

Foraging characteristics of an assemblage of four Sumatran hornbill species

YOK-YOK HADIPRAKARSA and MARGARET F. KINNAIRD

Summary

This study examines the diets of four hornbill species (Bushy-crested Hornbill *Anorrhinus galeritus*, Wreathed Hornbill *Aceros undulatus*, Rhinoceros Hornbill *Buceros rhinoceros* and Helmeted Hornbill *Buceros vigil*) common within our 9 km² study area in the Bukit Barisan Selatan National Park, Sumatra, Indonesia. Line transects and opportunistic sampling were used over one year to collect feeding data, including the tree species and strata in which birds fed, diet items, fruit characteristics and tree crop size. Hornbills fed on 64 species. Figs, non-fig fruits and animals comprised 23.4% ($n = 15$ species) 51.6% ($n = 33$ species) and 25% ($n = 16$ species) of the diet, respectively. Although there was overlap among the diets of the four species, only *B. rhinoceros* and *B. vigil* had a statistically significant overlap, primarily due to high fig consumption by both species. *B. vigil* fed almost exclusively on figs (98.6% of the diet) and a small proportion of animals (1.4%) while 23.1% of the *B. rhinoceros* diet comprised non-fig fruits and animals (23.1%), with 76.9% figs. *A. galeritus* and *A. undulatus* had distinct diets with drupaceous, oily fruits comprising 66.7% and 64.4% of the diets, respectively. We found no significant relationship between the numbers of hornbills visiting fruiting trees and the characteristics of the fruit (weight, length and width). However, maximum crop sizes of diet species significantly influenced the number of feeding hornbills. Hornbill species also differed in the strata in which they fed. *A. galeritus* and *B. rhinoceros* were seen in the middle of the canopy 56% and 50.8% of the time, respectively while *A. undulatus* and *B. vigil* were observed more frequently in the upper canopy (50% and 74.3% of the time, respectively). The lower part of the canopy was used infrequently by all species. This study suggests that the four hornbill species in our study partition food resources by food type and/or feeding location.

Introduction

All 54 species of hornbills are omnivorous but most rely heavily on fruit (Kemp 1995). Hornbill diets vary over seasons and years due to changes in food abundance and diversity. Diet shifts and changes in selection criteria may also be associated with behavioural changes such as breeding.

Diet selection and the spatial and temporal distribution of feeding may also be influenced by the presence of similar species. Rosenzweig (1995) showed that as the number of similar species increases in an area, each species specializes more narrowly. If coexisting species experience resource limitation, natural selection should result in spatial (Schoener 1974, Sunarto *et al.* 1999) or temporal partitioning of the ecological niche (Ricklefs 1973). Alternatively, coexisting species may select different resources, such as food items or nesting sites, in order to reduce competition (Schoener 1974, Cody 1985, Rosenzweig 1995).

Leighton (1982) found that exploitation of fruit resources varied among five species of coexisting Bornean hornbills as a function of morphology, interspecific behaviour and intergroup behaviour. The distribution, availability and characteristics of fruit resources strongly influenced feeding characteristics. For example, large-bodied hornbills tended to consume diet items of lower nutritional quality occurring in large patches while smaller-bodied hornbills were more efficient at exploiting patches containing low numbers of high-quality items.

This study used an approach similar to Leighton's (1982) to examine how an assemblage of four sympatric Sumatran hornbills exploits food resources and how food characteristics vary among species. Dietary composition of Bushy-crested Hornbill *Anorrhinus galeritus*, Wreathed Hornbill *Aceros undulatus*, Rhinoceros Hornbill *Buceros rhinoceros* and Helmeted Hornbill *Buceros vigil* were investigated. All commonly occur within a 9 km² study area in the Bukit Barisan Selatan National Park, Sumatra. We investigated the influence of fruit availability and fruit morphology on hornbill foraging and the degree of dietary overlap among hornbill species. We then asked whether those hornbill species exhibiting significant dietary overlap partitioned their resources temporally or spatially.

