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Characteristics of hornbill-dispersed fruits in a tropical seasonal forest in Thailand

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Summary

Asian hornbills are primarily frugivorous. We studied the characteristics of fruits consumed by four sympatric hornbill species in Thailand: Great Hornbill (*Buceros bicornis*), Wreathed Hornbill (*Aceros undulatus*), Austin's Brown Hornbill (*Anorrhinus austeni*) and Oriental Pied Hornbill (*Anthracoceros albirostris*). We compared the frequency of distribution of 11 variables for all fruit species collected in the study area ($n = 259$) and fruit species consumed by hornbills ($n = 73$). Our analysis revealed that fruits consumed by hornbills are: (1) large, (2) easily accessible within the canopy, (3) red, purple or black and (4) dehiscent or indehiscent with a thin husk. The range of fruit sizes eaten by hornbills in our study is comparable to that reported from other sites in Southeast Asia and Africa. The large gape width of hornbills enables them to consume large fruits that small frugivores would find difficult to consume.

Introduction

The relationships between fruits and frugivores in tropical forests are extremely diverse (Howe and Smallwood 1982, Turner 2001). Both animal-dispersed plants and frugivorous animals are dominant (Gautier-Hion *et al.* 1985). In extant tropical forests, 45–90% of tree species have adaptations for vertebrate dispersal (Fleming 1991, Howe and Smallwood 1982, McKey 1975, Turner 2001). Knowledge of fruit–frugivore interactions in forest ecosystems is an essential part of any conservation program (Corlett 2002, Hamann and Curio 1999). However, seed dispersers are not known for most plants, and the degree to which plants and animals rely on one another for successful reproduction and survival is also unknown. Studies of fruit–frugivore interactions have revealed that it is typical for several frugivorous animals to disperse the fruit of any particular plant species (Chapman and Chapman 1996, Gautier-Hion *et al.* 1985, Kitamura *et al.* 2002). Although the interaction between plants and seed dispersers is not usually characterized by strong species–species interactions (Wheelwright and Orians 1982), there are some specialized relationships (rhinoceros and *Trewia nudiflora*: Dinerstein 1991, gorillas and *Cola lizae*: Tutin *et al.* 1991, cassowaries and *Aglaia mackiana*: Mack 1995).

As both large fruit and/or seed size can limit the diversity of frugivore species able to consume and disperse their seeds (Gautier-Hion *et al.* 1985, Kitamura *et al.* 2002, Leighton and Leighton 1983, Noma and Yumoto 1997), the loss of a few, specialized dispersers may have dire consequences for a plant. Plants that produce large fruits and/or seeds may be especially vulnerable to extinction if they lose their natural seed dispersers. Large frugivores may therefore play an extremely important role as seed dispersers, yet are vulnerable to extinction in the face of selective hunting (Bennett and Robinson 2000), and habitat loss and degradation (Terborgh and Winter 1980).

Hornbills (family Bucerotidae) are the largest avian frugivores in Southeast Asia and are important members of the seed disperser community (Corlett 1998, 2002). Recent studies suggest that seed dispersal by hornbills affects forest structure in the African (Holbrook and Smith 2000, Holbrook *et al.* 2002, Poulsen *et al.* 2002, Whitney and Smith 1998, Whitney *et al.* 1998) and Asian tropics (Datta 2001, Kinnaird 1998, Kitamura *et al.* 2004). The seed dispersal process can be described using three phases of animal–plant–environment interactions (Garber and Lambert 1998): (1) The pre-dispersal phase, when frugivores are attracted to a fruit display. Fruit characteristics, such as fruit/seed size, colour, hardness, and nutritional and secondary metabolite content of the fruit, provide cues to the seed disperser. (2) The dispersal phase, when frugivores remove, destroy, drop or transport seeds. (3) The post-dispersal phase, when viable seeds must avoid predation, germinate and survive. Several studies have reported the characteristics of hornbill-dispersed fruits (Datta 2001, Kalina 1988, Kinnaird and O'Brien 1993, Leighton 1982, Poonswad 1993, Poonswad *et al.* 1998b, Poulsen *et al.* 2002, Suryadi *et al.* 1994). However, most of them recorded only the characteristics of fruits consumed by hornbills, ignoring other fruits. To expand on previous studies conducted in the Khao Yai National Park in Thailand (Poonswad *et al.* 1998b), we compare the characteristics of fruits in hornbill diet with the characteristics of all vertebrate-dispersed fruits collected in the forest. We assess the preference for particular fruit characteristics during the pre-dispersal phase among four sympatric hornbill species in a tropical seasonal forest in Thailand.

