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## Seed dispersal and movement patterns in two species of *Ceratogymna* hornbills in a West African tropical lowland forest

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**Abstract** We studied two species of *Ceratogymna* hornbills, the black-casqued hornbill, *C. atrata*, and the white-thighed hornbill, *C. cylindricus*, in the tropical forests of Cameroon, to understand their movement patterns and evaluate their effectiveness as seed dispersers. To estimate hornbill contribution to a particular tree species' seed shadow we combined data from movements, determined by radio-tracking, with data from seed passage trials. For 13 individuals tracked over 12 months, home range varied between 925 and 4,472 ha, a much larger area than reported for other African avian frugivores. Seed passage times ranged from 51 to 765 min, with *C. atrata* showing longer passage times than *C. cylindricus*, and larger seeds having longer gut retention times than smaller seeds. Combining these data, we estimated that seed shadows were extensive for the eight tree species examined, with approximately 80% of seeds moved more than 500 m from the parent plant. Maximum estimated dispersal distances for larger seeds were 6,919 and 3,558 m for *C. atrata* and *C. cylindricus*, respectively. The extent of hornbill seed shadows suggests that their influence in determining forest structure will likely increase as other larger mammalian dispersers are exterminated.

**Key words** Seed dispersal · Seed shadow · Hornbills · Telemetry · Tropical frugivory

### Introduction

Seed dispersal by vertebrates contributes significantly to the maintenance of tropical forest structure and diversity

(Gautier-Hion et al. 1985; Willson 1992; Howe 1993b; Finegan 1996; Hamann and Eberhard 1999). While the majority of tropical trees depend on vertebrate dispersers to move their seeds (Gentry 1982; Howe and Smallwood 1982; Willson and Crome 1989; Jordano 1992; Howe and Westley 1997), the effectiveness of fruit-eating vertebrates in dispersing tropical seeds remains poorly known (Wheelwright and Orians 1982; Murray 1988; Sun et al. 1997). Complicating the study of vertebrate seed dispersal in the tropics is the tremendous diversity of the vertebrates involved. For example, in the Afrotropics, these range from some of the smallest vertebrates, such as terrestrial rodents and small passerines, to some of the largest, such as hornbills (Bucerotidae), apes (Homidae), and elephants (*Loxodonta africana*) (Gautier-Hion et al. 1985; White et al. 1993; Graham et al. 1995; Whitney et al. 1998). It is very unlikely that animals as diverse as these disperse seeds in a similar fashion or affect forest structure in comparable ways (Howe 1989; Schupp 1993). Thus, understanding the ecological and evolutionary forces that produce and maintain forest diversity requires detailed information on individual dispersers (Graham et al. 1995; Sun et al. 1997; Kinnaird 1998).

One way to compare the effectiveness of individual dispersers is to estimate their contributions to a particular tree's "seed shadow" (Janzen 1971). However, obtaining accurate estimates of seed shadows for tropical tree species dispersed by vertebrates is difficult. While seed traps are effective for estimating seed shadows of wind-dispersed species, seed traps tend to be ineffective for vertebrate dispersers which often deposit seeds in clumped and non-random ways (Clark et al. 1999). Alternatively, seed shadows may be estimated by combining information on frugivore movements and gut passage rates of seeds. While several studies have examined gut passage rates of seeds (Levey 1986, 1987; Murray et al. 1994; Graham et al. 1995), or movement patterns of tropical avian frugivores (Poonswad and Tsuji 1994; Powell and Bjork 1994; Suryadi et al. 1998), only two studies have examined them in concert to estimate dis-

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perser-specific seed shadows (Murray 1988; Sun et al. 1997). In both cases, frugivores were found to disperse the majority of seeds away from the parent tree.

Expanding on previous work conducted on *Ceratogymna* hornbills in the Dja Reserve, Cameroon (Whitney and Smith 1998; Whitney et al. 1998), we combine data on hornbill movements and gut passage rates to estimate the seed shadows of trees important in the hornbill diet. Hornbills represent an excellent target species for this work as they are important members of the seed disperser community and are found throughout most of lowland tropical rain forest in equatorial Africa (Kemp 1995). Whitney et al. (1998) found three species in the genus *Ceratogymna* to be highly frugivorous and effective seed dispersers, showing that collectively they disperse 22% of the known tree flora, including many community dominants and economically important species. In addition, using germination trials and behavior watches at individual trees, Whitney et al. (1998) found that passage through the hornbill gut is gentle on seeds and that hornbills moved the majority of seeds away from the parent tree.

