DIFFERENTIAL RESOURCE USE BY PRIMATES AND HORNIBBLS:
IMPLICATIONS FOR SEED DISPERAL

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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-

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, Kinnaid 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 over-hunting 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-km² 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 m²) 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.

**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, Pieiou 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:

\[
R_0 = 1 - \frac{1}{2} \sum_{i=1}^{n} |p_{ij} - p_{ik}|
\]

where \(R_0\) 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 frugivores, 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-
Figure 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.

We then computed standardized overlap values to correct for monthly differences in dietary overlap resulting 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 $R_{S}$. 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
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 1.** Frequency (%), with total number of observations below (in parentheses), of feeding records by frugivores for each food category in 1998 in Cameroon.

<table>
<thead>
<tr>
<th>Species and monthly observations†</th>
<th>Fruit</th>
<th>Seed</th>
<th>Leaf</th>
<th>Flower</th>
<th>Insect</th>
<th>Other</th>
<th>Total no. observations</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Hornbills</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Ceratogymna atrata</em> [22.1 ± 17.7, 1–53]</td>
<td>97.8 (262)</td>
<td>0.0</td>
<td>0.4</td>
<td>0.0</td>
<td>1.9</td>
<td>0.0</td>
<td>268</td>
</tr>
<tr>
<td><em>Ceratogymna cydriclus</em> [20.8 ± 18.7, 0–54]</td>
<td>95.4 (248)</td>
<td>0.4</td>
<td>0.4</td>
<td>1.2</td>
<td>2.7</td>
<td>0.0</td>
<td>260</td>
</tr>
<tr>
<td><strong>Primates</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Lophocebus albigena</em> [40.1 ± 13.5, 20–62]</td>
<td>46.9 (246)</td>
<td>31.2</td>
<td>8.8</td>
<td>4.8</td>
<td>6.9</td>
<td>1.5</td>
<td>525</td>
</tr>
<tr>
<td><em>Cercopithecus pogonias</em> [30.3 ± 16.4, 6–52]</td>
<td>84.0 (335)</td>
<td>3.7</td>
<td>6.0</td>
<td>2.5</td>
<td>4.0</td>
<td>0.2</td>
<td>399</td>
</tr>
<tr>
<td><em>Cercopithecus nictitans</em> [38.1 ± 18.1, 8–64]</td>
<td>69.3 (339)</td>
<td>3.7</td>
<td>13.1</td>
<td>7.2</td>
<td>2.5</td>
<td>4.3</td>
<td>489</td>
</tr>
<tr>
<td><em>Cercopithecus cephus</em> [11.2 ± 7.4, 0–21]</td>
<td>80.4 (123)</td>
<td>3.3</td>
<td>5.2</td>
<td>2.6</td>
<td>5.2</td>
<td>3.3</td>
<td>153</td>
</tr>
<tr>
<td><em>Colobus guereza</em> [10.3 ± 4.8, 3–18]</td>
<td>31.1 (41)</td>
<td>23.5</td>
<td>36.4</td>
<td>3.8</td>
<td>1.5</td>
<td>3.8</td>
<td>132</td>
</tr>
</tbody>
</table>

† 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.

**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.

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

† Hornbills: ATR, *Ceratogymna atrata*; CYL, *C. cydriclus*; 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).

**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. cydriclus*; 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).
ly 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 foraged 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 frugivores 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.

### Table 3.

<table>
<thead>
<tr>
<th>Species</th>
<th><em>C. atrata</em></th>
<th><em>C. cylindricus</em></th>
<th><em>L. albigena</em></th>
<th><em>C. nictitans</em></th>
<th><em>C. pogonias</em></th>
<th><em>C. cephus</em></th>
<th><em>C. guereza</em></th>
</tr>
</thead>
<tbody>
<tr>
<td><em>C. atrata</em></td>
<td>46</td>
<td></td>
<td>36</td>
<td>34</td>
<td>27</td>
<td>17</td>
<td>17</td>
</tr>
<tr>
<td><em>C. cylindricus</em></td>
<td>83.6 / 80.7</td>
<td></td>
<td>31</td>
<td>32</td>
<td>26</td>
<td>18</td>
<td>15</td>
</tr>
<tr>
<td><em>L. albigena</em></td>
<td>65.4 / 27.9</td>
<td>54.3 / 24.0</td>
<td>86</td>
<td>75</td>
<td>47</td>
<td>31</td>
<td></td>
</tr>
<tr>
<td><em>C. nictitans</em></td>
<td>61.8 / 27.4</td>
<td>56.1 / 25.8</td>
<td>79</td>
<td>55</td>
<td>29</td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>C. pogonias</em></td>
<td>49.0 / 30.7</td>
<td>45.6 / 29.5</td>
<td>63.7 / 89.8</td>
<td>50</td>
<td>24</td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>C. cephus</em></td>
<td>30.9 / 28.3</td>
<td>31.6 / 30.0</td>
<td>44.3 / 91.7</td>
<td>56.8 / 83.3</td>
<td>12</td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>C. guereza</em></td>
<td>30.9 / 37.7</td>
<td>26.3 / 33.3</td>
<td>24.0 / 68.9</td>
<td>23.4 / 64.6</td>
<td>27.3 / 53.3</td>
<td>20.0 / 26.7</td>
<td></td>
</tr>
</tbody>
</table>

*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.
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 graviory.

