	Incub.	Nestling			Incub.	Nestling			Incub.	Nestling			Incub.	Nestling	
	Feb	Mar	Apr	May	Feb	Mar	Apr	May	Feb	Mar	Apr	May	Feb	Mar	Apr
ANNONACEAE															
Desmos chinensis	*0.8*	*3.2*			*0.7*	*2.1*			*0.1*	*0.3*			*1.0*	*4.0*	
Polyalthai jucunda		**8.2**	*8.0*			**11.7**	**13.7**			*3.0*	*2.3*			*9.3*	**9.2**
Polyalthia viridis		*1.2*	*1.8*	*14.1*		*1.4*	*2.7*	**14.7**		*0.9*	*1.0*	**15.4**		*1.4*	*2.2*
CELASTORACEAE															
Bhesa robusta	**18.9**	**14.0**	*3.6*		**37.9**	**22.1**	*6.7*		-	-	-		**29.4**	**21.9**	*5.6*
ELAEAGNEACEAE															
Elaeagnus latifolia	*2.7*	*0.5*			*2.0*	*0.3*			-	-			*1.6*	*0.3*	
LAURACEAE															
Beilschmiedia balansae			*1.5*				*1.0*				*0.5*				*1.4*
Beilschmiedia glabra			*1.2*	*2.2*			*1.4*	*1.9*			*1.7*	*6.1*			*0.4*
Beilschmiedia maingayi			*1.0*				*1.4*				-				*1.3*
Beilschmiedia sp.	-	-			-	-			-	-			-	-	
Cinnamomum subavenium	**41.4**	**45.9**	**11.0**		**37.3**	**32.4**	**9.2**		**93.4**	**85.7**	**15.5**		**24.8**	**27.6**	*6.7*
MALIACEAE															
Dysoxylum cyrtobotryum	*1.6*				*1.9*				*1.9*				*1.7*		
Dysoxylun densiflorum	*2.1*	**15.9**	**20.3**	**60.2**	*3.9*	**23.3**	**35.4**	**74.5**	-	-	-	-	*2.6*	**20.1**	**25.9**
Aglaia lawii		*2.5*				*3.2*				*7.0*				*2.9*	
Aphanamixis polystachya	*2.9*				*3.7*				-				*2.6*		
MORACEAE															
Ficus spp	**17.0**	*5.5*	**9.2**	*1.4*	**12.6**	*3.2*	*6.4*	*0.7*	*4.6*	*1.2*	*1.5*	*0.5*	**36.4**	**11.9**	**19.8**
MYRISTICACEAE															
Horsfiedia glabra		*0.7*	**41.9**	**22.1**		*0.3*	**22.0**	*8.2*		*1.8*	**77.3**	**78.1**		*0.5*	**27.1**
Knema elegans			*0.6*				*0.3*				*0.2*				*0.4*
RUBIACEAE															
Canthium glabrum	**12.6**	*1.8*			-	-			-	-			-	-	
SAPOTACEAE															
Sacrosperma arboria			-				-				-				-
STERCULIACEAE															
Sterculia sp.		*0.6*				-				-				-	
THEACEAE															
Ternstroemia wallichiana		*0.0*	*0.1*			-	-			-	-			-	-

Appendix Fb Important species (in bold) of fruit food species consumed by four hornbill species and percentage of pulp and multitional values in 2005 breeding season (Continued)

BH	ADF (%)				Calory (%)				Tannin (%)			
	Incub.	Nestling			Incub.	Nestling			Incub.	Nestling		
	Feb	Mar	Apr	May	Feb	Mar	Apr	May	Feb	Mar	Apr	May
ANNONACEAE												
Desmos chinensis	-	-			0.7	2.5			4.3	**8.8**		
Polyalthai jucunda		-	-			6.7	6.3			7.2	5.2	
Polyalthia viridis		2.5	9.3	**84.7**		1.0	1.5	11.2		0.8	0.9	5.0
CELASTORACEAE												
Bhesa robusta	-	-	-		**24.3**	**15.0**	3.7		-	-	-	
ELAEAGNEACEAE												
Elaeagnus latifolia	4.2	0.9			0.8	0.1			1.1	0.1		
LAURACEAE												
Beilschmiedia balansae			2.4				0.7				-	
Beilschmiedia glabra			3.9	8.5			1.2	2.1			0.0	0.1
Beilschmiedia maingayi			-				0.8				-	
Beilschmiedia sp.	-	-			-	-			-	-		
Cinnamomum subavenium	**68.0**	**85.0**	**47.4**		**55.1**	**50.7**	**11.6**		**69.2**	**37.8**	6.7	
MALIACEAE												
Dysoxylum cyrtobotryum	1.6				1.6				0.5			
Dysoxylun densiflorum	-	-	-	-	2.7	**17.5**	**21.4**	**61.4**	10.4	**39.2**	**37.0**	**77.1**
Aglaia lawii		1.9				2.8				2.8		
Aphanamixis polystachya	-				4.0				0.6			
MORACEAE												
Ficus spp	**26.2**	9.6	**37.1**	6.8	**10.7**	2.9	4.6	0.7	**13.8**	2.2	2.7	0.3
MYRISTICACEAE												
Horsfiedia glabra		-	-	-		0.9	**48.2**	**24.6**		1.1	**47.4**	**17.6**
Knema elegans			-				0.2				0.1	
RUBIACEAE												
Canthium glabrum	-	-			-	-			-	-		
SAPOTACEAE												
Sacrosperma arboria			-				-				-	
STERCULIACEAE												
Sterculia sp.		-				-				-		
THEACEAE												
Ternstroemia wallichiana		-	-			-	-			-	-	

Appendix Fb Important species (in bold) of fruit food species consumed by four hornbill species and percentage of pulp and multitional values in 2005 breeding season (Continued)

PH	Pulp (%)			Protein (%)			Fat (%)			Ca (%)		
	Incub.	Nestling		Incub.	Nestling		Incub.	Nestling		Incub.	Nestling	
	Mar	Apr	May	Mar	Apr	May	Mar	Apr	May	Mar	Apr	May
ANNONACEAE												
Desmos chinensis		0.8			0.8			0.1			1.0	
Polyalthai jucunda	3.3	**8.7**	3.6	**11.4**	**20.2**	7.3	2.1	3.0	0.9	5.1	**9.9**	4.8
Polyalthia viridis	0.4	6.9	7.2	1.0	**13.6**	**12.4**	0.5	**4.7**	3.8	0.6	**8.2**	10.1
CELASTORACEAE												
Bhesa robusta	2.9	0.5		**10.8**	1.3		-	-		6.0	0.8	
ELAEAGNEACEAE												
Elaeagnus latifolia	2.1			3.1			0.0			1.7		
LAURACEAE												
Beilschmiedia balansae		0.4			0.4			0.1			0.3	
Beilschmiedia glabra		0.1			0.2			0.2			0.0	
Beilschmiedia sp.		-			-			-			-	
Cinnamomum subavenium	**15.0**	**7.8**	0.4	**25.3**	8.9	0.4	**48.3**	**13.5**	0.5	**12.1**	4.7	0.2
MALIACEAE												
Dysoxylun densiflorum		4.2	**16.8**		**9.8**	**34.5**		-	-		5.2	**24.6**
Agaia lawii	5.6	0.4		**17.3**	0.7		**27.7**	0.9		**8.9**	0.4	
Aglaia spectabillis			**14.5**			**9.2**			3.8			**10.4**
MORACEAE												
Ficus spp	**15.4**	**21.0**	4.1	**21.6**	**19.8**	3.3	5.9	4.3	0.6	**44.4**	**44.6**	**10.2**
MYRISTICACEAE												
Horsfiedia glabra		**31.3**	**52.9**		**22.2**	**32.6**		**70.4**	**90.2**		**19.8**	**39.3**
Knema elegans			0.6			0.3			0.2			0.4
MYRTACEAE												
Syzygium sp.	**52.7**	**17.2**		9.5	2.1		**15.5**	2.7		**21.2**	5.1	
RHAMNACEAE												
Zizyphus attopoensis		0.3			-			-			-	
RHIZOPHORACEAE												
Carallia brachiata	0.5			-			-			-		
STERCULIACEAE												
Sterculia sp.	2.1	0.5		-	-		-	-		-	-	

