

Dja Hornbill Project / Projet Calao

Fourth Report – Summary of Weather, Phenology, and Abundance Data 1994 - 98



Submitted by:

**Kenneth D. Whitney
Donald Stauffer
Kimberly M. Holbrook
Aaron R. French
John R. Poulsen
Thomas B. Smith, Ph.D.**

**Mark K. Fogiel
Aaron Lamperti
Britta Denise Hardesty
Benjamin Wang
Connie J. Clark
V. Thomas Parker, Ph.D.**

**Center for Tropical Research
San Francisco State University
1600 Holloway Avenue
San Francisco, CA 94132 U.S.A.
Phone (415) 338-1089 Fax (415) 338-2295
E-mail tsmith@sfsu.edu**

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Summary

Seed dispersing animals are crucial to maintaining forest dynamics and ecological diversity of tropical forests. In 1993 we began a field study of three frugivorous hornbill species, the black-casqued hornbill, *Ceratogymna atrata*, the white-thighed hornbill, *Ceratogymna cylindricus albotibialis*, and the piping hornbill, *Ceratogymna fistulator*, in the semi-deciduous rain forest of the Dja Reserve, Cameroon. Collectively, the three hornbill species consumed fruits from 59 tree and liana species, and likely provide dispersal for 56 of them. Hornbill impact on forest composition may be significant as hornbill-dispersed trees composed 22% of the 260 tree species in the 25 km² study site. Germination trials showed that hornbill gut passage is gentle on seeds; 23 of 24 species germinated after passage by hornbills. Hornbill time spent foraging in a tree, visit frequencies, and seed passage times indicated that few seeds were deposited underneath parent trees. Seed shadows, modeled from seed passage data and daily movements of hornbills, were extensive, with approximately 80% of seeds moved more than 500 m from the parent plant. Home range analysis indicates that hornbills have extensive home ranges, from 925-4472 hectares. Hornbill populations showed strong seasonal changes in abundance in response to fruit availability. Radio telemetry studies conducted in 1996 determined that hornbills make large-scale movements in excess of 290 km.

Seed rain at the study site was highly variable, diverse, and unreflective of the adult community. Extrapolating the 297 seeds/m² in random seed traps to the entire study site, nearly seven million seeds fell in our research area in 1996. Twenty eight percent of the total seed rain, representing approximately 50% of the seed rain species, were handled by animals. Three of the top 10 handled species (*Uapaca*, *Ficus*, and *Xylopia*) are common vertebrate dispersed fruits and are important in the diets of hornbills and primates. Nearly 30% of all seeds handled were *Uapaca* sp. (3 species) suggesting that these species are important in the diets of frugivores.

Observations of fruiting trees demonstrated that the frugivore community in the study site was large, composed of over sixty animal species. This includes four species of hornbills, five species of primates (not including *Pan troglodytes* and *Gorilla gorilla*), at least five species of forest squirrels from three genera, and many small birds species. Analysis of competitive interactions at fruiting trees determined a social dominance hierarchy. Results showed a direct correlation between body mass and access to fruit resources. Social interactions, therefore, may dictate which frugivores eat and disperse a plant species. These interactions likely effect forest composition to the extent that frugivores differ in seed dispersal patterns.

To understand the differential patterns of hornbill and primate seed deposition, an array of nearly 750 seed traps was constructed under 90 individual trees representing 9 species. Preliminary results suggest that hornbill-dispersed tree species have longer seed shadow curves than either primate- or wind-dispersed tree species.

In an effort to determine the seed dispersal role of primates, the diets and feeding ecology of five species of arboreal primates, *Cercocebus albigena*, *Colobus guereza*, *Cercopithecus pogonius*, *Cercopithecus nictitans*, and *Cercopithecus cephus*, were studied in 1998. Results indicate that these species fed on 159 tree, liana, and shrub species. To date, fecal analysis of the four

Cercopithicine primates shows that they dispersed the seeds of 45 species. The set of plant species dispersed by primates differed largely from those dispersed by hornbills.

In sum, results suggest that hornbills and primates may have differential effects on forest composition determined by access to fruit resources, seed dispersal patterns, and the plant species dispersed. Thus, reduction in population sizes of either primates or hornbills caused by hunting or fragmented habitat may drastically change tropical forest composition. Due to the number of species for which they provide safe dispersal away from the parent plant, *Ceratogymna* hornbills may well be integral to healthy dynamics in equatorial African forests.

Preliminary Management Implications

Ceratogymna atrata and *Ceratogymna cylindricus* disperse seeds of 56 tree and liana species. Likewise, arboreal primates, *Cercocebus albigena*, *Cercopithecus nictitans*, *Cercopithecus pogonius*, and *Cercopithecus cephus* disperse at least 45 tree and liana species, and also impact the forest through the manipulations of substrate and seed predation. As such, healthy populations of these seed dispersers are necessary for forest regeneration and maintenance of forest dynamics.

1. Tree species known to be key resources in hornbill diets, especially those in the Annonaceae and Myristicaceae families, should be left standing in logging concessions and agricultural plots to promote visits and dispersal by *atrata* and *cylindricus*.
2. Hornbills depend on large trees as nesting cavities; and populations of cavity-nesting species have been shown to be subject to nest-site limitation (Kalina 1988; Wiens 1989). Large trees with natural cavities should be protected against extraction during logging or agricultural practices to encourage hornbill nesting.
3. As arboreal primates are frequently hunted by human populations, hunting should be restricted to a peripheral zone of the forest. This may best be accomplished by minimizing the number of trails that enter the forest. Protecting primate populations within the reserve will sustain hunting for the long-term as the reserve acts as a source for animals dispersing into the hunting zone.

