# DIFFERENTIAL RESOURCE USE BY PRIMATES AND HORNBILLS: IMPLICATIONS FOR SEED DISPERSAL

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*Abstract.* Arboreal frugivores, such as primates and hornbills, are important seed dispersers for many tropical plant species, yet the degree to which they use the same resources is unknown. If primates and hornbills consume the same fruit species, they may be redundant in their roles as seed dispersers, and the loss of one of these taxa may be compensated for by the other. To examine resource use by tropical frugivores, we quantified the feeding habits of two hornbill species, *Ceratogymna atrata* and *C. cylindricus,* and five primate species, *Colobus guereza, Lophocebus albigena, Cercopithecus pogonias, C. cephus,* and *C. nictitans,* in the lowland rainforest of south-central Cameroon. Based on over 2200 feeding observations recorded between January and December 1998, we characterized the diets and estimated dietary overlap among frugivore species. Previous studies have calculated dietary overlap by counting the number of diet species that two animals share, often leading to inflated estimates of overlap. Our method incorporated the proportional use of diet species and fruit availability into randomization procedures, allowing a clearer assessment of the actual degree of overlap. This added complexity of analysis revealed that, although the diets of a hornbill and a primate species may have as many as 36 plant species in common, actual dietary overlap is low. These results suggested that there are distinct hornbill and primate feeding assemblages, with primates consuming a greater diversity of plant species and higher levels of nonfruit items like leaves and seeds. Using Correspondence Analysis, we also identified two primate assemblages, separated largely by degree of frugivory and folivory. In addition, we found that hornbills feed at significantly higher strata in the forest canopy and eat fruits of different colors than primates. Averaged across the year, overlap between groups (hornbill–primate) was significantly lower than combined within-group overlap (primate–primate and hornbill–hornbill), showing that primates and hornbills have dissimilar diets and are not redundant as seed dispersers. In equatorial Africa, primate populations face greater declines than hornbill populations because of hunting. It is unlikely that seed dispersal by hornbills will compensate for the loss of primates in maintaining forest structure.

*Key words: Cameroon; Ceratogymna; Cercopithecus; Colobus; dietary overlap; frugivory; hornbill; Lophocebus; Monte Carlo methods; primate; seed dispersal.*

## INTRODUCTION

Seed dispersal by tropical frugivores plays a critical role in the maintenance of tropical forests (Estrada and Fleming 1986, Howe 1986, Fleming and Estrada 1993, Hamilton 1999, Hubbell et al. 1999). As many as 85% of woody, tropical forest species depend on frugivorous birds and mammals for dissemination of their seeds (Terborgh 1990). Without transport by vertebrate dis-

persers, seeds falling beneath the parent plant can face greater mortality due to competition for resources with their parent, higher levels of density-dependent seed predation, and higher frequencies of fungal attack (Janzen 1970, Connell 1971, Stiles 1992).

For a particular plant, however, not all seed dispersers are equal (McKey 1975, Howe and Estabrook 1977, Snow 1981, Levey 1987, Clark et al. 1999). Behavioral patterns of frugivore species, such as movements, foraging and defecating patterns, and habitat preferences affect seed dissemination (Richards 1996, Clark et al. 1999, Clark et al., *in press*). In addition, frugivores may differentially affect seed and seedling survival by digesting, scarifying, or discarding seeds unchanged, singly or in clumps (Howe 1989, 1990, Zhang and Wang 1995*b*, Lambert 1999). Many studies have reported distinct fruit preferences by frugivores that may affect dispersal. Plant characteristics, such as

fruit color, fruit and seed size, and plant life form, are often assumed to be specifically adapted for dispersal by particular species (McKey 1975, Charles-Dominique et al. 1981, Howe and Vande Kerckhove 1981, Knight and Siegfried 1983, Gautier-Hion et al. 1985, Wheelwright and Janson 1985, Fleming and Estrada 1993, Dew and Wright 1998).

Although frugivore species exhibit a diversity of seed dissemination patterns, most studies examine seed dispersal by a single species or a few closely related species. Few studies have examined in detail assemblages of species that exploit and disperse similar suites of plants (but see Gautier-Hion et al. 1985, Gautier-Hion 1990). Both primates and large frugivorous birds are seed dispersers that play an important role in tropical forest maintenance and regeneration (Gautier-Hion 1984, Rowell and Mitchell 1991, Chapman 1995, Zhang and Wang 1995b, Julliot 1996, Sun et al. 1997, Dew and Wright 1998, Kinnaird et al. 1998, Lambert and Garber 1998, Whitney et al. 1998, Andresen 1999, Holbrook and Smith 2000). Among frugivorous African birds, hornbills are some of the most important seed dispersers and may disperse as much as 22% of tropical plant species (Whitney et al. 1998). Because of their large size, one might assume that hornbills have diets similar to those of arboreal primates. Indeed, previous research in Central Africa suggests that hornbills and primates may disperse similar suites of plant species, indicating that animal-dispersed plant species possess alternative seed dispersal agents that may replace one another (Gautier-Hion et al. 1985, Gautier-Hion 1990). However, a review of resource use in the tropics found that birds and mammals, including primates, consume different sets of plant species (Fleming 1979).

The extent to which multiple species of frugivores consume and disperse the seeds of individual plant species has important implications for forest conservation. In Central Africa, arboreal primate populations have been reduced to a fraction of their historical size through hunting and habitat destruction (Redford 1992, Chapman 1995, Oates 1996, 1999, Chapman et al. 1999, Muchaal and Ngandjui 1999, Struhsaker 1999). The reduction of primate abundance may alter seed dispersal, seed predation, and seedling recruitment for tropical plants (Wright et al. 2000). In order to conserve tropical forests, it is important to determine whether the decline of primate populations will result in a reduction of seed dispersal rates for some plants (Hamann and Curio 1999); or whether large frugivorous birds such as hornbills might compensate for and replace the loss of seed dispersal services provided by primates.

The manner in which dietary overlap is calculated is of paramount importance when determining redundancy among seed dispersers. If frugivorous birds and primates are found to have high dietary overlap, they may be expected to disperse similar suites of fruit species. Previous estimates of dietary overlap between birds and primates have been calculated as the number of plant species that two animals consume in common (Fleming 1979, Gautier-Hion et al. 1985). However, assessing dietary overlap by comparing lists of diet species inflates the actual overlap, and may often lead to the conclusion that two species of frugivores are redundant in terms of the fruit species that they eat and disperse. Two frugivores must consume similar proportions of the same species within the same time period in order to have high dietary overlap. We present a statistical approach using randomization procedures that accounts for both the proportional use of diet species and fruit availability in calculating dietary overlap and allows us to assess the statistical significance of overlap between species.

The objective of this study is to determine whether a non-hunted community of frugivorous primates and hornbills represents a single feeding assemblage or two or more feeding assemblages. By identifying feeding assemblages, we examine whether the loss of primates would leave some plants without dispersers, or whether hornbills could be expected to replace primates if overhunting led to their decline. To address this objective, we characterize the diets of these hornbills and primates and estimate the degree of dietary overlap between these groups.

## METHODS

### Study site

This study was part of a larger project examining the role of hornbills as seed dispersal agents, conducted from January 1994 to December 1998 in the Dja Reserve, south-central Cameroon (Whitney et al. 1998, Whitney and Smith 1998, Holbrook and Smith 2000). The reserve encompasses 526 000 ha, making it the largest protected area in Cameroon (IUCN 1987). Our study area was a 25-km$^2$ site centered on the Bouamir Research Station. The vegetation is semideciduous tropical rain forest (Letouzey 1968) and has never been logged. Small-scale agriculture took place at one corner of the study site more than 90 yr ago (Whitney and Smith 1998), but the only evidence of farming is a small patch (<25 m$^2$) of thick *Marantaceae* shrubs devoid of large trees. The climate is characterized by two wet and two dry seasons; with major and minor rainfall peaks in September and May, respectively (Whitney and Smith 1998). Average annual rainfall is ~1600 mm (Laclavère 1980).

### Fruit abundance and rainfall

Relative fruit abundance was estimated in 1998 using the raked-trail survey method (Sabatier 1985, Zhang and Wang 1995a). A 4.3 km long, 0.7 m wide trail was sampled bimonthly for all non-wind-dispersed fruits. The trail sampled habitats in approximate proportion to habitat abundance: mature forest, swamp, and inselberg (rocky outcrop) habitats (Whitney and Smith 1998). Fruits encountered along the trail were identified

to species, and the number of mature and immature fruits was recorded. The trail was then cleared so that the fruits would not be counted on the next sampling date. Daily precipitation was recorded with a rain gauge located in a forest gap.

