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Habitat use and resource tracking by African *Ceratogymna* hornbills: implications for seed dispersal and forest conservation

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Abstract

Conservation of tropical forests requires an understanding of the seasonal patterns of abundance and distribution of important seed dispersers. In the forests of Central Africa, three species of hornbills in the genus *Ceratogymna* (Aves: Bucerotidae) provide dispersal for over 50 species of trees and lianas, yet their ecology is poorly known. We present the first empirical evidence for resource tracking and large-scale movements by two of these species, which were previously considered resident. Hornbill numbers and fruit production were estimated over a one-year period in the Dja Reserve, Cameroon. Monthly abundances of *C. atrata* and *C. cylindricus* varied four- and 12-fold, respectively, and were predicted by community fruit availability as measured by fruitfall on a 4·3 km trail. In contrast, *C. fistulator* abundances varied little and were not related to fruit availability. Synchronous population fluctuations in sites 22 km distant were observed for *atrata* and *cylindricus*, but not for *fistulator*. Together, these results indicate that *atrata* and *cylindricus* populations track fruit resources via seasonal emigrations, while the *fistulator* population appears to be relatively sedentary. Comparisons of hornbill densities in primary and secondary forests suggest that they are important dispersers in both habitats, and will likely play larger roles in central African forest regeneration as more vulnerable seed dispersers are removed by hunting. If large seasonal movements of hornbills turn out to be a general phenomenon, effective management of central African forest reserves will require greater emphasis on reserve connectivity and on seasonal and spatial patterns of fruit production.

INTRODUCTION

Changes in animal abundance in space and time are critically important when the species under consideration are integral to community processes. Seed dispersers provide a case in point. Because of their roles in the reproductive life histories of many plants (Howe, 1984, 1990; Stiles, 1992; Willson, 1992; Herrera, 1995), population fluctuations of seed dispersers can have substantial effects on communities. In the extreme case of extinction of the seed dispersing species, plant recruitment can be severely curtailed (Temple, 1977; Bond & Slingsby, 1984; Witmer & Cheke, 1991); conversely, large increases in seed disperser populations accompanying invasions of new habitats can have dramatic effects on plant community composition (e.g. Whittaker & Jones, 1994) and ecosystem function (e.g. Vitousek & Walker, 1989). Even less dramatic fluctuations, such as local increases in bird abundance that follow the construction of artificial perches, can change patterns of seed rain and alter the species diversity of the seedling bank (McDonnell & Stiles, 1983; McClanahan & Wolfe, 1993). In tropical forests, where 62–93% of the woody flora is adapted for vertebrate dispersal (Jordano, 1992), fluctuations in disperser abundances are likely to prove particularly important.

Disperser populations in tropical forests are affected by habitat disturbance and fragmentation. The combined effects of logging and land clearance for agriculture have resulted in vast changes in the availability of food, suitable breeding areas, and other resources that are important to animals. However, long-term studies that monitor disperser populations concurrently with changes in habitat structure and quality are scarce (but see Bierregaard & Lovejoy, 1988; Johns, 1989). In the absence of long-term data for many regions, comparing animal densities in adjacent undisturbed and disturbed forest sites (e.g. Johns & Skorupa, 1987) is an efficient method for

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evaluating the effects of disturbance on particular dispersers.

Disperser populations in tropical forests are also highly affected by the availability of fruit. Fruit exhibits a high degree of spatial and temporal patchiness in most tropical forests (Fleming, Breitwisch & Whitesides, 1987; Fleming, 1992; Jordano, 1992; van Schaik, Terborgh & Wright, 1993). Periods of fruit scarcity and abundance have been related to seasonal cycles of rainfall (Foster, 1982; Fleming *et al.*, 1987), temperature (Tutin & Fernandez, 1993), and insolation (White, 1994*a*), and are likely controlled by the interaction of these and a variety of other factors (van Schaik *et al.*, 1993). Spatially, large differences in fruit availability have been recorded over distances as small as 2 km (van Schaik, 1986). Frugivores can respond to this spatiotemporal patchiness through resource tracking, with consequences for their demography, physiology, foraging movements, social organization, and mating systems (Fleming, 1992). Resource tracking via daily and/or seasonal foraging movements has been demonstrated for many frugivore taxa; recent discussions include Fleming (1992), Jordano (1992), and van Schaik *et al.* (1993). Fleming *et al.* (1987) speculate that, because of a higher degree of spatiotemporal patchiness of fruit in the Old World, nomadic movements of frugivores may be more common in the Old World than in the New World. Their evaluation is based upon data from the Asian tropics and the Neotropics; further evidence is needed from the Afrotropics before this hypothesis can be evaluated, as data on frugivore movements in the Afrotropics are scarce (Thomas, 1983; White, 1994*b*).

Large hornbills in the genus *Ceratogymna* (Aves: Bucerotidae) are common members of the frugivore community throughout lowland tropical rain forest in Africa (Kemp, 1995), but their ecology has only recently been addressed quantitatively (Kalina, 1988; Whitney *et al.*, 1998). In the Dja Reserve in southern Cameroon, the black-casqued hornbill, *C. atrata*, the white-thighed hornbill, *C. cylindricus albotibialis*, and the piping hornbill, *C. fistulator sharpii* are large, 0·5–1·3 kg birds that consume the fruits and disperse the seeds of at least 56 species of trees and lianas belonging to at least 20 plant families (Whitney *et al.*, 1998). The majority of seeds swallowed are moved away from parent plants, seeds are rarely harmed during gut passage, and most species germinate at rates equal to or greater than controls, suggesting that *Ceratogymna* hornbills are important seed dispersers (Whitney *et al.*, 1998). *Ceratogymna subcylindricus* has been reported from the Dja Reserve (Christy, 1994) but is rare (R. Fotso, pers. comm.), and was not observed during this study. The remaining four species of hornbills in the Dja Reserve assemblage – *Tockus hartlaubi*, *T. camurus*, *T. albocristatus*, and *T. fasciatus* – are smaller and less frugivorous than the *Ceratogymna* species (K. Whitney, unpubl. data; Kemp, 1995).