I. Weather, Phenology, and Abundance Summary 1994 - 1998

1. Introduction

Project Scope

Research commenced within the Dja Reserve, Cameroon in 1993. The primary focus of the project was to determine the densities, habitat, diet, and the role as seed dispersers of two species of hornbills, the black-casqued hornbill/grand calao a casque noir, *Ceratogymna atrata*, and the white-thighed hornbill/calao a joues grises, *Ceratogymna cylindricus albotibialis*. In order to understand the relationship between these important seed dispersers and their environment, the general forest composition and seed rain patterns were assessed. To further understand how the natural history of hornbills can affect seed dispersal processes, we examined the breeding biology, foraging efficiency, home range and movement patterns of these species. Recently we studied the diets and seed dispersal by four species of Cercopithecine primates, the grey-cheeked mangabey/mangabe a joues grises, *Cercocebus albigena*, the white-nosed guenon/hocheur, *Cercopithecus nictitans*, the mustached monkey/moustac, *Cercopithecus cephus*, and the crowned guenon/cercopitheque pogonias, *Cercopithecus pogonius*, in an effort to understand the seed dispersal processes of the larger arboreal frugivore community. Finally, a comparative seed shadow study was conducted to examine the differential seed dispersal patterns of the hornbills and primates.

Study Site

The Bouamir Research Station (BRS) is located in the Dja Reserve, Cameroon. At 526,000 hectares, the Dja Reserve is the largest protected area in Cameroon. The vegetation is semi-deciduous tropical rain forest, and has affiliations with the Congo Basin forest to the south and, to a lesser extent, with the evergreen Atlantic coastal forest to the west. The climate is characterized by two wet and two dry seasons, with the major and minor rainfall peaks in September and May, respectively. Annual rainfall is approximately 1600 mm (Laclavere 1980). Topography in the Reserve is generally flat, with altitudes ranging from 400 – 800 m.

The Bouamir research Station (3°11'27"N, 12°48'41"E) is at the center of a 25 km² study area, 23 km from the nearest village or road. The study area has never been commercially logged, and has not been exploited agriculturally in the past 90 years. The Bouamir area is located on the spine of the reserve; headwaters of both north- and south-flowing streams are located within the study area. Reflecting this position, streams and their associated swamp forest are slightly less developed than elsewhere in the reserve. A feature unique to the study area and a few other localities in the reserve is the presence of inselbergs, outcroppings of rock characterized by thin soils and grassland vegetation. These include Bouamir (0.30 km²), Mbassako (0.14 km²), Lekenga (0.09 km²) and 9 small inselbergs.

2. Climate 1994 - 1998

Temperature and rainfall data at the Bouamir Research Station have been collected daily since January 1994, except for November 1997 through February 1998. Monthly averages of temperature and rainfall are provided in table 2.1. Figures 2.1 - 2.6 depict the monthly rainfall from 1994 to 1999.

Rainfall

Our results indicate that the climate at Bouamir was characterized by two distinct wet seasons and two distinct dry seasons. The major wet season started around the 1st of September and lasted until mid-November. This gave way to the major dry season, which lasted from November to mid-March. The second wet season, or minor wet season, began in mid-March and lasted approximately until the end of May. June, July and August constituted the minor dry season. The distinction between the minor wet and dry seasons was less pronounced and both contained periods of wet or dry weather. In the five-year period of our research, 1998 was the wettest year with 2008.5 mm of precipitation, and 1996 was the driest year with 1111.9 mm of precipitation.

Temperature

Average monthly temperatures ranged from 21.1 °C in September 1996 to 24.5 °C in April 1998. The highest temperature recorded during our study was 31.5 °C in March 1995. The lowest recorded temperature was 12.5 °C in January 1997. The highest average temperatures correspond with the peak of the major dry season, roughly February through April. The months proceeding the dry season, November through January, tended to have the lowest average minimum temperatures.

TABLE 2.1 Monthly average rainfall and temperature (Jan 1994 through Dec 1998).

Month	Rain (mm)	Average Max Temp (Celsius)	Average Min Temp (Celsius)	Average Temp (Celsius)
Jan 94	108.7	25.6	18.6	22.1
Feb 94	5.8	26.7	18.6	22.7
Mar 94	102.1	28.1	19.9	24.0
Apr 94	132.6	27.7	19.7	23.7
May 94	176.5	26.7	19.2	23.0
Jun 94	105.4	25.3	18.6	21.9
Jul 94	190.3	24.5	19.5	22.0
Aug 94	65.8	24.6	18.9	21.7
Sep 94	347.7	25.3	18.9	22.1
Oct 94	335.8	25.6	18.3	21.9
Nov 94	111.5	25.6	17.9	21.7
Dec 94	0.0	26.5	15.9	21.2
Jan 95	0.0	25.8	17.5	22.0
Feb 95	49.3	27.4	17.6	22.5
Mar 95	139.0	28.7	18.2	23.4
Apr 95	184.8	28.4	18.5	23.4
May 95	244.9	26.5	18.2	22.4
Jun 95	121.0	26.1	18.1	22.0
Jul 95	46.0	25.1	18.3	21.7
Aug 95	90.4	25.5	18.7	22.0
Sep 95	208.9	26.3	18.4	22.4
Oct 95	326.4	25.6	18.4	22.2
Nov 95	155.7	26.3	17.8	22.1
Dec 95	24.6	25.5	17.4	21.5
Jan 96	22.2	26.0	17.8	21.9
Feb 96	12.2	27.9	18.5	23.2
Mar 96	218.2	28.1	18.7	23.4
Apr 96	178.1	27.7	18.7	23.2
May 96	110.0	26.1	18.1	22.1
Jun 96	179.6	25.9	18.4	22.2
Jul 96	85.9	24.3	18.2	21.3
Aug 96	21.3	24.8	17.9	21.4
Sep 96	191.3	25.8	18.4	22.1
Oct 96	62.5	25.0	18.2	21.6
Nov 96	0.0	26.3	17.7	22.0
Dec 96	30.7	24.7	17.5	21.1
Jan 97	1.9	25.4	17.4	21.4
Feb 97	0.0	27.6	15.9	21.7
Mar 97	11.6	28.3	19.2	23.7
Apr 97	201.4	27.6	18.6	23.1
May 97	163.5	26.7	18.7	22.7

