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Breeding and nest site characteristics of the Black-casqued Hornbill *Ceratogymna atrata* and White-thighed Hornbill *Ceratogymna cylindricus* in south-central Cameroon

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The reproductive biology of two species of African hornbill, the Black-casqued Hornbill, *Ceratogymna atrata*, and the White-thighed Hornbill, *Ceratogymna cylindricus*, was investigated over a four-year period (1994–1997) on a 25km² site in lowland rainforest in south-central Cameroon. Nesting attempts varied considerably among years, with the percentage of successful nests highest in 1995, with 64% and 54% of Black-casqued and White-thighed Hornbill fledging offspring, respectively. There were no nesting attempts in 1994, despite the fact that hornbills were present in the study area. Large differences in fruit availability were also noted across years, suggesting that reproductive activity and success are related to fruit availability. Data collected from 38 nests, over four breeding seasons (1994–1997), showed a preference for nest cavities in larger trees within areas of the forest containing larger trees. Hornbills did not show preferences for particular tree species, with the possible exception of *Petersianthus macrocarpus*, in which nine of the active nest cavities were found. Comparisons showed few significant differences in cavity characteristics between the two species. While cavities may have been a limiting factor in nesting in 1995, the year with the highest fruit availability, cavities were not limiting during other years when fruit availability was lower. Hornbill diets, as determined from seed traps at cavities, showed significant year-to-year variation. Although courtship and exploratory behaviour of cavities by pairs took place in most years, females did not wall themselves into cavities unless fruit was plentiful. Hornbills appear to time reproduction to coincide with peak food supply and successfully reproduce only when food is plentiful, and may curtail or forego nesting in years when fruit availability is low.

Introduction

Hornbills in the genus *Ceratogymna* are large, primarily frugivorous species found throughout rainforest regions of Central Africa. Previous research has shown the larger species, the Black-casqued *C. atrata* and White-thighed *C. cylindricus*, are important seed dispersers for many rainforest tree species (Whitney *et al.* 1998, Whitney and Smith 1998, Poulsen *et al.* 2002). Both species are long-lived, believed to be monogamous, breed every one or two years, and lay one or two eggs (Fry *et al.* 1988, Kemp 1995). Until recently, however, the nesting biology of *Ceratogymna* hornbills has been poorly understood, even though the genus contains some of the more dominant species of frugivores in Central African rainforests (Whitney *et al.* 1998, Whitney and Smith 1998). Prior to Kalina's work (1988, 1989) in Uganda on the Grey-cheeked Hornbill (*C. subcylindricus*), relatively few nests of species in this genus had been described (Moreau 1937, Chapin 1939, Moreau and Moreau 1941, Fry *et al.* 1988, Kemp 1995).

The prominent role played by *Ceratogymna* hornbills in the dispersal of seeds of trees makes them important contributors to the maintenance of forest structure (Whitney *et al.* 1998, Whitney and Smith 1998, Hardesty 1999, Holbrook and Smith 2000, Poulsen *et al.* 2002). As with other tropical forests (Fleming *et al.* 1987, Fleming 1992, Jordano 1992, Van Schaik *et al.* 1993), Central African rainforests show considerable year-to-year variation in fruit availability (Gautier-Hion 1980, Gautier-Hion *et al.* 1985, White 1994, Whitney and Smith 1998). Previous studies found that Black-casqued and White-thighed Hornbills track resources, with hornbill abundance correlated with seasonal changes in fruit availability, and evidence of large-scale movements of more than 290km during food-lean periods (Whitney and Smith 1998, Holbrook and Smith 2000). Yet, the effect of inter-annual variation in fruit availability on hornbill reproductive effort is poorly understood. While food abundance is an important factor in regulating avian populations for cavity-nesting birds such as hornbills, the availability of suitable cavities may also be important (Newton 1994). Thus, determining the relative importance of each of these factors and how each is affected by anthropogenic influences is important not only for hornbill conservation, but also for the maintenance of rainforest, since hornbills are a major seed disperser (Whitney *et al.* 1998). The two species also differ in body mass, with Black-casqued Hornbills on average 5% larger than White-thighed Hornbills (Kemp 1995), and show differences in ecology (Whitney *et al.* 1998, Whitney and Smith 1998, Holbrook and Smith 2000).

The objectives of this study were to compare the breeding biology of the Black-casqued and White-thighed

Hornbills. Specifically, we examined: 1) nest-site characteristics and cavity availability, 2) the factors that determine timing and success of reproduction, especially the roles of fruit availability and rainfall, and 3) the composition of the diet of nesting hornbills. Finally, we discuss the implications of these factors in the conservation of hornbills and their habitats.

Methods

Study site
Research was conducted in the Dja Reserve, a 526 000 hectare Biosphere Reserve bound to the north and south by the Dja River, in central Cameroon (IUCN 1987). The 25km² study area was located approximately 23km south of the northern perimeter of the reserve, and is accessible only by foot (Whitney and Smith 1998). The reserve is comprised mostly of semi-deciduous rainforest (Letouzey 1968) that has not been commercially logged or cultivated (Figure 1). A distinctive feature of the study area is the presence of numerous inselbergs (rock outcrops) (Whitney and Smith 1998). The other major habitat type within the reserve (~7% of area) is swamp, which tends to be inundated year-round, and is dominated by the palm *Raphia monbuttorum*. Until recently, human activity was confined primarily to hunting by semi-nomadic Baka pygmies (Froment pers. comm.). Densities of arboreal frugivores are high, though the densities of large frugivores, such as the Forest Elephant (*Loxodonta africana*), Lowland Gorilla (*Gorilla gorilla*) and Chimpanzee (*Pan troglodyte*), are reduced (Poulsen *et al.* 2002), presumably from hunting pressure (Barnes 1996, Oyono 1998, Muchaal and Ngandjui 1999). Research began in late 1993, with most data in this study collected over a four-year period, from 1994–1997.