Methods

Study area

We conducted our study from September 1998 to December 1999 in the 3,568 km² Bukit Barisan Selatan National Park (BBSNP), located in south-western Sumatra, Indonesia (4°31'–5°57'S and 103°34'–104°43'E). The park is the third largest in Sumatra and contains some of the largest tracts of lowland rain forest remaining on the island (O'Brien and Kinnaird 1996). The Way Canguk Research Station is located at 50 m elevation in the southern section of the park. The study area surrounding the station is 9 km², consists of primary forest, burned forest and naturally disturbed forest and is divided by the Canguk river. The study area is contiguous with large tracts of primary forest, and areas disturbed by illegal logging and agricultural lands. Annual precipitation ranges from 1,600 mm in dry years to 4,000 mm in wetter years, with a short dry season generally occurring between June and September.

Hornbill species

All nine hornbill species known to occur on Sumatra (Kemp 1995, Rasmussen 2000 *in litt.*) have been observed in the study site but only Bushy-crested Hornbill *Anorrhinus galeritus*, Wreathed Hornbill *Aceros undulatus*, Rhinoceros Hornbill *Buceros rhinoceros* and Helmeted Hornbill *Buceros vigil*, are common enough to study. Population densities of these four species vary widely within the Way Canguk study area and fluctuate over time (Anggraini *et al.* 2000). *A. undulatus* occurs at the highest average density (7.5 birds/km²) while *B. vigil* occurs at the lowest average density (1.9 birds/km²). *A. galeritus* and *B. rhinoceros* occur at intermediate average densities of 3.05 and 2.6 birds/km², respectively.

Of the species studied, *A. galeritus* is the smallest in size (1,134–1,247 g), strictly territorial and lives in groups of 2–20, with one dominant breeding pair (Kemp

1995, Leighton 1986). Of the large-bodied hornbills in our study, *A. undulatus* (1,360–3,650 g) is believed to be non-territorial and ranges the most widely (Kemp 1995). Hornbills of the genus *Aceros* tend to live in pairs but will occasionally flock in large numbers. *Aceros* hornbills also are known to have some of the largest home ranges of all hornbill species (Poonswad and Tsuji 1994, Suryadi *et al.* 1998) and their numbers have been shown to fluctuate over time in response to changes in ripe fruit availability (Suryadi *et al.* 1994, Kinnaird *et al.* 1996). *B. rhinoceros* and *B. vigil* are the largest of the hornbills studied (2,180–2,580 g and 2,495–3,060 g, respectively), live in pairs and are reported to be territorial (Leighton 1982, Kemp 1995), although Anggraini *et al.* (2000) reported that *B. vigil* may not be territorial in southern Sumatra.

Data collection

We conducted our study from September 1998 to December 1999. Fixed transects and ad libitum sampling (Altmann 1974) were used to collect data. Approximately every 2 weeks we walked 12 transects on the southern side of Cangkuk river, and six on the north, each 2.2 km in length. Transects were separated by 200 m. Four different transects were surveyed each day, two in the morning (06h30–11h00) and two in afternoon (14h00–17h00). Opportunistic observations of feeding hornbills were noted, to augment feeding data collected during standardized walks (Leighton 1982).

Instantaneous scans (Altmann 1974) were used for all observations. Data were recorded on the initial observation of a bird, including: (1) hornbill species observed, (2) number of individuals, (3) position in the tree canopy (lower, middle or upper), (4) if feeding, diet item and fruit type, and (5) estimated crop size of fruiting trees (following methods of Leighton 1993 and Kinnaird *et al.* 1996). Food items were collected and identified at the field station's herbarium or by the Herbarium Bogoriense. Fruits were weighed wet, measured (longest length and width), and classified by morphology, fruit type (drupaceous, arilate, berry, multi-seeded capsule, and fig) and the characteristics of the endosperm (oily, watery, fleshy).

