Behavior and Ecology of the Mona Monkey in the Seasonally Dry Lama Forest, Republic of Bénin

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ABSTRACT

Behavior and Ecology of the Mona Monkey in The Seasonally Dry Lama Forest, Republic of Bénin

By Reiko Matsuda Goodwin

Advisor: Prof. John F. Oates

I investigated the behavior and ecology of the mona monkey (*Cercopithecus mona* Schreber, 1774) in the Lama Forest for 17 months, and estimated the population density and biomass of the anthropoid species in the forest.

I found that *Cercopithecus mona* forms mixed-sex groups and all-male groups. Multiple males in mixed-sex groups interacted amicably, but males belonging to different groups behaved aggressively towards each other during intergroup encounters. Male-male relationships in *C. mona* appear to differ from those reported in some other arboreal guenons (e.g., *C. diana*, *C. mitis*).

Fruits and legume seeds and arils were the most important foods for *C. mona*. Nearly 40% of its food came from *Dialium guineense* and *Diospyros mespiliformis*, the most common tree species. During the first major dry season, *C. mona* fed extensively on nectar and flower parts of *Ceiba pentandra*, immature seeds of *Dialium*, and arils of *Afzelia africana* legume seeds. During the second major dry season, *C. mona* fed mostly on *Afzelia* seed arils, mass-fruiting immature seeds of *Dialium*, and nectar of *Ceiba* flowers. Immature seeds were eaten when fleshy fruits were scarce. Factors such as low fleshy-fruit diversity, an abundance of Caesalpinioideae trees, and perhaps the superior nutritional quality of seeds and seed arils are all probably responsible for *C. mona*'s choice of the foods that they rely on when few ripe fleshy fruits are available.

The population density of *C. mona* at Lama is one of the highest of all the forests where it has been surveyed. In forests where members of *mona* species group occurs with few or no other sympatric primates, its biomass is high. In these forests, they thrive with year-round fruits, cultivated foods, or abundant alternative foods such as Caesalpinioideae seeds in seasons of scarcity. In contrast, their biomass is the lowest or second lowest of all arboreal guenons in wetter forests that are dominated by fleshy-fruit producing species, probably because members of the mona species group have a lesser ability to digest leaves and a lower competitive ability than sympatric guenons in territorial conflicts.

FOREWORD

I initially intended to habituate two mona monkey (*Cercopithecus mona*) groups that differ in size (large > 30 and small < 20) to examine the relationships between seasonality, group size, scramble (or exploitative) competition, and the size of food patches[*] in the Lama Forest, my study site. Scramble competition is an indirect form of competition in which an individual reduces the foods available for others by just being in the group and feeding on those foods. I was interested in finding out how seasonality influences within-group and between-group feeding competition in *C. mona* by collecting data on the daily path length[**] day range[***] size and interindividual distance as measures of scramble competition in large and small groups (Wrangham, 1980; Janson, 1985, 1988a, 1988b; Janson and van scahik, 1988; van Schaik, 1989; Isbell, 1991).

At the research station in the forest, I found out that the monkeys and other large mammals (e.g., duikers, bushbucks, bush pigs) that exist in the Lama Forest were subject to a steady level of hunting by local people. Although hunting was not on a large-scale, even small-scale hunting modifies primates' behavior (Muchaal and Ngandjui, 1999; Struhsaker, 2000). Regrettably, this fact was not evident during an initial summer 1994 reconnaissance visit. During the short visit, the monkeys appeared tame and habituation seemed possible. After arriving in July 1995, I found out that hunters entered the forest during the day, at night, at dawn, and at dusk. I started to hear gunshots while I was in and out of the forest. One late afternoon while I was working on a tree inventory in a drizzle in the forest, I heard a gunshot about 50 m away from me. More than once, in

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[*] a specific food tree or a cluster of trees that provides feeding sites for a group of primates.

[**] a distance a group of primates travels in one day from the time the members of the group wake up until theygo to sleep.

[***] an area covered by a group of primates in one day.

the middle of the night and at dawn, I was awakened by some gunshots and the subsequent series of loud calls given out by adult male *C. mona*. I also found metal snares and discarded gun cartridges in the forest.

When I started to try to habituate a tame-looking group, the group members gave alarm calls and fled into areas where there were no trails. I was not able to follow the group. The area where I decided to habituate two *C. mona* groups had three trails (Layon 12, 13, and 14) that are parallel to each other and separated by 1 km each, but it lacked a grid system. I began working with field assistants to create an extensive 100 m x 100 m grid system there between August 1995 and March 1996. While the grid system was laid out during the first five months, my hope for habituating at least one group was still high, but the monkeys kept on fleeing. I thought that this was just because of a lack of an extensive grid system and when the trail system was complete, I would be able to follow and habituate a group, but the monkeys kept a flight distance of more than 50 m. The sense of optimism faded when the New Year started. Behavioral observation was almost impossible, since every time I followed a group, it simply fled. I was not able to obtain much data while I was trying to habituate a group. After seven months, it became obvious that habituation was not possible at Lama under the current conditions. When I finally gave up on group habituation, I realized that I had to find an alternative way to study *C. mona*.

I was not able to use most of the research protocols and methods I proposed to use in research proposals I had submitted to funding agencies. I realized that none of the hypotheses I had intended to test would be testable. As a strategy to study unhabituated animals, instead of making myself visible and audible, I decided to slowly and quietly walk in the forest in search of any *C. mona* groups I could find. Given the fact that the Lama Forest is under surveillance by hunters from neighboring villages, my field assistants insisted that I walk with at least one assistant in the forest, but I decided that walking quietly alone was the best, if not only, way to obtain some behavioral data. When I found a group, I tried to remain silent and motionless to observe and record the behavior of the monkeys as long as possible while hiding behind trees. Consequently, this research went through some major transformations, and turned into something completely different from what had initially been intended. Naturally, sample sizes of *C. mona*'s behavioral data are limited and some of the conclusions I draw from this study remain tentative.

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TABLE OF CONTENTS

LIST OF TABLES

(List of Tables, cont'd)

LIST OF FIGURES

(List of Figures, Cont'd)

(List of Figures, Cont'd)

CHAPTER 1: INTRODUCTION

I. Study of Guenons in a Seasonally Dry Forest

Seasonality affects many, if not all, aspects of primate lives (van Schaik and Brockman, 2005). Changes in the availability of preferred foods have a profound influence on the activity levels, reproductive, social, and ranging behavior, and physiology in many primate species. Documenting how primates live through difficult seasons (i.e., fruit scarcity, increased feeding competition, periods of intense male-male competition for females in estrus, periods of high predator activities, decreased vegetation cover) is important, because this information can help us understand how natural selection has shaped their current biological existence. Natural selection is likely to act on many aspects of the biology of animals most strongly during periods of severe environmental challenges. Most primate species that live in seasonal environments appear to be equipped with an ability to cue into changes that take place in their habitats and respond to them appropriately, because their survival is dependent on it (van Schaik and Brockman, 2005). Climatic changes that occur in primate habitats are not limited to seasonal changes. Periodic fluctuations that occur in primate habitats that supersede seasonal changes can be more unpredictable and sometimes have long-lasting effects.

I investigated the behavior and ecology of the mona monkey (*Cercopithecus mona*) in the Lama Forest of the Republic of Bénin, a seasonally dry forest, in West Africa. Data were collected from unhabituated groups (6-8 groups) for 17 months between August 1995 and June 1997. I examined *C. mona*'s group structures, social and reproductive behavior, and feeding ecology in relation to seasonality. Particular attention was paid to their diet in relation to the temporal changes in food availability in their habitat. I also estimated the population density and biomass of *C. mona* and two sympatric species, the red-bellied guenon (*Cercopithecus erythrogaster*) and the olive colobus (*Procolobus verus*). The results of this study were compared with previous studies on other populations of the same species and with studies of other guenons to elucidate some ecological adaptations of the study species. This is the first long-term study focusing on *C. mona*'s behavior and ecology in a seasonally dry forest in mainland Africa. All previous surveys and observational studies on the species took place in much wetter forests.

The scientific and common names of guenon species and subspecies used in this dissertation are shown in Table 1.1. Most of the names I use in this dissertation follow the "Orlando Taxonomy" (Grubb *et al.*, 2003) except those of the terrestrial guenons (i.e., vervets, patas monkey, l'Hoest's monkey, and the sun-tailed monkey), for which I use *Chlorocebus*, since Tosi *et al.* (2005) have recently shown that these terrestrial taxa form a monophyletic group. I use the term "guenons" for all members of the tribe Cercopithecini and reserve the term "forest-living guenons" for all cercopithecins except the vervets and patas monkeys. I also use the term "swamp-living guenons" for the Allen's swamp monkey (*Allenopithecus nigroviridis*) and the talapoins (*Miopithecus talapoin* and *Miopithecus ogouensis*). Othe names of other African primate taxa used in this dissertation also follow the "Orlando Taxonomy" (Grubb *et al.*, 2003).

Table 1.1 Tribe Cercopithecini adapted from Grubb *et al.* (2003). The mona species group is shown in the shaded area.