Month	Rain (mm)	Average Max Temp (Celsius)	Average Min Temp (Celsius)	Average Temp (Celsius)
Jun 97	116.0	25.9	18.9	22.4
Jul 97	70.5	25.0	18.5	21.7
Aug 97	212.7	25.6	18.8	22.2
Sep 97	346.7	26.1	18.8	22.4
Oct 97	277.7	27.2	18.9	23.1
Nov 97	180.8	-	-	-
Dec 97	47.5	-	-	-
Jan 98	-	-	-	-
Feb 98	0.00	26.9	20.1	23.5
Mar 98	57.5	28.0	20.4	24.2
Apr 98	182.5	28.3	20.7	24.5
May 98	300.4	27.3	20.5	23.9
Jun 98	116.0	25.0	20.5	22.7
Jul 98	54.0	24.5	20.0	22.2
Aug 98	293.6	24.1	19.9	22.0
Sep 98	282.8	25.0	19.9	22.4
Oct 98	407.7	24.1	20.5	22.3
Nov 98	289.1	24.7	20.7	22.7
Dec 98	25.0	25.0	19.2	22.1
Total 1994	1682.2			
Total 1995	1591.0			
Total 1996	1111.9			
Total 1997	1630.3			
Total 1998	2008.5			

FIGURE 2.1. Monthly rainfall (mm) occurring at the Bouamir Research Station in 1994.

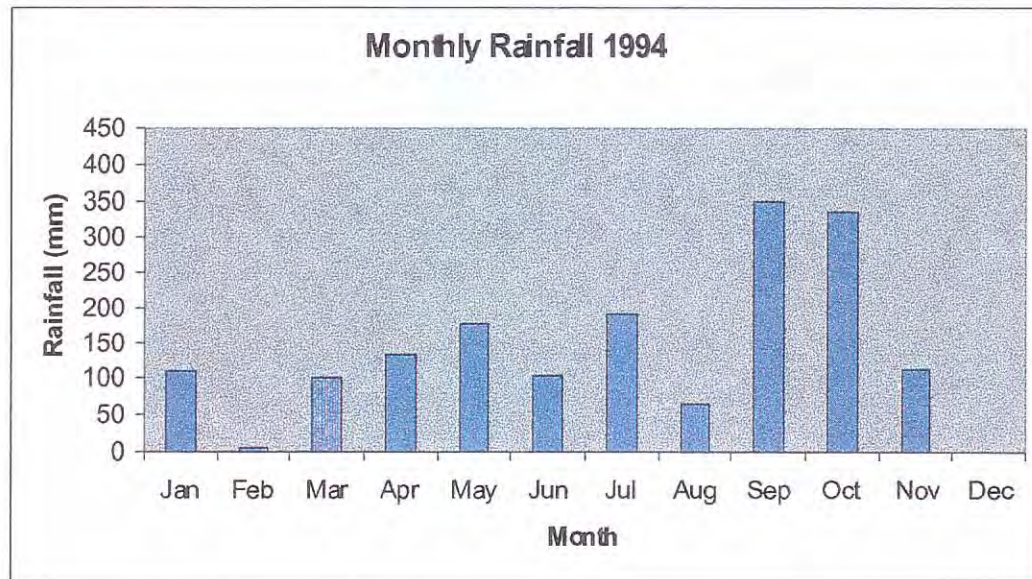


FIGURE 2.2. Monthly rainfall (mm) occurring at the Bouamir Research Station in 1995.