In this study we examined seed dispersal and movement patterns of two species of *Ceratogymna* hornbills: the black-casqued hornbill (*C. atrata*), and the white-thighed hornbill (*C. cylindricus*). We used radio-tracking to estimate the home range and movement patterns of the two hornbill species. Then, using wild-caught hornbills of each species, we measured seed passage rates for a variety of seeds of woody plants common in the hornbill diet. Combining these data, we then estimated hornbill-specific seed shadows for several tree species. Finally, we discuss the importance of hornbill seed dispersal to the maintenance of tropical forests in the region.

## Materials and methods

### Study area

Research was conducted from October 1995 through December 1996 in the Dja Reserve, southern Cameroon. Bounded to the north, west, and south by the Dja River, the reserve encompasses 526,000 ha, making it one of the largest protected areas in Central Africa. The vegetation is described as semi-deciduous lowland tropical rain forest (Letouzey 1968) between 400 and 800 m elevation. The climate is characterized by two wet and two dry seasons, with the major and minor rainfall peaks generally occurring in October and May, respectively. Annual rainfall averages 1,600 mm year<sup>-1</sup> (Laclavère 1980) with 1,549 mm recorded in 1996 (Holbrook 1999). The study site is 25 km<sup>2</sup>, and is centered on the Bouamir Research Station (3°11'N, 12°48'E), in the western central portion of the reserve, approximately 22 km from the nearest village. A unique geographic feature of the study area is the presence of inselbergs, or rock outcroppings, which rise as much as 400 m above the forest floor and, for our purposes, served as radio-tracking stations.

### Hornbill capture and radio telemetry

Radio telemetry was used to examine movement patterns and estimate hornbill home range. Pulley-mounted mist nets (Tsuji et al. 1987; Munn 1991; Hagan and Johnston 1992) were erected in the

canopy near fruiting trees, allowing individuals to be captured as they visited trees to feed. Typically, four nets (227 mm mesh, 12×2.8 m) were attached, top to bottom, so that they created a single 12×11.2 m net. Nets were raised level with a fruiting tree; placement varied in height from 20 to 40 m depending on the height of the fruiting tree. Once captured, each individual was removed from the net, hooded (to calm the individual), weighed, measured, and banded with a unique color band combination.

Radio transmitters were attached to 12 adult *C. cylindricus* and four adult *C. atrata* (Advanced Telemetry Systems Inc., Isanti, Minn., USA; 30 g each; Holohil Systems Ltd., Carp, Ontario, Canada; 6 g each). Body mass of *C. cylindricus* and *C. atrata* is approximately 1,038 and 1,431 g, respectively (Holbrook 1999). Each radio weighed less than 3% of the bird's mass, which should not affect bird movement (Cochran 1980). All radios were attached ventrally at the base of one or both of the central tail feathers. Prior to attachment, approximately 7 cm of a feather vane was trimmed (in the case of 30-g radios) cleaned with alcohol and allowed to dry. Radios were mounted on the shaft with a 5-min, fast-drying epoxy, and tied with a strong polyester thread (Kenward 1978). The antenna was tied off along the shaft every 5 cm and all knots glued to prevent unraveling. Weighing, measuring and attachment of the radio took approximately 30–45 min. After release, individuals were followed for a minimum of 2 h to monitor behavior and ensure that the radio package remained attached.

We estimated hornbill positions by triangulation using receivers and hand-held 3-element Yagi antennas (Telonics Inc., Mesa, Ariz., USA) following the methods of Kenward (1987) and White and Garrott (1990). Tracking stations were spaced from 260 to 4520 m apart and were located on inselbergs rising 100–300 m above the forest canopy. Two to three observers collected simultaneous bearings on 3–4 days per week locating each individual approximately every hour. Observers used two-way radios to ensure simultaneity of readings and to communicate about each individual's location and any inconsistent bearings. To ensure that morning and afternoon variations were accounted for, each tracking week consisted of one or two 5-h mornings, one or two 4-h afternoons, and an occasional full day of 10–12 h. Using transmitters placed in known locations we estimated that the maximum range of radio signals varied between 3 and 8 km, depending upon vegetation structure and topography.