Scientific Names	Common Names	T/ST/A*
Allenopithecus nigroviridis	Allen's swamp monkey	A
Miopithecus talapoin	Southern talapoin monkey	A
Miopithecus ogouensis	Northern talapoin monkey	A
Chlorocebus patas	Patas monkey	T
Chlorocebus aethiops	Green, Malbrouck, and Tantalus	T
	monkeys; Grivets, vervets	T
C. a. aethiops	Grivet monkey	T
C. a. djamdjamensis	Bale mountains monkey	T
C. a. tantalus	Tantalus monkey	T
C. a. sabaeus	Green monkey	T
C. a. cynosuros	Malbrouck monkey	T
C. a. pygerythrus	Vervet monkey	T
Chlorocebus lhoesti	L′ Hoest's monkey	T
Chlorocebus preussi	Preuss's monkey	T
C. p. preussi	Cameroon Preuss's monkey	T
C. p. insularis	Bioko Preuss's monkey	T
Chlorocebus solatus	Sun-tailed monkey	T
Cercopithecus diana	Diana and Roloway monkeys	A
C. d. diana	Diana monkey	A
C. d. roloway	Roloway monkey	A
Cercopithecus dryas	Dryad monkey	A
Cercopithecus neglectus	De Brazza's monkey	ST
Cercopithecus hamlyni	Owl-faced monkeys	ST
C. h. hamlyni	Northern owl-faced monkey	ST
C. h. kahuziensis	Mt. Kahuzi owl-faced monkey	ST
Cercopithecus petaurista	Lesser spot-nosed monkeys	A
C. p. petaurista	Eastern lesser spot-nosed monkey	A
C. p. buettikoferi	Western lesser spot-nosed monkey	A
Cercopithecus erythrogaster	White-throated monkeys	A
C. e. erythrogaster	Red-bellied monkey	A
C. e. pococki	Nigeria white-throated monkey	A
Cercopithecus sclateri	Sclater's monkey	A
Cercopithecus erythrotis	Red-eared monkeys	A
C. e. erythrotis	Bioko red-eared monkey	A
C. e. camerunensis	Cameroon red-eared monkey	A
Cercopithecus cephus	Moustached monkeys	A
C. c. cephus	Red-tailed moustached monkey	A
C. c. cephodes	Gray-tailed moustached monkey	A
C. c. ngottoensis	White-nosed moustached monkey	A

*T/ST//A = Terrestrial or Semi-Terrestrial or Arboreal

Scientific Names	Common Names	T/ST/A*
Cercopithecus ascanius	Red-tailed monkeys	A
C. a. ascanius	Black-cheeked red-tailed monkey	A
C. a. schmidti	Schmidt's red-tailed monkey	A
C. a. whitesidei	Yellow-nosed red-tailed monkey	A
C. a. katangae	Katanga red-tailed monkey	A
C. a. atrinasus	Black-nosed red-tailed monkey	A
Cercopithecus campbelli	Campbell's and Lowe's monkeys	A
C. c. campbelli	Campbell's monkey	A
C. c. lowei	Lowe's monkey	A
Cercopithecus mona	Mona monkey	A
Cercopithecus pogonias	Crowned and wolf's monkeys	A
C. p. pogonias	Golden-bellied crowned monkey	A
C. p. nigripes	Black-footed crowned monkey	A
C. p. grayi	Gray's crowned monkey	A
C. p. wolfi	Congo Basin Wolf's monkey	A
C. p. denti	Dent's monkey	A
C. p. elegans	Lamami River Wolf's monkey	A
C. p. pyrogaster	Fire-bellied Wolf's monkey	A
Cercopithecus nictitans	Putty-nosed monkeys	A
C. n. nictitans	Eastern putty-nosed monkey	A
C. n. martini	Stampfli's putty-nosed monkey	A
Cercopithecus mitis	Blue, Sykes's, and Golden monkeys; Samango	A
C. m. albotorquatus	Pousargue's white-collared monkey	A
C. m. kolbi	Kolb's white-collared monkey	A
C. m. albogularis	Zanzibar Sykes' monkey	A
C. m. monoides	Tanzania Sykes' monkey	A
C. m. francescae	Red-eared Sykes' monkey	A
C. m. moloneyi	Moloney's white-collared monkey	A
C. m. erythrarchus	Stair's white-collared monkey	A
C. m. labiatus	Samango	A
C. m. heymansi	Lomami river blue monkey	A
C. m. opisthostictus	Rump-spotted blue monkey	A
C. m. mitis	Pluto monkey	A
C. m. boutourlinii	Boutourlini's blue monkey	A
C. m. stuhlmanni	Stuhlmann's blue monkey	A
C. m. schoutedeni	Schouteden's blue monkey	A
C. m. doggetti	Doggett's blue monkey	A
C. m. kandti	Golden monkey	A

II. Introduction to Guenons

A. What are Guenons?

Cercopithecus mona belongs to one of the most geographically and ecologically diverse primate genera within the order Primates (Delson, 2000). *Cercopithecus* is placed within the tribe Cercopithecini along with *Allenopithecus, Miopithecus, and Chlorocebus*. Different authors recognize 19 to 36 species within the tribe (e.g., 20, Thorington and Groves, 1970; 21, Napier and Napier, 1967; 23, Hill, 1966, Butynski, 2002; 24, Oates, 1986; 25, Oates, 1996; 36, Groves, 2001a; 19, Grubb *et al.*, 2003).

Most guenons are forest-dwellers, and in most forests, two to several guenon species are sympatric. The arboreal species frequently join mixed-species groups that may include colobus monkeys (genera *Colobus* and *Procolobus*), mangabeys (genera *Lophocebus* and *Cercocebus*), some baboons (genus *Papio*), and mandrills and drills (*Mandrillus* spp.) (Haddow, 1952; Booth, 1956, 1958a, b, c; Sabater Pi and Jones, 1967; Jones and Sabetrr Pi, 1968; Struhsaker, 1969, 1981; Aldrich-Blake, 1977; Gartlan and Struhsaker, 1972; Gautier-Hion *et al.*, 1983; Galat and Galat-Luong, 1985; Cords, 1987a, 1987b; Mitani, 1991, 1992; Whitesides, 1991; McGraw and Bshary, 2002). Increased feeding efficiency and improved predator detection, which are probably not equally partitioned among participating species and individuals, are considered the two major advantages of mixed-species groups in guenons (Cords, 1987a, b; Bshary and Noë, 1997; McGraw and Bshary, 2002). Aside from human hunters, major predators of guenons living in rain forest habitats are the crowned hawk eagle (*Stephanoaetus coronatus*), the leopard (*Panthera pardus*), and the common chimpanzee (*Pan troglodytes*) (Cords, 1990; Struhsaker and Leakey, 1990; Cordeiro, 1992, 2003; Bshary and Noë, 1997; Noë and

Bshary, 1997; Zuberbühler *et al.*, 1997; Wilkie *et al.*, 1998; Treves, 1997; Shultz and Nöe, 2002; Cordeiro, 2003).

B. Social Structure and Behavior

Traditionally, forest-living guenons have been regarded as living in one-male groups of 2–30 individuals (Struhsaker, 1969; Cords, 1987a, 1988; Glenn, 1996; 1997; Peignot *et al.*, 2002). Although we still lack data on the group structure and social organization of more than half of the species within *Cercopithecus*, studies conducted in the last 20 years or so have revealed that social systems of guenons are complex and variable (Cords, 2000; Carlson and Isbell, 2001). Two well-studied forest-living species, *C. mitis* and *C. ascanius*, for example, usually form one-male groups, but in some years, extra males occasionally join these groups during some mating seasons (Henzi and Lawes, 1988; Cords *et al.*, 1986; Cords, 2000; Carlson and Isbell, 2001). A long-term two-male phase was also reported in *C. petaurista* groups in Taï Forest, Côte d'Ivoire (Buzzard, 2004). In contrast, multi-male groups appear to be the general pattern only in *Miopithecus*, *Allenopithecus*, and vervets among guenons. In two members of the mona species group (i.e. *C. campbelli* in Adiopodoumé, Côte d'Ivoire, Bourlière *et al.*, 1969, 1970; *C. campbelli* in Taï Forest, Côte d'Ivoire, Buzzard, 2004; *C. mona* in Mungo F.R., Cameroon, Howard, 1977; *C. mona* in Grand-Etang F.R., Grenada, Glenn, 1996), intraspecific and within-site variability in the number of males in mixed-sex groups have been reported. Furthermore, all-male groups or permanent associations of males have been reported in *C. campbelli* and *C. mona* (Bourlière *et al.*, 1969, 1970; Whitesides, 1981; Glenn, 1996; Buzzard, 2004).