Fruit availability and rainfall
The phenology of over 300 individual trees, representing 38 species, were monitored monthly over the four years for the presence of flowers and fruit (for methods see Whitney *et al.* 1998). Of these we chose 13 representative species known to be particularly important in hornbill diet (see Whitney and Smith 1998) to estimate fruit availability. These species included: ANNONACEAE, *Cleistopholis glauca*, *Enantia chlorantha*, *Polyalthia suaveolens*, *Xylopia hypolampra*; BURSERACECAE, *Canarium schweinfurthii*; EUPHORBIACEAE, *Ricinodendron heudelotii*; MYRISTIC-ACEAE, *Coelocaryon preussii*, *Staudtia stipitata*; OLACACEAE, *Strombosia grandiflora*, *Strombosia pustulata*, *Strombosiopsis tetranda*; RHAMNACEAE, *Maesopsis eminii*; and STERCULICACEAE, *Eribroma oblongum*. An index of overall fruit availability (Holbrook *et al.* 2002) was estimated using the equation:

$$FAI = \sum_{x=1}^{n} (bm_x * pf_x * ph_x)$$

where FAI is the community-wide fruit availability, bm_x is a biomass index representing the mean basal area per hectare for each species, pf_x is the proportion of fruiting individuals for species x and ph_x is the average phenology score of all sample individuals of species x.

Because of the importance of estimating temporal patterns in food abundance accurately we also used a raked-trail survey method for assessing fruit availability (Sabatier 1985, Zhang and Wang 1995, Whitney and Smith 1998). Rainfall was collected daily from 1994–1997, using a rain gauge and recorded to the nearest mm at the centre of the study area.

Nest searches
Searches for tree cavities were conducted both opportunistically and systematically. Opportunistic searches were conducted on foot with the assistance of local Baka guides. Cavities were deemed potentially suitable for hornbill nesting if they: 1) were located in the bole or large branch of a large tree, 2) had an opening that appeared to be at least 10 cm in length, width, or diameter, and 3) appeared to be deep enough to house an adult female and young. Occasionally, evidence of past hornbill use was indicated by the presence of debris at the base of a tree containing a cavity (including old feathers, piles of seeds, or dried mud used to seal cavity openings). Once located, cavities were monitored for nesting activity bi-weekly during the breeding season (April–October).

To ensure that all major habitat types were sampled proportionally, searches for cavities and nests were also conducted on three 25ha plots and along a previously established 5km transect (Whitney and Smith 1998). The location of comparison plots was determined by superimposing a grid of 25ha plots over a map of the study site, giving each plot a unique number and then using a random number table to select plots for analysis. Eleven 500m parallel transects, 50 metres apart, were marked in a north-south direction across the plot. Researchers then systematically walked the entire plot, searching for trees with suitable cavities.

Active nest cavities were checked for the presence or absence of hornbills, integrity of mud door etc., on a regular basis, approximately once a week for nests located far from camp (>5km), and twice or more times a week for those closer. Several were monitored intensively (several times per week, for several hours each time) by observers in blinds recording all behaviours observed (perching, flying, calling, feeding female, etc.). Typically, cavities were well hidden from the ground and observed from a distance of 50 or more metres from the base of the tree. For 10 active nests that were located after the female had already walled herself into the cavity we used the Mayfield method (Mayfield 1975) to estimate start dates.

Nest cavities and plots
Measurements were taken of all 38 nest trees, cavities, and nest plots in order to quantify characteristics (Table 1). For 18 of these, cavity and tree measurements were made directly by climbing the tree containing the cavity while others were measured indirectly from the ground following methods described by Poonswad (1995). Tree and cavity height were estimated with simple trigonometry and a clinometer.