From the bearings and known latitude and longitude coordinates of tracking stations (determined by a hand-held global positioning system; Garmin GPS 12), we used a computer program (J.F. Sartwell, Missouri Department of Conservation) to calculate each bird's universal transverse Mercator (UTM) location for subsequent home range analysis. We used the minimum convex polygon (MCP) home range estimator (Jennrich and Turner 1969) to calculate home range sizes at 95%, using the program CALHOME (Kie et al. 1994). Home range analysis includes all *C. atrata* and 9 of the 12 tagged *C. cylindricus* (three *C. cylindricus* departed the study site within 5 days of radio attachment and were therefore omitted from all analyses). Individual tracking periods ranged from 10 to 167 days per individual (mean=68 days). (The end of each bird's tracking period represented either a lost radio or an individual that was no longer within range.) A total of 1,233 and 713 locations were used to determine *C. atrata* and *C. cylindricus* home ranges, respectively. Home ranges were estimated by sex (for *C. cylindricus* only) and species using data collected throughout the period of the study, and compared statistically using ANOVA.

### Seed passage rates

To estimate seed passage rates, feeding trials were conducted with captive hornbills. One individual of each of the two hornbill species captured on the study site was confined in a 1×1×2 m cage for 24–48 h. Ripe fruits known to be important in hornbill diet were fed to each individual at approximately 45 min intervals from 0600 to 1400 hours. Based on availability in the forest, fruit species tested were: *Maesopsis eminii*, *Staudtia stipitata*, *Cleistopholis patens*, *Enantia chlorantha*, *Strombosia scheffleri*,

*Xylopia hypolampra*, *Rauwolfia macrophylla*, *Lannea* sp., and *Ficus* sp. These nine species include four of the six favored plant families in hornbill diets, and represent over 16% of all fruits consumed by the two species of hornbills studied (Whitney et al. 1998). As trial birds were captured approximately 1 month apart (*C. atrata*, weighing 1475 g, 19 April 1996 and *C. cylindricus*, 800 g, 29 May 1996), not all the same fruit species were available for trials.

Fruits that could be pierced with a needle were marked with short strands of colored cotton thread, allowing easy discrimination between fruits fed in different trials. Fruits not easily marked in this manner were only fed once within a 24-h period. Papaya and raisins were available as supplementary food. In each trial, 10–20 fruits were fed and a total of seven feeding trials were conducted for each individual. Fruits were placed in the rear of the throat and the bill closed to ensure swallowing. Each bird was observed continuously from 0600 to 1900 hours from a previously erected blind near the cage to determine seed passage times. Seeds were collected immediately after defecation, identified, and passage time was recorded. During the night, birds were checked at 1–3 h intervals with seeds assigned a minimum passage time corresponding to the beginning of the interval in which they were passed. To compare passage times for different seed sizes, all fruit species were grouped into two size classes (small < 8 mm; large > 10 mm). The small size class includes *X. hypolampra*, *R. macrophylla*, *Lannea* sp., and *Ficus* sp., and the large size class includes *M. emini*, *Staudtia stipitata*, *Cleistopholis patens*, *E. chlorantha*, and *Strombosia scheffleri*. Mean retention times were calculated, then tested for differences between and among hornbills, fruit species, and seed size, using a Mann-Whitney *U*-test.

#### Seed shadow estimation

We estimated seed shadows using movement data and seed passage times following a method similar to Murray (1988). Distances from the first location of the day (the "origin") were estimated at 60, 120, 180, 240, 300, 360, 420, 480 and 540-min intervals. Only individuals (3 *Ceratogymna atrata*, 6 *C. cylindricus*) for which we had locations every hour throughout the day for a minimum of 8–10 days were used in the movement analyses. Using the minimum distance between the origin and each location recorded for a given time interval, we calculated the probability that a bird would be in each of the following distance categories: <500, 1,000, 1,500, 2,000, 2,500, 3,000, 3,500, 4,000, 4,500, 5,000,

5,500, 6,000, and >6,500 m (see Murray 1988). Distance traveled by individuals of the same hornbill species in each time interval did not differ significantly (ANOVA,  $P > 0.12$  for all intervals), allowing data from individuals in each hornbill species to be combined. The probabilities of seed deposition (*D*) within each distance category were then summed over all time intervals to yield the seed shadow (see Murray 1988):

$$D = \sum(L_t \times P_d)$$

where *L* is the probability of an individual hornbill being a particular distance from the origin at *t* min, where *t* varies in 60-min intervals, between 60 and 540 min, where *P* is the probability of a hornbill passing a seed at *d* m, and where *d* varies in 500-m intervals.