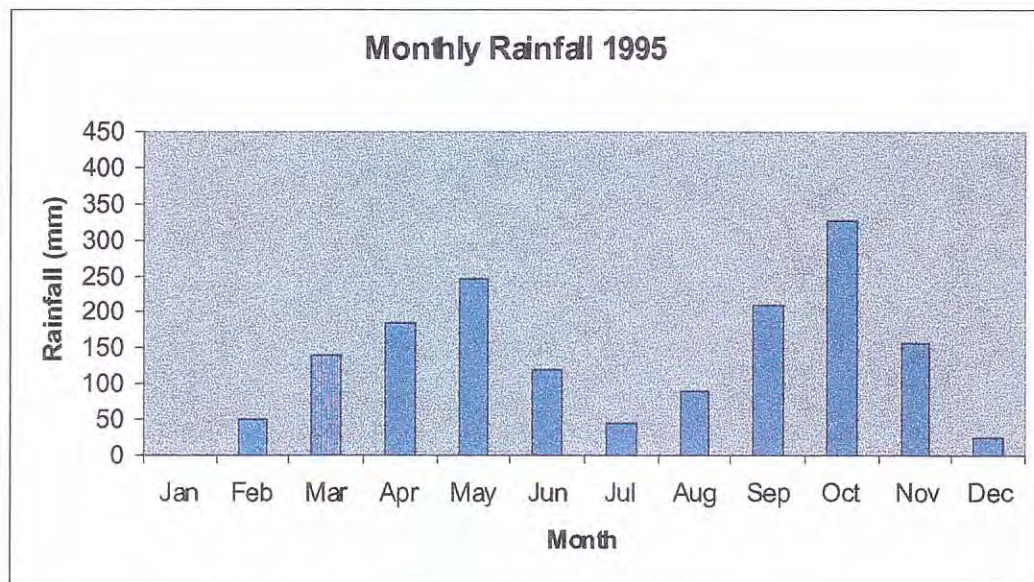


FIGURE 2.3. Monthly rainfall (mm) occurring at the Bouamir Research Station in 1996.

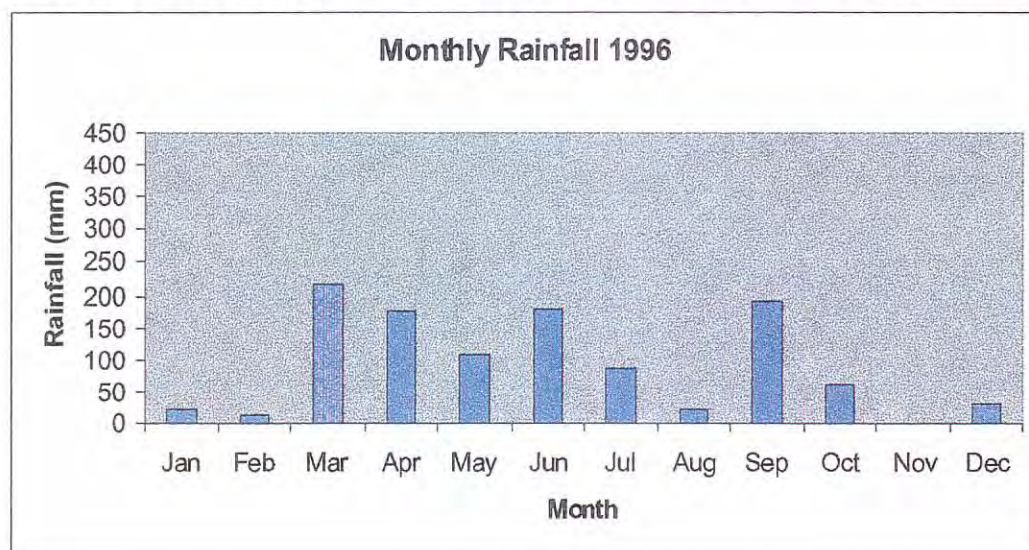


FIGURE 2.4. Monthly rainfall (mm) occurring at the Bouamir Research Station in 1997.

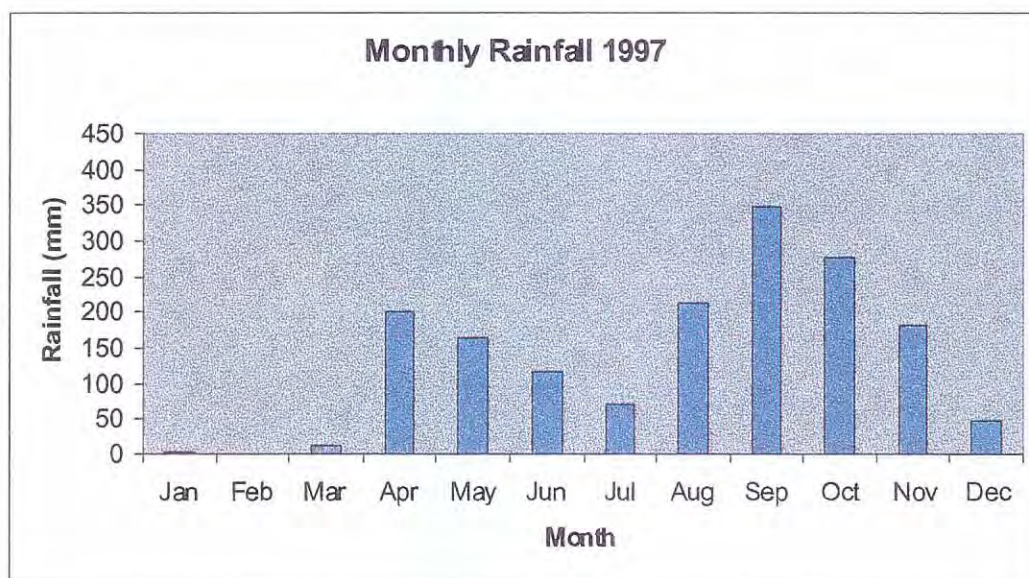
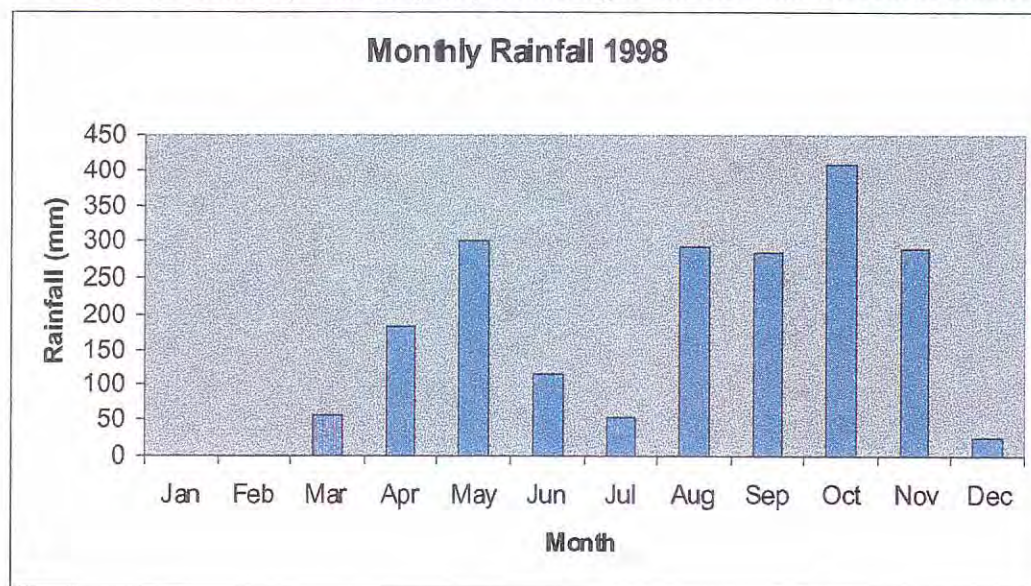