Cords (2000) examined several hypotheses that may explain seasonal and permanent presence of variable numbers of males in typically one-male and multi-male species of guenons. She proposed that the number of males per group in multi-male species (*Chlorocebus aethiops* and *Miopithecus talapoin*) is a function of the number of females per group. She also suggested that high population density could influence the rate of intergroup encounters that occur among neighboring groups, leading to male-male coalitions viable. Furthermore, she suggested that a relatively short mating season could elevate the number of females in estrous per day, leading to low defendability of females by single male. More recently, Buzzard (2004) showed that male relationships found in *C. campbelli* and *C. petaurista* are somewhat different from male relationships observed in *C. diana* in the Taï Forest.

What are the group structures of *C. mona* in the Lama Forest? Do all-male groups occur? If they do, do they persist for a long-term or only temporarily? How do male *C. mona* behave among themselves and in the presence of females? If mixed-sex groups exist, what are some factors that lead to multi-male sociality? In Chapter 6, I describe and examine group structures and social and reproductive behavior of *C. mona* in the Lama Forest and attempt to answer some of these questions. I also explore some factors that may explain some of the variations found among *C. mona* populations and other arboreal guenons.

C. Feeding Ecology

Most species groups within *Cercopithecus* contain at least one species that occupies tropical dry semi-deciduous forest or seasonally dry forest. In seasonally dry forests, fewer plant food species are usually available, especially those that produce fleshy fruits (Galetti and Pedroni, 1994). There is little documentation showing how medium-sized guenons living in this type of habitat cope with reduced availability of preferred food during the times of food scarcity (Chapman *et al.*, 2002). The only exceptions are studies conducted on *Cercopithecus mitis* living in Cape Vidal, a region with pronounced seasonality (Lawes, 1991). *Cercopithecus mitis* reduced fruit intake, but increased the intake of leaves during the long dry season (Lawes *et al.*, 1990).

In forests where *Cercopithecus mona* has been studied or surveyed to date, seasonality is moderate or minor and fruits were the most important food sources (Booth, 1954; Gartlan and Struhsaker, 1972; Whitesides, 1981; Howard, 1977; Glenn, 1996). As for other members of the mona species group, *Cercopithecus pogonias* at Makokou and Lopé in Gabon mostly fed on pulpy fruits, but at Makandé (Gabon) and Salonga (DRC) where Caesalpinioideae is the dominant tree family, *C. pogonias* fed on a significant amount of legume seeds of *Dialium* (Caesalpinioideae) (Brugière *et al.* 2002; Maisels *et al.*, 1994). *Cercopithecus campbelli* in the Taï Forest, Côte d'Ivoire increased the consumption of arthropods and, to a lesser extent, of leaves during the months of low fruits (Buzzard, 2004). What types of food does *C. mona* incorporate when pulpy fruits become scarce? Does it incorporate the same alternative foods during two major dry seasons? These became the central questions of this thesis. *Cercopithecus mona*'s response to the changes in resource availabilities is explored in detail in Chapter 5.

III. Study Species

A. Taxonomy

Over the last century, there have been many revisions to the classification of the mona monkey and its relatives. In 1907, Pocock recognized *Cercopithecus mona* as one of seven related species: *mona, campbelli*, *burnetti, denti*, *wolfi*, *grayi*, and *pogonias* (Pocock, 1907). Schwarz (1928), in contrast, examining the skull morphology of each form, concluded that *mona* is a polytypic species and recognized three sections: (1) *mona* section (*campbelli*, *lowei*, *mona*), (2) *pogonias* section (*pogonias*, *grayi*, *nigripes*), and (3) *wolfi* section (*wolfi*, *pyrogaster*, *elegans*, *denti*) as the most primitive one. Rode (1937) included two species in the *mona* group: *C. pogonias* and *C. mona*; *campbelli*, *denti*, and *wolfi* were considered subspecies of *mona*. Mainly based upon pelage colors and patterns, Booth (1955) recognized *mona*, *campbelli*, *pogonias*, *wolfi*, and *denti* as separate species, although he expressed uncertainty as to whether or not *denti* should be considered a subspecies of *wolfi*. He thought that drab colored pelages observed in West African forms were ancestral and more primitive than the brighter patterns seen in Central African forms. Hill (1966), Napier and Napier (1967), and Thorington and Groves (1970) followed Booth's (1955) classification. Wolfheim (1983) recognized the same five species, but Oates (1986) recognized only *mona*, *campbelli*, and *pogonias* as separate species.

Advances in chromosome and genetic studies prompted another revision among researchers. For example, Lernould (1988), Groves (1993), and Oates (1996) again acknowledged *wolfi* as a separate species and Kingdon (1997) and Groves (2001a) thought *denti* should be separated from *wolfi*. Most recently, however, Grubb *et al.*

(2003) recognized only *mona*, *campbelli*, and *pogonias* as full species based on vocalizations.

Although the monospecific status of *C. mona* stands firmly, the differences in opinion regarding the number of species within the *mona* group revolve around the relationships between *campbelli* and *lowei* and the relationships within the *pogonias* section. As for *campbelli* and *lowei*, most authors agree that the two are not distinct species (Napier and Napier, 1967; Struhsaker, 1970; Thorington and Groves, 1970; Oates, 1986, 1996; Butynski, 2002; Grubb *et al.*, 2003), but Kingdon (1997) and Groves (2001a), who support the Phylogenetic Species Concept, split them as separate species, since these two taxa possess diagnosably different patterns (Groves, 2004). The treatment of *wolfi* and *pogonias* populations has also been variable. Some authors list three *wolfi* subspecies (*C. w. wolfi*, *C. w. pyrogaster*, *C. w. elegans*) and four *C. pogonias* subspecies (*C. p. pogonias*, *C. p. grayi*, *C. p. nigripes*, *C. p. schwarzianus*) (Napier and Napier, 1967; Thorington and Groves, 1970; Groves, 2001a). Lernould (1988) listed four *C. wolfi* subspecies (*C. w. denti*, *C. w. elegans*, *C. w. pyrogaster*, *C. w. wolfi*) and three *C. pogonias* subspecies (*C. p. grayi*, *C. p. nigripes*, *C. p. pogonias*), confirming the existence and distribution of *elegans* and *wolfi* in the Congo river basin for the first time since the type specimens were obtained (Colyn and Verheyen, 1987). Oates (1986) originally considered *denti* and *wolfi* subspecies of *pogonias* on the basis of their distribution and similar vocalizations (Gartlan and Struhsaker, 1972), but later recognized *wolfi* as a full species distinct from *C. pogonias*, acknowledging Gooder's (1991) finding that *wolfi* possesses three derived features in its cranial and dental morphology (Oates, 1996). In contrast, the Orlando taxonomy subsumed all eight forms under *C. pogonias*

(*C. p. pogonias*, *C. p. nigripes*, *C. p. grayi*, *C. p. denti*, *C. p. wolfi*, *C. p. elegans*, *C. p. pyrogaster, C. p. petronellae*) (Grubb *et al.*, 2003). Grubb *et al.* (2003) recognized only one species of *C. pogonias*, noting that all the above forms had similar vocalizations and that there is a lack of sufficient data to delimit species (Grubb *et al.*, 2003).

B. Evolution

How did the various taxa in the mona species group evolve and radiate? Based upon the pelage and the distribution pattern of the *mona* species group, Booth (1955) hypothesized that *C. c. lowei* gave rise to *C. mona*. He believed that brighter pelage was more derived and *Cercopithecus mona* later gave rise to *C. p. denti* followed by *C. p. wolfi*, both of which have a brighter pelage than *C. mona*.

Struhsaker (1970), who examined several vocalizations of guenons, found that the hack call, an element of the male loud call, of *mona* and *campbelli* was most complex and concluded that *C. pogonias* was the ancestral form and that *C. mona* and *C. campbelli* were more derived. Grubb (1978) examined the species group's distribution pattern and hypothesized that *C. campbelli* gave rise to *C. mona* as it dispersed east, and that *C. p. pogonias*, *C. p. denti*, and *C. p. wolfi* were derived in a stepwise sequence. Ruvolo (1988) studied the serum and red cell proteins in guenons and found that *C. campbelli* and *C. mona* that live in West Africa possess a derived form of iron-transporting glycoprotein (a transferrin or a plasma protein) that is not possessed by *C. pogonias* or *C. wolfi* that live in Central Africa. Her study result supported the Central Africa to West Africa speciation scheme.

Gautier (1988) analyzed vocalizations of the mona species group and concluded that *C. mona* and *C. campbelli* were sister taxa that share "noisy warning sneezes" while a high-pitched alarm call evolved in the common ancestor of *C. pogonias pogonias* and *C. pogonias wolfi*. Dutrillaux *et al.* (1988) examined the chromosomes and hypothesized that *C. campbelli* (66 chromosomes) originated from *C. neglectus* (62), gave rise to *C. mona* (68), which later gave rise to *C. pogonias* (72 - the highest chromosome number within the genus). His conclusion agreed with Booth's (1955) idea of West to Central Africa migratory speciation.

Kingdon (1989, 1997) reviewed the facial pelage in guenons and hypothesized that the common ancestor of the group derived its facial feature from the ancestral stock of *C. erythrogaster* in the Upper Guinea forests. The common ancestor then radiated towards both east and west and through isolation, *C. c. campbelli* arose in the west and *C. c. lowei* arose in the east. Later, as *C. c. lowei* separated from *C. c. campbelli* and migrated east, it gave rise to *C. mona*. As *C. mona* moved into Central Africa, *C. pogonias* became differentiated.