## Results

### Hornbill movements and home range

Estimated mean home ranges using 95% minimum convex polygons were 2872 ha for *C. atrata* and 2716 ha for *C. cylindricus* (Table 1). Home ranges varied nearly 5-fold for *C. cylindricus* (925–4,472 ha), and 3-fold for *C. atrata* (1,265–3,607 ha). Because home range estimates are influenced by sample size (Jennrich and Turner 1969), those reported here are conservative, and would likely increase with more days of tracking. Home range size was not significantly different between the two species, nor were there significant differences between male and female *C. cylindricus* (Table 1). Home range data on *C. atrata* includes only one female, thus a comparison between the sexes was not possible. In addition, since sample size was small for *C. atrata* ( $n=4$ ), home range comparison between hornbill species may have been affected.

**Table 1** Home range size (ha) of adult male and female *Ceratogymna atrata* and *C. cylindricus* during 1996 (MCP minimum convex polygon: Jennrich and Turner 1969)

Species	Hornbill	Sex <sup>a</sup>	No. locations	No. days detected	Tracking period	95% MCP <sup>b</sup>
<i>C. atrata</i>	764	F	344	50	11 Jun–31 Oct	3,607
	579	M	500	77	6 Jul–20 Dec	3,258
	604	M	43	8	18–28 Sep	1,265
	882	M	346	46	4 May–13 Sep	3,059
					Mean (±SE)=2,872±1,100	
<i>C. cylindricus</i>	538	F	137	24	29 Jul–31 Oct	2916
	560	F	37	14	25 Jul–23 Oct	4,472
	704	F	33	9	27 Aug–23 Sep	1,895
	903	F	38	8	31 May–11 Jun	3,711
	505	M	27	7	1–12 Aug	1,375
	664	M	184	17	14 Jun–12 Jul	925
	684	M	150	33	22 Jul–8 Oct	3,420
	724	M	57	11	5–23 Sep	1,374
	943	M	50	18	20 Nov 95–26 Jan	4,360
						Mean (±SE) 2,716±1,360

<sup>a</sup>No significant difference between male and female *C. cylindricus* were found (ANOVA: 95% MCP,  $F_{1,7}=1.119$ ,  $P=0.325$ ). Unable to test differences between sexes for *C. atrata* as only one female captured

<sup>b</sup>No significant difference between hornbill species were found (ANOVA: 95% MCP,  $F_{1,11}=0.040$ ,  $P=0.845$ )

**Table 2.** Seed passage rates for one individual of *C. atrata* and *C. cylindricus* for 9 plant species

Bird species	Tree species	No. fruits fed (Percent recovered)	Seed diameter Mean±SE (mm)	Seed passage rate Mean±SE (min)
<i>C. atrata</i>	<i>Maesopsis eminii</i>	17 (100)	13.68±0.23	289±24
	<i>Staudtia stipitata</i> <sup>a,c</sup>	30 (100)	12.42±0.26	345±39
	<i>Cleistopholis patens</i>	27 (100)	11.98±0.32	212±28
	<i>Xylopia hypolampra</i> <sup>b,c</sup>	26 (57.7)	7.42±0.07	210±25
	<i>Rauwolfia macrophylla</i>	19 (94.7)	3.93±0.05	186±16
<i>C. cylindricus</i>	<i>Maesopsis eminii</i>	3 (100)	13.68±0.23	267±43
	<i>Staudtia stipitata</i> <sup>a,d</sup>	22 (95.5)	12.42±0.26	162±8
	<i>Enantia chlorantha</i>	6 (100)	11.60±0.13	288±66
	<i>Strombosia scheffleri</i>	19 (100)	10.85±0.47	251±30
	<i>Xylopia hypolampra</i> <sup>b,d</sup>	38 (100)	7.42±0.07	154±12
	<i>Lannea</i> sp.	20 (95)	7.10±0.10	198±17
	<i>Ficus</i> sp.	23 (100)	<1.00	209±24

<sup>a</sup> Within-plants between-hornbills: *C. atrata*>*C. cylindricus* for *S. stipitata* (Mann-Whitney *U*; *U*=117.5, *P*<0.001)

<sup>b</sup> *C. atrata* was not significantly different from *C. cylindricus* for *Xylopia hypolampra* (Mann-Whitney *U*; *U*=202.0, *P*=0.100)

<sup>c</sup> Within-hornbills between-plants: *S. stipitata*>*X. hypolampra* for *C. atrata* (Mann-Whitney *U*; *U*=107.0, *P*=0.004)

<sup>d</sup> *S. stipitata* was not significantly different from *X. hypolampra* for *C. cylindricus* (Mann-Whitney *U*; *U*=365.0, *P*=0.590)