In this paper, we use line transect methods to estimate the densities and biomasses of six of the seven species in the hornbill assemblage of the Dja Reserve, southern Cameroon. We contrast hornbill densities in mature and secondary forest sites in order to make some general predictions about the effects of habitat disturbance on hornbill populations, and about the types of habitats in which hornbills are likely to play an important role in seed dispersal. In addition, we examine within-site habitat use for the two largest and most common species, *atrata* and *cylindricus*. We use a measure of community fruit availability (the raked-trail survey) to examine whether *Ceratogymna* hornbill population fluctuations track seasonal changes in fruit availability. Finally, we evaluate evidence for intratropical migration using data on between-site synchrony in *Ceratogymna* hornbill abundances.

METHODS

Study sites

The study took place from January to December 1994 at two sites in southern Cameroon, one inside and one bordering the Dja Reserve. At 526 000 hectares, the Dja Reserve (Fig. 1) is the largest protected area in Cameroon and is an IUCN Biosphere Reserve (IUCN, 1987). The vegetation is semi-deciduous tropical rain forest (Letouzey, 1968), and has strong affiliations with other regions of the Congo Basin forest to the south and weaker affiliations with the evergreen Atlantic coastal forest to the west. Elevations in the Reserve range from 400–800 m. The climate is characterized by two wet and two dry seasons, with major and minor rainfall peaks in September and May, respectively. Average annual rainfall is approximately 1600 mm (Laclavère, 1980) and was 1669 mm during 1994.

Mature forest site: Bouamir Research Station

The mature forest site is a 25 km^2 square centered on the Bouamir Research Station (3°11'27"N, 12°48'41"E).

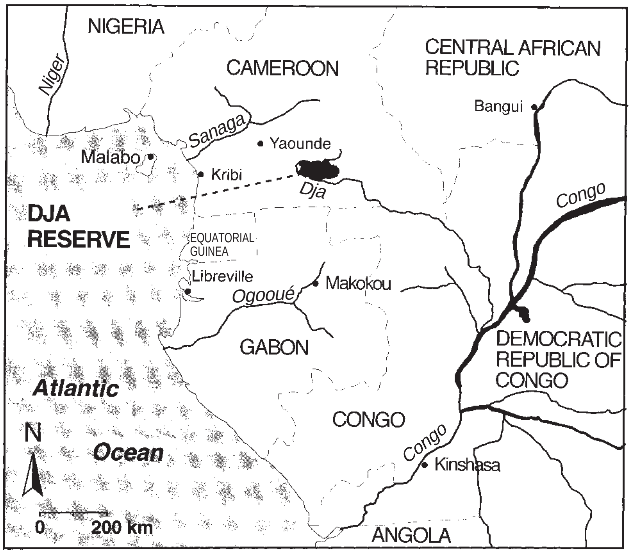

Fig. 1. Location of the Dja Reserve within the western Congo River basin.

Table 1. Characterization of habitat types in the mature and secondary forest sites, Dja Reserve

Habitat type	Extent[a]	Dominant trees[b]	Characteristics
Mature forest site: Bouamir Research Station			
Mature upland forest	83·0	*Desbordesia glaucescens* *Uapaca paludosa* *Terminalia superba*	
Inselberg-associated forest	3·3	*Lannea nigritiana* *Celtis mildbraedii* *Eribroma oblongum*	Distributed along edges of inselberg grasslands
Raphia swamp	6·8	*Raphia monbuttorum*	Year-round inundation
Uapaca swamp	6·8	*Uapaca paludosa* *Strombosiopsis tetranda* *Berlinia* sp.	Seasonal inundation
Secondary forest site: Somalomo			
Plantation	22·2	*Musanga cecropioides* *Albizia* sp. *Petersianthus macrocarpus*	Mosaic of cultivated fields (72%) and young secondary forest (28%)
Young secondary forest	31·9	*Musanga cecropioides*	≤ 30 years in age
Older secondary forest	40·4	—	> 30 years in age
Gilbertiodendron forest	3·4	*Gilbertiodendron dewevrei*	Monodominant stands
Uapaca swamp	2·1	*Uapaca paludosa*	Seasonal inundation

[a] Extent = percentage of the total area of each site. For the mature forest site, the relative extent of habitat types was determined through analysis of aerial photographs. *Raphia* swamp and *Uapaca* swamp are difficult to distinguish on photographs but were observed on the ground to be approximately equal in extent, thus, estimates were obtained by partitioning the observed swamp area equally between the two types. For the secondary forest site, analysis of older aerial photographs is not useful because of rapid habitat turnover. Instead, relative extent was estimated by the proportions occurring on animal survey transects.

[b] Dominants in the mature forest site were determined from (27) 40 × 40 m study plots (M. Fogiel, unpubl. data); dominants in the secondary forest site were determined by direct observation.

This area has never been commercially logged or farmed, has not been exploited for village agriculture in at least the past 90 years (J.-M. Froment, pers. comm.), and is 22 km from the nearest village or road. A feature unique to this site and a few other localities in the Reserve is the presence of inselbergs (‘rochers’), outcroppings of rock characterized by shallow soils and grassland vegetation. Four main habitat types occur in this site: upland forest, *Raphia* swamp, *Uapaca* swamp, and inselberg-associated forest (see Table 1). Currently, 230 species of trees are known from the site (M. Fogiel, unpubl. data).