Gooder (1991) analyzed the cranial morphology and the biogeographic pattern of distribution of the group using parsimony analysis. His cranial measurements of the members identified two subgroups: a West African group (*campbelli*, *lowei*), *mona*) and a Central African group – (*pogonias* (*denti* (*wolfi*, *pyrogaster*). His biogeographic examination of these forms found that all speciation events that occurred in the group were due to vicariance events. He reconstructed the speciation events as follows. The initial speciation event probably occurred as the crustal uplift in southwestern Cameroon caused the separation of the common ancestor into a West African form (northwest of River Sanaga) and a Central African form (Gabon and the Congo Basin). The second vicariance event fragmented the West African form at the Niger delta, leaving isolated populations in the west and east of the delta, but this event did not result in speciation. The third event took place in the Upper Guinea forests, prompting the separation of *C. mona* in eastern West Africa (Cameroon to Nigeria) from *C. campbelli* in western West Africa (Liberia to Ghana). The fourth separation occurred between *C. campbelli lowei* (Côte d'Ivoire–Ghanaian form) and *C. campbelli campbelli* (Liberia–Côte d'Ivoirian form). In the mean time, the Central African form, *C. pogonias*, separated into the Cameroon and Gabon form (*C. pogonias*) in the west and the Congo Basin forms (*denti*, *wolfi*, and *pyrogaster*) in the east. In the Congo Basin, as the area fragmented due to the river barriers, the East Central form became *C. pogonias denti*, the South Central form became *C. pogonias wolfi*, and the Kasai River separated *C. pogonias pyrogaster* from the rest. Gooder's (1991) findings are in contrast with Schwartz (1928), Booth (1955), Grubb's (1982), and Kingdon's (1999) stepwise allopatric speciation and migration scenario: *campbelli* → *mona* → *denti* → *wolfi* → *pyrogaster* →*pogonias*, but in agreement with Gautier (1988) and Dutrillaux *et al.*'s (1988) cladograms.

Tosi *et al.* (2005) recently reconstructed the phylogenetic history of guenons using fragments of X-chromosomes. They presented evidence that *C. aethiops*, *C. patas*, *C. solatus,* and *C. lhoesti* form a clade exclusive of all other *Cercopithecus*, reinforcing Tosi *et al.*'s (2002) finding using the Y-chromosomes. Tosi *et al.*'s (2005) preferred taxonomy places the non-arboreal forms into the genus *Chlorocebus* with several subgenera: *Chlorocebus aethiops*, *Chlorocebus* (*Erythrocebus*) *patas*, *Chlorocebus* (*Allochrocebus*) *lhoesti*, and *Chlorocebus* (*Allochrocebus*) *solatus*. They estimated that the divergence of arboreal forms from the last common ancestor of terrestrial and arboreal forms at 4.8 (± 1.2) Ma. They proposed that a divergence between the clade that contains the neglectus/mona/diana groups and the rest of arboreal guenons occurred at 4.5 (± 0.7) Ma and that the neglectus/mona/diana groups shared a common ancestry until 3.5 (± 0.6) Ma. The relationships within neglectus/mona/diana groups need to be sorted out with more genetic analyses, since morphological and behavioral data are incongruent with this phylogeny* (Gautier, 1988).

C. Physical Features

Cercopithecus mona is a medium-sized monkey with a long tail. On average, wild-living adult males weigh about 4.5–5 kg and adult females about 2.5–3 kg (Booth, 1960; Takeshita, 1962; Hill, 1966; Jones, 1970; Glenn, 1996; Glenn *et al.*, unpublished a; Gautier *et al.*, 1999). It is smaller than more folivorous *C. nictitans* or *C. mitis*, but larger than more insectivorous *C. ascanius* or *C. cephus* (Gautier-Hion, 1978; Cords, 1987a). Its crown is speckled with brown and black fur. The forehead is accentuated by a yellowish white brow-band. Below the forehead is a bluish-gray triangular area of bare skin that surrounds the eyes and the nose. A dark stripe connects the upper corner of the eye to the ear that has some black tufts at the tip. Below the nose are pink lips. The fur on the cheeks is golden yellow. The back and tail are tawny brown and the throat, chest, belly, and the inner part of the limbs are white. The outer side of the limbs is black. A round white patch on each side of the rump flanks the base of the tail. The major difference in the pelage that distinguishes *C. mona* from other taxa in the *mona* group,

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* *Cercopithecus diana* has many derived features (morphologically and socially) that are not shared with the mona species group and *C. neglectus* (Gautier, 1989). For example, *C. diana*'s dental, cranial, and pedal features are derived (Kingdon, 1988; Martin and MacLarnon, 1988). *Cercopithecus diana* also lacks boom calls that are possessed by both the mona species group and *C. neglectus* (Gautier, 1989). *Cercopithecus diana*, however, has the fewest chromosome numbers among the three (*C. diana* = 55, *C. neglectus* = 62, mona group = 66–72) (Dutrillaux *et al.*, 1988).

and all other guenons, is a pair of oval white patches at the base of the tail that is absent in other taxa. Like all other guenons, *C. mona* possesses a monogastric system (Booth, 1956; Hill, 1966).

D. Geographical Distribution

Sanderson (1940) was probably the first scientist who mapped the distribution of the *mona* species group in West Africa. About 15 years later, Booth (1954, 1955) shot and collected wild specimens, mapped the distribution pattern of the species group in West Africa, and discussed its evolution. More recently, the distribution of the species group has been more carefully surveyed, examined, and mapped by Colyn and Verheyen (1987), Colyn (1988), Lernould (1988), and Oates (1988a).

Cercopithecus mona is widely distributed in West Africa (range: 10˚N–8˚S, 0˚W–10˚E) (Booth, 1955; Colyn, 1988; Lernould, 1988; Oates, 1988a)(Fig. 1.1, adapted from Oates, 1988a). This species is more or less continuously distributed from the west of the Volta River (eastern Ghana) to south of the River Sanaga. The northern limit of *C. mona*'s range in Bénin is reported to be 9°14'N (Campbell, 2005). At the western bank of the Afram River, an upper western tributary of the Volta, *C. mona* shared a small area of sympatry with *C. c. lowei*. About fifty years ago, intermediate forms between *C. c. campbelli* and *C. c. lowei* were reported from Guiglo, which is located between the Sassandra-Nzo River and the Cavally River in Côte d'Ivoire (Booth, 1956, 1958a, b). *Cercopithecus mona* also occupies a wide area of sympatry with *C. p. pogonias* north of Sanaga River and a small area with *C. p. grayi* south of Sanaga River in Cameroon (Whitesides, 1981). Intermediate forms between *C. mona* and *C. p. pogonias* and between *C. mona* and *C. p. grayi* were observed at Idenau (4˚15'N, 10˚3'E) (north of

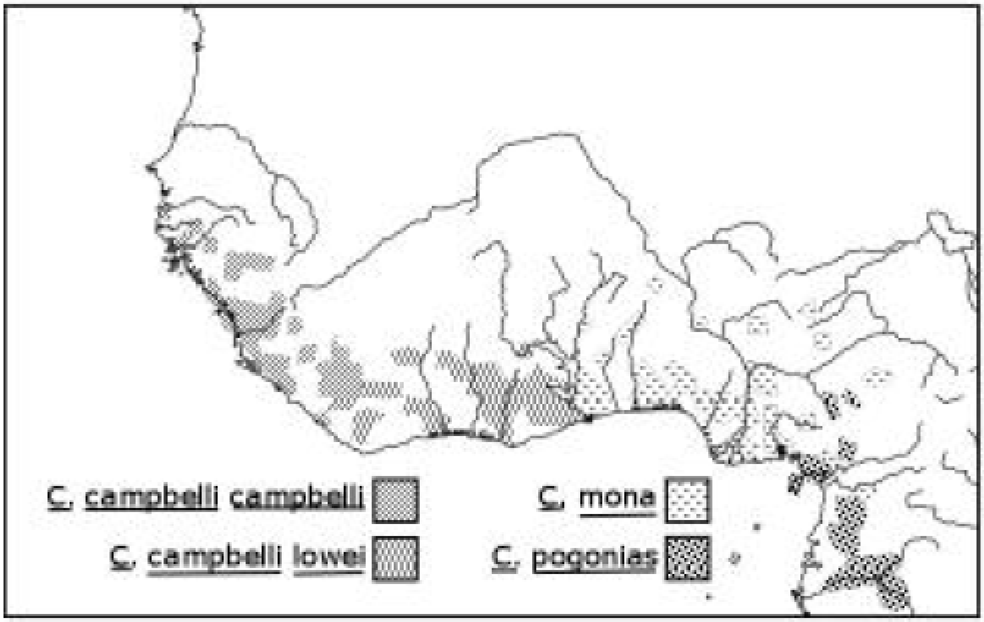

Fig. 1.1 Distribution of *mona* species group

Sanaga) and near Tinaso (3˚37'N, 9˚57'E) (south of Sanaga) in southwestern Cameroon, respectively, more than thirty years ago (Struhsaker, 1970). Hybrid individuals between *C. pogonias nigripes* and *C. pogonias grayi* have been recently observed in a large area along the Atlantic coast basin between Sanaga River, Ogooué River, and in the Congolese basin (Gautier-Hion *et al.*, 1999). Whether hybrid individuals still exist or not in the areas of sympatry between *C. mona* and *C. campbelli* and *C. mona* and *C. pogonias* has not been confirmed in recent years.