**Table 3** Minimum, maximum, and mean dispersal distances (m) of small (<8 mm) and large (>10 mm) seeds for *C. atrata* and *C. cylindricus*. Distances are calculated by combining seed passage

rates collected for small and large seeds with minimum, maximum, and mean distances moved within seed passage time categories

Bird species	Small seeds			Large seeds		
	Minimum	Maximum	Mean	Minimum	Maximum	Mean
<i>C. atrata</i>	95	6,919	1,422	216	6,919 <sup>a</sup>	1,620
<i>C. cylindricus</i>	87	5,698	1,127	87	3558	1,947

<sup>a</sup>An underestimation since the longest large seed passage time was 765 min and movement data were collected only up to 540 min

### Seed passage rates and dispersal distances

Average seed passage rates for *C. atrata* ranged from 186 to 345 min for *R. macrophylla* and *Staudtia stipitata*, respectively, and for *C. cylindricus* from 154 to 288 min for *X. hypolampra* and *E. chlorantha*, respectively (Table 2). Average gut passage rates were 284 min for large seeds and 197 min for small seeds in *C. atrata*, and 218 and 178 min, for large and small seeds, respectively in *C. cylindricus*. In both species, larger seeds took longer to pass than smaller seeds (Mann-Whitney *U*-test: *C. atrata*, *U*=785, *P*=0.003; *C. cylindricus*, *U*=1,024, *P*=0.027). There was also a trend for *C. atrata* to have longer passage times than *C. cylindricus* for large seeds (Mann-Whitney *U*-test: *U*=1,449.5, *P*=0.06). However, seed passage rates for small seeds did not differ significantly. In sum, the larger hornbill species (*C. atrata*) had longer seed passage times, and large seeds were retained longer than small seeds.

Estimated dispersal distances for small and large seeds are shown in Table 3. Average dispersal distances for large seeds were longer than small seeds in both hornbill species. The maximum dispersal distance for *C. atrata* for large seeds, based on movement data collected over 9 h, was 6,919 m.