### Frugivore diets

Two species of hornbills, the Black-casqued Hornbill *Ceratogymna atrata* and the White-thighed Hornbill *C. cylindricus* (Kemp 1995), and five primate species, the grey-cheeked mangabey *Lophocebus albigena,* the white-nosed guenon *Cercopithecus nictitans,* the crowned guenon *C. pogonias,* the mustached monkey *C. cephus,* and the black-and-white colobus *Colobus guereza* (Wilson and Reeder 1993), were chosen as target species. *C. atrata* and *C. cylindricus* were selected because they are the two largest and most frugivorous hornbills on the study site.

Diet records were compiled for each species from direct observations on unmarked individuals made at the Bouamir Research Station. To avoid disturbance associated with constructing a transect grid, researchers walked sections of a 34.5-km network of former hunting trails to make feeding observations. The trail system traverses all major habitats in the study area (Whitney and Smith 1998) and is composed of seven ''loops,'' ranging in length from 6.0 to 7.5 km, that collectively sample the entire study site. Surveys were walked during the morning (0600–1000) and afternoon (1500–1800). The loops were walked in sequence so that all seven loops were surveyed before the first loop was resampled. In addition, we alternated the direction in which a loop was sampled so that it was never walked in the same direction in two consecutive surveys. Each loop was walked at least three times per month, resulting in at least 21 surveys per month, with the exception of January, during which only 89 km of trail were surveyed (137.5 ± 16.2 km, mean ± 1 SD; range = 89–150 km). Whenever foraging hornbills or primates were encountered, the plant species and plant item (i.e., fruit, leaf, seed, bud, etc.) that they consumed were recorded. Each fruiting plant was considered a subject, and only one feeding observation was counted per frugivore species at a plant, irrespective of the number of individuals feeding. Furthermore, a fruit species was only designated a diet item if a frugivore was observed to ingest the fruit, or to regurgitate or defecate a seed. Observers frequently left the trail system to follow foraging hornbills or primates and to collect regurgitated or defecated seeds. The height in the canopy at which an individual frugivore was observed to feed was also recorded in 1998 as a series of height categories (0–10 m, 11–20 m, 21–30 m, >30 m). Feeding heights were not recorded for all species between January and April 1998, so we present data only for *L. albigena, C. pogonias,* and *C. nictitans* during that period.

Lists of food items in the diet were compiled from feeding observations made between January 1994 and May 1999 (Appendix). However, only feeding observations collected from January through December 1998 were used to estimate dietary overlap because sampling effort was consistent for all target species.

### Diets and dietary overlap estimates

We used Correspondence Analysis (CA) to compare diets among frugivores (Gorchov et al. 1995). As used here, CA projects a multidimensional swarm of data points onto a two-dimensional space (Gauch 1982, Pielou 1984) by maximizing the correspondence between row and column categories (frugivores and diet species). The data matrix consisted of the number of feeding observations recorded for each frugivore species on a plant species, and therefore accounted for both the presence or absence of a plant species in the diet and the amount of use of a plant species by a frugivore species. The resulting plot positions species with similar diets closer to each other. Correspondence analysis was done using the program PC-ORD.

The proportion of a food in the diet of the consumer depends on the consumer's electivity (preference for a food) and the availability of that food in the environment (Lawlor 1980, Gotelli and Graves 1996), and both of these factors are calculated in dietary overlap values described here. We calculated month-by-month indices of dietary overlap among pairs of frugivores using Schoener's (1974) overlap measure:

$$R_O = 1 - \frac{1}{2} \sum_{i=1}^{n} |p_{ij} - p_{ik}|$$

where $R_O$ is resource overlap, $p_{ij}$ and $p_{ik}$ are the proportions of observations in which the $i$th resource is consumed by the $j$th and $k$th species. This index generates a value ranging from 0 to 1, with 0 representing no overlap and 1 representing complete overlap.

We used Monte Carlo methods (Ricklefs and Lau 1980) to generate estimates of the expected monthly dietary overlap between species of frugivore, corrected for fruit availability, and to test the null hypothesis that the observed monthly dietary overlap between frugivores did not differ from that expected under the assumption that each species of frugivore consumes resources in relation to their availability in the environment. On a monthly basis, we simulated resource use of each of the $j$ species for each of the $i$ resource categories by randomly and independently redistributing the observed number of feeding observations for each species among the $i$ resource categories, with the probability of selecting the $i$th resource category equal to the proportion of all resources comprised by the $i$th category. We then used these simulated resource use values $E(p_{ij})$ to calculate the resultant overlap between the $j$th and $k$th species, employing Schoener's (1974) overlap index. We repeated this process 1000 times to generate the expected overlap for such Monte Carlo simulations and the variance in expected overlap. Be-
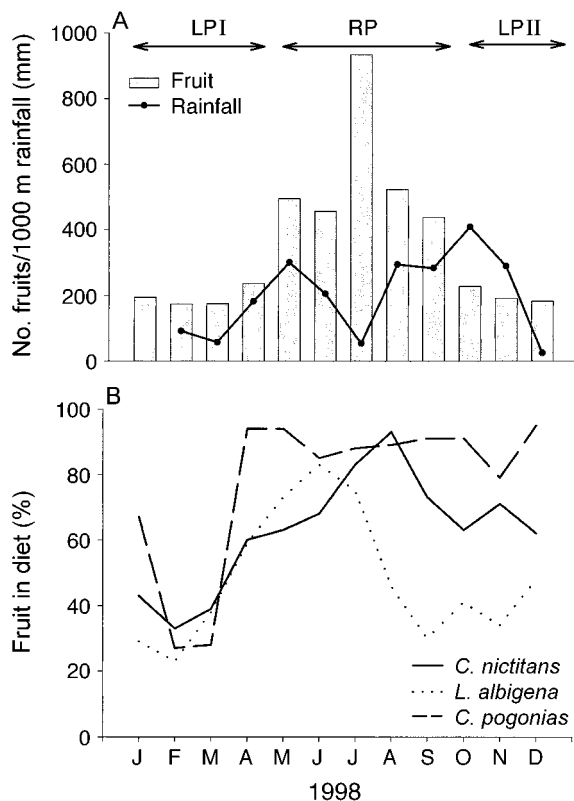
FIG. 1. (A) Abundance of fruits in 1998 based on raked-trail surveys and average monthly rainfall (mm) in the study area in Cameroon. Periods of fruit abundance are labeled as LPI (lean fruit period I), RP (rich fruit period), and LPII (lean fruit period II). (B) Percentage of fruit in diet per month for three primates (*Lophocebus albigena, Cercopithecus pogonias,* and *Cercopithecus nictitans*) during 1998. Hornbill diets did not vary significantly over the year and were therefore excluded from the figure. Likewise, because the number of feeding observations for *Cercopithecus cephus* and *Colobus guereza* were low in some months, seasonal comparisons were inappropriate.

cause of chance deviations from strictly proportional use of resources by individual species in Monte Carlo simulations, expected overlap between pairs of species will be less than 1 (but will approach 1 and exhibit less variance as the number of feeding observations increases for either or both species). We counted the number of times the observed overlap was less than or greater than the expected overlap. If the observed overlap was less than expected for 2.5% of the iterations or greater than 97.5% of the iterations, we rejected the null hypothesis that the observed monthly dietary overlap between frugivore species did not differ from that expected under the assumption that each species consumes resources in proportion to their availability in the environment at an $\alpha$ level of 5% (i.e., we concluded that one or both species consumed resources disproportionately from their relative availability).

We then computed standardized overlap values to correct for monthly differences in dietary overlap re-

sulting from sample size differences and differences in fruit availability between months, using Llewellyn and Jenkins' (1987) index:

$$PS_{std} = (PS_{obs} - PS_{exp})/[Var(PS_{exp})]^{1/2}.$$

Here, $PS_{std}$ represents the standardized dietary overlap for a particular month, $PS_{obs}$ represents the observed dietary overlap, and $PS_{exp}$ represents the expected dietary overlap value for that month. Although the notation of Llewellyn and Jenkins (1987) is used in the previous equation, PS is calculated with Schoener's overlap measure, and is equivalent to the symbol $R_O$. As a result of standardizing overlap values, raw overlap values on a 0–1 scale are replaced with scores centered on 0. A score of 0 indicates that the expected and observed values are the same. Therefore, negative numbers represent overlap less than that expected by chance, and positive numbers represent overlap greater than expected.