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. 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.

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.

<table>
<thead>
<tr>
<th>Taxa compared</th>
<th>Standardized overlap</th>
<th>Raw overlap</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Mean ± 1 SD</td>
<td>Range</td>
</tr>
<tr>
<td>All diet species</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Primate–primate</td>
<td>−3.87 ± 0.10</td>
<td>−10.55–2.15</td>
</tr>
<tr>
<td>Primate–hornbill</td>
<td>−5.83 ± 0.12</td>
<td>−13.17–0.36</td>
</tr>
<tr>
<td>Hornbill–hornbill</td>
<td>−1.62 ± 0.13</td>
<td>−3.58–0.05</td>
</tr>
<tr>
<td>Fruit species only</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Primate–primate</td>
<td>−2.55 ± 0.12</td>
<td>−6.88–0.37</td>
</tr>
<tr>
<td>Primate–hornbill</td>
<td>−5.11 ± 0.14</td>
<td>−14.74–0.37</td>
</tr>
<tr>
<td>Hornbill–hornbill</td>
<td>−1.91 ± 0.12</td>
<td>−3.36–0.49</td>
</tr>
</tbody>
</table>

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

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 Cerco-repus species averaged −5.35 ± 0.12 (mean ± 1 SD). Pairwise comparisons of standardized dietary overlap between primate species showed Cerco-repus monkeys to have diets more similar to those of congeneres 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 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 non-fruit species had no effect on our interpretation of feeding assemblages. Overlap between hornbills and primates was still much lower than overlap between hornbill 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 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.

<table>
<thead>
<tr>
<th>Species</th>
<th>Hornbills</th>
<th>Primates</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>C. atrata C. cylindricus</td>
<td>L. albigena C. Pogonias C. nictitans C. ceph us C. guereza</td>
</tr>
<tr>
<td>Ceratogymana atrata</td>
<td>-1.62</td>
<td>0.09</td>
</tr>
<tr>
<td>Ceratogymana cylindricus</td>
<td></td>
<td>0.12</td>
</tr>
<tr>
<td>Lophocebus albigena</td>
<td>-6.46</td>
<td>-7.29</td>
</tr>
<tr>
<td>Cercopithecus pogonias</td>
<td>-6.32</td>
<td>-6.67</td>
</tr>
<tr>
<td>Cercopithecus nictitans</td>
<td>-6.16</td>
<td>-6.95</td>
</tr>
<tr>
<td>Cercopithecus cephus</td>
<td>-4.39</td>
<td>-4.32</td>
</tr>
<tr>
<td>Colobus guereza</td>
<td>-4.50</td>
<td>-5.30</td>
</tr>
</tbody>
</table>

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 feeding 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.

<table>
<thead>
<tr>
<th>Month</th>
<th>Average within-group overlap</th>
<th>Average between-group overlap</th>
<th>( t )</th>
<th>( P )</th>
</tr>
</thead>
<tbody>
<tr>
<td>All months</td>
<td>0.337</td>
<td>0.159</td>
<td>3.974</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>January</td>
<td>0.495</td>
<td>0.350</td>
<td>1.167</td>
<td>0.209</td>
</tr>
<tr>
<td>February</td>
<td>0.271</td>
<td>0.025</td>
<td>4.755</td>
<td>0.016</td>
</tr>
<tr>
<td>March</td>
<td>0.188</td>
<td>0.294</td>
<td>-1.204</td>
<td>0.970</td>
</tr>
<tr>
<td>April</td>
<td>0.343</td>
<td>0.049</td>
<td>7.112</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>May</td>
<td>0.313</td>
<td>0.285</td>
<td>0.375</td>
<td>0.066</td>
</tr>
<tr>
<td>June</td>
<td>0.298</td>
<td>0.269</td>
<td>0.320</td>
<td>0.004</td>
</tr>
<tr>
<td>July</td>
<td>0.439</td>
<td>0.152</td>
<td>5.067</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>August</td>
<td>0.259</td>
<td>0.093</td>
<td>2.383</td>
<td>0.003</td>
</tr>
<tr>
<td>September</td>
<td>0.362</td>
<td>0.115</td>
<td>3.232</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>October</td>
<td>0.302</td>
<td>0.143</td>
<td>3.062</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>November</td>
<td>0.375</td>
<td>0.049</td>
<td>5.721</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>December</td>
<td>0.396</td>
<td>0.080</td>
<td>3.019</td>
<td>&lt;0.001</td>
</tr>
</tbody>
</table>

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.
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 (Olpot 1998). Despite the broad diets of primates, our data suggest that 30 plant species compose ~75% of primate and hornbill diets.

KINNAIRD et al. (1996) found strong evidence that hornbills disperse 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 frugivores, the rate of dispersal will probably be limited and seed deposition patterns altered, possibly influencing forest structure and composition.

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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.