Appendix Fb Important species (in bold) of fruit food species consumed by four hornbill species and percentage of pulp and multitional values in 2005 breeding season (Continued)

PH	Calory (%)			Tannin (%)		
	Incub.	Nestling		Incub.	Nestling	
	Mar	Apr	May	Mar	Apr	May
ANNONACEAE						
Desmos chinensis		*0.8*			*2.4*	
Polyalthai jucunda	*6.3*	**9.1**	*3.0*	*10.2*	**8.7**	*2.4*
Polyalthia viridis	*0.7*	*7.5*	*6.2*	*0.8*	*5.3*	*3.6*
CELASTORACEAE						
Bhesa robusta	*7.2*	*0.7*		-	-	
ELAEAGNEACEAE						
Elaeagnus latifolia	*1.3*			*1.5*		
LAURACEAE						
Beilschmiedia balansae		*0.2*			-	
Beilschmiedia glabra		*0.2*			*0.0*	
Beilschmiedia sp.		-			-	
Cinnamomum subavenium	**38.7**	**11.1**	*0.4*	**43.1**	*7.3*	*0.2*
MALIACEAE						
Dysoxylun densiflorum		*5.9*	**18.6**		**11.7**	**30.9**
Agaia lawii	**14.8**	*0.5*		**22.7**	*0.5*	
Aglaia spectabillis			*5.5*			*1.4*
MORACEAE						
Ficus spp	**18.8**	**14.0**	*2.1*	**21.7**	**9.6**	*1.2*
MYRISTICACEAE						
Horsfiedia glabra		**48.0**	**63.9**		**54.4**	**60.2**
Knema elegans			*0.2*			*0.1*
MYRTACEAE						
Syzygium sp.	**12.2**	*2.2*		-	-	
RHAMNACEAE						
Zizyphus attopoensis		-			-	
RHIZOPHORACEAE						
Carallia brachiata	-			-		
STERCULIACEAE						
Sterculia sp.	-	-		-	-	

Appendix G Percentage of fruit characteristic categories of 70 species of known hornbill food plant available during the breeding season (BS), the non breeding season (NBS) and year round.

Characteristics		Food				Non food			
		% of total availability				% of total availability			
		% species availabity	All year	BS	NBS	% species availabity	All year	BS	NBS
Lifeform	Climber	4.3	1.4	2.9	0.0	98.2	7.3	49.1	41.8
	Tree	95.7	12.9	40.0	42.9	1.8	0.0	0.0	1.8
Fruit presentation	Single fruit	35.2	5.6	14.1	15.5	42.0	18.0	18.0	6.0
	Cluster	64.8	9.9	28.2	26.8	58.0	30.0	24.0	4.0
Fruit type	Berry	41.4	1.4	17.1	22.9	25.0	0.0	23.1	1.9
	Capsule	14.3	0.0	4.3	10.0	25.0	1.9	9.6	13.5
	Drupe	31.4	1.4	20.0	10.0	32.7	5.8	17.3	9.6
	Legume	0.0	0.0	0.0	0.0	7.7	0.0	7.7	0.0
	Nut	0.0	0.0	0.0	0.0	5.8	0.0	0.0	5.8
	Samara	0.0	0.0	0.0	0.0	3.8	0.0	3.8	0.0
	Syconium	12.9	11.4	1.4	0.0	0.0	0.0	0.0	0.0
Fruit skin	Dull	40.0	2.9	20.0	17.1	63.6	25.5	34.5	3.6
	Shiny	60.0	11.4	22.9	25.7	36.4	16.4	16.4	3.6
Detachment of pulp from seed	Detached	75.7	12.9	31.4	31.4	32.7	7.3	18.2	7.3
	Non-detached	24.3	1.4	11.4	11.4	67.3	0.0	32.7	34.5
Dehiscence	Dehiscent	19.0	0.0	9.5	9.5	21.8	3.6	7.3	10.9
	Non-dehiscent	81.0	17.5	36.5	27.0	78.2	3.6	43.6	30.9
Color	Yellow	10.1	2.9	5.7	1.5	20.8	0.0	9.4	11.3
	Orange	12.0	4.2	6.3	1.5	9.4	0.0	5.7	3.8
	Red	33.8	8.8	11.8	13.2	17.0	1.9	9.4	5.7
	Green	1.5	0.0	0.0	1.5	13.2	1.9	7.5	3.8
	Black	42.7	1.5	23.5	17.7	39.6	3.8	18.9	17.0
UV Reflection	Reflection	46.0	11.1	12.7	22.2	24.5	0.0	12.2	12.2
	Non-reflect	54.0	3.2	30.2	20.6	75.5	4.1	42.9	28.6
Seed number per fruit	1 seed	55.7	4.3	27.1	24.3	48.0	2.0	24.0	22.0
	2-10 seeds	18.6	0.0	8.6	10.0	26.0	0.0	18.0	8.0
	11-50 seeds	11.4	0.0	5.7	5.7	18.0	0.0	10.0	8.0
	>50 seeds	14.3	11.4	0.0	2.9	8.0	0.0	2.0	6.0
Taste	Sweet	15.4	0.0	7.7	7.7	0.0	0.0	0.0	0.0
	Sweet and sour	3.8	0.0	0.0	3.8	0.0	0.0	0.0	0.0
	Sour	15.4	0.0	15.4	0.0	50.0	0.0	33.3	16.7
	Bitter	7.7	0.0	0.0	7.7		0.0	0.0	7.7
	Astringent	19.2	0.0	7.7	11.5	33.3			33.3
	Sweet and astringent	7.7	0.0	0.0	7.7	16.7	0.0	8.3	8.3
	Tasteless	30.8	30.8	0.0	0.0	0	0.0	0.0	0.0