To determine if the observed overlap in resource use is consistent with the hypothesis that hornbills might be able to replace the seed dispersal services provided by primates, we used a similar Monte Carlo procedure. We reasoned that, in order for hornbills to be able to replace the seed dispersal services provided by primates, they would first have to consume the same species of fruit in roughly the same proportions as primates. We compared the average overlap in resource use among pairs of primate species and among pairs of hornbill species to the average overlap between pairs of primate and hornbill species. We calculated the $t$ ratio comparing the within-group average to between-group overlap in resource use for the observed data, and compared this value to the distribution of $t$ values generated by the Monte Carlo procedure previously outlined.

### Analysis of fruit characteristics

We analyzed the characteristics of fruits found in hornbill and primate diets using morphological measurements on fruits and fruiting trees. For a particular frugivore species, we included the most frequently eaten species, representing ≥5% of all feeding observations for that frugivore during 1998. In total, we analyzed the fruit characters of 24 species. To test for morphological differences between the fruits preferred by hornbills and primates, we recorded plant form (liana, tall tree, medium tree, shrub), seed number (1, 2–10, >10), fruit color (green, yellow, orange, red, brown, violet), fruit length, fruit width, and the type of reward provided by the fruit (arillate fruit, succulent fruit, soft fruit, dry fruit, and seeds). Tall trees were usually emergent canopy trees (>30 m in height) and medium trees were 15–30 m in height. The number of seeds per fruit was treated as a categorical variable because the fruit species fell naturally into these categories. For fruits with more than one seed, the number of seeds varied, and the classification reflects this. Fruit

TABLE 1. Frequency (%), with total number of observations below (in parentheses), of feeding records by frugivores for each food category in 1998 in Cameroon.

| Species and monthly observations† | Fruit | Seed | Leaf | Flower | Insect | Other | Total no. observations |
|---|---|---|---|---|---|---|---|
| **Hornbills** | | | | | | | |
| *Ceratogymna atrata* | 97.8 | 0.0 | 0.4 | 0.0 | 1.9 | 0.0 | 268 |
| [22.1 ± 17.7, 1–53] | (262) | (0) | (1) | (0) | (5) | (0) | |
| *Ceratogymna cylindricus* | 95.4 | 0.4 | 0.4 | 1.2 | 2.7 | 0.0 | 260 |
| [20.8 ± 18.7, 0–54] | (248) | (1) | (1) | (3) | (7) | (0) | |
| **Primates** | | | | | | | |
| *Lophocebus albigena* | 46.9 | 31.2 | 8.8 | 4.8 | 6.9 | 1.5 | 525 |
| [40.1 ± 13.5, 20–62] | (246) | (164) | (46) | (25) | (36) | (8) | |
| *Cercopithecus pogonias* | 84.0 | 3.3 | 6.0 | 2.5 | 4.0 | 0.2 | 399 |
| [30.3 ± 16.4, 6–52] | (335) | (13) | (24) | (10) | (16) | (1) | |
| *Cercopithecus nictitans* | 69.3 | 3.7 | 13.1 | 7.2 | 2.5 | 4.3 | 489 |
| [38.1 ± 18.1, 8–64] | (339) | (18) | (64) | (35) | (12) | (21) | |
| *Cercopithecus cephus* | 80.4 | 3.3 | 5.2 | 2.6 | 5.2 | 3.3 | 153 |
| [11.2 ± 7.4, 0–21] | (123) | (5) | (8) | (4) | (8) | (5) | |
| *Colobus guereza* | 31.1 | 23.5 | 36.4 | 3.8 | 1.5 | 3.8 | 132 |
| [10.3 ± 4.8, 3–18] | (41) | (31) | (48) | (5) | (2) | (5) | |

† Below each species (in brackets) is the mean number of observations per month ± 1 SD and the range of observations per month for that species.

length and fruit width were measured with calipers. At least 10 fruits of each species were chosen randomly from under the canopies of fruiting trees, with the exception of two species for which we measured only six fruits (23 ± 16.32 fruits per plant, mean ± 1 SD; range = 6–55 fruits). Fisher's exact test was used to test for morphological differences between hornbill- and primate-preferred fruit species for categorical variables. We used $t$ tests to test for differences between the widths and lengths of fruits eaten by hornbills vs. primates.

## RESULTS

### Fruit abundance

During 1998, 18 173 fruits from 176 tree and liana species were counted along the raked fruit trail. Data from the raked-trail survey showed a single fruiting period between May and September in 1998 (Fig. 1A). Fruit abundance was highest in July, when it was four times higher than fruit abundance during times of fruit scarcity. These data suggest that the period from October to April 1998 represents a lean fruit period. To describe our results for 1998 more clearly, we divided the year into three fruit abundance periods: lean fruit period I (LPI) from January through April, rich fruit period (RP) from May through September, and lean fruit period II (LPII) from October through December. Previous years of study (1994–1997) demonstrated similar seasonal changes in fruit abundance, usually with a single rich fruit period peaking in July (Whitney and Smith 1998; T. B. Smith, *unpublished data*). Rainfall was bimodal, with peaks preceding and following the peak in fruit abundance (Fig. 1A).

TABLE 2. The percentage of observations at each feeding height (1, 0–10 m; 2, 11–20 m; 3, 21–30 m; 4, >30 m) and the sample size (*N*) for each period (LPI, January–April; RP, May–September; LPII, October–December) are listed for the two hornbill and five primate species studied.

| Species code† | Lean fruit period I (LPI) | | | | | Rich fruit period (RP) | | | | | Lean fruit period II (LPII) | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | 1 | 2 | 3 | 4 | (*N*) | 1 | 2 | 3 | 4 | (*N*) | 1 | 2 | 3 | 4 | (*N*) |
| ATR | | | | | | 1 | 18 | 37 | 44 | (170) | 0 | 20 | 33 | 47 | (36) |
| CYL | | | | | | 6 | 26 | 37 | 31 | (129) | 0 | 17 | 46 | 37 | (100) |
| ALB | 33 | 36 | 27 | 4 | (70) | 9 | 31 | 39 | 21 | (194) | 7 | 34 | 46 | 13 | (148) |
| CER | 48 | 31 | 16 | 5 | (80) | 10 | 35 | 43 | 12 | (389) | 8 | 32 | 54 | 6 | (242) |
| CEP | | | | | | 28 | 41 | 25 | 6 | (71) | 22 | 37 | 42 | 0 | (41) |
| GUER | | | | | | 12 | 27 | 37 | 24 | (59) | 0 | 24 | 48 | 28 | (29) |

*Notes:* Results of *G* tests of independence (all df = 3) for species pairs that foraged at significantly different heights for a period, with *P* values Bonferroni-corrected for sequential tests: ATR/CYL (RP, *G* = 10.61, *P* = 0.015); ATR/CER (RP, *G* = 79.78, *P* = 0.0001; LPII, *G* = 40.80, *P* = 0.0001); CYL/CER (RP, *G* = 24.01, *P* = 0.0001; LPII, *G* = 61.08, *P* = 0.0001); ATR/ALB (RP, *G* = 33.19, *P* = 0.0001; LPII, *G* = 22.00, *P* = 0.0001); CYL/ALB (LPII, *G* = 33.02, *P* = 0.001); ALB/CEP (RP, *G* = 37.28, *P* = 0.0001; LPII, *G* = 13.61, *P* = 0.0018); CEP/GUER (RP, *G* = 24.80, *P* = 0.0001; LPII, *G* = 34.23, *P* = 0.0001).

† Hornbills: ATR, *Ceratogymna atrata*; CYL, *C. cylindricus*. Primates: ALB, *Lophocebus albigena*; CEP, *Cercopithecus cephus*; GUER, *Colobus guereza*; CER, *Cercopithecus nictitans*, and *C. pogonias* (grouped because there was no difference in the heights at which they fed).

TABLE 3. Above diagonal: number of diet species shared between pairs of frugivores. Below diagonal: percentage of frugivore A's (column) diet species shared by frugivore B (row) and, following a slash (/), percentage of frugivore B's (row) diet species shared by frugivore A (column).

| | Hornbills | | Primates | | | | |
|---|---|---|---|---|---|---|---|
| Species | C. atrata | C. cylindricus | L. albigena | C. nictitans | C. pogonias | C. cephus | C. guereza |
| C. atrata | | 46 | 36 | 34 | 27 | 17 | 17 |
| C. cylindricus | 83.6 / 80.7 | | 31 | 32 | 26 | 18 | 15 |
| L. albigena | 65.4 / 27.9 | 54.3 / 24.0 | | 86 | 75 | 47 | 31 |
| C. nictitans | 61.8 / 27.4 | 56.1 / 25.8 | 66.6 / 69.4 | | 79 | 55 | 29 |
| C. pogonias | 49.0 / 30.7 | 45.6 / 29.5 | 58.1 / 85.2 | 63.7 / 89.8 | | 50 | 24 |
| C. cephus | 30.9 / 28.3 | 31.6 / 30.0 | 36.4 / 78.3 | 44.3 / 91.7 | 56.8 / 83.3 | | 12 |
| C. guereza | 30.9 / 37.7 | 26.3 / 33.3 | 24.0 / 68.9 | 23.4 / 64.6 | 27.3 / 53.3 | 20.0 / 26.7 | |

*Note:* The number of shared species was calculated from the diet list (see the Appendix) compiled after five years of study (1994–1998) in Cameroon.