To assess nest-site selection, 40m x 40m plots were established at known hornbill cavities, with plots centered on the cavity tree. These were then compared to 32 random vegetation plots previously established in the study area
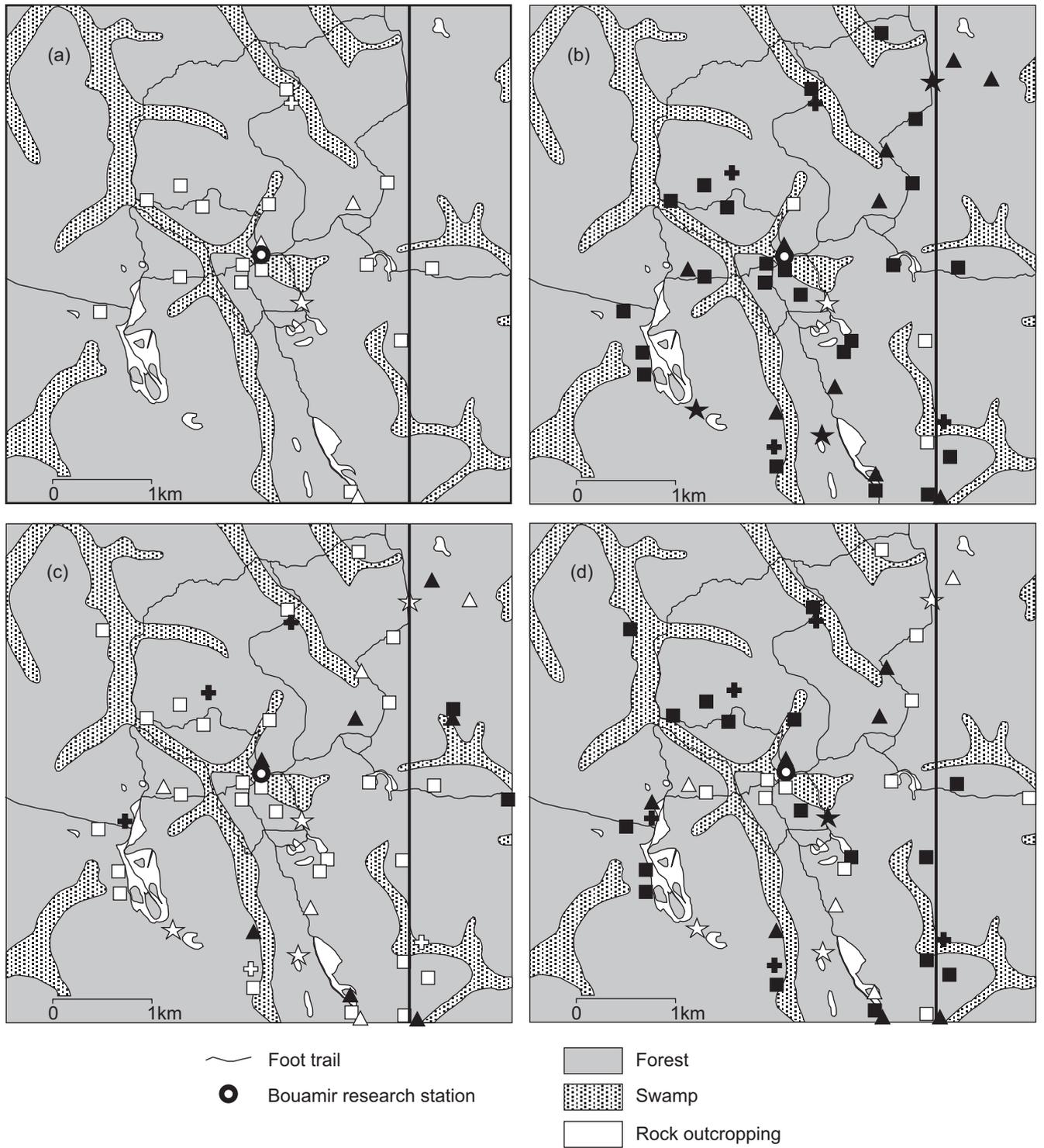
Figure 1: Locations of cavities and hornbill nests in years (a) 1994, (b) 1995, (c) 1996, (d) 1997. Open objects represent monitored cavities where no nesting attempt was made, while filled objects represent cavities with nesting attempts. Square — Black-casqued Hornbill (BCH), Triangle — White-thighed Hornbill (WTH), Cross — nest used by different species across years, Star — nest used by unknown species. The straight line that runs N–S on the eastern side of the study area is a transect line and foot trails

Table 1: Descriptions of nest and nest site variables

Category Variable	Description
Tree	
Species	
Dbh (cm)	Diameter of bole at breast height, measured with DBH tape
Nest height (m)	Measured with a clinometer
Tree (% live)	Estimated percentage of living canopy
Lowest limb height (m)	Measured with a clinometer
Nest cavity	
Cavity width (cm)	Measured directly
Cavity height (cm)	Measured directly
Cavity depth (cm)	Measured directly
Cavity volume (m^3)	Calculated by multiplying cavity width, height and depth
Opening width (cm)	Measured directly or estimated (*sensu* Poonswad 1995)
Opening height (cm)	Measured directly or estimated (*sensu* Poonswad 1995)
Opening area (cm^2)	Calculated by multiplying opening width by height
Opening thickness (cm)	Measured with a carpenter's tape
Cavity orientation	Measured with a compass weighted for equatorial Africa
Cavity pitch (° from vertical)	Measured with a clinometer
Plot	
Habitat	Forest, swamp or inselberg
Tallest tree in plot (m)	Measured with a clinometer
Rattan (# of stems)	Number and size (small, medium or large) of stems in each quadrant
Ground cover (%)	Measured as a percentage of 1m tape covered by foliage at ground
Cover at 1m (%)	Measured as a percentage of 1m tape covered by foliage at 1m
Canopy cover (%)	Measured with a densiometer
Trees in plots	
Density (trees ha^{-1})	Sum of trees in plot
Basal area (m^2 ha^{-1})	Sum of basal area, πr^2, of each tree in plot
Trees 10–12cm Dbh (trees ha^{-1})	From raw count in each plot
Trees 12–15cm Dbh (trees ha^{-1})	From raw count in each plot
Trees 15–20cm Dbh (trees ha^{-1})	From raw count in each plot
Trees 20–30cm Dbh (trees ha^{-1})	From raw count in each plot
Trees >30cm Dbh (trees ha^{-1})	From raw count in each plot
Dbh	Diameter of bole at breast height, measured with DBH tape
Distance and orientation	To nest tree, measured with a tape and compass

(Fogiel in prep.) and representing all habitat types. All trees over 10cm Dbh were counted and placed into one of five size classes.