Data analysis

Opportunistic data and transect data were combined, as a chi-square analysis found no significant difference between the distribution of feeding records between transect observations and opportunistic data for any species ($P > 0.1$). Chi-square analysis was used (Sokal and Rohlf 1981) to test for differences between species in the distributions of feeding strata, food items (fig fruits, non-fig fruits, animal) and fruit type or morphology. Cole's (1949) Index of Interspecific Association was calculated to examine dietary overlap among species. Cole's index measures zero if two species are distributed independently of each other, approaches +1 if species are completely associated, and -1 if they are not associated. The index is tested for significance with chi-square contingency tables. We also used step-wise multiple regression (Sokal and Rohlf 1981) to examine the relationship between hornbill number and fruit characteristics (crop

size and fruit size). For this analysis, we used the maximum number of hornbills observed visiting a particular fruiting tree during the study and the maximum crop size observed during the study for each tree species (Leighton 1982). We took the natural log of crop size in order to linearize the data. Fruit length, width, and weights of fleshy parts were averaged for a species and entered into the model as separate variables.

Results

The hornbill diet, for all species combined, was 23.4% fig fruits ($n = 15$ species), 51.6% non-fig fruits ($n = 33$ species) and 25% small animals ($n \geq 16$ species). There were significant differences among the species in the percentage of fig, non-fig fruit and animals in the diet ($\chi^2 = 134.47$, $df = 6$, $P < 0.001$). *B. vigil* and *B. rhinoceros* fed more than expected on fig fruit; this difference contributed the greatest amount to the overall chi-square statistic.

Fruit types (49 species of 5 fruit types) consumed by the different hornbill species were not evenly distributed ($\chi^2 = 54.142$, $df = 12$, $P < 0.001$; Table 1). Overlap was observed among the diets of the four hornbill species, but only *B. rhinoceros* and *B. vigil* showed significant overlap in the diet species consumed ($C_7 = 0.21 \pm 0.09$, $\chi^2 = 5.48$, $df = 1$, $P = 0.05$, $n = 48$). This overlap is due to the high degree of fig consumption by both these species.

Hornbills were found in every canopy stratum of the feeding trees, although the four species were not distributed evenly among them ($c^2 = 22.4$, $df = 6$, $P < 0.001$; Figure 1). *B. vigil* was observed more frequently than expected in the upper canopy and less than expected in middle canopy, and contributed the most to the chi-square statistic.

Step-size multiple regression analysis showed a significant positive relationship between the maximum number of all hornbills observed feeding in a tree and the maximum crop size for the tree species ($F_{1,46} = 26.117$; $P = 0.001$; $r^2 = 0.4$; Figure 2); all other factors (mean fruit weight, length and width) were insignificant and were removed from the model. There was a positive relationship between hornbill numbers and maximum crop size for the larger hornbills *A. undulatus* ($F_{1,46} = 8.91$, $r^2 = 0.16$, $P < 0.005$), *B. rhinoceros* ($F_{1,46} = 30.3$, $r^2 = 0.39$, $P < 0.001$) and *B. vigil* ($F_{1,46} = 21.96$, $r^2 = 0.32$, $P < 0.001$). There was no significant relationship between hornbill numbers and crop size for the smaller-bodied *A. galeritus* ($P = 0.1$).

Discussion

Our results demonstrate that an aggregation of four Sumatran hornbills coexist, in part, by partitioning their diet and by foraging at different levels in the canopy. Two species, *A. galeritus* and *A. undulatus*, feed on a variety of foods but rely more on lipid-rich drupaceous fruits whereas the larger species, *B. vigil* and *B. rhinoceros*, rely heavily on strangling figs. These findings are similar to those of Leighton (1982, 1986) for the same species in Borneo.

The important role that figs play in hornbill abundance and distribution is well documented (Leighton 1982, Poonswad *et al.* 1986, Kinnaird *et al.* 1996, Suryadi

Table 1. Family, species and characteristics of fruit consumed by four hornbill species during the study (Ag, *Anorrhinus galeritus*; Au, *Aceros undulatus*; Br, *Buceros rhinoceros*; Bv, *Buceros vigil*).