Some researchers have postulated that during dry phases in the Pleistocene, the Dahomey Gap* and, to a lesser extent, the Baoulé-V in central Côte d'Ivoire were devoid of forests and that these areas acted as important barriers to the distributions of many vertebrate species and subspecies, although different species were affected in different ways (Booth, 1958; Shiøtz, 1967; Oates, 1988a). In addition, some large rivers such as Volta, Cross, Niger, and Sanaga have acted as faunal distributional barriers in the past (Booth, 1958; Schiøtz, 1967; Robbins, 1978; Oates, 1988a). *Cercopithecus mona*'s current wide distribution in Ghana, Togo, Bénin, Nigeria, and Cameroon indicates that its distribution may be hindered, but not stopped, by rivers, except the Volta and Sanaga (Whitesides, 1981; Oates, 1988a).

Introduced populations of *C. mona* occur in the evergreen forest on the island of Grenada in the Caribbean and on the islands of São Tomé and Príncipe in the Gulf of Guinea, West Africa. *Cercopithecus mona* probably reached Grenada on slave ships when the slave trade to the Americas was at its peak during the late16th to 17th Century.

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* In Appendix B, I describe the characteristics of the Dahomey Gap and the factors that produce low rainfall in the region. I also examine authors' opinions regarding the influence of the Dahomey Gap on the faunal distributions in West Africa.

The island populations of *C. mona* have been studied and surveyed by Glenn and her colleagues (Glenn, 1996; Glenn *et al.*, unpublished a).

E. Habitats

Across its wide geographical distribution, *C. mona* inhabits diverse types of habitat [e.g., rain forest, mangrove forest, swamp forest, riverine forest, dry forest, woodland, and derived savanna (Booth, 1956; Struhsaker, 1969; Gartlan and Struhsaker, 1972; Oates, 1988a)]. Among forest-living guenons, *C. mona*'s ability to occupy such diverse habitats is comparable only with that of the blue monkey (*C. mitis*), a highly polytypic species, which occurs in northeastern Africa, eastern Central Africa, East Africa, and southern Africa (Gartlan and Brain, 1968; Aveling, 1984; Cords, 1987a; Lawes, 1990; Lawes and Piper, 1992; Lawes *et al.*, 1990). While *C. mitis* inhabits rain forest, montane forest, dry forest, swamp forest, woodland, and grassland, *C. mona* also thrives near the water: in mangrove, swamp forest, riparian forest, and seasonally inundated dry and wet forest (Booth, 1954; Gautier and Gautier-Hion, 1969; Gartlan and Struhsaker, 1972; Whitesides, 1981; Oates, 1988a; Dunn, 1993; Werre, 2000).

Where *C. mona* is sympatric with another taxon of the *mona* group, *C. mona* shows a strong preference for seasonally inundated forests. Booth (1955) noted that there is a slight difference in ecological preferences between *C. c. lowei* and *C. mona* along the Volta R., where there is an area of sympatry: *C. mona* at riverbanks and *C. c. lowei,* in the forest interior. In southern Cameroon, where *C. mona* and *C. pogonias* are sympatric, *C. mona* was more abundant in the mangrove swamp, seasonally inundated forest, and secondary forest than in mature forests where *C. pogonias* was more abundant (Gartlan and Struhsaker, 1972). *Cercopithecus campbelli*, on the other hand, prefers *terre firme* forests (Kuntz, 1999-2000). *Cercopithecus campbelli lowei* in Adiopodoumé, western Côte d'Ivoire, did not enter water even though streams and lagoons were near (Bourlière *et al.*, 1970). In Gashaka Gumti National Park in eastern Nigeria at the mountainous border with Cameroon, *C. mona* was more common in montane forest where secondary tree species were abundant than in lowland forest (Dunn, 1993). Furthermore, *C. mona* appears to be able to inhabit somewhat drier habitats than *C. campbelli* or *C. pogonias*.

Beyond *C. mona*'s range, *C. pogonias* prefers rain forests, gallery forests (Struhsaker, 1969; Quris, 1976; Colyn and Verheyen, 1987; Colyn, 1988; Oates, 1988a), and swamp forest in northern Congo (Mitani, 1992). In some parts of its range, *C. pogonias* also prefers secondary forests (Thomas, 1991; Gautier-Hion and Brugière, 2005).

Across their wide range of distribution, all species within the *mona* species group appear to have higher tolerance to habitat disturbances and human activities than other sympatric guenons (Matthews and Matthews, 2002).

IV. Study Site

A. Background

This study was conducted in the northern part of the Lama Forest (*la forêt classée de la Lama*) (a.k.a. the Kô Forest (*la forêt de Kô*) (6˚55'-7°00'N, 2˚04'-2°12'E; 60-120m a.s.l.) in southern People's Republic of Bénin (formerly the Kingdom of Dahomey or Danhomey) (Fig. 1.2). The Lama Forest is situated in the center of the Lama depression, a clay plain that occurs between the Kouffo River to the west and the Ouémé River to the east, and between Ekpé village to the south and Agrimé village to the north (Juhe-

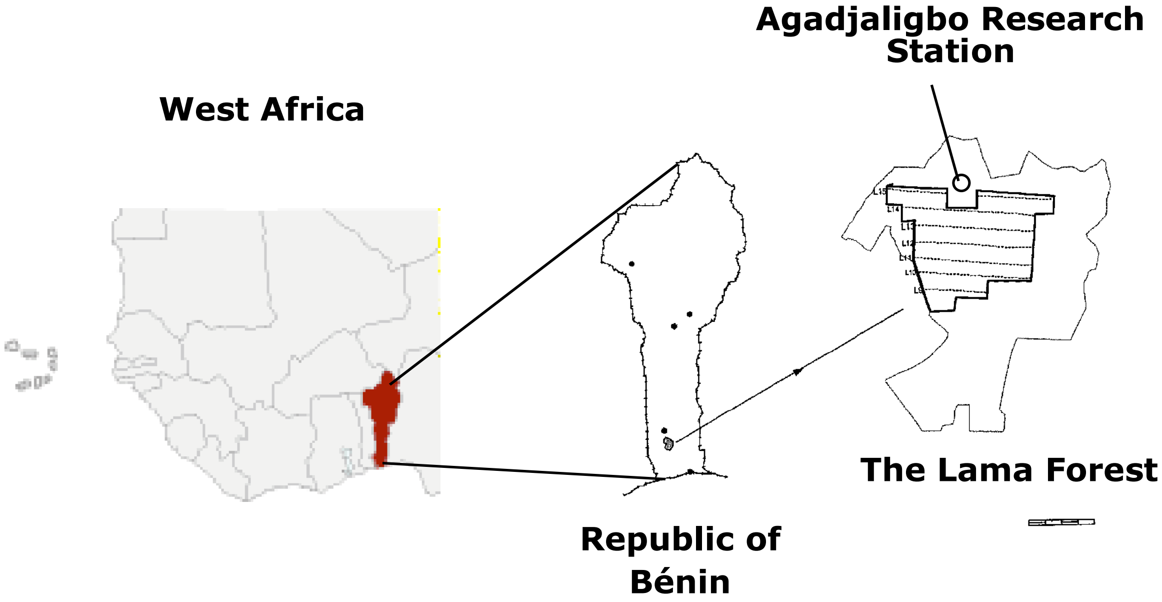


Fig. 1.2 The Lama Forest of Benin in West Africa

Beaulaton, 1995). Lama Forest (16,250 ha) became classified as a "*forêt classée*" (i.e., forest reserve) by government decree in December 1946. Extensive deforestation and destruction has dramatically reduced the size of natural forest in the last 50 years. During the 1970's, under the auspices of a development project sponsored by the Food and Agriculture Organization (FAO) of the United Nations (UN), a group of forestry experts, *Mission Forestière Allemande* (MIFOR) from the German Agency for Technical Cooperation (GTZ) (*Deutsche Gesellschaft für Technische Zusammenarbeit*) recommended large-scale timber production and reforestation projects in cooperation with the *Office National du Bois* (ONAB). The project areas were estimated to cover about 6,500 ha in total. To protect the natural vegetation of the forest, the ONAB/MIFOR project set aside about 4,777 ha *Noyau Central* (the "central core") where no human exploitation was permitted. The *Noyau Central* contains a mosaic of dense forest and disturbed forest (combined total of about 1,900 ha) interspersed with farm bush (about 2,585 ha), and tree plantation areas (292 ha) (Marsch, 1976; Biglo and Guedegbe, 1995). Since the project began, it has planted teak (*Tectona grandis*) (Verbenaceae), *Gmelina arborea* (Verbenaceae), *Terminalia superba* (Combretaceae), *Khaya senegalensis* (Meliaceae), and other economically important species for timber production outside the *Noyau Central*. *Triplochiton scleroxylon* (Sterculiaceae) has also been planted in the *Noyau Central* (M.A. Moumouni, pers. comm..)