Diets

Hornbill diet was estimated from ejected material at nest cavities. In both 1995 and 1996, seeds were collected from traps located underneath active hornbill nests. The traps were constructed from 1m^2 polyethylene sheets mounted approximately 1m off the forest floor on wooden poles. Traps were located so as to capture the highest possible concentration of material ejected from the nest, as debris tended to fall in a concentrated and discernable plume. A total of 25 traps were installed under nest cavities in 1995. Four additional traps were installed in 1996, three under newly discovered nests, and one under a nest discovered after the breeding season in 1995. Trapped seeds were collected weekly, counted, and the species was identified using a reference collection of known seeds (Poulson *et al.* 2002).

Statistical analysis

Differences between continuous variables from nest cavities of Black-casqued and White-thighed Hornbills were evaluated using one-way ANOVAs. Variables that remained non-normal after log or arcsine transformation were evaluated using non-parametric Mann-Whitney U-tests. Orientations of nest openings were tested using Rao's spacing test (Batschelet 1981, Rendell and Robertson 1994). Data were also analysed using forward stepwise multivariate logistic regression (Hosmer and Lemeshow 1989).

Results

Nesting success

Nesting activity and success varied greatly across years. In 1994, although hornbills were present, none were found breeding (Figure 1a). In 1995, 38 active hornbill nests were found, 25 Black-casqued and 13 White-thighed Hornbills (Figure 1b, Table 2). In addition, a Piping Hornbill (PPH), *Ceratogymna fistulator*, nested in one cavity and another nest contained an unknown *Ceratogymna* species. There were 10 nests in 1996 (three Black-casqued and seven White-thighed; Figure 1c) and 21 in 1997 (15 Black-casqued and six White-thighed; Figure 1d). Nesting success was highest in 1995, a period of maximal fruit production (see below); 64% and 54% of Black-casqued and White-thighed

Table 2: Cavity use and nesting success for Black-casqued Hornbill (BCH) and the White-thighed Hornbill (WTH)

	1994[a]		1995[b]		1996[c]		1997[d]	
	BCH	WTH	BCH	WTH	BCH	WTH	BCH	WTH
Nesting attempts	0	0	25	13	3	7	15	6
Nesting success[e]	0	0	16	7	1	2	10	2
Percent successful	0	0	64	54	33.3	28.6	66.7	33.3

[a] 20 cavities were monitored with no observed nesting
[b] 40/45 cavities (89%) monitored were used; 38 by BCH or WTH, 1 by PPH, 1 unknown
[c] 14/50 cavities (28%) monitored were used; 10 by BCH or WTH, 1 by PPH, 3 unknown
[d] 30/48 cavities (62.5%) monitored were used; 21 by BCH or WTH, 1 by PPH, 8 unknown
[e] Nesting success did not differ between species ($\chi^2 = 2.0$, $P > 0.1$)
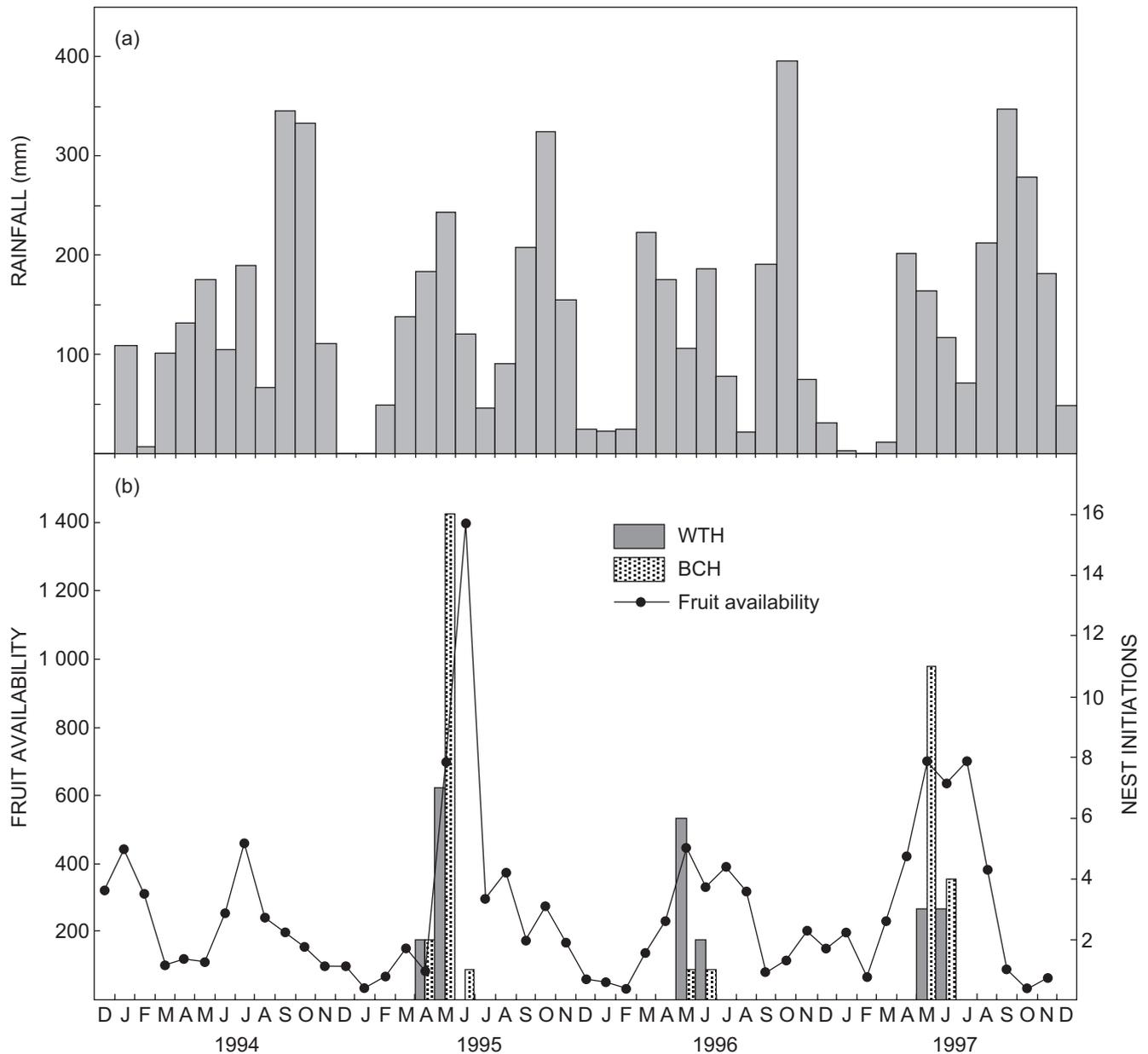