Methods

Study site

The study was conducted from June 1998 to March 2002 in Khao Yai National Park (KY). This park was established in 1962, and was the first national park in Thailand (Smitinand 1977). It covers an area of 2,168 km^2 in the lower northeastern part of the country. The park lies at latitude 14°05′–15′N and longitude 101°05′–50′E in the Dongruk mountain range. Its elevation ranges from 250 to 1,351 m. Based on stand structure and species composition, the vegetation can be classified into six communities: moist evergreen forest, hill evergreen forest, mixed deciduous forest, dry evergreen forest, tropical grassland and disturbed or secondary forest (Smitinand 1977, Kutintara 1993). The main study area, about 70 km^2 around the headquarters in KY, has an altitudinal range of 600–800 m and comprises moist evergreen forest.

The moist evergreen forest of KY covers approximately 64% of the total park area, or 1,375 km^2, ranging from 400 m to 1,000 m (Smitinand 1977). The trees reach 45 m in height, and the density of trees over 10 cm in diameter at breast height is 371 ha^{-1}, with a basal area cover of 32 m^2 ha^{-1} (Kutintara 1993). The mean annual rainfall is 2,326 mm (1993–2001), and there is a marked wet season from May until October, with relatively dry conditions from November until April. The mean monthly maximum temperature ranges from 21°C (December and January) to 32°C (April and May). Although ripe fruits are available year-round (Poonswad *et al.* 1998a), fruit diversity and abundance are relatively high in the rainy season and lowest at the beginning of the dry season (S. Kitamura unpublished data).

Four hornbill species occur in KY: Great Hornbill (*Buceros bicornis*), Wreathed Hornbill (*Aceros undulatus*), Oriental Pied Hornbill (*Anthracoceros albirostris*) and Austen's Brown Hornbill (*Anorrhinus austeni*). Hornbill diets were determined by previous studies in KY (Kitamura *et al.* 2002, Poonswad 1993, Poonswad *et al.* 1998b). Since the diet overlap of fruit species among four hornbill species in KY was high (Poonswad *et al.* 1998b), in this study, hornbill-dispersed fruits were defined as fruit species that were consumed by at least one hornbill species.

Analysis of fruit characteristics

We use "fruits" and "seeds" in their ecological, not anatomical, sense. Whenever it was possible, ripe fruits were collected in the study area. The following characteristics were recorded: length, transverse diameter, wet weight of fruit/seed, ripe fruit colour (for dehiscent fruits, the displayed colour of the inner part of the fruits was described), number of seeds in a fruit, and sugar concentration of the fruit pulp. The sugar concentration was measured using a pocket refractometer (Belingham and Stanley Ltd, BS-R70) that determined the sucrose equivalents of the juice. In the case of several dehiscent fruits, such as *Michelia baillonii*, we treated the arillate seeds as the dispersal units, since they separate quite easily in the ripe fruit and are apparently removed individually by animals. These data were collected for at least 15 samples of each fruit species (except *Artocarpus gomezianus*, for which only four intact fruit were found). Fruit with obvious damage was excluded from the measurements. No attempt was made to look at variation among individuals within species; samples were chosen representing the typical size range. The measurements were taken within a day after fruit was collected. The life form and fruit type of each species were defined as follows (see Gautier-Hion *et al.* 1985): *Life form*: epiphyte (EP); herb (HE); liana (LI); arboreal shrub (< 7 m) (SH); small tree (7–15 m) (ST); middle-sized tree (15–30 m) (MT); tall tree (> 30 m) (TT). *Fruit type*: dehiscent fruit (D); indehiscent fruit with a thin husk (I); indehiscent fruit with a thick husk (T). The complete datasets of the fruit characteristics for this study were extracted from Kitamura *et al.* (2002). In that study, characteristics of fruit were examined for 259 species of 65 families. These included 73 species that were known to be included in the diets of hornbills. Those 73 species were distributed across 39 families.