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Family/Species	ET	LF	SS	FP	Fruit Characteristic									Seed Characteristic						Color				
					FS	DP	DH	FT	FW	FL	FW1	FW2	FV	SF	SW	SL	SW1	SW2	SV	CC	C	UVC	UV	UVD
ALANGIACEAE																								
Alangium kurzii	1	1	2	2	1	2	1	1	0.64	13.11	9.54	8.23	0.57	1	0.13	9.06	6.32	3.97	0.11	100 100 100 60	5	not change	5	2
ANACARDIACEAE																								
Buchanania latifolia	0	1	1	2	2	2	1	1	0.54	10.88	8.93	7.67	0.44	1	0.48	12.48	9.56	9.53	0.59	100 100 100 -	3	not change	3	2
Choerospondias axillaris	0	1	2	1	1	2	1	1	8.34	25.11	21.94	22.31	7.88	1	0.27	6.80	6.98	6.64	0.25	- 20 100 10	4	100 100 80 30	3	1
Rhus cochichinensis	0	1	2	2	1	1	2	3	0.29	8.29	6.39	6.63	.	2	0.04	5.37	2.86	2.38	.	- 80 80 10	3	- 60 80 10	3	1
Average									3.06	14.76	12.42	12.20	4.16		0.26	8.22	6.46	6.18	0.42					
SD									5.28	10.35	9.52	10.11	3.72		0.22	4.26	3.09	3.35	0.17					
ANNONACEAE																								
Alphonsea boniana	1	1	1	2	1	1	1	3	16.24	33.47	26.96	27.95	15.57	2	0.63	14.92	9.29	6.01	0.51	10 40 80 -	3	not change	3	2
Desmos chinensis	1	2	1	2	1	1	1	3	1.95	39.00	6.45	6.45	.	2	0.09	6.15	4.46	4.42	.	100 100 100 10	5	not change	5	2
Miliusa lineata	1	1	2	2	2	2	1	3	6.80	26.63	21.63	20.33	6.57	2	0.34	12.94	8.00	4.90	0.27	- 80 80 -	3	30 80 80 -	3	1
Platymitra macrocarpa	1	1	1	1	1	2	1	7	140.45	73.37	58.04	56.36	134.33	2	3.12	27.07	16.31	9.74	2.87	40 60 100 -	3	not change	3	2
Polyalthia jucunda	1	1	1	2	2	1	1	3	7.60	29.92	20.68	19.18	7.33	1	3.79	23.63	15.01	14.22	3.45	100 100 100 -	5	not change	5	2
Polyalthia viridis	1	1	1	2	2	1	1	3	7.28	28.11	20.68	20.15	6.93	1	3.49	23.56	15.09	14.46	3.38	100 100 80 -	5	not change	5	2
Uvaria cordata	1	2	1	2	2	1	1	3	14.12	60.57	18.81	18.84	13.93	3	0.42	11.78	10.37	5.03	0.34	20 100 100 -	4	80 100 100 -	4	1
Average									27.77	41.58	24.75	24.18	30.78		1.70	17.15	11.22	8.40	1.80					
SD (+/-)									112.67	31.79	33.29	32.18	103.56		2.09	9.92	5.09	6.07	1.65					
APOCYDACEAE																								
Alstonia scholaris	0	1	1	2	1	1	1	4	0.92	329.60	6.38	1.35	1.30	3	.	.	.	.	.	80 80 80 30	5	not change	5	2
Alstonia sp.	0	1	1	.	1	1	1	4	0.89	277.93	2.36	2.38	0.90	3	0.003	5.98	1.65	0.36	0.003	80 100 100 10	4	not change	4	2
Melodinus cambodiensis	0	2	2	1	2	2	1	3	174.00	69.03	64.05	63.87	173.33	4	0.18	10.62	7.66	2.95	0.17	- 80 40 30	4	10 30 30 60	5	1
Average									58.60	225.52	24.26	22.53	58.51		0.09	8.30	4.66	1.65	0.08					
SD									115.40	104.08	39.78	41.33	114.82		0.09	2.32	3.00	1.30	0.08					
AQUIFOLIACEAE																								

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Family/Species	**ET**	**LF**	**SS**	**FP**	**Fruit Characteristic**									**Seed Characteristic**						**Color**				
					FS	**DP**	**DH**	**FT**	**FW**	**FL**	**FW1**	**FW2**	**FV**	**SF**	**SW**	**SL**	**SW1**	**SW2**	**SV**	**CC**	**C**	**UVC**	**UV**	**UVD**
ARECACEAE																								
Areca laolensis	0	1	1	2	2	1	1	1	10.84	37.79	22.30	21.99	10.23	1	5.08	36.87	15.25	15.24	4.50	60 100 80 -	4	60 100 40 -	6	1
Areca triandra	0	1	3	2	2	1	1	1	.	.	.	.	.	.	.	.	.	.	.	.	4	.	.	.
Average									10.84	37.79	22.30	21.99	10.23		5.08	36.87	15.25	15.24	4.50					
SD									0	0	0	0	0		0	0	0	0	0					
ASCLEPIADACEAE																								
Asclepias curassavica	0	1	2	.	1	1	2	4	.	.	.	.	.	1	.	.	.	.	.	.	5	not change	5	2
BURSERACEAE																								
Canarium euphyllum	1	1	1	2	1	1	1	1	14.07	40.01	24.73	24.21	12.67	1	4.98	37.28	16.35	16.60	4.10	100 100 100 30	5	not change	5	2
CASEALPINIOIDEAE																								
ErytrophLeum teysmanii	0	1	1	2	1	1	1	4	1.34	130.72	16.49	1.46	.	.	0.001	1.69	1.44	0.99	0.03	100 100 100 -	5	not change	5	2
CELASTRACEAE																								
Bhesa robusta	1	1	1	1	1	1	2	1	1.66	19.56	10.86	10.47	1.50	1	0.64	14.54	8.39	7.15	0.61	- 60 100 -	3	- 30 100 -	3	1
CORNACEAE																								
Mastixia pentandra	1	1	2	2	1	1	1	1	5.10	27.40	17.55	16.96	4.60	1	2.24	22.85	12.97	11.92	1.82	100 100 60 10	5	not change	5	2
Nyssa javanica	0	1	2	.	1	2	1	1	1.93	16.60	13.94	13.49	1.93	1	0.34	13.80	9.44	4.54	0.25	30 - 80 -	1	not change	1	2
Average									3.51	22.00	15.74	15.22	3.27		1.29	18.33	11.20	8.23	1.03					
SD									1.59	5.40	1.80	1.73	1.33		0.95	4.52	1.77	3.69	0.78					
DIPTEROCARPACEAE																								
Dipterocarpus glacilis	0	1	1	1	1	1	2	6	4.66	135.37	20.08	1.82	4.65	.	4.60	.	.	.	.	60 20 80 30	1	not change	1	2
EBENACEAE																								
Diospyros glandulosa	0	1	2	1	1	2	1	3	12.67	28.42	26.69	26.10	11.43	1	1.02	15.18	11.64	11.50	0.96	- 20 80 -	5	not change	5	2
ELAEGNACEAE																								
Elaeagnus latifolia	1	1	1	1	2	2	1	1	9.43	34.20	19.75	19.82	.	1	0.79	28.80	7.05	6.55	.	- 80 100 10	3	40 - 80 100	3	1
ELAEOCARPACEAE																								
Sloanea sigun	0	1	2	1	2	2	1	2	19.66	52.83	47.47	44.07	17.67	3	0.13	9.06	5.45	4.56	0.16	- 30 80 -	2	20 60 100 -	3	1