### Seed shadows

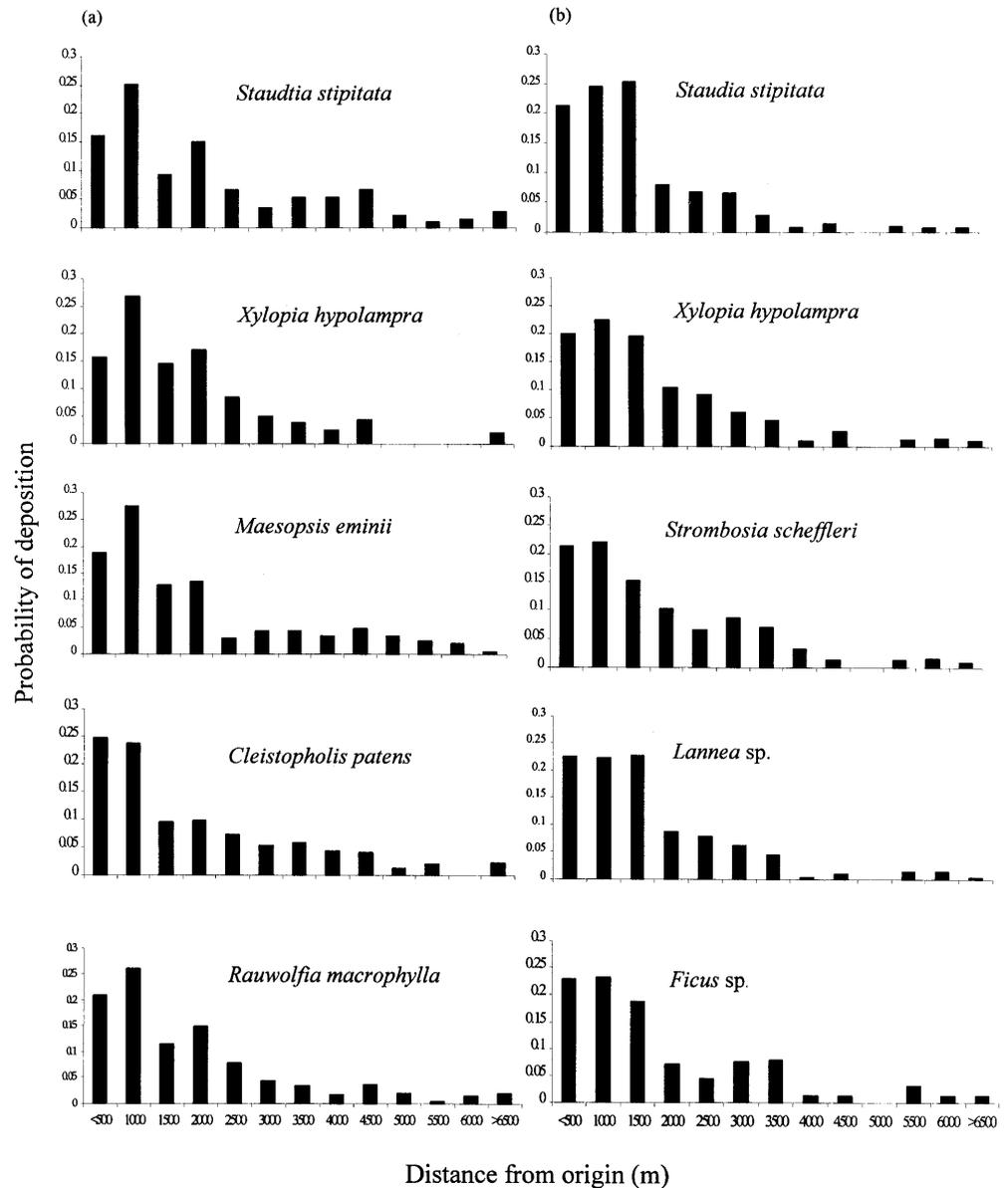
Estimated seed shadows for eight tree species important in hornbill diet are shown in Fig. 1. *C. atrata* deposited only 15–25% of ingested seeds within 500 m of a parent tree, and all fruit species show a peak seed deposition at 1,000 m (Fig. 1a). Seed shadows produced by *C. cylindricus* were similar with only 20–23% of seeds deposited within 500 m of the trees, with peaks occurring at 1,000 and 1,500 m (Fig. 1b). Both hornbill species produced extensive seed shadows, with approximately 80% of seeds deposited at more than 500 m from the parent tree. Contrary to many conventional descriptions of seed shadows for tropical vertebrates (Harper 1977; Fleming and Heithaus 1981; Clark et al. 1999), the shape of these seed shadows does not fit a simple negative exponential. Rather, they suggest a Poisson distribution with most peaks in seed deposition occurring at 1,000 m from the source, with very long thin tails that may exceed 6.5 km.

## Discussion

### Movements and home range

Our estimates of home range (925–4472 ha) are much larger than those reported by Brosset and Erard (1986),

**Fig. 1 a** Estimated seed shadows of *Staudtia stipitata*, *Xylopiya hypolampra*, *Maesopsis eminii*, *Cleistopholis patens* and *Rauwolfia macrophylla* produced by *Ceratogymna atrata*. *Origin* refers to the parent tree. **b** Estimated seed shadows of *Staudtia stipitata*, *X. hypolampra*, *Strombosia scheffleri*, *Lannea* sp. and *Ficus* sp. produced by *C. cylindricus*. *Origin* refers to the parent tree. (*M. eminii* and *E. chlorantha* were left out of analyses because of small sample size in seed passage trials)



who estimated that home ranges of *C. atrata* and *C. cylindricus* varied between 150 and several hundred hectares, but are likely conservative since home range estimates typically increase with increasing sample size (Jennrich and Turner 1969). In addition, it is likely that hornbill home ranges shrink during the breeding season, when females are walled into nest cavities, and are being fed by males. For example, both Poonswad and Tsuji (1994), and Suryadi et al. (1998) suggest smaller home ranges for breeding Asian hornbills. In the current study, several hornbills made nesting attempts, but the majority of nests failed by mid-season and none of the tagged birds attempted to nest.

In comparison with Asian hornbills, *Ceratogymna* hornbills have small home ranges. The great (*Buceros bicornis*), brown (*Ptilolaemus tickelli*), and wreathed hornbills (*Rhyticeros undulatus*) are reported to have home

ranges that vary from 3,700 to 28,000 ha (Poonswad and Tsuji 1994), and that of the Sulawesi red-knobbed hornbill (*Aceros cassidix*) is reported to average 4,690 ha (Suryadi et al. 1998). Nevertheless, *Ceratogymna* hornbill home range estimates exceed those reported for most other tropical frugivores. For example, one of the largest avian frugivores, the great blue turaco (*Corythaeola cristata*) is estimated to have a home range of approximately 150 ha (C. Sun, personal communication). Smaller terrestrial frugivores have very small ranges (e.g., agoutis, squirrels, and most rodents, less than 2 ha) (Eisenberg 1981, 1989; Smythe 1989). Larger primates such as black howler monkeys (*Alouatta pigra*), mantled howling monkeys (*A. palliata*), and patas monkeys (*Erythrocebus patas*) have home range sizes from 1 to 2,680 ha (Zucker et al. 1996; Gonzales-Martinez 1998; Ostro et al. 1999), and western lowland gorilla home

ranges (*Gorilla gorilla*) are estimated at 2,290 ha (Remis 1997).