Fruit species	Fruit characteristic	Hornbill species			
		Ag	Au	Br	Bv
Family Anacardiaceae					
<i>Dracontomelon dao</i>	Aril — fleshy		X		
Family Apocinaceae					
<i>Leuconotis eugeniflora</i>	Drupe — oily			X	
Family Annonaceae					
<i>Cananga odorata</i>	Drupe — oily	X	X		
<i>Polyalthia lateriflora</i>	Drupe — oily		X		
Family Burseraceae					
<i>Canarium denticulatum</i>	Drupe — oily		X		
Sp1	Drupe — oily		X		
Sp2	Drupe — oily		X		
Sp3	Drupe — oily			X	
Sp4	Drupe — oily	X	X		
Sp5	Drupe — oily	X			
Sp6	Drupe — oily		X		
Sp7	Drupe — oily		X		
Family Combretaceae					
<i>Terminalia balerica</i>	Drupe — oily			X	
Family Cluciaceae					
<i>Garcinia dioica</i>	Aril — fleshy		X		
Family Cucurbitaceae					
<i>Coccinia</i> sp1	Multi — seed	X			
<i>Coccinia</i> sp2	Multi — seed	X			
Family Connaraceae					
<i>Connarus monocarpus</i>	Aril — fleshy	X			
Family Lauraceae					
<i>Beilschmiedia lucida</i>	Drupe — oily	X			
<i>Criptocarya ferrea</i>	Drupe — oily	X	X	X	
<i>Litsea garciae</i>	Drupe — oily			X	
<i>Litsea resinosa</i>	Drupe — oily		X		
<i>Litsea</i> sp.	Drupe — oily		X		
Family Meliaceae					
<i>Diospyros truncata</i>	Aril — fleshy		X		
<i>Dysoxylum arborescens</i>	Aril — fleshy	X	X		
<i>Dysoxylum excelsum</i>	Aril — fleshy	X	X	X	
Sp8	Aril — fleshy		X		
Family Moraceae					
<i>Antiaris toxicaria</i>	Drupe — oily	X	X	X	
<i>Ficus albifila</i>	Fig	X	X	X	X
<i>Ficus altissima</i>	Fig		X	X	X
<i>Ficus crassiramera</i>	Fig		X	X	X
<i>Ficus drupaceae</i>	Fig	X	X	X	X
<i>Ficus globosa</i>	Fig	X		X	
<i>Ficus microcarpa</i>	Fig				X
<i>Ficus stupenda</i>	Fig	X	X	X	X
<i>Ficus sundaica</i>	Fig				X
<i>Ficus benyamina</i>	Fig				X
<i>Ficus</i> sp1	Fig	X	X	X	X
<i>Ficus</i> sp2	Fig		X	X	X
<i>Ficus</i> sp3	Fig			X	X
<i>Ficus</i> sp4	Fig			X	X
<i>Ficus</i> sp5	Fig			X	
<i>Ficus</i> sp6	Fig			X	

Table 1. Continued.

Fruit species	Fruit characteristic	Hornbill species			
		Ag	Au	Br	Bv
Family Myristicaceae					
<i>Horsfieldia bracteosa</i>	Aril — fleshy			X	
<i>Knema maxima</i>	Aril — fleshy		X		
<i>Knema</i> sp1	Aril — fleshy	X			
<i>Knema</i> sp2	Aril — fleshy		X	X	
Family Rubiaceae					
<i>Zucacarinia macrophylla</i>	Berry — sugar	X	X		
Family Sterculiaceae					
<i>Sterculia</i> sp	Aril — fleshy		X		