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Family/Species	**ET**	**LF**	**SS**	**FP**	**Fruit Characteristic**									**Seed Characteristic**						**Color**				
					FS	**DP**	**DH**	**FT**	**FW**	**FL**	**FW1**	**FW2**	**FV**	**SF**	**SW**	**SL**	**SW1**	**SW2**	**SV**	**CC**	**C**	**UVC**	**UV**	**UVD**
EUPHORBIACEAE																								
Baccarea ramiflora	0	1	1	2	1	2	1	3	4.72	22.20	21.15	21.05	4.86	2	0.06	5.20	4.12	4.04	0.05	- - 60 10	6	100 100 80 -	5	1
Balacata baccata	0	1	1	2	1	2	1	3	1.01	12.79	13.77	9.49	0.98	1	0.06	4.67	4.90	4.21	0.50	80 100 40 60	3	not change	3	2
Bischofia javanica	0	1	2	2	1	2	1	1	0.26	7.48	7.71	7.66	0.20	1	0.24	9.17	4.80	6.65	0.16	40 60 80 -	5	not change	5	.
Bridelia retusa	1	1	1	1	2	1	1	3	0.56	10.02	7.98	7.98	0.50	1	0.20	9.35	5.24	5.28	0.25	80 100 60 60	5	not change	5	2
Chaetocarpus castanocarpus	0	1	2	2	1	2	1	2	0.76	16.07	14.86	14.39	.	1	1.95	17.00	13.65	13.26	1.65	100 100 30 100	2	not change	2	.
Excoecaria oppositifolia	0	1	2	1	2	2	2	2	13.68	51.74	47.24	46.88	15.67	3	0.49	15.63	10.11	5.92	0.42	10 - 80 30	2	not change	2	2
Glochidion lanceolarium	0	1	2	1	2	1	1	2	0.21	4.53	9.78	9.27	0.20	1	0.14	4.71	6.48	5.98	0.11	80 100 30 80	3	not change	3	2
Macaranga gigantea	0	1	1	2	1	2	1	2	0.10	4.96	7.73	4.70	0.12	2	0.02	3.23	3.50	3.44	0.02	60 60 80 -	5	not change	5	2
Mallotus philippensis.	0	1	1	2	1	2	1	1	0.36	6.00	8.11	8.40	0.25	2	0.02	3.57	3.32	3.07	0.03	60 100 100 -	4	100 100 80 -	4	1
Phyllanthus emblica	0	1	2	1	2	2	1	1	2.93	15.63	17.40	17.30	2.77	1	0.48	11.02	9.42	9.44	0.56	10 - 60 20	2	not change	2	2
Average									2.70	16.25	16.37	15.52	3.20		0.40	8.78	6.76	6.27	0.40					
SD									11.22	36.60	31.67	32.17	12.83		1.59	8.64	7.09	7.13	1.28					
FAGACEAE																								
Castanopsis accuminatissima	0	1	2	2	2	1	2	5	1.09	15.47	13.06	10.72	1.15	2	0.33	6.55	4.94	3.95	0.08	30 - 60 -	5	100 100 100 10	5	1
Lithocarpus rassa (mig.)	0	1	2	2	2	2	1	5	4.43	22.91	19.04	18.99	3.95	1	3.88	18.42	18.57	18.47	3.33	100 100 100 -	5	not change	5	2
Lithocarpus thomsonii	0	1	2	2	2	2	1	5	4.38	30.10	20.37	20.02	4.70	1	3.24	23.55	17.01	17.01	3.60	10 10 40 30	2	not change	2	2
Average									3.30	22.83	17.49	16.58	3.27		2.48	16.18	13.51	13.14	2.34					
SD									1.13	7.27	2.88	3.44	1.43		1.39	7.38	5.06	5.33	1.26					
FLACOURTIACEAE																								
Casearia grewiaefolia	1	1	2	1	2	1	2	2	5.44	24.27	21.08	20.68	5.50	3	0.02	5.99	3.07	2.11	0.02	- 100 60 -	4	40 100 60 -	4	1
Casearia sp.(big size G38)	1	1	2	1	2	1	2	2	36.99	45.34	37.57	37.18	.	3	0.10	6.34	4.65	3.94	0.10	- 100 60 -	4	40 100 60 -	4	1
Casearia sp.2 (small size)	1	1	2	1	2	1	2	2	1.17	15.17	12.16	12.02	1.25	3	0.02	4.81	3.49	2.49	0.02	10 100 80 -	4	not change	4	2
Average									14.54	28.26	23.60	23.29	3.38		0.05	5.72	3.73	2.85	0.05					
SD									22.46	17.08	13.97	13.88	2.13		0.05	0.63	0.91	1.09	0.05					
GUTTIFERAE																								
Garcinia speciosa	0	1	1	1	1	2	1	3	24.72	33.60	37.84	35.71	23.47	3	0.01	3.36	2.16	2.10	0.01	- 60 80 -	4	40 100 100 -	4	1

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					FS	**DP**	**DH**	**FT**	**FW**	**FL**	**FW1**	**FW2**	**FV**	**SF**	**SW**	**SL**	**SW1**	**SW2**	**SV**	**CC**	**C**	**UVC**	**UV**	**UVD**
HAMAMELIDACEAE																								
Altingia excelsa	0	1	3	2	1	1	2	1	2.05	13.70	16.52	16.02	0.50	1	.	.	.	.	.	40 60 80 80	5	not change	5	2
ICACINACEAE																								
Apodytes dimidiata	1	1	2	2	2	2	1	3	0.52	11.90	7.59	7.91	0.47	1	0.22	9.04	7.71	4.21	0.02	40 100 80 -	4	100 100 100 -	5	1
Gonocaryum lobbianum	0	1	2	1	2	2	1	1	8.39	40.95	20.70	18.91	8.07	1	11.64	24.75	27.56	24.51	9.03	100 100 100-	1	not change	1	2
Platea latifolia	1	1	2	2	1	1	1	1	8.05	34.07	20.06	19.87	7.38	1	4.33	32.16	15.93	15.93	3.78	- 80 100 -	3	30 100 100 -	4	1
Average									5.65	28.97	16.12	15.56	5.31		5.40	21.98	17.06	14.88	4.28					
SD									2.74	11.98	4.58	4.30	2.76		6.25	10.18	10.49	9.62	4.75					
JUGLANDACEAE																								
Engelhardtia spicata	0	1	1	2	1	1	1	6	0.05	44.74	8.78	0.17	0.10	3	0.03	5.66	3.83	0.86	.	80 40 40 -	5	not change	5	2
LABIATAE																								
Gmelina arborea	0	1	1	2	2	2	1	1	8.01	22.74	22.60	22.70	.	1	7.12	40.66	19.41	17.69	6.83	60 20 100 -	5	not change	5	2
LAURACEAE																								
Beilchimiedia balansae	1	1	1	2	1	1	1	1	3.87	30.02	14.93	14.74	.	1	2.78	29.04	13.30	13.17	.	100 100 80 -	5	not change	5	2
Beilschmiedia maingayi	1	1	1	2	2	1	1	1	.	.	.	.	.	.	.	.	.	.	.	.	5	.	.	.
Beilschmiedia villosa	1	1	1	2	1	1	1	1	5.42	32.63	15.13	15.47	4.53	1	3.53	31.17	13.05	13.06	2.73	100 100 80 -	5	not change	5	2
Cinnamomum glaucescen	1	1	2	2	2	1	1	3	.	.	.	.	.	.	.	.	.	.	.	.	5	.	.	.
Cinnamomum subavenium	1	1	1	2	2	1	1	1	0.82	13.84	9.32	9.25	0.89	1	0.42	11.84	7.16	7.22	0.36	100 100 100 -	5	not change	5	2
Cryptocarya impressa	1	1	1	2	2	1	1	3	.	.	.	.	.	.	.	.	.	.	.	.	5	.	.	.
Lindera communis	1	1	1	.	1	1	1	1	2.77	30.02	12.38	12.11	2.43	1	2.04	28.56	11.13	11.09	1.50	100 100 80 -	5	not change	5	2
Litsea beusekomii	1	1	2	2	1	1	1	1	12.00	36.10	24.12	23.12	10.94	1	6.43	28.85	19.60	18.29	5.73	100 100 100 80	5	not change	5	2
Litsea monopetala	0	1	2	.	1	1	1	1	0.30	9.09	7.22	7.13	0.27	1	0.12	7.34	5.16	4.89	0.14	100 100 100 -	5	not change	5	2
Neolitsea latifolia	1	1	1	2	1	1	1	1	3.07	17.28	17.46	17.26	3.43	1	0.69	12.96	10.28	10.03	0.69	100 100 100 60	5	not change	5	2
Average									4.04	24.14	14.37	14.15	3.75		2.29	21.40	11.38	11.11	1.86					
SD									7.97	11.96	9.76	8.97	7.19		4.14	9.77	8.22	7.18	3.87					
LYTHRACEAE																								
Lagerstroemia balansae	0	1	2	2	1	2	2	2	0.22	12.03	8.39	8.42	0.24	4	0.01	11.29	5.54	0.71	0.01	60 80 60 60	5	not change	5	2
Lagerstroemia speciosa	0	1	2	2	1	2	2	2	1.03	17.81	14.93	14.75	.							60 60 60 -				
Average									0.62	14.92	11.66	11.58	0.24		0.01	11.29	5.54	0.71	0.01					
SD									0.41	2.89	3.27	3.17	0		0	0	0	0	0					