Figure 2: (a) Pattern of rainfall over the four years of the study and (b) fruit availability and nest starts for Black-casqued Hornbill (BCH) and White-thighed Hornbill (WTH). There were no recorded nests in 1994

Hornbills which attempted to breed (females walling in) fledged offspring, respectively.

Correlates of breeding activity

In the Dja, rainfall is bimodal, with a major wet season in September and October, and a minor one that stretches from March through June (Figure 2a). December through February is dry and a minor dry season occurs from June through August. We found no significant differences in rainfall across years (ANOVA, $F_{2,33}$ = 0.04, P = 0.96). Coefficients of variation of rainfall across years for this region of Cameroon average 12% and are similar to patterns found here (Smith 1990). In years that hornbills bred, they initiated nesting at the end of the minor dry season and the beginning of the minor wet season (Figure 2).

Variation in hornbill nesting activity across years was compared with fruit availability (Figure 2). The largest spike in the fruit availability index occurred in June and July 1995 and coincided with the year of greatest hornbill nests and highest reproductive success (Figure 2). Smaller spikes also occurred during the same periods in 1996 and 1997. The onset of nesting — the date the female walled herself into the nest (nest initiations) — occurred between May and July and coincided roughly with peak fruit production. While a similar magnitude peak occurred in 1994, when there was no breeding, the peak in 1996 was broader, suggesting more overall food availability (Figure 2).

There was a significant correlation between the large fruit availability peaks and nest initiation (r_s = 0.431, P = 0.002, n = 48). It appeared that pairs sealed their cavities during periods when fruit availability was increasing (Figure 2). In 1996 and 1997 nest starts were fewer, whereas during 1994 there were no nests. There was a significant difference in fruit availability across all years by month (ANOVA, $F_{11,36}$

= 3.104, P = 0.004). Fruit abundance estimated using the raked-trail method showed a similar pattern.

Cavity availability, characteristics and habitat associations

Of the 25 Black-casqued and 13 White-thighed Hornbill nest cavities examined, all but two (one of each species) were in living trees. Most cavities were in the boles of trees, but three (one Black-casqued and two White-thighed Hornbills) were in large branches. The cardinal orientation of cavity openings did not differ significantly from random for either species (Rao's spacing test, U = 114.5, P > 0.10) and there was no significant difference in orientation between species (t_{34} = 1.54, P = 0.132). A comparison of cavity characteristics of the Black-casqued and the White-thighed Hornbill revealed a significant difference only in cavity pitch (whether the cavity opening faced up or down). The pitch was slightly downward (negative) for Black-casqued Hornbill cavities, and slightly upward (positive) for White-thighed Hornbill cavities (Table 3).

A comparison of nesting success (1995–1997) for both species, combined or singly, found no significant influence of either negative or positive cavity pitch (Mann-Whitney U-test, z = –1.273, P = 0.203, n = 53, combined; z = –0.873, n = 32, P = 0.404, for Black-casqued; and z = –1.358, n = 18, P = 0.258 for White-thighed).

The availability of suitable nest cavities apparently did not limit reproductive activity. In each year, the total available cavities exceeded the number of nesting hornbills (Table 2), although cavity use neared the total number known to be available in 1995, with 45 of 50 available cavities used for nesting.