FIGURE 2.5. Monthly rainfall (mm) occurring at the Bouamir Research Station in 1998.



3. Phenology of Fruiting Trees 1994 – 1998

Knowledge of the temporal patterns of fruit production is important to understand frugivore-forest dynamics. We have shown that fruit availability can be used to predict monthly abundances of hornbills, which track fruit resources (Whitney 1998). Food availability also likely affects hornbill breeding behavior and home ranges which in turn determine the amount and quality of seed dispersal in a particular habitat. While the tree species in this study were chosen for their importance in hornbill diets, they are also important diet resources for other frugivores. As such, fruit availability may affect the densities, movements, and diet of primates and other seed dispersing animals within the forest community.

Methods

Phenology of Hornbill Diet Species - Canopy Fruit Census

The study site was initially searched for individuals of known or suspected hornbill dispersed tree species. Adult individuals of these species located were evaluated for crown visibility. The first 5 to 20 individuals of a species identified with suitable crown visibility were chosen for monitoring. Generally, a sample size of 10 was chosen, but 20 individuals were monitored for a few species initially perceived as being abundant in the forest. A few individuals each of 5 additional species were also monitored. All trees in the study were measured (diameter at breast height) and permanently marked with aluminum tags.

Monitoring phenology commenced in November 1993. More than 300 individuals in 38 species were checked at monthly intervals. Monitoring consisted of visual inspection of the crown with binoculars. Trees were graded on a scale of 0 to 4 in regard to flower buds, flowers, immature fruits, and mature fruits. The 0 to 4 scale reflected percent of full flowering or fruiting (0 = 0%, 1 = 1 to 25%, 2 = 26 - 50%, 3 = 51 - 75%, 4 = 76 - 100%). Observers record the proportion of leaf flush and leaf cover for each individual, using the same 0 to 4 scale reflecting proportion cover.

Community Fruit Production - Raked Trail Survey

Total fruit production by the forest community is measured by recording fruit fall onto a 4.3 km, 1-m wide trail (Gautier-Hion 1985b.). The trail is walked biweekly. For each patch of fruits found on the trail, the species, ripeness, and approximate number are recorded. Fruits are then removed so that they are not counted on the next census.

Results

The period from April until September appears to be the peak fruiting period for hornbill diet species and the forest community as a whole. November through February is consistently the time of greatest fruit scarcity within the study area. Fruit availability, however, varies within the peak fruiting period and between years. General patterns of peak fruiting periods are depicted in Figure 3.1 and Figure 3.2.

Five years of phenology data on hornbill diet species indicate that 1998 was the year with the lowest fruit availability (Figure 3.4). 1995 had the highest fruit abundance (Figure 3.3). Community fruit production measured by the raked trail survey indicated 1997 as the year of greatest fruit availability (Figure 3.2). This disparity can be attributed to the number and species of plants measured by each method. Canopy fruit census on hornbill diet species only evaluated a subset of the tree species found in

the study site; whereas the raked trail survey of community fruit production recorded fruit availability for all species within the study site.

Despite the discordance of the two methods in evaluating overall fruit availability, fruit production by the plant community and the hornbill diet species followed similar temporal patterns of fruit production. Community fruit production, measured by the raked trail survey, more than doubled in 1997 compared to the three previous years (Figure 3.2). The canopy fruit census, which focuses on hornbill diet species, did not detect the increase in 1997 fruit availability. This can partially be accounted for by increased fruit production of wind-dispersed liana species.

Since 1994, over 300 species of fallen fruit from trees and lianas have been recorded along the 4.3 km trail censused by the raked trail survey. We have tagged over 2500 individuals, and continue to add new individuals and species with each survey.

FIGURE 3.1. Fruit and ripe fruit abundances calculated from the canopy fruit census graphed for 1994-97. This figure depicts the phenology of 38 hornbill diet species.