Appendix H: List of eaten (**ET =** 1) and non-eaten fruit (**ET =** 2) in different season with their fruit characteristics included. **LF** (Lifeform, 1= tree, 2 = climber); **SS** (Season, 1 = breeding, 2 = non-breeding, 3 = all year); **FP** (Fruit presentation, 1= single, 2 = cluster); **FS** (Fruit skin, 1= dull, 2 = shining); **DP** (Detachment of pulp, 1 = non-detached, 2 = detached); **DH** (Dehiscent, 1 = non-dehiscent, 2 = dehiscent); **FT** (Fruit type, 1= drupe, 2 = capsule, 3 = berry, 4 = legume, 5 = nut, 6 = samara, 7 = syconium); **FW** (Fruit weight); **FL** (Fruit length); **FW1** (Fruit greatest width); **FW2** (least width); **FV** (Fruit volume); **SF** (Seed number per fruit, 1= 1 seed, 2 = 2-10 seeds, 3 = 11-50 seeds, 4 =>50 seeds); **SW** (Seed weight); **SL** (Seed length); **SW1** (Seed greatest width); **SW2** (Seed least width); **SV** (Seed volume); **CC** (Color chart): **C** (Color detected from human eyes, 1= green, 2 = yellow, 3 = orange, 4 = red, 5 black, 6 = purple); **UVC** (color chart under UV light); **UV** (color detected from human eyes under UV light); **UVD** (Changing of color, 1 = changing, 2 = not changing) (Continued)

Family/Species	**ET**	**LF**	**SS**	**FP**	**Fruit Characteristic**									**Seed Characteristic**						**Color**				
					FS	**DP**	**DH**	**FT**	**FW**	**FL**	**FW1**	**FW2**	**FV**	**SF**	**SW**	**SL**	**SW1**	**SW2**	**SV**	**CC**	**C**	**UVC**	**UV**	**UVD**
MAGNOLIACEAE																								
Michelia baillonii	1	1	2	1	2	1	1	3	116.29	89.83	48.72	46.36	110.90	4	0.05	7.37	4.47	2.65	0.05	- 80 80 -	3	40 80 100 30	4	1
MALVACEAE																								
Hybiscus macrophyllus	0	1	1	1	1	2	1	2	1.54	28.28	20.89	19.31	2.98	4	0.03	5.32	2.25	0.27	0.06	30 30 80 10	5	not change	5	2
MELASTOMATACEAE																								
Memecylon plebejum	1	1	1	1	2	2	1	3	0.89	9.64	11.80	11.56	0.75	1	0.15	4.95	6.49	6.27	0.11	100 100 100 60	5	not change	5	2
MELIACEAE																								
Aglaia lawii	1	1	2	1	2	2	2	2	11.28	27.9	27.41	26.91	.	2	1.20	17.51	10.20	8.34	0.96	- 80 80 10	3	30 100 80 10	4	1
Aglaia edulis	0	1	1	1	2	1	2	2	1.15	15.17	14.89	10.27	1.01	2	0.34	9.78	7.97	7.86	0.23	- - 20 -	2	10 - 100 -	1	1
Aglaia elaeagnoidea	0	1	2	1	1	2	2	3	1.64	15.57	13.73	13.28	1.70	2	0.32	11.62	9.26	4.60	0.33	- 30 - -	4	not change	4	2
Aglaia spectabilis	1	1	1	1	2	2	2	2	71.65	56.5	51.69	48.07	69.53	2	5.89	29.52	18.98	14.50	5.39	10 80 100 -	3	30 40 100 -	3	1
Aphanamixis polystechya	1	1	2	2	2	2	1	2	7.99	25.63	22.06	21.05	.	2	0.94	13.42	10.62	9.16	.	10 80 100 -	3	not change	3	2
Azadirechta indica	0	1	1	.	1	2	1	3	0.13	5.83	6.01	5.67	.	2	0.21	9.63	7.97	3.23	0.16	100 100 100 10	2	not change	2	2
Dysoxylum cyrtobotryum	1	1	1	2	2	1	2	2	6.12	32.33	20.86	19.97	5.94	2	0.92	15.49	10.06	7.91	0.88	100 100 100 -	5	not change	5	2
Dysoxylum densifloram	1	1	1	2	2	1	2	2	11.40	22.96	30.98	26.92	.	2	1.41	12.59	15.60	11.51	1.20	- 80 100 -	3	not change	3	2
Sandoricum indicum	0	1	1	1	1	2	1	3	78.83	47.96	53.46	54.14	77.00	2	2.94	26.12	15.96	11.85	2.55	- -10 -	2	not change	2	2
Toona macrocarpa	0	1	2	2	1	2	1	2	0.38	18.82	10.19	10.16	0.67	3	0.00	13.36	3.04	0.09	0.01	40 60 80 60	5	not change	5	2
Walsura robusta	1	1	1	2	1	2	1	3	3.10	18.65	15.09	16.64	2.82	1	1.16	13.13	11.70	10.25	0.89	- - 10 -	2	not change	2	2
Walsura robusta	1	1	1	2	1	2	1	3	1.02	15.11	11.57	10.09	0.99	1	0.53	11.71	9.66	7.06	0.53	- - - -	2	not change	2	2
Average									16.22	25.20	23.16	21.93	19.96		1.32	15.32	10.92	8.03	1.19					
SD									62.60	31.28	30.30	32.21	57.04		4.57	14.19	8.06	6.47	4.20					
MIMOSOIDEAE																								
Archidendron clypearia	0	1	1	2	1	2	1	4	1.00	163.84	29.42	1.65	.	3	0.06	6.69	5.49	1.74	0.05	60 80 100 10	3	not change	3	2

Appendix H: List of eaten (**ET =** 1) and non-eaten fruit (**ET =** 2) in different season with their fruit characteristics included.
LF (Lifeform, 1= tree, 2 = climber); **SS** (Season, 1 = breeding, 2 = non-breeding, 3 = all year); **FP** (Fruit presentation, 1= single, 2 = cluster); **FS** (Fruit skin, 1= dull, 2 = shining); **DP** (Detachment of pulp, 1 = non-detached, 2 = detached); **DH** (Dehiscent, 1 = non-dehiscent, 2 = dehiscent); **FT** (Fruit type, 1= drupe, 2 = capsule, 3 = berry, 4 = legume, 5 = nut, 6 = samara, 7 = syconium); **FW** (Fruit weight); **FL** (Fruit length); **FW1** (Fruit greatest width); **FW2** (least width); **FV** (Fruit volume); **SF** (Seed number per fruit, 1= 1 seed, 2 = 2-10 seeds, 3 = 11-50 seeds, 4 =>50 seeds); **SW** (Seed weight); **SL** (Seed length); **SW1** (Seed greatest width); **SW2** (Seed least width); **SV** (Seed volume); **CC** (Color chart): **C** (Color detected from human eyes, 1= green, 2 = yellow, 3 = orange, 4 = red, 5 black, 6 = purple); **UVC** (color chart under UV light); **UV** (color detected from human eyes under UV light); **UVD** (Changing of color, 1 = changing, 2 = not changing) (Continued)