A simple ordination technique, principal component analysis (PCA), was used to illustrate fruit selection by hornbills. The PCA was performed using the statistical software package STATISTICA 5.1 (StatSoft 1995). The PCA was carried out in order to collapse eight variables (fruit weight, fruit length, fruit diameter, sugar content, number of seeds per fruit, seed weight, seed length and seed diameter) into a new set of principal components that incorporated the relationships between these variables. Thus, principal components important in explaining the variation in fruit selection by hornbills were generated. They incorporate a known fraction of the variation explained by the original variables. We used a *t*-test to test for differences between these factor scores (hornbill fruit species vs all fruit species). For the principal component analysis, log transformations of the data were performed. Fisher's exact test was used to test for morphological differences between the preferred fruits of hornbills and all the fruits collected in the forest, for categorical variables (fruit colour, life form and fruit type).

Results

In the 73 hornbill fruit species, the most common families were the Moraceae (14 species), Lauraceae (10 species), Annonaceae (7 species) and Meliaceae (5 species). Within these, figs (*Ficus* spp.) were the most common (10 species). A summary of the characteristics of fruits consumed by hornbills is shown in Table 1. Since half the fruit species did not have enough juice in the pulp to measure sugar content using the refractometer, the sample size for the measurement of sugar content was a subset of the 73 diet species.

From eight variables (Table 1), PCA extracted three principal components that explained 96% of the total variance. The first component (PCA1: 42% of the total variance) had a high positive loading for fruit size (fruit weight, fruit length, fruit diameter). Fruit species with high scores on this axis were large, such as *Trichosanthes tricuspidata*, *Artocarpus lakoocha* and *Ficus* spp. The second component (PCA2) explained an additional 41% of the total variance. PCA2 had a high positive loading for seed size (seed weight, seed length, seed diameter), and a high negative loading for number of seeds per fruit. Fruit species with high scores on this axis were fruits with a single large-sized seed, such as *Horsfieldia glabra*, *Aglaia spectabilis*, *Areca triandra*, *Canarium euphyllum* and *Platea latifolia*. The third component (PCA3) explained 11% of the total variance and was negatively correlated with the sugar content. Fruit species with high scores on this axis had a high sugar content in the fruit pulp, such as *Chionanthus ramiflorus*, *Tetrastigma* sp.1, *Morinda* sp.SK042. There were significant differences between the fruits in the diet of hornbills and all the fruits collected in the forest for PCA1 (t-test, $t = 2.93$, $df = 330$, $P = 0.004$). However, there was no difference in PCA2 ($t = 0.91$, $df = 330$, $P = 0.36$) and PCA3 ($t = 1.14$, $df = 330$, $P = 0.25$). Thus, in this forest, hornbills tended to consume large fruits.

All three categorical variables were significantly different between hornbill fruits and all the fruits collected in the forest (Fisher's exact test, $P = 0.045$ for fruit color, $P = 0.002$ for life form, $P = 0.008$ for fruit type). Hornbills preferred to consume fruits that were red, purple and black. They tended to consume the

Table 1. Summary of the measurements of fruits eaten by hornbills in Khao Yai National Park, Thailand. Data extracted from Kitamura *et al*. (2002).