### Overall diets

From January 1994 to May 1999, 6436 individual feeding observations were collected on the two hornbill and five primate species, of which one-third (2226) were collected in 1998 (Table 1). The total number of foods recorded for the seven species was 242, representing 187 plant species. The foods included fruits from 157 species, leaves from 45, flowers from 24, seeds from 11, and pith from 7 species (Appendix). Of the 242 different foods eaten by the frugivore community, the fruits of only seven species (3%) were shared by all seven target animal species, representing 4.5% of the 157 fruit species. Eighty-four (34%) of all species recorded as diet items were recorded for only one animal species. The number of feeding observations per month for frugivore species was significantly correlated with their monthly abundance in 1998 ($r = 0.774$, $N = 84$, $P < 0.001$). Observations for *Colobus guereza* and *Cercopithecus cephus* are relatively few, and diet lists are likely to be incomplete.

In 1998, fruit was the most frequently selected food item for six of the seven target species. The exception, *C. guereza,* had a diet dominated by leaves. The hornbill species were the most frugivorous of the target species, with fruit making up an average of 97% of their diets (Table 1). Primate diets were more diverse than those of hornbills and included greater percentages of seeds, leaves, flowers, pith, and insects. The three *Cercopithecus* primates (*C. nictitans, C. pogonias,* and *C. cephus*) were also highly frugivorous, averaging 78% fruit in their diets. *Lophocebus albigena* had a diverse diet of fruit (47%) and seeds (31%), and is best characterized as a frugivore–granivore.

Three primates, *L. albigena, C. nictitans,* and *C. pogonias,* showed significant seasonal differences in the types of food consumed (Fig. 1B). *L. albigena, C. nictitans,* and *C. pogonias* consumed significantly lower percentages of fruit during the lean fruit season (LPI) than during the rest of the year (*G* test for equality of proportions: $G = 4.99$, df = 2, $P = 0.03$; $G = 23.36$, df = 2, $P < 0.01$; and $G = 30.92$, df = 2, $P < 0.01$, respectively). Fruit consumption by *L. albigena* roughly reflected monthly fruit availability, with peak fruit consumption in June and July. *L. albigena* also consumed significantly lower percentages of fruit in LPII compared to the rich fruit season, May–September (*G* $= 40.103$, df = 2, $P < 0.01$). During periods of fruit scarcity, *L. albigena* switched to a diet of seeds and leaves. Between September and December, *L. albigena* specialized on the seeds of *Erythrophloem suaveolens,* which accounted for 41% of *L. albigena*'s diet and reached a high of 61% in September. *C. pogonias,* and to a lesser degree, *C. nictitans,* sustained high levels of frugivory in LPII despite decreased fruit availability. There was no significant difference in the amounts of fruit consumed by *C. pogonias* and *C. nictitans* in the October–December period compared to the rich fruit period (*G* test for equality of proportions: $G = 0.12$, df = 2, $P = 0.91$; and $G = 3.26$, df = 2, $P = 0.07$, respectively). From September to November, all *Cercopithecus* species depended largely on the fruits of *Uapaca* species. During these months, the diets of *C. pogonias, C. cephus,* and *C. nictitans* consisted of 44%, 41%, and 31% *Uapaca* species, respectively.

Several species of frugivores fed at different heights in the canopy. *Ceratogymna atrata* foraged significantly more often in the upper strata than *Ceratogymna cylindricus* during RP, but there was no significant difference in feeding heights for LPII (Table 2). Both species of hornbill fed at significantly different heights in the canopy than did the primates, except that there was no significant difference in the feeding heights of *L. albigena* and *C. cylindricus* during RP. Hornbills foraged more often in the upper (>30 m) and mid-high strata (20–30 m) than did the primates in both RP and LPII.

The only detectable pattern of feeding height stratification among the primates was found in *C. cephus,* which foraged significantly lower in the canopy for RP and LPII than did the other primates. There was no difference in feeding heights between *C. nictitans* and *C. pogonias* for any season. Therefore, they were grouped as ''*Cercopithecus*'' for comparison with other frugivore species. Both *Cercopithecus* and *L. albigena* concentrated their feeding at the mid and mid-low strata, and *L. albigena* and *C. guereza* did not differ in feeding heights during RP and LPII.

*Diets and dietary overlap*

Based on five years of study, frugivore species shared between 12 and 86 plant species in their diets (Table 3). Large percentages of the plant species eaten by *C. atrata* (65%) and *C. cylindricus* (54%) were also consumed by at least one primate. Hornbills consumed only about 30% of the species in primate diets.

Correspondence analysis (CA) of the seven frugivores and 161 of their diet species identified three major feeding assemblages of frugivores (Fig. 2A). The first axis accounted for 63% of the variance, and separated hornbills and their diet species from primates and their diet species. The second axis represented 45% of the remaining variance, and distinguished the primate species with contrasting diets and different degrees of frugivory. The diets of the more frugivorous species, *C. pogonias, C. cephus, C. nictitans,* and *L. albigena,* were most similar, whereas that of the more folivorous *Colobus guereza* diverged strongly (Fig. 2A).

Because the separation of hornbills and primates accounted for the greatest part of the variance, CA of the five primates and their 154 diet species was used to further examine similarity of diet among the primates. Correspondence analysis separated the primates into three feeding groups: *C. guereza, L. albigena,* and the three *Cercopithecus* species (Fig. 2B). The first axis separated *C. guereza* from the other primates and accounted for 46% of the variance. This axis probably separated primates by their consumption of plant species for leaves. The second axis accounted for 32% of the remaining variance and separated *L. albigena* from the other primates, based largely on degree of granivory.

Because the positioning of frugivores along the axes may have been caused by important nonfruit diet species, we conducted CA after eliminating all nonfruit foods, including leaves, flowers, and seeds. *C. guereza* is a seed predator in the Dja Reserve and was removed from this analysis so that this CA represents the potential seed dispersal assemblages. Correspondence analysis of the six species of frugivores and the 127 species of fruit in their diets identified three feeding guilds. The first axis represented 60% of the variance and separated the hornbills from the primates. The second axis represented 21% of the remaining variance. Axis 2 grouped *C. pogonias, C. nictitans,* and *C. cephus,* and separated *L. albigena* from the other primates (Fig. 2C).

Examination of dietary overlap values revealed patterns similar to those produced by correspondence analysis. Overall, pairwise dietary overlap was less than expected by chance (Fig. 3). The two hornbill species showed the highest standardized dietary overlap, with an average value of −1.62 (Table 4). Dietary overlap between pairs of primate species averaged −3.87. Comparisons between hornbill and primate species pro-
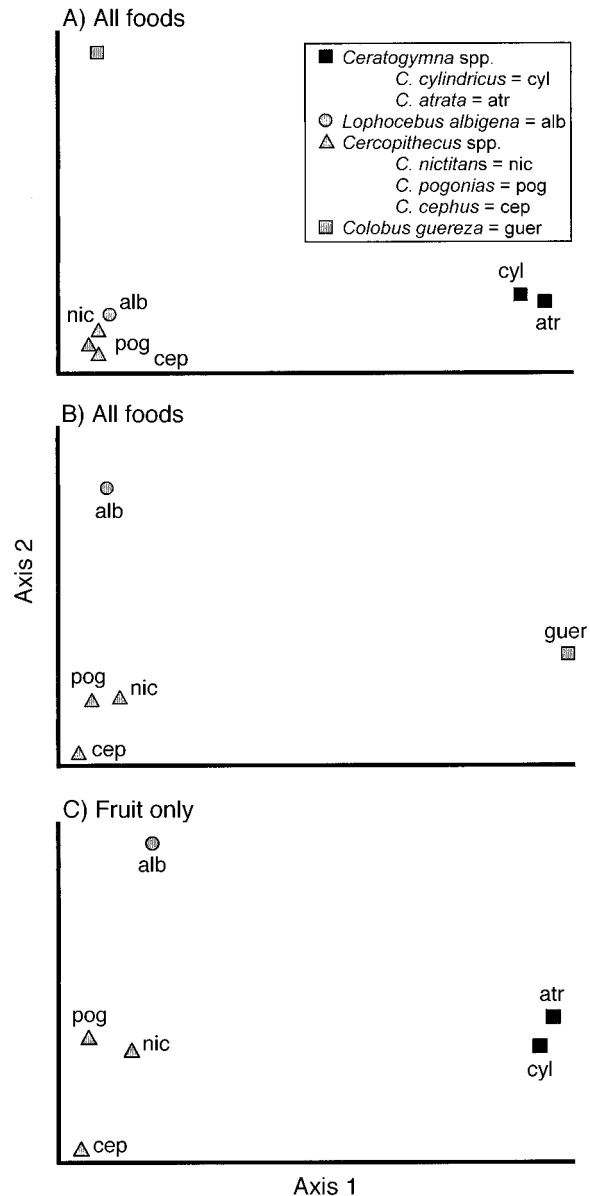