Family/Species	ET	LF	SS	FP	Fruit Characteristic									Seed Characteristic						Color				
					FS	DP	DH	FT	FW	FL	FW1	FW2	FV	SF	SW	SL	SW1	SW2	SV	CC	C	UVC	UV	UVD
MORACEAE																								
Antiaris toxicaria	1	1	1	1	1	2	1	1	2.16	21.85	12.82	12.10	.	1	0.90	13.84	9.39	8.87	.	30 100 40 30	4	80 100 100 -	5	1
Artocarpus lakoocha	1	1	2	1	1	1	1	3	13.68	28.64	25.74	25.38	13.27	2	0.22	7.10	5.89	5.68	0.19	10 100 100 10	4	40 100 - 30	6	1
Fig sp. 1	1	1	3	1	2	1	1	7	3.26	21.00	16.92	16.85	3.67	4	.	.	.	.	.	- 20 100 -	2	10 - 100 -	2	1
Fig sp. 2	1	1	3	1	2	1	1	7	0.65	9.61	10.62	10.51	0.57	4	.	.	.	.	.	10 80 60 10	3	20 60 60 10	3	1
Fig sp. 3	1	1	3	1	2	1	1	7	0.33	9.82	8.49	12.54	.	4	.	.	.	.	.	- 40 80 -	3	not change	3	2
Fig sp. 4	1	1	3	1	2	1	1	7	2.47	16.24	16.67	16.41	2.48	4	.	.	.	.	.	80 100 100 60	5	100 100 100-	5	1
Fig sp. 5	1	1	3	1	2	1	1	7	0.78	12.27	11.20	11.02	0.81	4	.	.	.	.	.	10 80 60 -	3	100 100 100 -	5	1
Fig sp. 6	1	1	3	1	1	1	1	7	0.35	8.77	8.18	8.31	0.33	4	.	.	.	.	.	30 80 80 -	3	80 100 80 -	6	1
Fig sp. 7	1	1	3	1	2	1	1	7	2.04	15.36	15.57	15.68	.	4	.	.	.	.	.	- 40 80 10	3	80 100 80 30	4	1
Fig sp. 8	1	1	3	1	2	1	1	7	1.28	13.97	12.13	12.35	.	4	.	.	.	.	.	- 60 100 10	3	- - 100 10	2	1
MORACEAE																								
Fig sp. 9	1	2	3	1	2	1	1	7	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Average									2.70	15.75	13.83	14.12	3.52		0.56	10.47	7.64	7.28	0.19					
SD									10.9775	12.8822	11.905	11.262	9.75005		0.3403	3.3687	1.7518	1.5927	0					
MYRSINACEAE																								
Ardisia colorata	0	1	2	2	1	2	1	3	0.24	6.18	6.94	6.88	0.22	1	0.06	4.17	4.12	4.11	0.06	100 100 80 -	5	not change	5	2
MYRSTICACEAE																								
Gnetum montanum	1	1	1	2	2	1	2	1	1.11	14.34	9.18	9.20	.	1	0.79	13.36	8.00	7.94	.	- 80 80 10	3	30 80 80 10	3	1
Knema elegans	1	1	1	1	2	1	2	1	8.42	28.44	26.97	23.71	5.29	1	2.11	18.34	13.57	13.49	1.98	40 100 80 10	4	80 100 30 -	6	1
Knema globularia	1	1	2	1	2	1	2	1	2.23	19.27	13.49	13.57	2.21	1	1.01	15.52	10.36	10.23	0.88	10 100 80 -	3	40 100 80 -	3	1
Average									3.92	20.68	16.55	15.49	3.75		1.30	15.74	10.64	10.55	1.43					
SD									4.50	7.76	10.42	8.21	1.54		0.80	2.60	2.93	2.94	0.55					
MYRSTICEAE																								
Cleistocalyx operculatus	1	1	1	1	2	1	1	3	.	.	.	.	.	.	.	.	.	.	.	.	5	.	.	.
Horsfieldia glabra	1	1	1	2	2	1	2	1	8.11	30.49	25.01	21.22	3.32	1	2.20	17.75	13.96	14.00	2.09	- 60 100 -	3	not change	3	2
Syzygium cuminii	1	1	2	1	1	1	1	3	0.41	7.07	7.33	7.84	.	1	0.12	4.62	4.96	5.02	.	100 100 8030	5	not change	5	2
Syzygium grande	1	1	2	1	1	1	1	1	13.04	34.51	27.26	26.00	12.47	1	5.31	22.31	20.12	19.19	4.40	40 100 60 -	1	30 80 40 -	4	1
Syzygium sp.1 (white)	1	1	2	1	2	1	1	3	0.54	12.49	9.78	9.97	0.53	1	0.16	5.00	5.54	5.36	0.11	- - 10 -	2	not change	2	2
Syzygium sp.2 (big)	1	1	2	1	2	1	1	3	6.09	24.68	19.12	18.50	.	1	1.25	17.58	9.39	9.04	1.02	100 100 100 -	5	not change	5	2

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Family/Species	**ET**	**LF**	**SS**	**FP**	**Fruit Characteristic**									**Seed Characteristic**						**Color**				
					FS	**DP**	**DH**	**FT**	**FW**	**FL**	**FW1**	**FW2**	**FV**	**SF**	**SW**	**SL**	**SW1**	**SW2**	**SV**	**CC**	**C**	**UVC**	**UV**	**UVD**
Syzygium sp.3 (Km33)	1	1	2	1	2	1	1	3	0.44	10.57	8.34	8.99	0.43	1	0.19	6.51	6.66	6.61	0.93	60 100 80 60	5	not change	5	2
Syzygium sp.4 (medium)	1	1	2	1	2	1	1	3	1.15	13.91	11.35	11.17	1.02	1	0.24	9.00	5.89	5.97	0.19	100 100 100 60	5	not change	5	2
Cleistocalyx operculatus	0	1	1	1	2	1	1	3	0.58	10.83	9.08	9.07	0.56	1	0.13	7.37	5.69	5.52	0.11	80 100 100 30	2	- 60 80 -	2	1
Average									3.79	18.07	14.66	14.10	3.05		1.20	11.27	9.03	8.84	1.26					
SD									9.25	16.44	12.60	11.91	9.41		4.11	11.04	11.10	10.35	3.14					
OLEACEAE																								
sp. 1	0	1	2	.	1	1	1	2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
PALMAE																								
Livistona speciosa	1	1	1	2	1	1	1	1	8.66	26.27	24.18	22.39	7.72	1	3.83	22.09	18.00	15.59	2.95	100 100 60 60	5	not change	5	2
Livistona speciosa (raw)	0	1	3	2	2	1	1	1	.	.	.	.	.	.	.	.	.	.	.	.	5	.	.	.
Average									8.66	26.27	24.18	22.39	7.72		3.83	22.09	18.00	15.59	2.95					
SD									0	0	0	0	0		0	0	0	0	0					
PODOCARPACEAE																								
Dacrydium elatum	0	1	3	1	2	2	1	3	0.27	12.90	7.20	5.51	0.21	2	0.35	16.70	10.24	3.11	2.57	30 80 80 -	2	not change	2	2
POLEMONIACEAE																								
Phoebe Cathia	1	1	2	2	2	1	1	3	.	.	.	.	.	.	.	.	.	.	.	.	5	.	.	.
PROTEACEAE																								
Helicia exelsa	0	1	1	2	1	2	1	1	20.71	40.41	34.59	32.11	18.83	4	0.01	3.25	2.30	1.29	0.03	80 30 100 -	1	not change	1	2
RHAMNACEAE																								
Ziziphus attepoensis	1	1	2	2	1	1	1	3	2.36	15.72	13.72	14.30	1.79	1	0.67	13.02	10.34	7.09	0.58	- 80 80 10	3	- 30 80 -	3	1
RHIZOPHORACEAE																								
Caralia brachiata	1	1	1	1	1	2	1	3	0.33	6.43	7.58	7.89	.	1	0.08	4.12	4.02	4.80	.	40 100 80 -	4	100 80 30 -	4	1
RUTACEAE																								
Acronychia pedunculator	0	1	2	2	1	2	1	1	5.51	21.96	21.18	19.87	5.53	1	1.34	17.10	13.17	11.65	1.18	30 10 80 -	1	not change	1	2
Acronychia sp.	0	1	2	2	1	2	1	1	5.15	15.99	26.92	21.85	5.18	2	1.68	16.36	14.53	13.42	1.53	60 80 100 -	3	60 60 100 -	3	1
Clausena exocaria	1	1	2	2	2	1	1	3	0.67	13.27	9.95	9.71	0.61	1	0.23	7.93	4.87	5.14	0.28	- 30 30 -	3	10 - 30 -	3	1
Glycosmis mauritiana	0	1	1	2	2	1	1	3	0.62	8.13	10.46	10.33	0.63	1	0.69	14.30	8.18	8.32	0.61	- 80 100 -	1	not change	1	2
Average									2.99	14.84	17.13	15.44	2.99		0.99	13.93	10.19	9.63	0.90					
SD									2.52	7.12	9.79	6.41	2.54		0.70	3.18	4.34	3.79	0.63					