To evaluate hornbill nest plot characteristics, random plots were compared with 40m x 40m plots surrounding hornbill

Table 3: Nest characteristics of Black-casqued and White-thighed Hornbills. With the exception of cavity pitch, none of the characteristics differed significantly between the species

Characteristic	Black-casqued (n = 25)		White-thighed (n = 13)	
	Mean	SE	Mean	SE
Dbh (cm)	98.0	8.1	92.2	11.4
Nest ht. (m)	22.8	1.2	21.4	2.3
Tree (% live)	88.5	4.1	83.5	7.5
Lowest limb ht. (m)	25.9	1.6	24.7	1.1
Cavity width (cm)	41.2	4.3	45.4	4.2
Cavity height (cm)	151.0	12.9	112.9	22.8
Cavity depth (cm)	47.7	8.2	30.8	2.6
Cavity volume (m³)	3.6	1.5	1.5	0.4
Opening width (cm)	9.6	0.5	9.4	0.9
Opening height (cm)	13.5	1.1	10.4	0.7
Opening area (cm²)	132.2	15.6	168.3	73.7
Opening thickness (cm)	14.6	1.6	11.3	3.5
Cavity orientation	Random	–	Random	–
Cavity pitch (° from vertical)*	–1.3	1.1	5.3	4.1
Tallest tree in plot (m)	43.7	2.1	40.9	2.6
Rattan (# of stems)	16.6	4.3	9.0	4.9
Ground cover (%)	31.7	1.6	33.1	3.2
Cover at 1m (%)	18.4	3.6	15.8	2.9

* P = 0.04, multivariate linear regression

Table 4: Comparisons between hornbill nests and random plots

Characteristic	Hornbill nest plots (n = 38)		Random plots (n = 32)	
	Mean	±SE	Mean	±SE
Trees ha^{-1}	422.0	13.2	437.5	15.5
Basal area ha^{-1}**	37.9	2.3	29.5	1.9
Trees <12cm ha^{-1}**	59.4	4.6	82.8	5.8
Trees 12–15cm ha^{-1}	85.0	4.9	93.5	5.5
Trees 15–20cm ha^{-1}	99.3	5.4	90.4	5.5
Trees 20–30cm ha^{-1}	87.3	5.7	82.4	5.8
Trees >30cm ha^{-1}*	90.9	5.1	88.5	5.5
Canopy (% cover)	97.6	2.7	93.0	4.2

* P < 0.05
** P < 0.01, multivariate linear regression

Table 5: Tree species where hornbill nests were located

Family/species	Black-casqued	White-thighed
Apocynaceae		
Alstonia boonei	1	1
Caesalpinioideae		
Anthonotha macrocarpa	1	–
Chrysobalanaceae		
Maranthes glabra	1	–
Clusiaceae		
Allanbackia floribunda	1	–
Combretaceae		
Terminalia superba	3	2
Euphorbiaceae		
Drypetes sp.	1	–
Faboideae		
Pterocarpus soyaxii	1	1
Irvingaceae		
Desbordesia glaucescens	1	–
Lecythidaceae		
Petersianthus macrocarpus	4	5
Meliaceae		
Entandrophragma candollei	1	–
E. cylindricus	–	1
Mimosoideae		
Piptadeniastrum africanum	–	1
Olacaceae		
Ongokea gore	1	–
Strombosiopsis tetranda	1	–
Sapindaceae		
Blighia welwitschii	1	–
Eriocoelum macrocarpum	2	1
Sapotaceae		
Baillonella toxisperma	2	
Sterculiaceae		
Nesgordonia papaverifera	1	3
Ulmaceae		
Celtis mildraedii	1	–

nest trees (not including the nest tree). To maximise sample size, plots from both species of hornbill were combined. Using a forward stepwise multivariate logistic regression (Hosmer and Lemeshow 1989), significant differences in three variables were found (Table 4). Hornbill plots had fewer trees in the smallest tree class measured (Dbh <12cm), more trees in the largest size class (Dbh >30cm), and larger total tree basal area (m^2 ha^{-1}) than in the random plots. These patterns suggest that hornbills prefer cavities in areas with larger trees. Trees with active cavities had significantly larger diameters than trees located in the random plots (mean ± SE, 95 ± 6.52cm vs 23.3 ± 0.36, respectively; Mann-Whitney U-test, z = –9.975, P < 0.001, n = 4 939). Within plots, cavity trees were taller than the surrounding trees (mean ± SE, 41.0 ± 1.98m, vs 28.5 ± 1.61, respectively; Mann-Whitney U-test, z = –10.01, P < 0.001, n = 2 368).

Nest cavities of both species were in trees in mature upland forest (n = 33), with a few located in swamp forest (n = 2) or near inselbergs (n = 3). However, this distribution was not statistically different from the distribution of habitat types found at the study site (χ^2 = 0.734), indicating that hornbills did not show a preference for a particular habitat.

Hornbills did not show preferences for tree species, with the possible exception of *Petersianthus macrocarpus*, in which nine of the active nest cavities were found. It is unclear whether this tree species is more prone to having cavities than other species of tree. In total, hornbills used cavities in 19 tree species across 16 families with similar preferences exhibited by Black-casqued and White-thighed Hornbills (Table 5).

Diets

Species of seeds found in the seed traps differed significantly between years (Figure 3). Of the five most common, there were significantly more seeds of *Polyalthia suaveolens* (ANOVA, $F_{1,13}$ = 5.065, P = 0.042), *Pycanthus angolensis* (ANOVA, $F_{1,16}$ = 6.296, P = 0.023), and rattan spp. (Family Arecaceae) (ANOVA, $F_{1,16}$ = 5.091, P = 0.038) in 1995 than in 1996. There was no significant difference for *Cleistopholis* spp. (either *Cleistopholis glauca* or *Cleistopholis patens*) (ANOVA, $F_{1,16}$ = 0.836, P = 0.374), and *Enantia chlorantha* (ANOVA, $F_{1,15}$ = 2.728, P = 0.119). Additionally, for these same five species, there were no significant differences between traps under Black-casqued and White-thighed cavities: *Polyalthia suaveolens* (ANOVA, $F_{51,83}$ = 1.031, P = 0.444), *Pycanthus angolensis* (ANOVA, $F_{34,100}$ = 1.031, P = 0.756), rattan spp. (Family Arecaceae) (ANOVA, $F_{38,96}$ = 1.475, P = 0.066), *Cleistopholis* spp. (either *C. glauca* or *C. patens*) (ANOVA, $F_{25,109}$ = 1.421, P = 0.111), and *Enantia chlorantha* (ANOVA, $F_{23,111}$ = 1.225, P = 0.239).