FIG. 2. (A) Correspondence analysis (CA) of seven frugivore species and all foods ($N = 161$) showing one hornbill feeding assemblage and two primate feeding assemblages. With the exception of the folivorous *Colobus guereza,* the primates were grouped closely. (B) CA of five primate species and all foods ($N = 154$) separates *Colobus guereza* from the more frugivorous primate species. *Lophocebus albigena* is also distinguished from the *Cercopithecus* species based on its consumption of plant species for seeds. (C) CA of six frugivore species and fruit species only ($N = 127$) separates the hornbill species from the primate species. This CA represents the potential seed dispersal assemblages. *Colobus guereza* was excluded because it acts as a seed predator rather than as a seed disperser. *Lophocebus albigena* was also distinguished from the other primates. The variance represented by each axis is reported in the text.

FIG. 3. Monthly dietary overlap values for all pairs of hornbill and primate species. Symbols represent standardized overlap values for each pair of species in each month. Horizontal dotted lines represent the approximate upper (97.5) and lower (2.5) percentiles of the expected distribution of standardized overlap values. Standardized overlap values below $-1.96$ represent species pairs that overlap in diet significantly less than expected. Bold lines indicate the best-fit curve for dietary overlaps between hornbill species, among primate species, and between primates and hornbills. On average, comparisons between primates and hornbills show the lowest standardized overlap values, suggesting that these two groups of frugivores consume and disperse different suites of plant species.
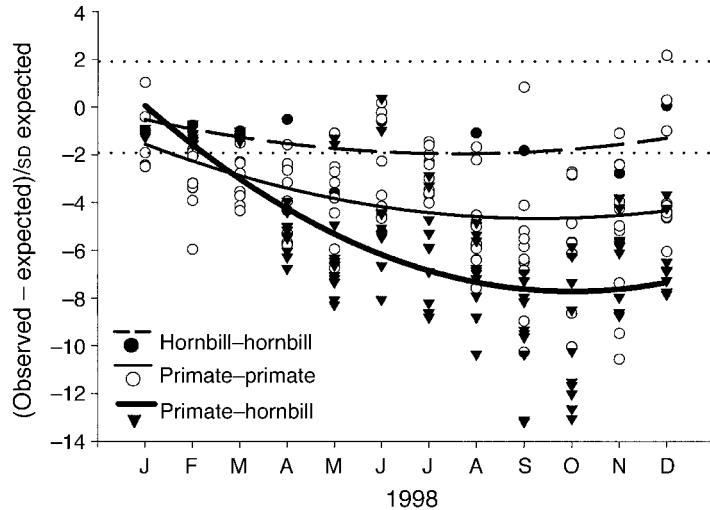
duced the lowest dietary overlap, averaging $-5.83$. Even when *L. albigena* and *C. guereza,* the least frugivorous primate species, were excluded, dietary overlap between the hornbill species and the three *Cercopithecus* species averaged $-5.35 \pm 0.12$ (mean $\pm$ 1 SD). Pairwise comparisons of standardized dietary overlap between primate species showed *Cercopithecus* monkeys to have diets more similar to those of congeners than to those of *L. albigena* and *C. guereza* (Table 5).

Dietary overlap values were also calculated for those fruit species that might be dispersed by primates or hornbills, by excluding all species for which seeds, leaves, flowers, etc., were the focus of the consumer (Table 4). The overlap between hornbills was slightly lower than when all diet species were included ($-1.91$), but overlap among primates ($-2.55$) and between primates and hornbills increased ($-5.11$). The changes in dietary overlap resulting from the elimination of nonfruit species had no effect on our interpretation of feeding assemblages. Overlap between hornbills and primates was still much lower than overlap between horn-

bill species or among primate species. The increase in overlap between primates and hornbills and among primates was expected because removing foods that most frugivore species do not have in common could only increase overlap. The decrease in dietary overlap between hornbills was caused by the change in relative fruit abundances associated with the elimination of plant species from the analysis.

To determine whether hornbills and primates could replace each other as seed dispersers, we tested if the average between-group overlap (hornbill–primate overlaps) was significantly less than combined within-group overlap (hornbill–hornbill overlaps + primate–primate overlaps). Again, these tests included only fruit species that might be dispersed by hornbills and primates, excluding all nonfruit diet species. Averaging across months, between-group overlap was significantly lower than within-group overlap ($P < 0.001$; Table 6), indicating that primates and hornbills have very dissimilar diets. When tests were performed for each month, between-group overlaps were significantly

TABLE 4. Comparison of standardized and raw dietary overlap values of the major taxa studied, based on the mean of monthly dietary overlap values among all species pairs.

| Taxa compared | Standardized overlap | | Raw overlap | |
|---|---|---|---|---|
| | Mean $\pm$ 1 SD | Range | Mean $\pm$ 1 SD | Range |
| All diet species | | | | |
| Primate–primate | $-3.87 \pm 0.10$ | $-10.55$–$2.15$ | $0.29 \pm 0.17$ | $0.00$–$0.79$ |
| Primate–hornbill | $-5.83 \pm 0.12$ | $-13.17$–$0.36$ | $0.10 \pm 0.10$ | $0.00$–$0.44$ |
| Hornbill–hornbill | $-1.62 \pm 0.13$ | $-3.58$–$0.05$ | $0.54 \pm 0.11$ | $0.10$–$0.68$ |
| Fruit species only | | | | |
| Primate–primate | $-2.55 \pm 0.12$ | $-6.88$–$0.37$ | | |
| Primate–hornbill | $-5.11 \pm 0.14$ | $-14.74$–$0.37$ | | |
| Hornbill–hornbill | $-1.91 \pm 0.12$ | $-3.36$–$0.49$ | | |

*Note:* Standardized dietary overlap values calculated by Schoener's index were corrected for differences in monthly sample sizes and fruit availability, whereas row overlap values, also calculated by Schoener's index, were not corrected for these two factors.

TABLE 5. Average raw overlap values (above diagonal) and pairwise standardized dietary overlap (below diagonal) for plant foods eaten by primates and hornbills. The monthly dietary overlap values between species pairs were averaged to calculate the average overlap; negative numbers indicate that overlap was less than expected by chance.

| Species | Hornbills | | Primates | | | | |
|---|---|---|---|---|---|---|---|
| | *C. atrata* | *C. cylindricus* | *L. albigena* | *C. Pogonias* | *C. nictitans* | *C. cephus* | *C. guereza* |
| *Ceratogymna atrata* | | 0.49 | 0.09 | 0.07 | 0.10 | 0.11 | 0.03 |
| *Ceratogymana cylindricus* | −1.62 | | 0.12 | 0.13 | 0.14 | 0.15 | 0.05 |
| *Lophocebus albigena* | −6.46 | −7.29 | | 0.35 | 0.32 | 0.28 | 0.29 |
| *Cercopithecus pogonias* | −6.32 | −6.67 | −5.16 | | 0.38 | 0.40 | 0.19 |
| *Cercopithecus nictitans* | −6.16 | −6.95 | −6.05 | −4.34 | | 0.42 | 0.19 |
| *Cercopithecus cephus* | −4.39 | −4.32 | −3.77 | −2.06 | −2.02 | | 0.12 |
| *Colobus guereza* | −4.50 | −5.30 | −3.13 | −4.16 | −4.34 | −3.55 | |

*Note:* Both raw and standardized dietary overlap values are calculated using Schoener's index; the latter are corrected for differences in monthly sample sizes and fruit availability; the former are not type.

lower than within-group overlaps for all months except for three of the initial five months (Table 6).