According to FAO/UNEP (United Nations Environment Program) (2000), 2,650,000 ha of forests remained in Bénin in 1999, although 70,000 ha were lost between 1990 and 2000. The Lama Forest is the largest remnant of the original dry forest vegetation that once covered much of the southern Bénin. The second largest is found in

Pobé along the lower Ouémé River, located southeast of the Lama Forest. A history of the Lama Forest deforestation and destruction is described and discussed in detail in Appendix A.

B. Climatic and Physical Features

The Lama Forest has an annual rainfall of about 1,100 mm. Although there is a general trend of declining annual precipitation elsewhere in West Africa, the average rainfall in the Lama Forest does not appear to have changed since the 1920's (Aubréville, 1937; Paradis and Houngnon, 1977; Lieberman, 1982). There are two wet seasons per year: April through June (major wet season), and August through October (minor wet season). A short minor dry season that lasts for about a month around July usually interrupts the two wet seasons. Following the minor wet season, there is a major dry season from November through February or March. During the two dry seasons, which span about four to six months of the year, there is little or no rain. During the wet seasons, many areas in the forest become inundated. This inundation may start as early as May and usually continues until the beginning of the major dry season (Paradis and Houngnon, 1977). During the major dry season, when rainfall is near zero, many trees lose leaves, and each year some natural and artificial forest fires occur and sometimes rapidly spread to a wide area. During the major dry seasons, patrol guards with binoculars keep a watchful eye out for such fires at three watchtowers approximately 25 m high that are located at the perimeter of the *Noyau Central*. Because of the extreme seasonal nature of the forest, some researchers call this type of forest a "tropical flood forest" (J. Kamstra, pers. comm.). In Chapter 2, I examine the rainfall and temperature of the Lama Forest during this study in more detail.

The soil of the Lama Forest is largely vertisol that is dark and high in clay (40–60%). The soil is rich in organic carbon and nitrogen and the dark topsoil is particularly high in organic matter, but the amount of potassium is low. The pH is slightly acidic (Gaiser *et al.*, 2000). The soil goes through cycles of swelling and shrinkage throughout the year. When it swells, it is sticky and muddy. When it shrinks, it is brittle and cracks easily; the forest floor forms many crevices, which can have a maximum depth of about 6 m. This type of soil is probably damaging to certain plant species that are not adapted to a poor drainage. Prolonged forest inundation has caused high mortality in certain species (M.A. Moumouni, pers. comm.). During the dry seasons, the clay rich soil is beneficial for many plants, because the soil retains moisture and provides high atmospheric humidity when there is little or no rain (Clayton, 1958; Paradis and Houngnon, 1977).

C. Flora

Common large tree species (> 10 m tall) in the dense forest in the *Noyau Central* include *Afzelia africana* (Caesalpnioideae), *Ceiba pentandra* (Bombacaceae), *Dialium guineense* (Caesalpnioideae), *Diospyros mespiliformis* (Ebenaceae), *Lonchocarpus sericeus* (Papilionioideae), and *Anogeissus leiocarpus* (Combretaceae). Among these, the tallest are *Ceiba* trees, reaching to height of over 30 m. Among small trees (≤ 10 m), *Drypetes floribunda* (Euphorbiaceae) and *Celtis brownii* (Ulmaceae) are common. In the dense understory, *Sorindeia warneckei* (Anacardiaceae), *Cremaspora triflora* (Rubiaceae), *Chassalia kolly* (Rubiaceae), *Pancovia bijuga* (Sapindaceae), and *Gardenia triacantha* (Rubiaceae) are found. In the undergrowth, *Culcasia saxatilis* (Araceae), *Geophila obvallata* (Rubiaceae) and *Oplismenus hirtellus* (Poaceae) are dominant

(Paradis and Houngnon, 1977). In the disturbed forest, *Ficus* spp. (Moraceae), *Anogeissus leiocarpus* (Combretaceae), and the oil palm, *Elaeis guineensis* (Arecaceae) are abundant. These species grow in areas that were once cultivated by the Holi, the indigenous peasant population. Where no cultivation took place, these species are absent. Most areas of farm bush are dominated by the perennial shrub, *Chromolaena odorata* (Asteraceae), which forms a dense thicket 2–6 m in height. *Chromolaena odorata*, which originally came from the West Indies, was introduced from Southeast Asia to mainland Africa between 1920 and 1940. It has been a dominant weed in the Guinea Zone since the 1970's (Holou and Sinsin, 2001; Beier *et al.*, 2002). Saplings of *Ficus sur* (Moraceae), *Acacia caffra* (Mimosoideae), *Nauclea latifolia* (Rubiaceae), *Ceiba* and the oil palm are interspersed through the area. Some of these trees have been planted in the ONAB's reforestation project.

Tall trees that are common in fragmented areas of wet forests in southwestern Bénin, such as Pobé, but absent from or rare in the Lama Forest include *Triplochiton scleroxylon*, *Terminalia superba*, and *Piptadeniastrum africanum* (Mondjannagni, 1969). In comparison with wetter forests west and east of the Dahomey Gap, the Lama Forest is species-poor. Liana species diversity may turn out to be high, but botanical studies focusing on climbers have not been conducted to date. Epiphytes are not abundant (Paradis and Houngnon, 1977).

The vegetation of the Lama Forest is examined in detail in Chapter 3, but all recurring names of the vascular plants that occur in the Lama Forest are listed in Appendix C. All species that belong to family Leguminosae are placed in their subfamilies.

D. Primate Community

In addition to *C. mona*, diurnal anthropoid species inhabiting the Lama Forest are the tantalus monkey (*Chlorocebus aethiops tantalus*), red-bellied guenon (*Cercopithecus erythrogaster erythrogaster*), olive colobus (*Procolobus verus*), and the white-thighed colobus monkey (*Colobus vellerosus*) (Table 1.2). The red-bellied guenon is endemic to Bénin (Oates, 1995, 1996) and eastern Togo (G. Campbell, pers. comm.). *Cercopithecus e. erythrogaster* is an endangered subspecies that demands immediate conservation attention (Oates, 1996; Baillie *et al.*, 2004).

I personally never clearly observed *C. vellerosus* during the entire study, although once during my preliminary visit to Lama in July 1994 and three times during this study, I had incomplete sightings of some monkeys that I suspected to be *C. vellerosus.* The characteristic loud calls of the black-and-white colobus monkeys that I am familiar with from previous trips to Kenya (*Colobus guereza*) and Sierra Leone (*Colobus polykomos*) were never heard during the entire study period. P. Bekhuis (unpublished), however, reported that she observed a few individuals of *C. vellerosus* in the *Noyau Central.* The population size of this species in the Lama Forest must be extremely small and is probably on the verge of local extinction. It has been reported, however, that Mt. Kouffé (about 200 km north of Lama) sustains a healthier population (J. Kamstra, pers. comm.).

In addition to the above anthropoid species, Sayer and Green (1984), who conducted a survey of large mammals in Bénin between 1974 and 1979, reported that *Cercopithecus nictitans* occurs in the Lama Forest and *Cercopithecus petaurista* in the Lama vicinity. These two guenons were never observed in Lama or in the lower Ouémé delta during more recent surveys conducted by Bekhuis (unpublished) and Kassa (2001).

Table 1.2 Anthropoid species of the Lama Forest

Scientific Name	Local Name in Yoruba Nagot	Common Name	Common Name in French
Cercopithecus mona	Akko	Mona monkey	*le mona*
Cercopithecus erythrogaster erythrogaster	Agbé	Red-bellied guenon	*le singe ventre rouge*
Chlorocebus aethiops tantalus	Eiyaifo	Tantalus monkey	*le singe vert*
Colobus vellerosus	Eduoko	White-thighed black-and-white colobus monkey	*le singe noir et blanc*
Procolobus verus	Ochiké	Olive colobus	*le colobe vert*

It is likely that Sayer and Green (1984) mistook *C. erythrogaster* for *C. nictitans* and *C. petaurista*. Furthermore, Sayer and Green (1984) noted that the potto (*Perodicticus potto*) and the common chimpanzee (*Pan troglodytes*) occurred near the Lama Forest in the past. I never observed these species at Lama. The only nocturnal Strepsirrhini I observed were Demidoff's dwarf bushbaby (*Galagoides demidovii*) and the lesser bushbaby (*Galago senegalensis*). Pottos (*P. potto*) may be present, but my few nocturnal observations were unable to confirm their presence.

During this study, the *Noyau Central* was patrolled by eight security guards. Nevertheless, hunting by firearms, trapping of animals by ground snares, and illegal cutting of trees and lianas for construction and honey collection were evident throughout the entire study period. In Chapter 7, I examine the population density of the anthropoid species.