Since our sample sizes were not equivalent for the two species, home range comparisons between species may be affected. Only further radio-tracking of a larger numbers of individuals will be able to detect possible differences. In addition, further work examining movements over a longer period is required to determine whether hornbill home ranges vary with respect to season, age, or sex, and, if so, whether potential changes in home range size are due more to fluctuations in food availability, breeding behavior, or other factors. One dramatic finding was the discovery that the two species also make long distance movements, possibly in excess of 290 km, during times when food is scarce, suggesting an important link between movement patterns and food availability (K.M. Holbrook and T.B. Smith, unpublished work).

#### Seed passage rates

Hornbill gut passage rates are among the longest reported for large avian frugivores with averages ranging between 154–345 min. Other studies report seed passage rates from 45 min for crested guans (*Penelope purpurascens*) (Howe and Kerckhove 1981) to 240 min for Ruwenzori turacos (Sun et al. 1997). Murray et al. (1994) indicate that seed viability decreases with increasing retention time, but that rapid passage rates have negative consequences on parent reproductive success, due to the increased probability of a seed being deposited near the parent tree. Though clearly there is a tradeoff between these two functions, Murray et al. (1994) still found that the proportional germination rate was higher on seeds that had passed through the gut. While we do not have data on seed viability as a function of retention time, Whitney et al. (1998) did find that seed passage by *Ceratogymna* hornbills had either positive or neutral effects on germination for 75% of seeds of the 1,411 seeds tested in germination experiments.

Levey (1986) examined seed passage rates through nine avian species in the Emberizidae and Pipridae and found rates increased with bird mass and increasing firmness of fruit pulp. He also found that large seeds tended to have shorter passage times than small seeds. Murray (1988) found differences in passage rates among fruits of similar size and texture in three species in the families Muscicapidae, Capitonidae, and Ptilogonatidae, and suggested that perhaps the fruits with the shortest seed passage rates contained a chemical laxative. In contrast, Sun et al. (1997) found no correlation between seed size and passage time in the Ruwenzori turaco (*M. johnstoni*). We found the larger *C. atrata* had longer passage rates than *C. cylindricus*, which agrees with Levey (1987), who found seed passage rates increased with bird mass. In contrast to Levey (1987), however, both hornbill species were found to have significantly longer seed passage times for large seeds. Several factors may have

affected seed passage estimates. First, wild birds kept captive are inactive and likely experiencing stress, and thus, may not pass seeds at normal rates. Secondly, the number and combination of fruits fed in a trial probably do not reflect foraging in the wild, which could affect results (Levey 1986). Finally, although we performed repeated trials, only one individual of each species was examined, making it impossible to detect individual variation in seed passage rates.

#### Seed shadows

The extensive seed shadows reported here are produced by long seed retention times and large daily movements, suggesting that the two hornbill species effectively move 80% of the seeds they consume a distance greater than 500 m from the parent plant. These results support the conclusions of Whitney et al. (1998) who combined tree watch data with seed passage times to show *Ceratogymna* hornbills conservatively deposited 69–100% of seeds away from the parent tree.

Recent evidence suggests that forest fragments may represent a significant barrier to gene flow for some tropical tree species dependent on vertebrate dispersers (Bruna 1999; Hamilton 1999). Because of long seed retention times and the ability to move large distances, hornbills may potentially deposit seeds as much as 6.9 km from the parent tree. This suggests that hornbills not only provide dispersal away from the parent tree, but may also be responsible for the colonization of gaps and the maintenance of gene flow between contiguous forests and forest fragments.