### Fruit characteristics of hornbill- and primate-preferred diet species

Diet species of hornbills and primates differed significantly in fruit color (Fisher's exact test, $P = 0.002$). Primates tended to consume green and brown fruits, whereas hornbills consumed more red and violet fruits (Fig. 4). There were no significant differences between hornbill- and primate-preferred fruit species for plant form (Fisher's exact test, $P = 0.092$), seed number (Fisher's exact test, $P = 0.706$), fruit length ($t = 0.756$, df = 27, $P = 0.456$), fruit width ($t = 0.893$, df = 26, $P = 0.380$), or type of fruit reward (Fisher's exact test, $P = 0.187$).

### DISCUSSION

#### Hornbill and primate feeding assemblages

Based on diet, feeding heights, and preferred fruit colors, we identified one hornbill and two primate feed-

ing assemblages, separated by their intake of fruit and other food items. The average dietary overlap between hornbills and primates was lower than overlap between hornbill species or overlap among the primate species. In general, hornbills were more frugivorous, fed on a smaller suite of plant species, and fed higher in the canopy than did primates.

We found dietary overlap between hornbills and primates to be significantly lower than expected by chance. These results are in stark contrast to measures of dietary overlap calculated as the number of plant species that two animals consume in common. Using the latter method, we would have calculated that primates consume, albeit infrequently, as much as 65% of the same plant species as hornbills. Although this method has been used in other studies to estimate dietary overlap (Fleming 1979, Gautier-Hion et al. 1985, Tutin et al. 1997), it neglects the proportion of a food species in the diet of the consumer and the availability of the fruit in the environment.

Primates were differentiated by dietary preference,

TABLE 6. Comparisons of combined within-group dietary overlaps (hornbill–hornbill + primate–primate) with between-group overlaps (primate–hornbill) for fruit species only, across all months and on a monthly basis. Significant $P$ values are shown in boldface.

| Month | Average within-group overlap | Average between-group overlap | $t$ | $P$ |
|---|---|---|---|---|
| All months | 0.337 | 0.159 | 3.974 | <0.001 |
| January | 0.495 | 0.350 | 1.167 | **0.209** |
| February | 0.271 | 0.025 | 4.755 | **0.016** |
| March | 0.188 | 0.294 | −1.204 | 0.970 |
| April | 0.343 | 0.049 | 7.112 | <**0.001** |
| May | 0.313 | 0.285 | 0.375 | 0.066 |
| June | 0.298 | 0.269 | 0.320 | **0.004** |
| July | 0.439 | 0.152 | 5.067 | <**0.001** |
| August | 0.259 | 0.093 | 2.383 | **0.003** |
| September | 0.362 | 0.115 | 3.232 | <**0.001** |
| October | 0.302 | 0.143 | 3.062 | <**0.001** |
| November | 0.375 | 0.049 | 5.721 | **0.002** |
| December | 0.396 | 0.080 | 3.019 | <**0.001** |

*Notes:* Averaged across all months, between-group overlap is significantly less than within-group overlap. Between-group overlap is significantly less than the within-group overlaps for all months, except January, March, and May.
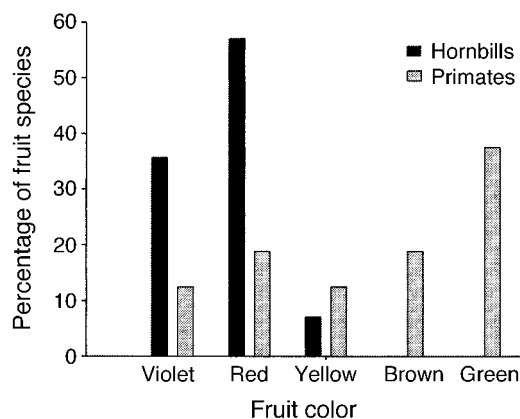
Fig. 4. Percentages of fruits in hornbill and primate diets by color. Twenty-four species of fruits were analyzed for fruit characteristics.

specifically the percentages of food items (fruit, leaves, seeds, etc.) in their diets. Two feeding assemblages of primates emerged from the CA: one folivorous feeding assemblage composed of *Colobus guereza,* and a more frugivorous feeding assemblage that included the *Cercopithecus* primates (*C. pogonias, C. nictitans,* and *C. cephus*) and *Lophocebus albigena.* The *Lophocebus–Cercopithecus* feeding assemblage may be better divided into two separate assemblages: one composed of the frugivorous *Cercopithecus* primates and another composed of *L. albigena,* because of its high consumption of seeds and ability to eat larger, harder fruits than the smaller *Cercopithecus* species (Tutin et al. 1997). The diet of *L. albigena* was seasonally quite distinct from the *Cercopithecus* species when examined at the plant species level. Dietary overlap between *L. albigena* and the *Cercopithecus* primates was lowest from September to November. During these months, *L. albigena* specialized in the seeds of *Erythrophloem suaveolens,* while the *Cercopithecus* species consumed higher frequencies of succulent fruits, especially *Uapaca* and *Cissus* species.

Hornbills were found to have more specialized diets than primates, and were more frugivorous overall. After five years of study, we recorded 57 and 55 plant species consumed by *C. atrata* and *C. cylindricus,* respectively (34 ± 6.7 species/yr, mean ± 1 SD). Hornbills in Gabon (*Ceratogymna subcylindricus*) and Asia (*Rhyticeros cassidix*) were found to consume 33 and 24 fruit species, respectively, in a single year of study (Kalina 1988, Suryadi et al. 1994). In contrast, studies of frugivorous primates often report between 75 and 100 diet species (Gautier-Hion 1988, Ham 1994, Tutin et al. 1997). Primates appear to have highly varied diets and show considerable flexibility in the types of foods eaten seasonally (Chapman 1987) and between years (Olupot 1998). Despite the broad diets of primates, our data suggest that 30 plant species compose ~75% of primate and hornbill diets.

Fleming (1992) suggested that, because of their greater mobility, birds should be more frugivorous year-round than strictly arboreal or terrestrial species. Similarly, specialization by hornbills on fewer diet species is consistent with their greater mobility relative to primates. Flight may allow hornbills to track fruit resources of particular species more efficiently than other arboreal species. For example, Asian hornbills track fig production over potentially long distances (Kinnaird et al. 1996). Whitney and Smith (1998) found strong evidence for resource tracking by hornbills in the Dja Reserve, and hornbills flew as far as Gabon (150 km) during the lean fruit season (Holbrook 1999). Primates, on the other hand, are more limited in mobility and would be under greater selective pressure to diversify their diets. However, other factors may contribute as well. For example, greater diversity of primate diets may also result from their greater strength and dexterity relative to hornbills that would allow them to manipulate a greater variety of resources.

Differences in feeding heights may also explain differences in resource use between hornbills and primates. We found hornbills to forage higher in the forest canopy than primates. Large frugivorous birds observe the forest while in flight, and thus are more likely to detect fruits in the upper strata of the canopy. Primates are more likely to detect fruits in the middle strata, where they travel through the forest. A concurrent study of seed rain in the Dja Reserve determined that hornbills dispersed seeds from emergent trees of the upper canopy, whereas primates disseminated seeds from mid- and low-canopy trees and lianas (Clark et al., *in press*).

Analysis of fruit characteristics supported the separation of primate and hornbill diets. Fruits eaten by hornbills differed in color from those eaten by primates. Primates preferred green and brown fruits, whereas the majority of hornbill fruits were red and violet. Birds in Gabon, Costa Rica, French Guyana, and Peru similarly prefer combinations of red, violet, and black fruits (Charles-Dominique et al. 1981, Gautier-Hion et al. 1985, Wheelwright and Janson 1985). Knight and Siegfried (1983) determined that birds favor black, orange, and red, whereas mammals favor species with yellow, orange, and green fruits. Our study confirms the seemingly universal choice by birds of purple-black and/or red fruits.

Monkeys may be more flexible with respect to fruit color preferences. Old World primates (Catarrhini) possess trichromatic vision, enabling the detection of ripe fruit against the green background of forest foliage (Mollon 1989, Osorio and Vorobyev 1996). We found monkeys to be largely attracted to green and brown fruits. Although Gautier-Hion et al. (1985) found *Cercopithecus* monkeys to avoid those colors, Leighton and Leighton (1983) found the monkey *Cercopithecus albogularis* to eat fruit of a wide range of colors, including brown and green.

Our results support those of Tutin (1999) that diets of closely related frugivore species overlap more than do those of distantly related species. Hornbill species had the greatest dietary overlap, and the closely related *Cercopithecus* species shared more similar diets with each other than with *L. albigena* or *C. guereza.* Relatively low overlap between hornbills and primates is not surprising, as distantly related species may differ markedly in body size, group size, foraging behavior, and morphology.