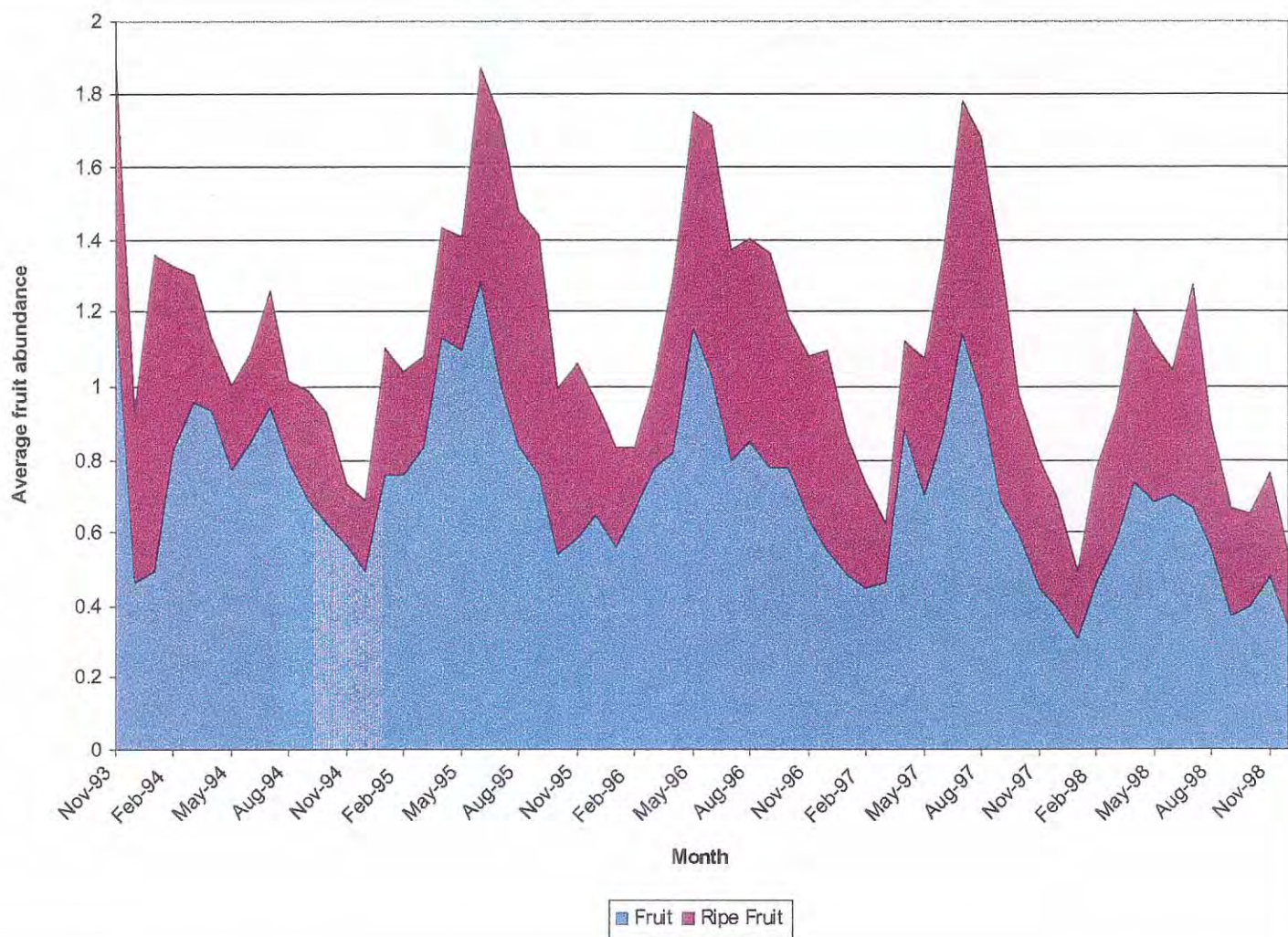
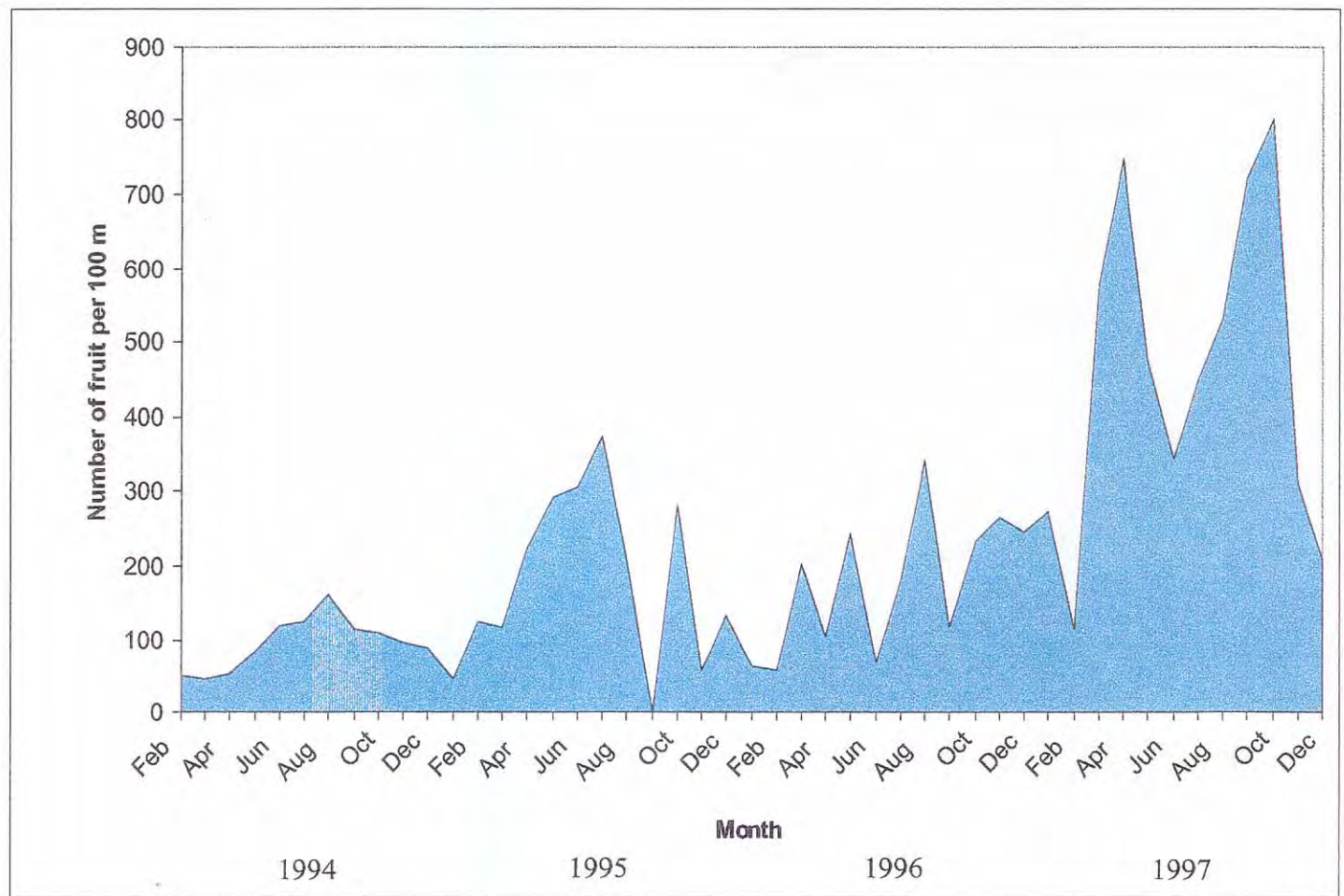