Secondary forest site: Somalomo

The secondary forest site is located in and surrounding the village of Somalomo (3°22'24"N, 12°43'53"E), 22 km to the north of the Bouamir Research Station and just outside the Dja Reserve on the Dja River. This area is characterized by slash-and-burn agriculture, and is a mosaic of active plantations and regenerating forest. When mature forest is cleared for cultivation, some large trees are left (De Wachter, 1995); after abandonment, the site is dominated by a mix of these remaining trees and newly colonizing species, particularly *Musanga cecropioides* (Moraceae). We recognized four major habitat types in this site (Table 1): plantations (including coffee, cocoa and staple crops), young secondary forest (<30 years), older secondary forest (>30 years), and *Gilbertiodendron* forest. While *Raphia* and *Uapaca* swamps are also present at this site, they are not extensive and will not be considered further.

Hornbill survey methods

Hornbills were surveyed using modified line-transects, based on the distance sampling methods of Buckland *et al.*, (1993). To avoid the disturbance associated with constructing a transect grid, surveys were carried out on a 25 km network of former hunting trails at the mature forest site, and on 18 km of plantation and hunting trails at the secondary forest site. Trails were mapped using a topofil distance measurer and compass, and were then subject to zonation into habitat types (see Table 1). Approximately 30 km of surveys were conducted every two weeks at the mature forest site from January to December 1994 (726 km total). Approximately 20 km of surveys were conducted monthly at the secondary forest site exclusive of January, August and October 1994 (177 km total).

Surveys were conducted between 06.00–11.00 and 14.00–18.00 by one researcher and one local guide working together. Trails were walked at a pace of approximately 2·5 km h^{-1}; surveys were temporarily suspended during rainshowers. For each group of one or more hornbills encountered, the species, group size, observer-to-group distance, compass bearing of the trail, compass bearing of the group, time, and habitat type were recorded. Distances were estimated by eye to the nearest meter and were calibrated using an optical rangefinder. Observers occasionally left the trail to confirm group size, but all groups were initially detected from the transect line.

Density and biomass estimates

Densities of hornbill groups were estimated from the transect data using the program DISTANCE (Laake *et al*., 1993), which implements the analysis described in Buckland *et al.* (1993). Time of day had no significant effect on the number of hornbill group sightings ($\chi^2 = 7{\cdot}60$, d.f. = 12, $P = 0{\cdot}797$ for *atrata* groups; $\chi^2 = 14{\cdot}95$, d.f. = 12, $P = 0{\cdot}300$ for *cylindricus* groups; $\chi^2 = 6{\cdot}40$, d.f. = 6, $P = 0{\cdot}421$ for *fistulator* groups), so data from morning and afternoon surveys were pooled. Approximately 10% of the observations – those farthest from the transect line – were excluded from the analysis to improve model estimation (see Buckland *et al*., 1993), resulting in a truncated transect width of 325 m. Densities of individuals were calculated as the product of group density and mean group size, where mean group sizes were based on a subset of the observations for which we were confident that all group members were counted. Calculation of standard errors of individual densities follows Raj (1968):

$$\text{SE(individual density)} = \text{(group density)}^2 \times \text{SE(group size)} + \text{(group size)}^2 \times \text{SE(group density)} + \text{SE(group size)} \times \text{SE(group density)}$$

Hornbill densities in different habitats were compared using pairwise z tests and a 0·05 significance level. Hornbill biomass was estimated using an average of the midpoints of mean adult male and female masses from Kemp (1995).

Temporal patterns of fruit availability and hornbill abundance

Fruit availability at the mature forest site was measured using the raked-trail survey method (Sabatier, 1985; Zhang & Wang, 1995). Fruit falling onto a 4·3 km, 1 m-wide trail was surveyed biweekly. For each fruit patch (produced by an individual tree or liana) encountered on the trail, the species and the approximate numbers of ripe and unripe fruits were recorded. The trail was then cleared so that the fruits would not be counted on the next sampling date. Fruits of understory and of wind-dispersed species were uncommon and were not recorded. While not randomly placed, the trail sampled habitats in rough proportion to habitat abundance; mature forest, swamp, and inselberg habitats represented 75·4, 23·3, and 1·3% of the raked trail and 83·0, 13·7, 3·3% of the site, respectively. Two monthly indices of fruit availability are employed to represent the raked-trail results: 'number of individuals in fruit' is the number of all fruit patches found on the trail, and 'number of species in fruit' is the number of species comprising those individuals. Measurements of fruit availability were not made at the secondary forest site, where they likely would have been compromised by human foot traffic.

Monthly abundance indices of hornbills were determined from the transect data in the following manner: for each sampling period, all hornbill groups encountered within 100 m of the transect line were tabulated (thus transect width was set at 200 m), and this number was multiplied by the mean monthly group size to determine the number of individuals encountered. The monthly abundance indices are expressed as individual birds encountered per 100 km. Temporal patterns of hornbill abundance were compared using the Pearson correlation coefficient and single-factor ANOVA ($\alpha = 0{\cdot}05$).

Indices of hornbill abundance and fruit availability in the mature forest site were compared using regression. To determine if relationships remained significant after accounting for possible temporal autocorrelation (Verdú & García-Fayos, 1994), simple and partial Mantel tests were employed using the 'R' Package (Legendre & Vaudor, 1991). Mantel tests were carried out using 1000 permutations of the matrices.