### *''Replaceability'' of seed dispersers*

Both the proportional use of diet species and fruit availability are important factors in determining whether frugivores can replace each other as seed dispersers. First, a primate that opportunistically eats a fruit is unlikely to provide the same level of seed dispersal for the plant as a hornbill that feeds predominantly on the same species of fruit (Schupp 1993). Second, the timing of fruit consumption may affect treatment of the fruit by the frugivore. In our study, primates occasionally consumed immature fruits for their seeds weeks before hornbills fed on the mature fruits; primates preyed upon the seeds, whereas hornbills dispersed them. Thus, the manner in which dietary overlap is calculated has important conservation implications. High dietary overlap may imply that one seed disperser can replace another, and methods that overestimate dietary overlap may falsely lead to the conclusion that some frugivores can be extirpated from a forest community without affecting subsequent patterns and rates of seed dispersal.

For hornbills and primates to replace each other as seed dispersers, they would first have to consume the same species of fruit in roughly the same proportions. However, we found that dietary overlap between groups (hornbill–primate overlaps), averaged across months, was significantly less than combined within-group overlap (hornbill–hornbill overlaps + primate–primate overlaps) for fruit species. Thus, hornbills and primates have very dissimilar diets, and it is probable that neither group is able to replace the seed dispersal services provided by the other. Dietary overlap between groups and within groups did not differ in three of the initial five months, suggesting that during very resource lean periods, the diets of frugivores may converge as hornbills and primates rely upon the same scarce fruits. Further study will be necessary to examine patterns of interannual variation in dietary overlap in relation to resource-rich and resource-lean years.

We have found that hornbills and primates have different diets, and are therefore unlikely to replace each other in their roles as seed dispersers. The extirpation of either one of these groups of animals from the forest may inhibit the ability of some plants to regenerate, as their fruits and seeds fall to the forest floor below the parent plant, where they often face the highest rates of mortality (Janzen 1970, Connell 1971). Without the movement of seeds away from the parent plant by fru-givores, the rate of dispersal will probably be limited and seed deposition patterns altered, possibly influencing forest structure and composition.

### Literature Cited

Andresen, E. 1999. Seed dispersal by monkeys and the fate of dispersed seeds in a Peruvian rain forest. Biotropica **31**: 145–158.

Chapman, C. A. 1987. Flexibility in diets of three species of Costa Rican primates. Folia Primatologica **49**:90–105.

Chapman, C. A. 1995. Primate seed dispersal: coevolution and conservation implications. Evolutionary Anthropology **4**:74–82.

Chapman, C. A., A. Gautier-Hion, J. F. Oates, and D. A. Onderdonk. 1999. African primate communities: determinants of structure and threats to survival. Pages 1–37 *in* J. G. Fleagle, C. Janson, and K. E. Reed, editors. Primate communities. Cambridge University Press, Cambridge, UK.

Charles-Dominique, P., M. Atramentowicz, M. Charles-Dominique, H. Gerard, A. Hladik, C. M. Hladik, and M. F. Prevost. 1981. Less mammifères frugivores arboricoles nocturnes d'une forêt guyanaise: interrelations plantes–animaux. Revue d'Ecologie (Terre et Vie) **35**:341–435.

Clark, C. J., J. R. Poulsen, and V. T. Parker. *In press.* Impact of frugivores on seed rain patterns in a central African tropical forest. Biotropica.

Clark, J. S., M. Silman, R. Kern, E. Macklin, and J. HilleRisLamers. 1999. Seed dispersal near and far: patterns across temperate and tropical forests. Ecology **80**:1475–1494.

Connell, J. H. 1971. On the role of natural enemies in preventing competitive exclusion in some marine animals and in rain forest trees. Pages 298–312 *in* P. J. Den Boer and P. R. Gradwell, editors. Dynamics of populations. Pudoc, Wageningen, The Netherlands.

Dew, J. L., and P. Wright. 1998. Frugivory and seed dispersal by four species of primates in Madagascar's eastern rain forest. Biotropica **30**:425–437.

Estrada, A., and T. H. Fleming, editors. 1986. Frugivores and seed dispersal. Kluwer Academic Publishers, Dordrecht, The Netherlands.

Fleming, T. H. 1979. Do tropical frugivores compete for food? American Zoologist **19**:1157–1172.

Fleming, T. H. 1992. How do fruit- and nectar-feeding birds and mammals track their food resources? Pages 355–391 *in* M. D. Hunter, T. Ohgushi, and P. W. Price, editors. Effects of resource distribution on animal–plant interactions. Academic Press, San Diego, California, USA.

Fleming, T. H., and A. Estrada, editors. 1993. Frugivory and

seed dispersal: ecological and evolutionary aspects. Kluwer Academic Publishers, Dordrecht, The Netherlands.

Gauch, H. G. 1982. Multivariate analysis in community ecology. Cambridge University Press, Cambridge, UK.

Gautier-Hion, A. 1984. La dissémination des graines par les cercopithèques forestiers africains. Revue d'Ecologie (Terre et Vie) **39**:159–165.

Gautier-Hion, A. 1988. The diet and dietary habitats of forest guenons. Pages 257–283 *in* A. Gautier-Hion, F. Bourliere, J. P. Gautier, and J. Kingdon, editors. Primate radiation: evolutionary biology of the African guenons. Cambridge University Press, Cambridge, UK.

Gautier-Hion, A. 1990. Interactions among fruit and vertebrate fruit-eaters in an African rain forest. Pages 219–230 *in* K. S. Bawa and M. Hadley, editors. Reproductive ecology of tropical forest plants. UNESCO, Paris, France.

Gautier-Hion, A., J.-M. Duplantier, R. Quris, F. Feer, C. Sourd, J.-P. DeCoux, G. Dubost, L. Emmons, C. Erard, P. Hecketsweiler, A. Moungazi, C. Roussilhon, and J.-M. Thiollay. 1985. Fruit characters as a basis of fruit choice and seed dispersal in a tropical forest vertebrate community. Oecologia **65**:324–337.

Gorchov, D. L., F. Cornejo, C. F. Ascorra, and J. Jaramillo. 1995. Dietary overlap between frugivorous birds and bats in the Peruvian Amazon. Oikos **74**:235–250.

Gotelli, N. J., and G. R. Graves. 1996. Null models in ecology. Smithsonian Institution Press, Washington, D.C., USA.

Ham, R. M. 1994. Behaviour and ecology of the grey-cheeked mangabeys (*Cercocebus albigena*) in the Lope Reserve, Gabon. Dissertation. University of Stirling, Stirling, UK.

Hamann, A., and E. Curio. 1999. Interactions among frugivores and fleshy fruit trees in a Philippine submontane rainforest. Conservation Biology **13**:766–773.

Hamilton, M. B. 1999. Tropical tree gene flow and seed dispersal. Nature **401**:129–130.

Holbrook, K. 1999. Seed dispersal and movement patterns of *Ceratogymna* hornbills in Cameroon. Thesis. San Francisco State University, San Francisco, California, USA.

Holbrook, K., and T. B. Smith. 2000. Seed dispersal and movement patterns in two species of *Ceratogymna* hornbills in a West African tropical lowland forest. Oecologia **125**:249–257.

Howe, H. F. 1986. Seed dispersal by fruit-eating birds and mammals. Pages 123–189 *in* R. David, editor. Seed dispersal. Academic Press, London, UK.

Howe, H. F. 1989. Scatter- and clump-dispersal and seedling demography: hypotheses and implications. Oecologia **79**: 417–426.

Howe, H. F. 1990. Seed dispersal by birds and mammals: implications for seedling demography. Pages 191–218 *in* K. S. Bawa and M. Hadley, editors. Reproductive ecology of tropical forest plants. The Parethenon Publishing Group, Paris, France.

Howe, H. F., and G. F. Estabrook. 1977. On intraspecific competition for avian dispersers in tropical trees. American Naturalist **111**:817–832.

Howe, H. F., and G. A. Vande Kerckhove. 1981. Removal of wild nutmeg (*Virola surinamensis*) crops by birds. Ecology **62**:1093–1106.

Hubbell, S. P., R. B. Foster, S. T. O'Brien, K. E. Harms, R. Condit, B. Wechsler, S. J. Wright, and S. Loo de Lao. 1999. Light-gap disturbances, recruitment limitation, and tree diversity in a Neotropical forest. Science **283**:554–557.