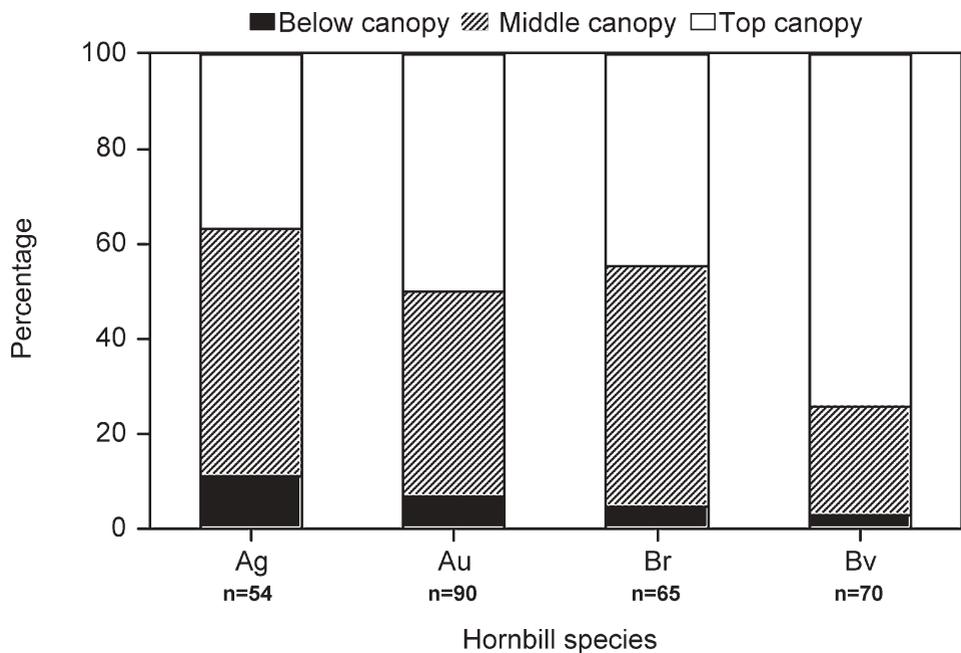


Figure 1. The percentage of observations of four hornbill species in the lower, middle and upper strata of the canopy. Au, *Aceros undulatus*; Ag, *Anorrhinus galeritus*; Br, *Buceros rhinoceros*; Bv, *Buceros vigil*.

et al. 1994). Leighton and Leighton (1983) and Leighton (1986) argue that hornbills and other frugivores prefer lipid-rich fruits and that they choose figs only when these foods are scarce. A growing body of evidence, however, suggests that figs are preferred foods for many hornbills rather than substitutes (O'Brien *et al.* 1998, Kinnaird *et al.* 1999, Sitompul *et al.* 2004). Our study shows that *B. vigil* in southern Sumatra rely almost entirely on figs despite low fig densities relative to other sites.

Figs occur at densities of 0.51 reproductive figs/ha at the Way Canguk study site (Anggaraini *et al.* 2000) compared with densities of up to 6.6 figs/ha in

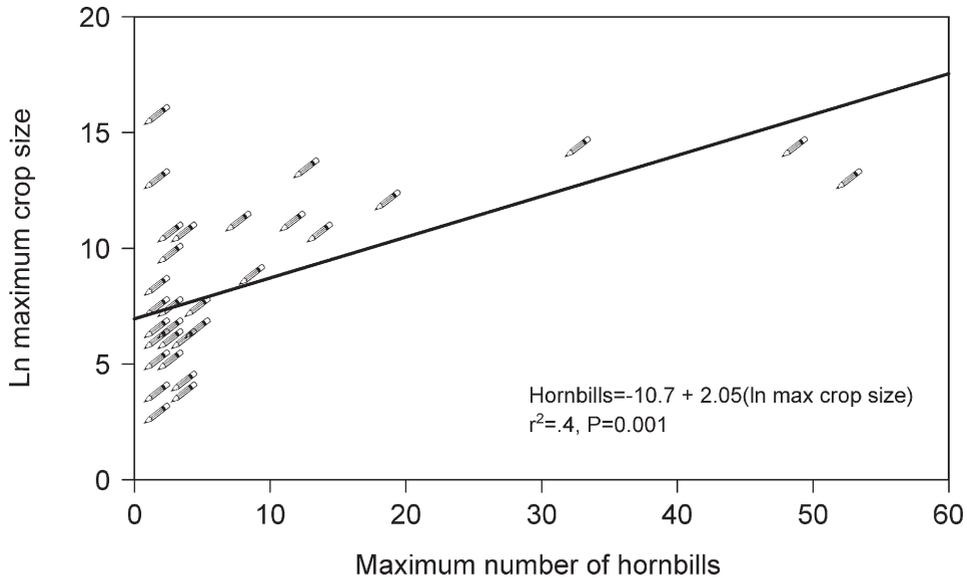


Figure 2. Relationship between the maximum number of hornbill sightings and the natural log of the maximum crop size for tree species over 15 months of study.