E. Other Fauna

Other common mammals present at Lama include Maxwell's duiker (*Cephalophus maxwelli*), red-flanked duiker (*Cephalophus rufilatus*), bushbuck (*Tragelaphus scriptus*), red river-hog (*Potamochoerus porcus*), and Cusimanse mongoose (*Crossarchus obscurus*) (Refisch, 1998). These species, along with primates, were included in a census study by Kassa (2001) after the termination of this study.

The avifauna of the *Noyau Central* has received some attention, with 106 species reported thus far, but frugivorous species are scarce (Birdlife International, 2005). Raptors include the long-crested eagle (*Lophaetus occipitalis*) (Accipitridae) and Wahlberg's eagle (*Aquila wahlbergi*)(Accipitridae), which are probably the major predators of the guenons (Waltert and Mühlenberg, 1999).

The diversity of amphibians and reptile species appears to be great. During the wet seasons, especially during the time of inundation, frogs and snakes become a prominent presence, but to date, no studies have been conducted on these fauna.
A few groups of insects, including grasshoppers (Orthoptera), beetles (Coleoptera), and butterflies (Lepidoptera) have received some attention in the Lama Forest. Entomologists from Freiburg University (Germany) in association with the IITA (International Institute of Tropical Agriculture) in Abomey-Calavi in southern Bénin, have been visiting the *Noyau Central* to study the variegated grasshopper (*Zonocerus variegatus*) and other insects since the late 1980's and their study results have been published (Boppré *et al.*, 1993, Fischer and Boppré, 1995; Nansen *et al.*, 2001). According to Boppré *et al.* (1993), the weedy shrub, *Chromolaena odorata* suppresses the regeneration of primary forest trees and provides feeding niches for *Zonocerus* and other pests (Boppré *et al.*, 1992). More recently, Fermon *et al.* (2001) identified 83 butterfly species that occur at low canopy levels and in the understory in the *Noyau Central*. Forty of the 83 spp. were recorded for the first time in Bénin.

F. Human Factors

The inhabitants of the Lama Forest, the Holi (sometimes written as Holli), are migrants from north of Pobé and southwestern Nigeria who settled in this region around the 1950's. Their current population density is 30–200/km^2 with a rate of increase of 3.3 % per annum (in 1999)(Sayer *et al.*, 1992). The Holi people have practiced slash-and-burn agriculture since they settled in the Lama Forest. Their cultivation of maize (*Zea mays*) has resulted in forest degradation, fragmentation, conversion, and reduction. The reduction of the forest started in the south and continued north. It has been estimated that between 1957 and 1985, 100–150 ha per year of the Lama Forest were deforested (Marsch, 1976; Paradis and Houngnon, 1977). In 1984, the inhabitants were relocated outside the *Noyau Central*, because their destructive effects on the forest were becoming increasingly obvious. In the past, hunting and eating of some primates was considered to be a taboo in "*forêts sacreés*" (sacred forests or sacred groves) in the Lama Depression, but as of today no such forests where people voluntarily inhibit themselves from hunting the wild monkeys remain near the Lama Forest. Nevertheless, some small (< 1–5 km^2) sacred forests are still found in the lower Ouémé delta, where *C. e. erythrogaster* and *C. mona* have been recently reported to live within villages (P. Bekhuis unpublished; Sayer *et al.*, 1992).

In the eyes of most inhabitants, monkeys are nuisances, a potential meal, or a source of income. According to the local farmers, all three guenons come to feed on the maize and other food crops planted in the farms just outside the forest. I observed only a few incidents of *C. aethiops*, but not *C. mona* or *C. erythrogaster*, raiding crops during this study. Several inhabitants told me that *C. aethiops* raids crops more often than *C. mona*, and *C. mona* raids crops more than *C. erythrogaster*. In Mungo Forest Reserve in southwestern Cameroon, Howard (1977) studied mixed-species associations among three guenons (*C. mona*, *C. nictitans*, *C. erythrotis*) and found that *C. mona* was the only species that raided the farm crops.

In Appendix B, I discuss the history of deforestation, examples of illegal activities, and possible remedies for these problems in the Lama Forest.

V. Previous and Subsequent Studies

The first long-term study on the natural history and behavior of *C. mona* was initiated by Howard (1977) who studied mixed-species associations among unhabituated *C. erythrotis*, *C. mona*, and *C. nictitans* in Mungo F.R. in southwestern Cameroon from January 1972 to February 1973. His research provides important data regarding *C. mona*'s group size, social behavior including vocalization, reproductive behavior, and the diet. The average rainfall at his site recorded in 1953–1971 was 2,613.6 mm, but the year he conducted his study was an exceptionally dry year (2,070 mm) for the site. Hunting and trapping occurred in this forest.

The second long-term study was conducted by Glenn (1996) on the island of Grenada in the West Indies, where *C. mona* was introduced via the slave trade from West Africa 150–300 years ago (Glenn, 1996, 1998). She (1996) conducted a 28-month study on *C. mona* from September 1992–April 1995 in the Grand-Etang Forest Reserve. *Cercopithecus mona* at Grand-Etang is regularly hunted. Unable to habituate a wild group, Glenn (1996) had to obtain behavioral and ecological information from many commensal individuals that frequented her research station as well as from wild monkeys.

From June to October 1998, Glenn and her colleagues (unpublished a) also conducted population surveys in the central mountains of São Tomé and Príncipe of the Gulf of Guinea islands, where *C. mona* was introduced from mainland West Africa about 150–500 years ago. Their survey areas included primary rain forest, montane rain forest, secondary rain forest, and abandoned farmland. On both islands, *C. mona* was being hunted. More recently (between April and June 1999), Glenn *et al.* (unpublished b) conducted a study in the Bimbia Bonadikombo Community Forest on the coast of southwestern Cameroon, which consists of primary rain forest, secondary forest, farmland, and mangrove forest. This forest receives 4,060 mm of rain per year (Glenn, 1996).

After the end of my study, Kassa (2001) conducted a census study of the large mammals, including *C. mona,* in the Lama Forest. Most recently, Sinsin and Assogbadjo (2002) conducted a census study of the primates in the swamp forest of Lokoli (7˚03', 2˚15°12'E), a 500 ha forest surrounded by three villages: Lokoli, Koussoukpa, and Dèmè, northeast of the Lama Forest from October 2001 to February 2002. Annual rainfall of these forests is similar to that of the Lama Forest (approx. 1,100 mm/yr). About 1,500 indigenous agriculturists who belong to the Fon ethnic group live in the villages.

Within the *mona* species group, the behavioral ecology of *C. campbelli* has been more extensively studied than that of other members of the species group especially during the last 10 years. Bourlière *et al.* (1969, 1970) and Hunkeler *et al.*'s (1972) studies of a commensal group of *C. c. lowei* in Adiopodoumé, western Côte d'Ivoire, were landmark studies on this guenon's behavior and ecology. Their studies provided important information regarding the diet, locomotory, reproductive, social, and ranging behavior of *C. campbelli*. In the Taï forest, also in Côte d'Ivoire, Galat-Luong and Galat, (1979) initiated their ecological studies on seven anthropoid species including *C. campbelli* during 1980's (Galat and Galat-Luong, 1985). McGraw (1994, 1996, 1998a, b, c) and colleagues have followed up on this and studied the locomotory behavior, mixed-species association, population size and density, of *C. campbelli* and other cercopithecids. More recently, Zuberbühler and his colleagues conducted experimental field studies on the vocalization of *C. campbelli* and *C. diana* (Zuberbühler *et al.*, 1997; Zuberbühler, 2001, 2002a, b; Wolters and Zuberbühler, 2003; Eckardt and Zuberbühler, 2004). Most recently, Buzzard (2004) completed his dissertation on competition and cooperation among *C. diana*, *C. campbelli*, and *C. petaurista*. His study provides valuable information on the social structure, feeding ecology, and mixed-species association of the three guenons.

Data on mixed-species associations, group size, density and primate biomass of *C. c. campbelli*, as well as other primates, are also available from a number of studies conducted on Tiwai Island, Sierra Leone (semi-deciduous lowland moist forest) by a group of researchers from University of Miami, Hunter College of the City University of New York, University College London, and Njala University College (Sierra Leone) between 1982 and 1991 (Whitesides *et al.*, 1988; Oates and Whitesides, 1990; Oates *et al.*, 1990; Dasilva, 1994; Fimbel, 1992, 1994a, 1994b; Oates, 1999).