RESULTS

Hornbill densities, biomass and habitat use

Six of the seven species in the hornbill assemblage of the Dja Reserve (all but *T. hartlaubi*) were recorded frequently enough to allow density estimations. Densities of these species in the mature and secondary forest sites ranged from 0·6 to 13·3 birds km^{-2}, and overall hornbill assemblage biomass was estimated at 20·0 and 27·3 kg km^{-2} for the mature and secondary forest sites, respectively (Table 2).

Between-site habitat preferences: mature vs. secondary forest

Each of the three *Ceratogymna* species showed significant differences in usage of the mature and secondary forest sites, while none of the three *Tockus* species did so (Table 2). Densities of *atrata* were significantly higher in the mature forest site than in the secondary forest site. In contrast, both *cylindricus* and *fistulator* densities were significantly lower in the mature forest site compared with the secondary forest site. Overall, the hornbill assemblage reached a higher density in the secondary forest site (30·9 birds km^{-2}) than in the mature forest site (20·2 birds km^{-2}).

Within-site habitat preferences

Sample sizes were large enough to analyze within-site habitat preferences for *atrata* and *cylindricus*, but not for other hornbill species. At the mature forest site, *atrata* reached significantly higher densities in inselberg-associated forest than in any other habitat type (z test, $P \leq 0{\cdot}036$ in all comparisons; Table 3). There was no significant preference apparent in their use of upland forest, *Uapaca* swamp, and *Raphia* swamp habitats. In the secondary forest site, *atrata* densities were not significantly different between habitat types, with the exception of *Gilbertiodendron* forests in which no *atrata* individuals were ever recorded.

Table 2. Comparison of hornbill assemblages in the mature and secondary forest sites, Dja Reserve, 1994. Densities are given ± SEM.

		Mature forest site (Bouamir Research Station)			Secondary forest site (Somalomo)			
Species	Mass (kg)[a]	n	Density (indiv. km^{-2})	Biomass (kg km^{-2})	n	Density (indiv. km^{-2})	Biomass (kg km^{-2})	P[b]
Ceratogymna atrata	1·20	647	8·7 ± 0·6	10·5	89	5·7 ± 1·0	6·9	0·008**
C. cylindricus	1·13	286	7·2 ± 1·0	8·1	147	13·3 ± 1·8	15·0	0·004**
C. fistulator	0·55	36	1·4 ± 0·4	0·7	55	8·1 ± 1·9	4·5	0·001**
Tockus albocristatus	0·31	39	0·7 ± 0·2	0·2	10	0·6 ± 0·2	0·2	0·536
T. fasciatus	0·26	78	1·2 ± 0·3	0·3	29	2·5 ± 0·7	0·7	0·083
T. camurus	0·10	92	1·0 ± 0·2	0·1	21	0·6 ± 0·2	0·1	0·178
T. hartlaubi	0·10	3	—	—	0	—	—	
Totals			20·2	20·0		30·9	27·3	

[a] Mean body masses are based on the midpoint of mean adult male mass and mean adult female mass from Kemp (1995).

[b] P-value of z test for whether densities are similar in the mature and secondary forest sites.

** $P < 0.01$.

n, number of hornbill groups encountered in surveys. Models used in density estimation were: uniform (*C. fistulator* and *T. camurus* in mature forest, *T. albocristatus* in secondary forest), composite models (*C. atrata* and *C. cylindricus*, see Table 3) and half-normal (all other estimates).

Table 3. Densities (± SEM) of *C. atrata* and *C. cylindricus* by habitat. Site averages are area-weighted averages (see Table 1).

	C. atrata			*C. cylindricus*		
Site / habitat	n	groups km^{-2}	indiv. km^{-2}	n	groups km^{-2}	indiv. km^{-2}
Mature forest site: Bouamir Research Station						
Mature upland forest	443	4·3 ± 0·3	8·5 ± 0·7	201	2·6 ± 0·3	7·6 ± 1·1
Inselberg-associated forest	108	8·3 ± 1·3	16·5 ± 2·7	66	5·4 ± 1·1	16·0 ± 3·4
Raphia swamp	37	4·8 ± 1·0	9·5 ± 2·0	6	0·5 ± 0·2	1·5 ± 0·5
Uapaca swamp	59	3·3 ± 0·6	6·5 ± 1·2	13	1·2 ± 0·4	3·6 ± 1·3
Site average		4·4 ± 0·3	8·7 ± 0·6		2·4 ± 0·3	7·2 ± 1·0
Secondary forest site: Somalomo						
Plantation	16	2·2 ± 0·6	4·5 ± 1·4	74	10·0 ± 1·9	22·1 ± 4·3
Young secondary forest	42	3·5 ± 0·8	7·3 ± 1·7	62	8·1 ± 1·6	17·8 ± 3·6
Older secondary forest	31	2·5 ± 0·7	5·3 ± 1·4	11	1·1 ± 0·4	2·5 ± 1·0
Gilbertiodendron forest	0	0·0	0·0	0	0·0	0·0
Site average		2·8 ± 0·4	5·7 ± 1·0		6·0 ± 0·8	13·3 ± 1·8

n, number of hornbill groups encountered in surveys. Models used in estimation were the: half-normal (*cylindricus* in mature upland forest, *Uapaca* swamp and young secondary forest), hazard rate (*atrata* in *Uapaca* swamp, *cylindricus* in inselberg-associated forest and plantation), and uniform (all other estimates).