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Family/Species	ET	LF	SS	FP	Fruit Characteristic									Seed Characteristic						Color				
					FS	DP	DH	FT	FW	FL	FW1	FW2	FV	SF	SW	SL	SW1	SW2	SV	CC	C	UVC	UV	UVD
SAPINPACEAE																								
Lepisanthes rubiginosa	0	1	1	2	1	2	1	3	0.76	13.99	8.05	7.90	.	1	0.26	12.30	5.37	5.38	.	100 100 80 -	5	not change	5	2
Nephelium melliferum	0	1	1	2	2	2	1	1	9.32	33.62	26.61	24.80	9.10	1	2.29	21.73	13.10	11.07	1.67	-100 100 -	4	not change	4	2
Average									5.04	23.80	17.33	16.35	9.10		1.28	17.02	9.23	8.23	1.67					
SD									4.28	9.82	9.28	8.45	0		1.01	4.72	3.86	2.85	0					
SONNERATIACEAE																								
Duabanga grandiflora	0	1	3	1	1	1	2	2	2.98	26.44	36.25	35.80	3.12	1	0.03	5.47	4.07	4.02	0.01	80 80 100 10	1	not change	1	2
STERCULIACEAE																								
Sterculia balanghas	1	1	2	2	1	1	2	2	10.40	71.22	23.84	19.04	.	2	0.76	13.94	12.73	7.59	0.70	100 100 100-	5	not change	5	2
Sterculia sp.1	1	1	2	.	1	1	2	2	4.95	58.40	32.23	28.55	.	2	0.37	11.26	6.78	6.97	0.36	100 100 100 -	5	not change	5	2
Average									7.68	64.81	28.03	23.80	.		0.57	12.60	9.76	7.28	0.53					
SD									2.73	6.41	4.19	4.75	.		0.19	1.34	2.97	0.31	0.17					
THEACEAE																								
Eurya nitida	0	1	1	1	2	2	1	3	0.20	6.73	7.48	7.46	0.20	3	1.10	12.13	12.65	12.59	0.99	100 100 80 -	2	not change	2	2
Schima wallichii	0	1	1	1	1	2	1	2	0.92	12.55	13.86	13.83	1.17	2	0.06	8.39	5.59	0.56	0.13	40 40 40 10	5	not change	5	2
Average									0.56	9.64	10.67	10.65	0.68		0.58	10.26	9.12	6.58	0.56					
SD									0.36	2.91	3.19	3.19	0.48		0.52	1.87	3.53	6.01	0.43					
THYMELAEACEAE																								
Aquillaria crassna	0	1	1	1	1	2	2	2	7.21	34.32	30.59	29.07	14.00	2	0.16	13.74	7.24	6.24	0.20	40 80 10 -	1	not change	1	2
ULMACEAE																								
Celtis tetrandra	1	1	2	1	1	2	1	1	0.25	8.34	6.44	6.44	0.20	1	0.09	6.20	4.39	4.37	0.05	10 60 80 -	3	10 40 60 -	3	1
Gironniera nervosa	1	1	3	1	1	2	1	1	0.15	8.40	6.48	5.23	0.14	1	0.02	4.06	4.02	2.59	0.06	40 30 80 -	2	not change	2	2
Average									0.20	8.37	6.46	5.83	0.17		0.06	5.13	4.21	3.48	0.06					
SD									0.05	0.03	0.02	0.60	0.03		0.03	1.07	0.18	0.89	0.01					
Aidia chinensis	1	1	2	2	2	2	1	3	0.32	9.8	7.34	7.27	0.30	4	0.001	1.68	1.04	0.84	0.001	100 100 100 80	5	not change	5	2
Mahad (thai)	1	1	2	.	1	2	1	3	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.

Summary: Eaten 70 species, non-eaten 57 species

Appendix I Nutritional values of 50 hornbill fruit-food and 14 non-food species
T = Taste: 1 = sweet, 2 = sweet and sour, 3 = sour, 4 = bitter, 5 = astringent, 6 = tasteless, 7 = sweet and astringent

Family/Species	Food	Calory kal/g	Moisture g%	Protein g%	Fat g%	CHO g%	Ash g%	Fiber g%	Ca g%	P g%	NDF g%	ADF g%	Tannin g%	Taste
ALANGIACEAE														
Alangium kurzii	eaten	5847	76.09	15.24	.	.	6.15	.	0.78	0.014	.	.	7.04	.
ANNONACEAE														
Desmos chinensis	eaten	4466	61.38	5.38	1.87	75.92	2.76	14.07	0.63	0.05	.	.	10.63	.
Polyalthia jucunda	eaten	4724	84.05	11.59	6.36	60.22	6.3	15.53	0.57	0.015	.	.	3.36	.
Polyalthia viridis	eaten	4940	66.94	9.9	12.78	48.32	4.33	24.67	0.6	0.013	36.17	35.2	2.59	.
Uvaria cordata	eaten	4392	67.06	5.33	2.54	51.61	2.93	37.59	0.55	0.01	51.94	47.6	0.51	3
Average		4630	69.86	8.05	5.89	59.02	4.08	22.97	0.59	0.02	44.06	41.40	4.27	3.00
SD		309	14.19	3.54	6.89	16.90	2.22	14.63	0.04	0.03	7.89	6.20	6.36	0.00
BURSERACEAE														
Canarium euphyllum	eaten	6011	50.23	4.17	30.53	52.65	4.89	7.76	0.8	0.05	37.86	36.1	0.4	5
CELASTRACEAE														
Bhesa robusta	eaten	6196	73.41	12.75	.	.	2.59	.	0.78	0.009	.	.	.	.
CORNACEAE														
Mastixia pentandra	eaten	5223	65.7	4.41	2.78	59.25	5.87	27.69	0.68	0.008	31.32	31	0.41	6
ELAEGNACEAE														
Elaeagnus latifolia	eaten	1500	85.99	4.81	0.12	85.99	1.2	7.88	0.29	0.06	13.19	28.52	0.77	3
EUPHORBIACEAE														
Bridelia retusa	eaten	4136	61.28	2.77	1.99	81.74	1.81	11.69	0.26	0.005	.	.	0.63	.
FLACOURTIACEAE														
Casearia grewiaefolia	eaten	6397	45.08	14.48	.	.	2.47	.	0.5	0.024	.	.	1.13	.
ICACINACEAE														
Apodytes dimidiata	eaten	5891	72.96	5.86	.	.	4.87	.	0.34	0.011	.	.	2.55	4
Platea latifolia	eaten	2063	64.91	3.24	.	.	1.09	2.92	0.66	0.01	10.6	13.78	0.1	.
Average		3977	68.94	4.55	.	.	2.98	2.92	0.50	0.01	10.60	13.78	1.33	4.00
SD		1914	4.02	1.31	.	.	1.89	0.00	0.16	0.00	0.00	0.00	1.23	0.00

Appendix I Nutritional values of 50 hornbill fruit-food and 14 non-food species
T = Taste: 1 = sweet, 2 = sweet and sour, 3 = sour, 4 = bitter, 5 = astringent, 6 = tasteless, 7 = sweet and astringent (Continued)