FIGURE 3.2. Total fruit production by the forest community depicted as fruit abundance per 100 m for 1994 – 97. *No data was collected for September 1995.



4. Hornbill and Primate Abundances 1994 - 1997

Establishing the densities of hornbills and primates in the Dja Reserve has been one of our primary goals. By determining frugivore abundances, we can monitor the effects of hunting, agriculture, reserve management and other human impacts on animal populations. Moreover, this data may be used as a yardstick to judge human pressures and effects on other forest in southern Cameroon.

Before this study, very little was known regarding the densities of forest hornbills in Africa. Characterized as "resident" (Fry 1988; Dowsett 1993; Christy 1994) with fixed home ranges of 150 hectares (Brosset & Erard 1986), the long-distance movements and the resulting effects on the forest system were unknown. Hornbill abundance results already demonstrated monthly abundance of *atrata* and *cylindricus* varied four- and 12-fold, respectively (Whitney 1998). Baseline data on hornbill densities may further explain the magnitude of density fluctuations and the underlying cause for hornbill movements.

Clearly, the seed dispersal quality of a frugivore depends on its population density. Without an adequately large population, even a voracious frugivore will contribute little to seed dispersal processes. The fluctuation of animal abundances and densities in time may also determine which species of plant are fed upon, and therefore, dispersed.

Primate populations have been shown to be variable across Africa and may elucidate historical events or ecological limits, like prolonged periods of fruit scarcity, that explain population levels of animals (Tutin 1997). As primate populations have been studied more in-depth than hornbill populations, they serve as one means of comparison of the Dja forest to other well-studied forests across Central Africa.

Methods

Densities of large frugivorous birds and primates are determined using a modified line-transect method, based on (Whitesides 1988). Trails are walked at a steady pace of approximately 2.0 km/hr. For each animal group encountered (seen or heard), the species, number, observer-to-group distance, compass bearing of the trail, and compass bearing of the group are recorded.

Two types of trails are surveyed: random trails throughout the study area, and four 2 to 2.5 km transects. The trails cut through all the habitat types represented at Bouamir: mature forest, *Raphia* swamp, *Uapaca* swamp, and inselberg. Currently, we walk each of the seven different line transect "loops" three times per month. Thus, approximately 143 kilometers of line transects are walked each month.

Relative abundances of large frugivorous birds and primates were determined by calculating the number of animals encountered in 100 km of trails. Since primary forest is dense and primates are shy, accurate estimation of primate groups proved difficult. We counted each primate encounter as a group encounter for this report. Mean group sizes borrowed from the literature (Tutin 1997) were multiplied by the number of groups sightings to derive the relative abundances of primates. This manner of calculating abundances, although used in other studies, ignored possible monthly or seasonal changes in group size.

Results

Census results indicate animal abundances vary monthly, seasonally, and inter-annually. Among the largest hornbills, *atrata* was more abundant than *cylindricus*. *Albigena* was more abundant than other primates in the study area, followed by *nictitans*, *pogonius*, *cephus*, and *guereza* (Table 4.1).