In the mature forest site, *cylindricus* showed a pattern similar to *atrata*, with higher densities in inselberg-associated forest than in any other habitat type (z test, $P \leq 0.020$ in all comparisons; Table 3). However, unlike *atrata*, *cylindricus* densities were significantly higher in upland forest compared with either *Uapaca* swamp or *Raphia* swamp (z test, $P = 0{\cdot}019$ and $0{\cdot}001$, respectively). In the secondary forest site, *cylindricus* showed no significant difference in its use of plantation and young secondary forest habitats. However, densities were significantly lower in older secondary forest than in either of the younger habitats (z test, $P < 0{\cdot}001$ in both comparisons). No *cylindricus* were ever recorded in *Gilbertiodendron* forests.

Fruit availability

Over 350 individuals of 102 species of fruiting trees and lianas were recorded during the raked-trail survey at the mature forest site. Of these, at least 10 species (represented by 29 individuals on the trail) are consumed by *Ceratogymna* hornbills (Whitney *et al.*, 1998). General trends in fruit production by the tree and liana community were well represented by two indices, the number of individuals in fruit and the number of species in fruit (Fig. 2). The two indices were highly correlated (Pearson's $r = 0{\cdot}875$; $P < 0{\cdot}001$). When measured by either index, fruit availability was lowest from January to April, and highest from May to December (no. individuals in fruit, $F = 32{\cdot}98$, d.f. = 1,23, $P < 0{\cdot}001$; no. species in fruit, $F = 39.77$, d.f. = 1,23, $P < 0{\cdot}001$). When compared to rainfall during the same month or during either of the two previous months, both indices were most closely correlated with rainfall one month previous, although correlations did not reach statistical significance (no. individuals in fruit, $r = 0{\cdot}429$, $P = 0{\cdot}164$; no. species in fruit, $r = 0{\cdot}516$, $P = 0{\cdot}086$).

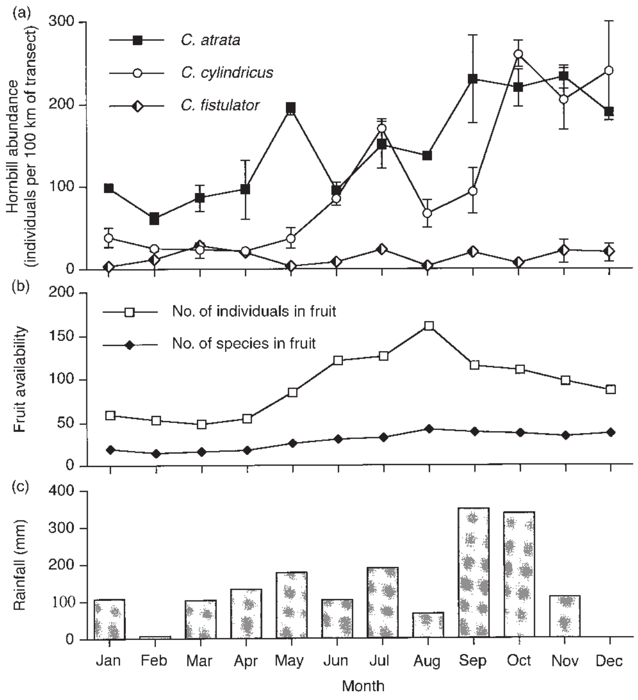

Fig. 2. Temporal patterns of hornbill abundance, fruit availability, and rainfall at the mature forest site, 1994. (a) Monthly hornbill abundance indices (individuals per 100 km of transect ± SEM). When standard errors are very small, error bars do not appear. (b) Community fruit availability measured on a 4·3 km trail. (c) Monthly rainfall (mm).

Hornbill responses to fruit availability

Monthly abundances (birds per 100 km of transect) of both *atrata* and *cylindricus* were highly variable at the mature forest site (Fig. 2). *Ceratogymna atrata* abundances varied nearly four-fold, while *cylindricus* abundances varied 12-fold. This contrast between peaks and valleys of abundance is consistent with a scenario in which as much as 74 and 92% of the *atrata* and *cylindricus* populations, respectively, leave the study area on a seasonal basis. Sightings throughout the year of a *cylindricus* individual with distinctive plumage markings indicate that populations do not turnover completely, however. Both species were less abundant from January through April, and more abundant from May to December (*atrata*, $F = 22{\cdot}19$, d.f. = 1,22, $P < 0{\cdot}001$; *cylindricus*, $F = 13{\cdot}53$, d.f. = 1,22, $P = 0{\cdot}001$), reaching peaks in October (*atrata*) and November (*cylindricus*). Monthly abundances of *atrata* and *cylindricus* at the mature forest site were highly correlated ($r = 0{\cdot}699$, $P = 0{\cdot}011$). These results suggest that the two species respond similarly to fruit production and/or other temporal factors affecting abundance.

During 1994, the monthly availability of fruit was a good predictor of *atrata* and *cylindricus* abundances in the mature forest site. Abundances of *atrata* and *cylindricus* were each significantly positively related to both the number of fruiting species and the number of fruiting individuals (Table 4). Analysis using partial Mantel tests found that the relationships between fruit availability and *atrata* and *cylindricus* abundances remained significant or nearly significant after controlling for temporal autocorrelation ($P < 0{\cdot}05$ in all comparisons except *atrata vs.* fruiting individuals for which $P = 0{\cdot}139$; Table 4).

In contrast to *atrata* and *cylindricus* responses, *fistulator* showed no significant population response to fruit availability. Abundances were fairly constant throughout the year at the both the mature and secondary forest sites (Figs 2 and 3); January–April and May–December abundances were not significantly different within either site (mature forest, $F = 0{\cdot}25$, d.f. = 1,22, $P = 0{\cdot}624$; secondary forest, $F = 1{\cdot}13$, d.f. = 1,30, $P = 0{\cdot}296$). Regression analysis found no significant relationship between either index of fruit availability and *fistulator* abundance at the mature forest site (Table 4).