While only eight cavities contained walled-in females in 1996, 26 traps accumulated some seeds during the breeding season. Of the 18 traps located under cavities where females were not walled in, most of the deposition occurred at the end of May and the beginning of June. Many of the seeds from these traps also appeared to be old, which suggests that hornbills may have been discarding refuse from the cavity.

Discussion

Fruit availability and nesting
Results suggest that although courtship and exploratory behaviour of cavities by pairs takes place in most years, females do not wall themselves into cavities unless fruit is
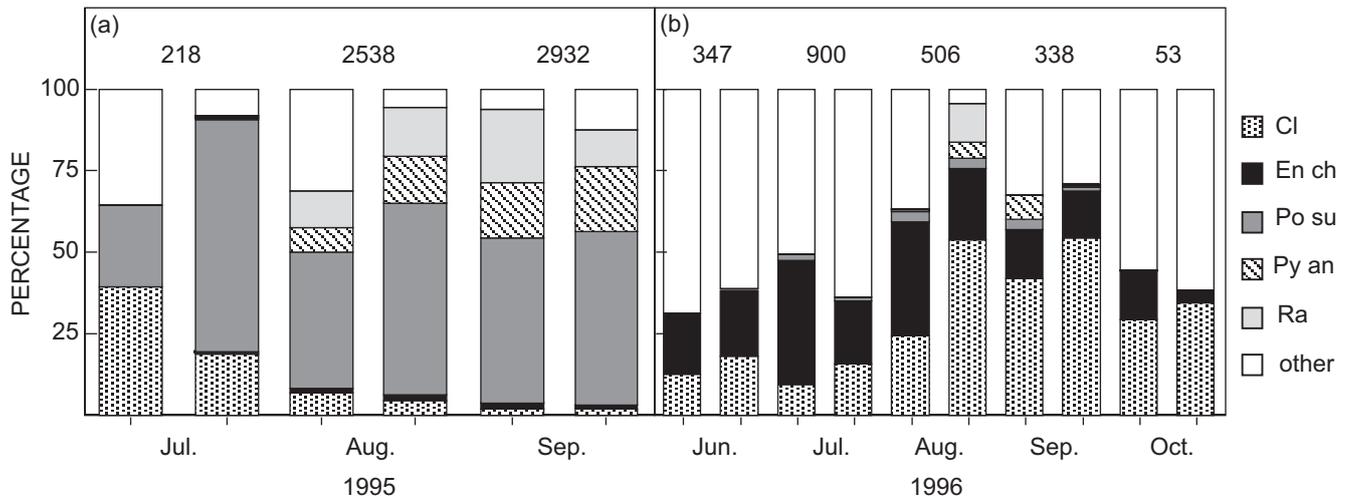
Figure 3: Proportions of different seed species collected in seed traps below nest cavities in (a) 1995 and (b) 1996; sample sizes are given above each bar for each month. See text for number of nests examined. Cl— *Cleistopholis* spp., En ch — *Enantia chlorantha*, Po su — *Polyathia suaveolens*, Py an — *Pycanthus angolensis*, Ra — rattan spp.

plentiful. This pattern suggests that hornbills time reproduction to coincide with peak food supply and nest when food becomes plentiful. Furthermore, data indicate that hornbills may curtail or forego nesting altogether in years when fruit availability does not show a sharp peak, as it did in 1994 when there was no breeding. Martin (1987) listed four possible responses to food limitation. First, parents could increase the number of surviving young by compromising offspring quality, i.e. egg size. Second, parents could invest additional energy into egg production, which could have negative effects on their own survival or on resources available for developing nestlings. Third, parents could delay egg production until adequate energy reserves are stored. Fourth, parents could forego nesting during a particular season. Being long-lived, it seems unlikely that hornbills would trade future reproductive success during a year of limited resources, especially given the energy needed for incubation and possible predation risk for females while in cavities. Moreover, hornbills are limited in the number of eggs they can lay (Fry *et al.* 1988, Kemp 1995). Thus one might expect, as results suggest, that pairs forego nesting in a year with limited resources, given the likelihood of their survival to the next breeding season (Ricklefs 1983, Boyce and Perrins 1987).

One factor believed to be important to the timing of breeding in tropical species is rainfall (Bourne 1955, Marchant 1960, Smith 1990). Research on other species of hornbill has shown that rainfall, coupled with the availability of fruit, is correlated with breeding (Kemp 1995). For example, Kalina (1988), working with the Grey-cheeked Hornbill, and Kemp and Kemp (1991) found that the onset of nesting is correlated with the beginning of the rainy season, which is followed by an increase in food supply. Poonswad *et al.* (1987) noticed a pattern with drought and nesting, finding that in years with little rainfall, nesting in four species of Asian hornbill was limited. Kinnaird and O'Brien (1993) found that hornbills in Indonesia commenced breeding at the

end of the rainy season, irrespective of other factors. The absence of a consistent pattern in the Dja suggests that rainfall probably does not always predict breeding. Whereas pairs did appear to set up territories independent of fruit availability (pers. obs.), pairs do not appear to wall the female into a cavity unless food is plentiful (Figure 2).