Family/Species	Food	Calory kal/g	Moisture g%	Protein g%	Fat g%	CHO g%	Ash g%	Fiber g%	Ca g%	P g%	NDF g%	ADF g%	Tannin g%	Taste
LAURACEAE														
Beilchimiedia balansae	eaten	2676	51.31	4.65	6.93	80.88	1.9	5.64	0.45	0.11	.	10.97	.	.
Beilschmiedia maingayi	eaten	4842	55.25	9.92	.	.	4.9	.	0.68	0.009	.	.	.	.
Beilschmiedia villosa	eaten	5970	56.26	8.34	32.84	50.96	5.53	2.33	0.17	0.12	38.09	23.16	0.2	.
Cinnamomum glaucescen	eaten	1718	73.56	1.8	1.37	91.01	1.41	4.41	0.84	0.01	6.12	6.25	.	.
Cinnamomum subavenium	eaten	6391	54.27	5.71	31.92	37.38	7.87	17.12	0.3	0.005	31.09	29.91	3.16	.
Cryptocarya impressa	eaten	6512	46.7	12.73	26.69	49.28	2.86	8.44	0.52	0.1	35.69	27.71	2.08	.
Lindera communis	eaten	5728	51.33	7.97	33.85	37.52	12.67	7.99	0.2	0.076	.	.	0.82	.
Litsea beusekomii	eaten	5302	75.84	10.4	9.79	61.5	5.58	12.73	0.36	0.007	45.91	12.61	2.75	.
LAURACEAE														
Neolitsea latifolia	eaten	3935	69.04	5.88	32.07	28.68	3.92	29.45	0.44	0.011	.	.	1.68	.
Average		4786	59.28	7.49	21.93	54.65	5.18	11.01	0.44	0.05	31.38	18.44	1.78	.
SD		1726	16.56	5.24	11.92	36.36	7.49	18.44	0.40	0.07	14.53	11.48	1.38	.
MAGNOLIACEAE														
Michelia baillonii	eaten	6760	48.12	6.18	45.01	39.28	1.57	7.96	0.32	0.015	.	.	3.37	.
MELASTOMATACEAE														
Memecylon plebejum	eaten	4079	63.21	3.45	2.39	55.36	2.71	36.09	0.77	0.003	43.89	39.71	0.26	.
MELIACEAE														
Aglaia lawii	eaten	6493	56.29	10.32	48.47	27.38	4.5	9.33	0.59	0.006	15.47	12.4	4.42	.
Aglaia spectabilis	eaten	2201	65.78	3.67	6.39	80.78	1.05	8.11	0.31	0.06	11.58	12.58	0.5	.
Aphanamixis polystechya	eaten	6490	56.45	8.01	.	.	2.37	.	0.44	0.016	.	.	0.42	.
Dysoxylum cyrtobotryum	eaten	4654	57.57	7.4	16.33	51	6.16	19.11	0.52	0.15	17.77	17.96	0.63	.
Dysoxylum densifloram	eaten	6356	65.37	11.84	.	.	5.58	.	0.63	0.015	.	.	9.44	.
Walsura robusta	eaten	3654	84.83	4.6	4.74	79.17	4.22	7.27	0.42	0.008	.	.	0.16	3
Average		4975	64.38	7.64	18.98	59.58	3.98	10.96	0.49	0.04	14.94	14.31	2.60	3.00
SD		1519	20.45	4.20	29.49	21.20	2.18	8.16	0.15	0.11	2.83	3.65	6.85	0.00
MORACEAE														
Antiaris toxicaria	eaten	4671	57.51	12.18	11.84	64.27	5.21	6.5	0.4	0.014	.	.	1.92	.
Artocarpus lakoocha	eaten	4114	72.91	5.27	9.83	66.18	2.85	15.87	0.4	0.007	.	.	1.68	.

Appendix I Nutritional values of 50 hornbill fruit-food and 14 non-food species
T = Taste: 1 = sweet, 2 = sweet and sour, 3 = sour, 4 = bitter, 5 = astringent, 6 = tasteless, 7 = sweet and astringent (Continued)

Family/Species	Food	Calory kal/g	Moisture g%	Protein g%	Fat g%	CHO g%	Ash g%	Fiber g%	Ca g%	P g%	NDF g%	ADF g%	Tannin g%	Taste
Ficus altissima	eaten	5264	70.88	10.13	16.63	27.88	6.43	38.93	1.28	0.012	.	.	4.45	6
Ficus heterepheura	eaten	629	86.85	1.04	.	.	1	3.44	1.51	0.005	4.01	4.63	.	6
Ficus kurzii	eaten	4389	67.13	4.04	1.78	42.52	4.56	47.1	0.03	0.008	45.16	32.83	1.72	6
Ficus nervosa	eaten	4271	63.93	4.43	3.91	57.91	5	28.75	1.01	0.008	49.18	48.05	1.12	6
Ficus religiosa	eaten	4419	82.38	9.5	5.18	66.12	7.9	11.3	1.31	0.016	42.12	42.1	0.21	6
Ficus sagittata	eaten	917	73.57	1.5	1.19	93.04	1.47	2.8	1.89	0.008	10.18	9.89	.	6
Ficus sp. (B22)	eaten	4231	73.79	7.07	1.73	23.76	6.97	60.47	1.54	0.012	71.56	58.59	0.2	6
Ficus sp. (climber)	eaten	629	86.85	1.04	.	.	1	3.44	4.01	4.63	1.51	0.005	.	6
Average		3353	73.58	5.62	6.51	55.21	4.24	21.86	1.34	0.47	31.96	28.01	1.61	6.00
SD		1910	13.27	6.56	10.12	37.83	3.66	38.61	2.67	4.16	39.60	30.58	2.84	0.00
MYRSTICACEAE														
Knema globularia	eaten	4955	78.53	5.93	18.2	63.2	2.68	9.99	0.68	0.01	.	.	1.65	.
Gnetum montanum	eaten	4656	8.87	13.2	2.33	21.11	4.05	59.31	0.45	0.016	53.52	43.69	1.42	.
Average		4806	43.70	9.57	10.27	42.16	3.37	34.65	0.57	0.01	53.52	43.69	1.54	.
SD		150	34.83	3.64	7.94	21.05	0.69	24.66	0.12	0	0	0	0.12	.
MYRSTICEAE														
Horsfieldia glabra	eaten	6939	45.9	3.56	41.61	43.94	1.36	9.53	0.32	0.004	.	.	5.86	.
Cleistocalyx operculatus	eaten	.	83.07	5.83	.	.	.	.	.	.	.	.	.	5
Syzygium cuminii	eaten	3937	77.73	4.06	5.69	84.75	1.92	3.58	0.32	0.006	23.27	21.56	3.32	7
Syzygium grande	eaten	571	85.8	0.61	2.91	95.42	0.37	0.69	0.15	0.02	2.57	5.66	.	.
Syzygium sp.2 (big)	eaten	4146	81.03	5.97	0.07	86.19	4.16	3.61	0.21	0.09	.	.	2.15	1
Syzygium sp.4 (medium)	eaten	4453	37.28	2.03	.	.	3.24	.	0.05	0.012	.	.	11	7
Average		4009	68.47	3.68	12.57	77.58	2.21	4.35	0.21	0.03	12.92	13.61	5.58	5.00
SD		2930	17.33	2.29	29.04	17.85	1.95	5.18	0.11	0.06	10.35	7.95	5.42	2.00
PALMAE														
Livistona speciosa	eaten	5473	50.19	4.16	30.61	47.73	4.83	12.67	0.26	0.013	36.28	35.06	1	5
POLEMONIACEAE														
Phoebe Cathia	eaten	2393	64.18	2.92	25.66	65.02	1.28	5.12	0.54	0.06	5.8	10.92	.	.

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