Between-site synchrony in hornbill abundances

To look for evidence that *Ceratogymna* hornbills may make large-scale seasonal movements, we examined the synchrony of hornbill abundances in the mature and secondary forest sites, which are separated by 22 km. As with responses to fruit availability, *atrata* and *cylindricus* show one pattern, while *fistulator* shows another (Fig. 3). *Ceratogymna atrata* and *cylindricus* abundances at the mature forest site were significantly and

Table 4. Results of regression analysis and partial Mantel tests of monthly fruit availability and hornbill abundances in the mature forest site, 1994. Bird and fruit data were log-transformed prior to analysis. Mantel's *r* is standardized.

Index of fruit availability	Hornbill species	Regression		Mantel test[a]	
		r^2	*P* value	Mantel's *r*	*P* value
Number of species in fruit	*C. atrata*	0·66	0·001*	0·96	0·012*
	C. cylindricus	0·69	0·001*	0·68	0·016*
	C. fistulator	0·00	0·858*	–0·17	0·329
Number of individuals in fruit	*C. atrata*	0·36	0·037*	0·29	0·139
	C. cylindricus	0·49	0·011*	0·62	0·032*
	C. fistulator	0·03	0·595*	–0·07	0·470

[a] Significant results indicate that monthly bird abundance remains significantly predicted by fruit availability after controlling for temporal autocorrelation.
* $P < 0{\cdot}05$.

positively correlated with their abundances at the secondary forest site (*atrata*, $r = 0·659$, $P = 0·053$; *cylindricus*, $r = 0·834$, $P = 0·005$). This evidence is consistent with movements on a regional scale, and suggests that populations of these species perceive the mature and secondary forest sites as part of the same resource patch. *Ceratogymna fistulator* abundances showed no such correlation between sites (Fig. 3; $r = 0·163$; $P = 0·676$), corroborating evidence (see above) that this species does not track fruit availability via large-scale movements.

DISCUSSION

Hornbill densities, biomass and habitat use

One possible source of bias in transect sampling of hornbills is related to their cavity-nesting habit. Because nesting females are walled into their nesting cavities for several months, density estimates may be biased low during nesting periods. However, extensive searches and monitoring of previously used cavities determined that no breeding occurred in the mature and secondary forest sites during 1994, and thus this source of error is not applicable. Another source of bias that does apply is related to the use of non-linear transects. Foot trails, such as those used in the present study, are useful for sampling volant or arboreal species whose movements and habitat use are not likely to be affected by terrestrial trails. Several studies have successfully used hunting trails (Thomas, 1991), other types of non-linear, non-random trails (Defler & Pintor, 1985) or even roads (Skorupa, 1988) as transects. However, non-linear transects underestimate density because the estimated sampling area is greater than the actual area sampled (J. L. Laake, pers. comm.). For this reason, density estimates presented in this study should be treated as conservative.

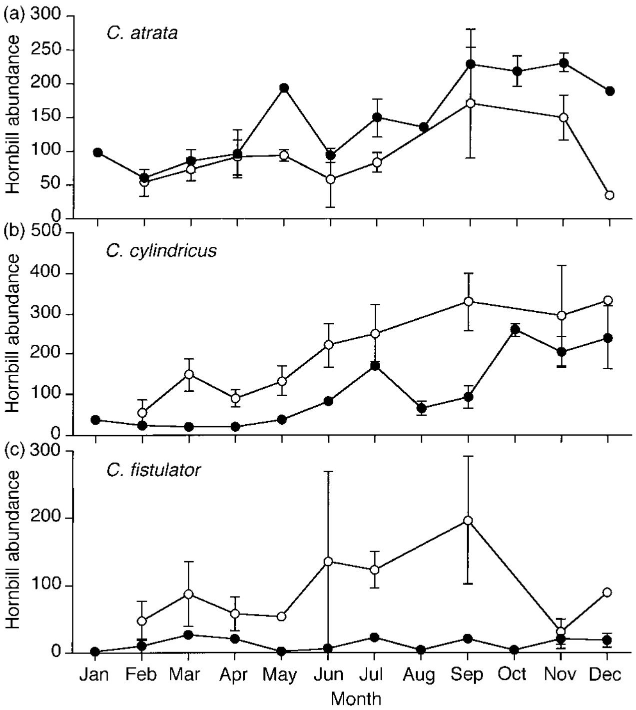

Fig. 3. Comparison of hornbill abundances in the mature forest (●) and secondary forest (○) sites, 1994. These sites are separated by 22 km of mature forest. Monthly abundance indices (individuals per 100 km of transect) are ± SEM; when standard errors are very small, error bars do not appear. The December estimates in secondary forest are based on a single sample. (a) *C. atrata* ($r = 0·659$; $P = 0·053$). (b) *C. cylindricus* ($r = 0·834$, $P = 0·005$). (c) *C. fistulator* ($r = 0·163$, $P = 0·676$).

Frugivore assemblage biomasses are useful in comparisons among different sites, and potentially will be useful in assessing the impacts of different groups on seed dispersal once more data become available. To date, this is the only known study to estimate the densities and biomass of an African hornbill assemblage. Kalina (1988) studied *C. subcylindricus* in the Kibale Forest, Uganda, and while biomass of the other species (*T. alboterminatus*) in the two-species hornbill assemblage was not established, biomass of *subcylindricus* ranged from 16·7 to 36·2 kg km^{-2}. Elsewhere in the Old World tropics, hornbill assemblage biomass ranges from 8·6 to 121·7 kg km^{-2} (Kinnaird *et al.*, 1996). Our estimate of the biomass of the Dja hornbill assemblage (20·0–27·3 kg km^{-2}) thus falls within the known ranges from other sites.