Although biomass estimates are not available here, data will be forthcoming and offer a better inter-species comparison. Qualitatively, however, comparisons can be drawn from abundance data. Considering the high abundances of *albigena* relative to the other primates and its rank as the second largest arboreal primate, our data suggests that it dominated the frugivore community in biomass. *Guereza* abundances were the lowest of the primates; however its position as the largest of the primates considered here suggests that it may rank as the third dominant species in biomass. Of the *Cercopithecus* monkeys, *nictitans* was the largest and had the greatest abundances in all four years.

When considered with diet data reported in Section 1 of the Project Report for 1998, these preliminary data suggest that the omnivorous habits of *albigena* allowed it to dominate the frugivore community in numbers and biomass. Abundances of *guereza* were likely limited by its greater body mass and perhaps by the concentration of leaves in its diet. Of the more frugivorous primate and hornbill species, the largest primate, *nictitans* dominated. Given heavier body masses, primate abundances and biomass were greater than the hornbills for all years, except 1997. It appears that *atrata* may have ranked higher in biomass than *cephus* in 1997.

Atrata reported greater abundances than *cylindricus* for the 1994-97 period. Calculations for 1994 indicate that *atrata* also had greater densities (8.7 ± 0.6 ind./km²) compared to *cylindricus* (7.2 ± 1.0 ind./km²) and greater biomass (10.5 kg km²) to (8.1 kg km²) (Whitney 1998). Our data suggest this trend was consistent over the four year period.

TABLE 4.1. Average abundances of 5 primates and 2 hornbills, as determined by line-transect censuses conducted between 1994-1997.

Species	Avg. Abund. 1994	Avg. Abund. 1995	Avg. Abund. 1996	Avg. Abund. 1997
Primates				
<i>Cercocebus albigena</i> Grey-cheeked mangabey Mangabe a joues grises	516.45	370.02	623.16	929.30
<i>Cercopithecus nictitans</i> White-nosed guenon Hocheur	458.50	285.47	453.52	709.06
<i>Cercopithecus pogonius</i> Crowned guenon Cercopitheque pogonias	404.86	182.79	319.87	420.70
<i>Cercopithecus cephus</i> Moustached monkey Moustac	148.69	105.50	114.39	117.11
<i>Colobus guereza</i> Black-and-white colobus Colobe guereza	83.35	80.56	71.50	115.61

Species	Avg. Abund. 1994	Avg. Abund. 1995	Avg. Abund. 1996	Avg. Abund. 1997
Hornbills				
<i>Ceratogymna atrata</i> Black-casqued hornbill Grand calao a casque noir	173.58	161.95	177.58	391.42
<i>Ceratogymna cylindricus</i> White-thighed hornbill Calao a joues grises	101.75	72.39	93.36	62.96

The monthly abundances of primates and hornbills fluctuated widely by month and season (Figure 4.1, 4.2). While variations in primates are less clear, hornbill abundances are highly correlated with fruit abundance. In 1994, monthly abundances of *atrata* and *cylindricus* varied four- and 12-fold, respectively. Comparisons with fruit abundance indicated that *atrata* and *cylindricus* populations track fruit resources via seasonal emigrations (Whitney 1998). Radio telemetry results strongly supported these findings by tracking hornbill movements outside of the reserve (Holbrook 1999). Figure 3.3 demonstrates the hornbill abundance patterns, and the consistency of these patterns over four years of study. *Cylindricus* abundances peaked in July and again in October through December. *Atrata* abundances followed a similar, though less marked, pattern with increased abundances May through August and relatively high abundances October through December, except for 1995. Hornbill abundances were consistently low during the major dry season, January to April.

Patterns in changes in primate relative abundances are less understood. There appears to be a slight trend towards increased abundances during times of greater fruit abundance (Figure 4.4, 4.5). However, this is the timing and degree of fluctuation is highly variable between years and species. To better understand primate abundance patterns, future analysis will compare primate abundances with phenological patterns of primate diet species. In addition, abundances will be examined with fruiting patterns of key diet species like *Uapaca* spp., *Xylopia* spp., and *Erythrophloeum suaveolens* to detect whether single tree species can affect abundance patterns.

Abundances of *albigena*, *nictitans*, *pogonius*, and *guereza* appear to have increased from 1994 to 1997 (Figure 4.2). The highest abundance of *albigena* was recorded in April 1994 at 719 individuals per 100 km. In 1997, an abundance of 1209 individuals was reported, a 68% (490) increase of mangabeys over a four year period. Table 4.1. depicts the change in relative abundance over the four-year period for each of the primate and hornbill species studied. More data is necessary to conclude whether primate populations have increased at the study site or if this is solely a phenomenon in 1997.

Increased animal abundances may be explained by changes in fruit production. Increased primate and hornbill abundances corresponded with increased community fruit production measured by the raked trail survey doubled in 1997 (Figure 4.2). This increase in fruit availability was not accounted for by the canopy fruit censuses of hornbill diet species (Figure 4.1). Although more analysis needs to be done, this may suggest that these animals foraged on species not measured by our canopy fruit census methodology. Or, perhaps primates and hornbills don't discriminate between species, and are drawn to areas of greater fruit production. If an area of forest shows high fruit production, general fruiting conditions may be good, and therefore, chances are high that plants of value to frugivores are fruiting.

While we await the 1998 census results, one possible reason for this increase in primate abundance may be that larger-bodied monkeys sought refuge from hunting pressures on the periphery of the reserve. It may also be possible that these species have become more habituated to our presence in the study area, and therefore are easier to detect. Additional data must be collected to answer this question of increasing primate abundances.

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