The nutritional content of fruit and availability of insects may be involved in nesting and nesting success. For example, calcium requirements may increase as much as five times during the breeding season and birds may alter their diet to increase food rich in calcium (Robbins 1993). Preliminary nutritional analysis of fruits consumed by the Dja hornbills in 1995 (Lamperti, unpublished data) provides evidence of two temporal peaks in calcium. Calcium peaks, as measured by the ratio of calcium to phosphorus, peaked during the period that female hornbills walled themselves into their nests, a time when calcium would be needed for producing eggshells. In addition, the proportion of hornbill diet comprised of insects (a ready source of protein) peaked in August 1995, when male hornbills were provisioning nests filled with growing chicks. It is not known whether this reflects relative availability of insects in the Dja or whether hornbills specifically seek insects during this period.

Other factors that affect the timing of nesting may relate to the availability of specific fruit. For at least part of the 1995 nesting season, a significant fraction of the hornbills' diet was composed of rattan. Data indicate rattan fruited heavily in 1995 and little in 1994 or 1996, which corresponded well to the hornbill nesting pattern. If hornbills commonly use rattan, this could have an important influence on the distribution and maintenance of this important non-timber forest product.

Nest cavity availability

There is considerable evidence that availability of suitable nest cavities, especially for secondary hole-nesting birds such as hornbills, limits both the prevalence of breeding and the density of bird populations (Newton 1994). For instance,

nest cavities appear limiting to the Great Pied Hornbill, *Buceros bicornis*, due to extensive deforestation in its native habitat in India (Kannan 1994, Kannan and Mudappa 1997). On the other hand, the availability of suitable nest cavities does not appear to limit nesting in the Red-knobbed Hornbill, *Aceros cassidix,* in Sulawesi (Kinnaird and O'Brien 1999). With the possible exception of the 1995 breeding year, the number of available cavities greatly exceeded the numbers of breeding pairs, which suggests that the availability of nest cavities does not limit breeding. In a given year, however, a large percentage of the adult hornbills seen in the Dja did not breed. Evidence suggests that lack of availability of suitable fruits at the onset of the breeding season may limit breeding.

As only those cavities that had been used as nests by hornbills were counted in the totals of available cavities, other factors may have influenced the desirability of certain cavities by hornbills. For instance, flying squirrels (*Anomalurus* sp.) compete with birds for nest cavities (Stabb *et al.* 1989). There were two observations of flying squirrels inside unoccupied hornbill nest cavities in the Dja. However, no interactions between flying squirrels and hornbills were observed, so the importance of this to cavity availability is unknown.

Cavity characteristics

Black-casqued Hornbills are approximately 5% larger than the White-thighed Hornbills (Kemp 1995), but, with the exception of cavity pitch, this did not translate into any significant differences in nest cavity or nest site characteristics between the species. Although no influence of cavity pitch on reproductive success was found here, Kalina (1988), in working in Uganda on the congeneric Grey-cheeked Hornbill (*Ceratogymna subcylindricus*), found that cavity openings with a downward pitch had a higher success rate that those with an upward pitch. She surmised that upward-facing openings were more exposed to rain, and lead to nest failure through exposure to moisture. In addition, Radford and Du Plessis (2003), working on Green Woodhoopoe (*Phoeniculus purpureus*), suggested nesting success may be reduced, due to flooding, when cavity openings are directed upward.

In 1995, Black-casqued Hornbill densities were higher than White-thighed Hornbill in primary forest, whereas secondary forest showed the reverse pattern (Whitney and Smith 1998). Similarly, the number of confirmed Black-casqued nest cavities in primary forest was higher than that for White-thighed. This possibly indicates that Black-casqued Hornbills are largely a primary forest species and White-thighed Hornbills are for the most part a secondary forest species. If nest cavities are relatively common in secondary forest and are used substantially by the White-thighed Hornbill, then it would be evidence supportive of this hypothesis. However, data collected in 1998 suggest that there were equal numbers of Black-casqued Hornbills and White-thighed Hornbills nesting in secondary forest adjacent to the Dja reserve (Wang in prep.).

Conservation implications

Trees with cavities used by hornbills were among the largest, and presumably oldest, in the study area. In some cases, trees with cavities may have wood that is not as resistant to rot as others, making them unsuitable for lumber. With little economic incentive to harvest these species, it may be possible to convince loggers and farmers to spare them when clearing tracts of forest. However, at least one tree species whose cavities are used by hornbills, *Baillonella toxisperma*, is an exception. Due to its large size and massive bole, it is prized by the lumber industry (Debroux and Delvingt 1998).

In the face of increased disturbance from logging, agriculture or activities such as fuel wood removal (Du Plessis 1995), loss of large trees could potentially have negative impacts on hornbill reproduction and demography. Given the mounting evidence of the hornbills' critical role in seed dispersal (Whitney *et al.* 1998, Poulsen *et al.* 2002), this impact, in turn, could have an adverse effect on forest regeneration. The practice of leaving some large trees standing in coffee and cocoa plantations could help ameliorate this situation. In addition, future studies should also explore the possible use of artificial nest boxes as a means of increasing hornbill numbers, and seed rain in regions where suitable cavities for nesting are scarce.

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