Variables	N	Median	Minimum	Maximum
Fruit weight (g)	73	2.5	0.14	145.4
Fruit length (mm)	73	18.9	6.6	70.8
Fruit diameter (mm)	73	15.2	5.4	68.6
Sugar content (%)	43	13.9	4.5	26.1
Number of seeds per fruit	73	1.0	1.0	100 >
Seed weight (g)	73	0.3	0.01	7.2
Seed length (mm)	73	11.1	0.5	35.6
Seed diameter (mm)	73	8.1	0.3	20.3

fruit of taller trees and lianas (TT, MT, LI), but were occasionally observed to consume the fruits of smaller trees (ST, SH). They were never observed eating indehiscent fruits with a thick husk.

Discussion

Characteristics of hornbill-dispersed fruits in KY

In this study, we focused on the characteristics of the fruits consumed by hornbills in KY. Our results are more useful in elucidating the characteristics of hornbill-dispersed fruits than previous studies, as the characteristics of those fruits consumed by hornbills and those fruits not consumed by hornbills were examined and compared. We characterize hornbill-dispersed fruits as: (1) large, (2) easily accessible within the canopy, (3) red, purple or black and (4) dehiscent or indehiscent with a thin husk.

Large fruits tend to attract larger frugivores, possibly due to improved foraging efficiency, especially for birds (Lambert and Marshall 1991). The relationship of frugivory with gape size was first demonstrated by Wheelwright (1985), who found that smaller frugivorous birds have smaller gape size, which restricts the consumption of larger fruits, while larger frugivorous birds which are not gape-limited can eat a much wider range of fruits, both large and small. The principal component analysis clearly showed that in KY, hornbills preferred the large fruits found in the forest. Indeed, in KY, the fruits consumed by hornbills are known to be significantly larger than those found in the diet of small frugivorous birds, such as bulbuls (Kitamura *et al.* 2002). Despite their large body size, hornbills were also observed to consume small fruits (5–69 mm in fruit diameter; Table 1). Previous studies also reported that Asian hornbills consumed various sizes of fruits in Borneo (4–40 mm; $n = 120$; Leighton 1982), Sulawesi (6–33 mm; $n = 23$; Suryadi *et al.* 1994) and India (6–30 mm; $n = 26$; Datta 2001). Since the diameters of the fruits consumed by hornbills are not significantly different among these study sites (Kruskal–Wallis test, H (3, 242) = 7.3, $P > 0.05$), it may be generalized that Asian hornbills tend to consume similar-sized fruit species (from small-sized to large-sized fruits), irrespective of their habitat.

Hornbills preferred the fruits of canopy trees or lianas and rarely used the fruits of small trees or arboreal shrubs. Fruits consumed by hornbills in KY have the characteristics that are associated with "bird-dispersed fruits", i.e. thin husks, or purple/black or red colour (Corlett 1996, Janson 1983, Knight and Siegfried 1983, Wheelwright and Janson 1985). In this respect, our results reflect a similar fruit choice as observed for hornbills elsewhere in Asian (Datta 2001, Leighton 1982, Suryadi *et al.* 1994) and African hornbills (Gautier-Hion *et al.* 1985, Kalina 1988, Poulsen *et al.* 2002). The fruits of Annonaceae, Lauraceae, Moraceae and Meliaceae were the most common fruits in hornbill diets in KY, as well as in other study sites. Hornbills prefer large dehiscent fruits or indehiscent fruits with a thin husk that grow in tall trees or lianas, especially the ripe colours of black/purple or red. But other factors, such as crop size, phenological patterns, tree distribution and nutrition in fruit pulp also influence fruit preference by hornbills.

Evidence from a number of studies suggests that seeds that are not dispersed by frugivores simply fall from the parent's canopy to the ground and have a low probability of survival (Becker and Wong 1985, Chapman and Chapman 1996, Howe *et al*. 1985). These findings support the idea that seed dispersal by frugivores is important for the maintenance of animal-dispersed tree populations, since the survival of fallen seeds under the mother tree does not appear to be sufficient to maintain populations of many tropical tree species (Chapman *et al*. 1992). However, the functions of large frugivorous animals in the Southeast Asian forest ecosystem are not well understood (Corlett 1998). Hornbills represent a good target taxon for the study of seed dispersal in the region; additional studies should be undertaken with urgency, given the high human pressures on hornbills.

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