Borneo (Leighton 1982) and 8.3 figs/ha in Sulawesi (Kinnaird *et al.* 1996). Fig specialization by such large-bodied birds will require that they find big crops, as postulated by Leighton (1982), and move over ranges large enough to provide big crops reliably. Our data for *B. vigil* and *B. rhinoceros* numbers show that larger fig crops attract larger numbers of hornbills and are consistent with this idea. Reliance on figs and the associated long-distance movements necessary to maintain a consistent diet of figs may inhibit territoriality. Anggraini *et al.* (2000) speculate that *B. vigil* and *B. rhinoceros* in southern Sumatra may practice facultative territoriality (Kinnaird 1992), exhibiting territoriality only when resources are limiting and defensible; the smaller, territorial species *A. galeritus* has the most generalized diet and the highest percentage of animal prey. Poonswad (1993) reports similar diet composition for the small-bodied and territorial Austen's Brown Hornbill *Anorrhinus austeni*, and Oriental Pied Hornbill *Anthracoceros albirostris*. O'Brien (1997) also shows a generalized diet for the Sulawesi Tarctic Hornbill *Penelopides exarhatus exarhatus*. These are species that are group-living, are constrained in their movement patterns by territorial boundaries, and display a higher degree of flexibility in exploitation of food resources. *A. galeritus* often sub-groups while foraging (Leighton 1982, Y. H. pers. obs.), visits small crops of lipid-rich fruits, forages on lianas as well as trees, relies heavily on protein-rich invertebrate prey, and when available visits fruiting figs. Large fruit crops had no relationship to numbers of visiting *A. galeritus* at our site, consistent with the idea that smaller-bodied birds can harvest entire meals and satisfy energetic requirements from smaller crops. Foraging in sub-groups within a territory also enhances the likelihood of a given individual harvesting an entire meal. Alternatively, *A. galeritus* may be forced to forage on smaller crops due to competitive exclusion by larger hornbills.

Our study showed that only *B. vigil* and *B. rhinoceros*, the largest hornbills, overlap significantly in diet, primarily due to their high intake of figs. We would expect competition for resources to be greatest between these species. Although we did not observe interspecific aggression, we did find spatial partitioning in feeding trees. Three-quarters of our observations of foraging *B. vigil* were in the upper canopy while approximately half our observations of foraging *B. rhinoceros* were in the mid-canopy. Leighton (1982) reported that displacement among hornbill species was hierarchical, following body size, although he did not observe displacements between *B. vigil* and *B. rhinoceros*. *B. vigil* is slightly larger than *B. rhinoceros* and is also reported to be a potential predator on *B. rhinoceros* chicks (Hetharia 1941 in Kemp 1995), therefore, we may be observing competitive displacement or simply avoidance of *B. vigil* by *B. rhinoceros*. Similarly, we would expect, based on foraging strata, that *A. undulatus* and *B. rhinoceros* would experience competition while foraging but these species have no significant overlap in diet composition. Although we cannot conclude that there has been competitive exclusion between species pairs, our results are consistent with the hypothesis that this hornbill assemblage is partitioning food resources through diet selection and foraging strata.

Conclusion

Four hornbill species that commonly occur in the Way Canguk study area of southern Sumatra, Indonesia, showed variability in their dietary composition and may be partitioning resources by selecting different diet species and food types. Two species showing significant dietary overlap foraged at different strata in the canopy, thereby partitioning the resources spatially and possibly reducing competition. Although we found a high diversity of fruits in the study area, figs still played an important role in the diets of the hornbill species studied, especially the larger-bodied species of the genus *Buceros*. Large fruit crops, which may provide an entire meal, were important in attracting the larger-bodied hornbills whereas smaller crops with high lipid content tended to attract the smaller-bodied hornbill. We believe this reflects the differences in foraging efficiencies relative to body size and supports similar findings for Bornean hornbills.

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YOK-YOK HADIPRAKARSA¹ and MARGARET F. KINNAIRD^{1,2}

¹Wildlife Conservation Society — Indonesia Program, Jln. Pangrango No. 8, P.O. Box 311, Bogor 16003, Indonesia (e-mail: y.hadiprakarsa@wcsip.org)

²Wildlife Conservation Society — Asia Program, 2300 Southern Blvd., Bronx, NY 10460, U.S.A.