The shapes of hornbill-produced seed shadows are all relatively similar regardless of the species of tree and contrast with those recently described for tropical vertebrates (Clark et al. 1999). Seed shadows are often assumed to be highly leptokurtic, with the majority of seeds being deposited under the parent tree (Harper 1977; Fleming and Heithaus 1981). However, our findings suggest that seed shadows follow a Poisson distribution, exhibiting long thin tails with peaks at 1,000 and 1,500 m. Willson (1992) argued that, although the peak portion of the seed shadow often receives the most attention, perhaps the tail distribution should receive more attention. Our data support this assertion; the long tails suggest that hornbill seed dispersal may have substantive impacts on plant community structure and may contribute to increased gene flow (Schupp 1993; Hamilton 1999; Shilton et al. 1999). Long-distance dispersal by hornbills may also facilitate the dispersal of rare species and colonization to gaps or more suitable germination sites.

Several other studies have noted that seed shadow distributions deviate from a negative exponential (Murray 1988; Willson 1993; Sun et al. 1997). Hornbill seed shadows estimated here are very similar in shape to those described by Sun et al. (1997) for turacos in the African montane forests of Rwanda. Nevertheless, seed

shadows estimated from a single frugivore likely represent a mere fraction of the total seed shadow for a given tree (Willson 1993; Sun et al. 1997). For example, A. French and T.B. Smith (unpublished work) conducted tree watches for the same tree species (with the exception of *S. scheffleri* and *C. patens*) on the same site, and found that the number of vertebrate seed dispersers ranged from 7 to 17 species. Thus, considerably more work will be necessary to estimate the actual seed shadow from the standpoint of the tree.

### Hornbills as important seed dispersers

Results support previous work by Whitney et al. (1998) that *Ceratogymna* hornbills disperse the majority of seeds away from the parent tree. In conjunction with the finding that hornbill gut passage has a positive or neutral effect on seed germination rates (Whitney et al. 1998), this suggests that hornbills are likely important in determining forest structure and contributing to increased gene flow. The eight tree species tested are most likely adapted to be scatter-dispersed (Howe 1989) as they are primarily dispersed by smaller frugivores. Additionally, since hornbills are scatter-dispersers during the non-breeding season, when they are not restricted by nest cavity locations (Whitney et al. 1998), and are wide-ranging, they likely decrease density-dependent seed and/or seedling mortality by transporting seeds away from parent plants (Janzen 1970; Connell 1971; Howe 1989; Loiselle 1990). Recent studies confirm the importance of distance and/or density-dependent factors. In a 4-year study on Barro Colorado Island, Panama, Harms et al. (2000) found that negative density-dependent recruitment contributed significantly to an increase in diversity from seeds to seedling recruits. Additionally, Packer and Clay (2000) reported that although both distance to parent and neighborhood density were significant predictors of seedling survival, distance had a stronger effect on survival. These studies suggest that seeds of a given species are less likely to become established as the density of conspecific seedlings increases and emphasize the importance of seed dispersers such as hornbills.

Seed dispersal distances reported here exceed not only those of African turacos, estimated to be up to 304 m (Sun et al. 1997), but also those reported for other tropical and temperate birds (Howe and Primack 1975; Herrera and Jordano 1981; Howe and Kerckhove 1981; Murray 1988; Mack 1995), and terrestrial and volant mammals (Janzen et al. 1976; Fleming 1981; De Steven 1994; Fragoso 1997). Clearly, different frugivores influence plant recruitment in different ways. In a study by Howe (1993a), seeds dispersed by large toucans and guans were more likely to survive than those dispersed by smaller trogons and motmots. While the research presented here would certainly have benefited from investigations of seed and seedling survival, it was beyond the scope of this study. Still, many other questions remain

regarding the larger-scale processes determining tropical forest structure and regeneration. However, while we know little of how individual tropical frugivores impact forest structure, it is likely that focusing on individual dispersers may shed some light. For example, Fragoso (1997), looking at tapir-generated seed shadows, found that tapirs (*Tapirus terrestris*) have unique dispersal behavior that results in definable forest structure. His study in Brazil showed that past seed dispersal by tapirs had created distinct patches (or clumps) of adult palm trees.

The importance of hornbills as primary dispersers is amplified by their large home ranges and the fact that they are not currently heavily exploited as food, unlike many mammalian dispersers (Whitney et al. 1998). In addition, both species traverse secondary forest, degraded areas, roads, and rural regions in undergoing large-scale movements (Holbrook 1999). Thus, dispersal by hornbills may contribute to increased gene flow between plant populations and forest regeneration. Given the increasing rates of tropical deforestation, forest fragmentation, and loss of large mammalian frugivores (WRI 1992; Laurance et al. 1998; Oates 1999) the influence of hornbill seed dispersal on forest structure will likely increase.

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