IUCN (International Union for the Conservation of Nature). 1987. The IUCN directory of Afrotropical protected areas. International Union for the Conservation of Nature, Gland, Switzerland.

Janzen, D. H. 1970. Herbivores and the number of tree species in tropical forests. American Naturalist **104**:501–528.

Julliot, C. 1996. Seed dispersal by red howling monkeys (*Alouatta seniculus*) in the tropical rain forest of French Guiana. International Journal of Primatology **17**:239–258.

Kalina, J. 1988. Ecology and behaviour of the black-and-white casqued hornbill *Bycanistes subcylindricus subquadratus* in Kibale forest, Uganda. Dissertation. Michigan State University, Lansing, Michigan, USA.

Kemp, A. C. 1995. The hornbills. Oxford University Press, Oxford, UK.

Kinnaird, M. F., T. G. O'Brien, and J. R. Sinclair. 1998. The role of Sulawesi red-knobbed hornbills *Aceros Cassidix* in seed dispersal. Pages 1–336 *in* P. Poonswad, editor. The Asian hornbills: ecology and conservation. Thai Studies in Biodiversity, Bangkok, Thailand.

Kinnaird, M. F., T. G. O'Brien, and S. Suryadi. 1996. Population fluctuation in Sulawesi red-knobbed hornbills: tracking figs in space and time. Auk **113**:431–440.

Knight, R. S., and W. R. Siegfried. 1983. Inter-relationships between type, size, and colour of fruits and dispersal in southern African trees. Oecologia **56**:405–412.

Laclavère, G. 1980. Atlas of the United Republic of Cameroon. Editions Jeune Afrique, Paris, France.

Lambert, J. E. 1999. Seed handling in chimpanzees (*Pan troglodytes*) and redtail monkeys (*Cercopithecus ascanius*): implications for understanding hominoid and Cercopithecine fruit-processing strategies and seed dispersal. American Journal of Physical Anthropology **109**:365–386.

Lambert, J. E., and P. A. Garber. 1998. Evolutionary and ecological implications of primate seed dispersal. American Journal of Primatology **45**:9–28.

Lawlor, L. R. 1980. Overlap, similarity, and competition coefficients. Ecology **61**:245–251.

Leighton, M., and D. R. Leighton. 1983. Vertebrate response to fruiting seasonality within a Bornean rain forest. Pages 181–196 *in* S. L. Sutton, T. C. Whitmore, and A. C. Chadwick, editors. Tropical rain forest ecology and management. Blackwell Science, London, UK.

Letouzey, R. 1968. Études phytogéographiques du Cameroun. Editions Paul Lechavlier, Paris, France.

Levey, D. J. 1987. Seed size and fruit-handling techniques of avian frugivores. American Naturalist **129**:471–485.

Llewellyn, J. B., and S. H. Jenkins. 1987. Patterns of niche shift in mice: seasonal changes in microhabitat breadth and overlap. American Naturalist **129**:365–381.

McKey, D. 1975. The ecology of coevolved seed dispersal systems. Pages 159–191 *in* L. E. Gilbert and P. H. Raven, editors. Coevolution of animals and plants. University of Texas Press, Austin, Texas, USA.

Mollon, J. D. 1989. 'Tho' she kneel'd in the place where they grew. . . '. The uses and origins of primate colour vision. Journal of Experimental Biology **146**:21–38.

Muchaal, P. K., and G. Ngandjui. 1999. Impact of village hunting on wildlife populations in the western Dja Reserve, Cameroon. Conservation Biology **13**:385–396.

Oates, J. F. 1996. Habitat alteration, hunting and conservation of folivorous primates in African forests. Australian Journal of Ecology **21**:1–9.

Oates, J. F. 1999. Myth and reality in the rain forest. University of California Press, Berkeley, California, USA.

Olupot, W. 1998. Long-term variation in mangabey (*Cercocebus albigena johnstoni* Lydekker) feeding in Kibale National Park, Uganda. African Journal of Ecology **36**:96–101.

Osorio, D., and M. Vorobyev. 1996. Colour vision as an adaptation to frugivory in primates. Proceedings of the Royal Society London **263**:593–599.

Pielou, E. C. 1984. The interpretation of ecological data. Wiley, New York, New York, USA.

Redford, K. H. 1992. The empty forest. BioScience **42**:412–422.

Richards, P. W. 1996. The tropical rain forest. Cambridge University Press, Cambridge, UK.

Ricklefs, R. E., and M. Lau. 1980. Bias and dispersion of overlap indices: results of some Monte Carlo simulations. Ecology **61**:1019–1024.

Rowell, T. E., and B. J. Mitchell. 1991. Comparison of seed dispersal by guenons in Kenya and capuchins in Panama. Journal of Tropical Ecology **7**:269–274.

Sabatier, D. 1985. Saisonnalité et déterminisme du pic de fructification en forêt guyanaise. Revue d'Ecologie (Terre et Vie) **40**:289–320.

Schoener, T. W. 1974. Some methods for calculating competition coefficients from resource utilization spectra. American Naturalist **108**:332–340.

Schupp, E. W. 1993. Quantity, quality and the effectiveness of seed dispersal by animals. Vegetatio **107/108**:15–29.

Snow, D. W. 1981. Tropical frugivorous birds and their food plants: a world survey. Biotropica **13**:1–14.

Stiles, E. W. 1992. Animals as seed dispersers. Pages 87–104 *in* M. Fenner, editor. Seeds: the ecology of regeneration in plant communities. CAB International, Wallingford, UK.

Struhsaker, T. T. 1999. Primate communities in Africa: the consequences of long-term evolution or the artifact of recent hunting? Pages 298–294 *in* J. G. Fleagle, C. Janson, and K. E. Reed, editors. Primate communities. Cambridge University Press, Cambridge, UK.

Sun, C., A. R. Ives, H. J. Kraeuter, and T. C. Moermond. 1997. Effectiveness of three turacos as seed dispersers in a tropical montane forest. Oecologia **112**:94–103.

Suryadi, S., M. F. Kinnaird, T. G. O'Brien, J. Supriatna, and S. Somadikarta. 1994. Food preferences of the Sulawesi red-knobbed hornbill during the non-breeding season. Tropical Biodiversity **2**:377–384.

Terborgh, J. 1990. Seed and fruit dispersal—commentary. Pages 181–190 *in* K. S. Bawa and M. Handley, editors. Reproductive ecology of tropical forest plants. The Parthenon Publishing Group, Paris, France.

Tutin, C. E. G. 1999. Fragmented living: behavioural ecology of primates in a forest fragment in the Lope Reserve, Gabon. Primates **40**:249–265.

Tutin, C. E. G., R. M. Ham, L. J. T. White, and M. J. S. Harrison. 1997. The primate community of the Lope Reserve, Gabon: diets, responses to fruit scarcity, and effects on biomass. American Journal of Primatology **42**:1–24.

Wheelwright, N. T., and C. H. Janson. 1985. Colors of fruit displays of bird-dispersed plants in two tropical forests. American Naturalist **126**:777–798.

Whitney, K. D., M. F. Fogiel, A. M. Lamperti, K. M. Holbrook, D. J. Stauffer, B. D. Hardesty, V. T. Parker, and T. B. Smith. 1998. Seed dispersal by *Ceratogymna* hornbills in the Dja Reserve, Cameroon. Journal of Tropical Ecology **14**:351–371.

Whitney, K. D., and T. B. Smith. 1998. Habitat use and resource tracking by African *Ceratogymna* hornbills: implications for seed dispersal and forest conservation. Animal Conservation **1**:107–117.

Wilson, D. E., and D. M. Reeder, editors. 1993. Mammal species of the world: a taxonomic and geographic reference. Smithsonian Institution Press, Washington, D.C., USA.

Wright, S. J., H. Zeballos, I. Domínguez, M. M. Gallardo, M. C. Moreno, and R. Ibáñez. 2000. Poachers alter mammal abundance, seed dispersal, and seed predation in a Neotropical forest. Conservation Biology **14**:227–239.

Zhang, S., and L. Wang. 1995*a*. Comparison of three fruit census methods in French Guiana. Journal of Tropical Ecology **11**:281–294.

Zhang, S., and L. Wang. 1995*b*. Fruit consumption and seed dispersal of *Ziziphus cinnamomum* (Rhamnaceae) by two sympatric primates (*Cebus apella* and *Ateles paniscus*) in French Guiana. Biotropica **27**:397–401.

## APPENDIX

A table providing a diet list (plant species and plant parts) for primates and hornbills in this study is available in ESA's Electronic Data Archive: *Ecological Archives* E083-006-A1.