Between-site habitat preferences: mature vs. secondary forest

While densities of *Tockus* hornbills were not significantly different between sites, there is a clear divergence in habitat preferences of *Ceratogymna* species in the Dja Reserve. *Ceratogymna atrata* reaches its highest densities in mature forest habitats, while *cylindricus* and *fistulator* attain their highest densities in secondary forests associated with village agriculture. These differences may be related to differences in hunting pressures, differences in nest cavity abundance and size, and/or differences in vegetation composition (which in turn determine food availability).

Hunting is unlikely to be a factor in generating the observed patterns of hornbill densities. Relative to other game species, hunters in the Dja region rarely take *Ceratogymna* hornbills (K. Whitney, pers. obs.). The overall density of *Ceratogymna* hornbills is higher in the secondary forest site, where hunting for all animal species is much more intense, than in the mature forest site (Table 2).

Populations of many cavity-nesting species are subject to nest-site limitation (Wiens, 1989), and hornbill populations are likely to be limited in this way (Kemp, 1995). The availability of suitable hornbill nesting cavities may differ between logged and unlogged habitats because of differences in the abundance of large-diameter trees (Kalina, 1988). It may be that *cylindricus* and *fistulator*, which are smaller in size than *atrata*, are able to use smaller trees for nesting. The availability of suitable nest cavities in the mature and secondary forest sites is unknown, and thus we cannot evaluate potential nesting habitat effects on hornbill densities. However, it is important to note that the observed habitat preferences occurred in a non-nesting year, indicating that differences in fruit resources may play a more important role in generating the observed patterns.

Vegetation composition of the mature and secondary forest sites has not been directly contrasted. However, De Wachter (1995) characterized similar mature forests and plantations near Ekom, 34 km to the west of the Somalomo secondary forest site. He found that cultivated fields retained 4·5% of the number of smaller stems (10–70 cm dbh) and 57% of the larger stems (>70 cm dbh) found in mature forest. This pattern occurs because farmers do not cut all trees when preparing a plantation site. Large-diameter trees, especially those with hard woods, are left standing in cultivated fields because of the difficulty in felling them. These trees persist in the regenerating forest after cultivation is abandoned. De Wachter (1995) lists the 22 tree species most frequently left standing in Dja plantations; fruits from five of these (*Ficus* sp., *Pycnanthus angolensis*, *Xylopia* sp., *Margaritaria discoidea* and *Cleistopholis patens*) are consumed by at least one *Ceratogymna* species (Whitney *et al.*, 1998). Thus, a subset of the fruit resources available to hornbills in mature forest is also available in these secondary forest habitats. Unique fruit resources are available in secondary forest as well. *Musanga cecropioides* and *Ficus exasperata* are rare in mature forest, but are common in regenerating forest. *Ficus exasperata* is planted in cocoa plantations in the Dja region as a shade species (De Wachter, 1995). These species and others in the Moraceae were major sources of food for *cylindricus* and *fistulator* in the secondary forest site in 1994 (K. Whitney, unpubl. data). Our observations are in accord with other data suggesting that figs are often rare in mature forests but common in secondary forests in Africa (Gautier-Hion & Michaloud, 1989).

The observed habitat-use patterns of *Ceratogymna* hornbills are thus consistent with species-specific responses to differing fruit resources in the mature and secondary forest sites. Whether nest-site availability differs between these two habitats, and whether it contributes to hornbill habitat-use patterns, remain to be elucidated. Because secondary forests are created by multiple mechanisms, work is needed to refine our understanding of hornbill responses to habitat disturbance. Because of the agricultural practice of leaving large trees, secondary forests produced by shifting agriculture (including those in this study) are probably much different than secondary forests produced by logging, in which large hardwoods are selectively removed. Hornbill populations are likely to respond differently to these two types of secondary forest, and the high hornbill densities found in village-associated secondary forest in this study are not a guarantee that similar densities would be supported in logged forests. So far, data on the effects of selective logging on hornbill densities are ambiguous. In Uganda, Kalina (1988) compared two unlogged plots with one logged plot and found that *C. subcylindricus* densities were equal in one logged and one unlogged plot, while higher in the other unlogged plot. In Malaysia, Johns (1987) and Lambert (1992) observed little change in abundances of several hornbill species following selective logging, but small sample sizes make interpretation difficult.

Within-site habitat preferences

Ceratogymna cylindricus was observed to have relatively low densities in *Raphia* swamp habitats (Table 3). *Raphia monbuttorum* is a palm which produces large (4–6 cm long) drupes. Although *cylindricus* is known to occasionally take *Raphia* fruits (Whitney *et al.*, 1998), the species may be restricted to only the smallest fruits. In terms of fruit resources, there is little else in this habitat to attract *cylindricus*.

Inselberg-associated forest was heavily utilized by *Ceratogymna* hornbills. This forest has a distinct composition and contains species of hornbill feeding trees which are rare elsewhere; in particular, *Lannea welwitschii*, *Eribromum oblongum*, and *Maesopsis eminii* reach high basal areas within 20 m of the grassland–forest interface but are not well represented in any other habitat types at the mature forest site (M. Fogiel, unpubl. data). One of these inselberg-associated species in particular, *Lannea welwitschii*, produced abundant fruit from early June to mid-September 1994 and was heavily fed upon by *Ceratogymna* hornbills. Inselberg-associated forest comprises only 3% of the mature forest site and is even less frequent in the Dja Reserve as a whole. Further work on the role of this habitat type in influencing hornbill movements and distribution would be valuable.

Gilbertiodendron forests are monodominant stands of *G. dewevrei* (Caesalpinioideae), which mast fruits at intervals of two to three years (Hart, 1995). *G. dewevrei* was not observed to fruit during 1994; furthermore, its fruits are large woody pods and are unlikely to be eaten by hornbills. It is thus of little surprise that no hornbills of any species were recorded in these forests.

Resource tracking and large-scale movements

This study provides the first empirical evidence for resource tracking and large-scale movements by African hornbills. The larger species occurring in the Dja Reserve, *atrata* and *cylindricus*, track fruit resources through seasonal emigrations and show synchronous population fluctuations in distant sites. Perhaps as much as three-quarters of their populations are involved. The spatial scale of their movements remains to be determined, as does whether their movements represent true seasonal migrations, or nomadism. In any case, previous characterizations of these species as ‘resident’ (Fry *et al.*, 1988; Dowsett & Dowsett-Lemaire, 1993; Christy, 1994) with fixed home ranges of 150 to ‘several hundred’ hectares (Brosset & Erard, 1986) are not supported by the data. A smaller species, *fistulator*, does not track fruit resources (at least, not on the same scale as its congeners) and does not exhibit between-site synchrony in abundance, indicating that it is relatively sedentary. These patterns may be related to the degree of frugivory among the three species. While all are highly frugivorous, *fistulator* is less so than the other two species (Whitney *et al.*, 1998).

Where do *atrata* and *cylindricus* hornbills from the Dja go during the early part of the year? Although fruit resources can change substantially over short distances (<10 km), it is interesting to note that drastically different rainfall regimes (and by logical extension, fruit production regimes) occur within a few hundred kilometers of the Dja Reserve. To the west, rainfall increases and becomes unimodal in its yearly distribution; by Kribi (300 km from the Dja and on the Atlantic coast, see Fig. 1), the annual rainfall of 3000 mm is twice that of the Dja and has a single peak in August (Laclavère, 1980). To the south, rainfall remains bimodal, but by Makokou (250 km from the Dja and in Gabon) the major and minor dry seasons are reversed (comparison of data from Laclavère, 1980, and from Gautier-Hion *et al.*, 1985). Smith (1990) suggested that such regional differences in rainfall might be the cause of the likely seasonal migrations of some forest granivores in Cameroon. Documentation of regional fruit and frugivore abundance patterns in the Afrotropics is an important area of future study.

Wandering movements, perhaps in response to fruit availability, have been anecdotally recorded for African hornbill species of patchy habitats. In montane forests in Malawi, *C. brevis* and *C. bucinator* both show long-range movements; *brevis* in particular has been noted in forest patches over 100 km from breeding areas (Dowsett-Lemaire, 1989). The same two species apparently range widely in patchy woodland, coastal, and riparian habitats in East Africa (Britton, 1980). However, resource tracking and large-scale movements have never before been demonstrated for lowland, continuous-forest hornbill species in Africa. These new results are consistent with the movements of several Asian hornbill species. On Borneo, Leighton & Leighton (1983) found large seasonal fluctuations in the densities of *Rhyticeros* hornbills and other frugivores; emigrations from their site were related to food-lean periods. Populations of *Aceros undulatus* are nomadic, frequently crossing stretches of open water including that between Bali and Java (Kemp, 1995). On Sulawesi, Kinnaird *et al.* (1996) found that fig fruit densities predicted abundances and flock sizes of Sulawesi red-knobbed hornbills (*Aceros cassadix*). The scarcity of observations suggesting large-scale movements by African hornbills of the forest block may be related less to biological fact than to the difficulties in studying vagile species in continuous lowland forests.

Conservation implications

The current study has several implications for conservation of Central African *Ceratogymna* hornbills and their lowland forest habitats. First, if current trends in the disappearance of more vulnerable seed dispersers (e.g. forest elephants, *Loxodonta africana cyclotis*, and primates) continue, hornbills are likely to play increasingly larger roles in the dynamics of forest regeneration. Because elephants, primates, and hornbills disperse substantially different groups of species (Whitney *et al.*, 1998), changes in forest composition over the long term are possible, potentially in the direction of increased presence of hornbill-dispersed species.

Second, the results show that *Ceratogymna* hornbills are active in seed dispersal in both mature and secondary forests. As the forest block becomes increasingly fragmented, an important question is whether hornbill seed dispersal will continue to contribute to regeneration in isolated forest patches. To reach such patches, hornbills would have to travel through a matrix of degraded habitat, including plantations, open space, and urban areas. Hornbill species of naturally patchy habitats apparently regularly cross inhospitable areas (e.g. East African *Ceratogymna* species; Britton, 1980; Dowsett-Lemaire, 1989), but further work is needed to understand whether and when lowland, continuous-forest species (such as *atrata* and *cylindricus*) will cross matrix areas.

Finally, that lowland, continuous-forest hornbill species make unsuspected large-scale movements is intriguing, and adds credence to speculation (Thomas, 1983; Thiollay, 1985; Fleming *et al.*, 1987) that nomadic or migratory movements of paleotropical frugivores may be more extensive than previously thought. Confirmation that other large seed dispersers make large-scale movements would require us to rethink our approach to the conservation of central African forests (for a related situation in the Neotropics, see Powell & Bjork, 1994, 1995). The effective design and management of a system of reserves would need to take into account both how the reserves are connected, and the seasonal and spatial patterns of fruit production necessary for sustaining disperser populations.

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