Habitat surveys and community-level studies that were conducted during the 1960's and 1970's often included *C. mona*, *C. campbelli*, and *C. pogonias*. Struhsaker (1969, 1970) reviewed social behavior and social organization of the guenons, including *C. mona* and *C. pogonias*. His study provided some important information regarding the social behavior, including vocal behavior, of *C. c. lowei*, *C. mona*, *C. p. grayi*, and *C. p. pogonias*. His study also commented on *C. mona*/*C. pogonias* hybridization. Gartlan and Struhsaker's (1972) study in Cameroon provided information regarding the group size, vocalizations, mixed-species associations, and microhabitat preferences of *C. mona* and *C. pogonias*, and other sympatric primates. Whitesides' (1981) 11-month-study in 1977 on the anthropoid primates in the Douala-Edéa Reserve in Cameroon, an evergreen lowland rain forest, also offers some detailed information regarding population size, density, biomass, use of vertical space, and behavior of *C. mona* and *C. pogonias* during mixed-species association. Studies in Makandé and Makokou (M'passa Reserves) in Gabon conducted by French researchers at CNRS (*Centre National de la Recherche Scientifique*) under the direction of J.-P. Gautier and A. Gautier-Hion have provided valuable data regarding the vocal, feeding, and social behavior, and group size, population size, and biomass of unhabituated *C. pogonias* during the last thirty years (Gautier-Hion and Gautier, 1976,1979; Gautier-Hion, 1980; Gautier-Hion *et al.*, 1980, 1985; Gautier-Hion and Tutin, 1988). Primate studies in Lopé Reserve in Gabon (rainfall 1,548 mm/yr), a semi-deciduous lowland moist forest, also offer various data on the *C. pogonias* population (Tutin *et al.*, 1997a, b; Tutin, 1999). *Cercopithecus pogonias* has also been a focus of community-wide seed dispersal studies that have been conducted in Dja Reserve in south-central Cameroon (Poulsen *et al.*, 2001a, 2001b, 2002). Furthermore, surveys on the primate population in Campo-Ma'an area in southwestern Cameroon by Mitani (1991) and Matthews and Matthews (2002) before and after the area was logged include information regarding the behavior and ecology of *C. pogonias*. Table 1.3 summarizes the most significant studies mentioned above.

VI. Research Objectives

The primary objective of this study is to obtain ecological and behavioral data from the wild population of *C. mona,* to elucidate how this species copes with intense seasonality. What is the extent of seasonality in the Lama Forest? When exactly do fleshy fruits become scarce? What does *C. mona* feed on when fleshy fruits become scarce? Does it incorporate a significant amount of leaves, seeds, or insects as alternative

Table 1.3 Previous field studies on the members of the mona species group
Research sites are listed from East to West. Studies on *C. mona* are indicated in shaded areas.

Research Site*		Forest Type & Rainfall (mm/yr)	Study Period	Species	Focus of Study	Major Reference
DRC	Ituri	Mixed Lowland Moist Forest (1,802)	Jan. – Jun. 1996	All anthropoids including *C. pogonias*	Population density	Thomas 1991
	Botsima (Salonga)	Seasonally Flooded Forest (1,774)	1989 – 1991	All anthropoids including *C. pogonias*	Diet, population density	Gautier-Hion & Maisels 1994
Gabon	Makandé (south Lopé)	Mixed Seasonal Lowland Rain Forest (1,802)	1993 - 1996	*C. pogonias* and other sympatric primates	Vocal, fieeding, social behavior, group size, biomass	Fleury & Gautier-Hion 1997, Brugière *et al.* 2002
	M'passa (Makokou)	Lowland Moist Forest (1,755)	1962 - present day	*C. pogonias* and other sympatric primates	Vocal, fieeding, social behavior, group size, biomass	Gautier-Hion 1980; Gautier-Hion & Gautier 1978, 1980; Gautier-Hion *et al.* 1980, 1985; Gautier-Hion & Tutin, 1988; Tutin *et al.* 1997
	North Lopé	Semi-Deciduous Lowland Moist Forest (1,531)	1980's - present day	*C. pogonias* and other sympatric primates	Vocal, fieeding, social behavior, group size, biomass	Gautier-Hion 1980; Gautier-Hion & Gautier 1978, 1980; Gautier-Hion *et al.* 1980, 1985; Gautier-Hion & Tutin, 1988; Tutin *et al.* 1997
Cameroon	Dja	Semi-Deciduous Lowland Rain Forest (1,600)	1990's	7 diurnal primates including *C. pogonias*	Resource use and seed dispersal	Poulsen *et al.* 2001, 2002
	Douala-Edéa	Evergreen Lowland Rain Forest (1,900*)	Feb. – Dec. 1977	All anthropoids including *C. mona* and *C. pogonias*	Group size, density, biomass, vertical space use, and mixed-species association	Whitesides 1980

** Names such as "Forest", "Forest Reserve" and "Community Forest" were not noted. * in Aug. 1976 –Jul. 1977

(Table 1.3 Cont'd)

Research Site*		Forest Type & Rainfall (mm/yr)	Study Period	Species	Focus of Study	Major Reference
Cameroon	Mungo	Lowland Rain Forest (2,870 in 1972)	2,489 hrs between Jan. 1972 and Feb. 1973	*C. mona, C. nictitans, C. erythrotis*	Mixed-species association, vocalization, habitat preferences	Howard 1977
	Bimbia Bonadikombo	Evergreen Seasonal Lowland Forest (>11,000)	Jun. 1996 - Oct. 1998	*C. mona*	Population density	Glenn *et al* .unpublished b
	Idenau, Bukundu, Campo, Dja, Sanje, etc.	Evergreen Lowland Rain Forest (8,567, Idenau; 2,694, Bukundu)	Nov. 1966 – May 1968	All anthropoids including *C. mona* , *C. p, grayi, C. p. pogonias*	Mixed-species association, vocal & social behavior, habitat preferences	Struhsaker 1969, 1970; Gartlan & Struhsaker 1972
Ghana	Boabeng-Fiema	Seasonally Dry Semi-Deciduous Forest (1,250)	43 days in 1989-1991	*C. campbelli* and *Colobus vellerosus*	Group size, density, biomass	Fargey 1992, Saj et al., 2005; Porter 2005
Côte d'Ivoire	Adiopodoumé	Lowland Moist Forest (2,000)	Sept. 1967 – Jan. 1970, June 1977 – 1983	*C. c. lowei*	Feeding, locomotory, reproductive, social, and ranging behavior	Bourlière *et al.* 1969, 1970; Hunkeler *et al.* 1972; Galat-Luong & Galat 1979, 1983
	Täi	Evergreen Seasonal Lowland Forest (1,942)	Sept. 1967, Jun. 1970, 1976 ~ present day	7 diurnal primates including *C. c. campbelli*	Vocalization, locomotion, mixed-species associaiton, interspecific competition	Galat & Galat-Luong 1985; McGraw 1996, 1998; Zuberbühler 2001, 2002a, b; Wolters & Zuberbühler 2003; Buzzard 2004; Eckardt & Zuberbühler 2004
Sierra Leone	Tiwai Island	Semi-Deciduous Lowland Moist Forest (2,708)	Oct. 1982 - Jun. 1984; 1991	All anthropoids including *C. c. campbelli*	Mixed-species association, primate biomass, habitat use	Whitesides *et al.* 1988; Oates & Whitesides 1990; Oates *et al.* 1990; Fimbel 1994

(Table 1.3 Cont'd)

Research Site[**]		**Forest Type & Rainfall (mm/yr)**	**Study Period**	**Species**	**Focus of Study**	**Major Reference**
Sào Tomé & Príncipe		Evergreen Lowland Forest 4,060 (Sào Tomé) ≥3,000 (Príncipe)	Jun. 1996 - Oct. 1998	*C. mona*	Population density	Glenn *et al* . unpublished a
Grenada	Grand Etang	Evergreen Lowland Forest (2,614)	1992 - 1995	*C. mona*	Group structure, group size, population density, habitat use, vocalization, morphometry,	Glenn 1996, 1998

** Names such as "Forest", "Forest Reserve" and "Community Forest" were not noted.

foods to ripe fleshy fruits? These are central questions addressed in this document. The second aim was to compare the data obtained in this study with previous and subsequent studies on the same species and other guenon species to contribute to our understanding of the extent of within population variation and interspecific variation. All-male groups were observed in Grenada. Do male *C. mona* in the Lama Forest also form all-male groups? Both one-male and multi-male groups have been observed in previous research. What is the structure of mixed-sex *C. mona* groups in the Lama Forest? The third aim was to gather general behavioral and ecological data on *C. erythrogaster* and other primate species that occur at the study site, to better understand the primate community. Other goals were to describe the vegetation composition and structure of the forest and to understand the seasonality of this little known forest ecosystem as a whole.

In Chapter 2, I examine the climate of the Lama Forest. In Chapter 3, I examine the diversity of the trees, lianas, and shrubs and spatial distribution of some trees. Comparisons will be made with previous studies that were conducted in the Lama Forest. In Chapter 4, I present the data on temporal variation in the availability of plant resources obtained by the direct observation of the phenophases of the trees, shrubs, and lianas along with a trail survey of the fruits. In Chapter 5, I examine data on *C. mona*'s diet in relation to the seasonal changes in the availability of plant resources and explore possible differences that exist in the guenons' abilities to digest certain foods. In Chapter 6, I describe group structures, social behavior including vocalizations, and mating behavior of *C. mona*, examining how some of these elements may be influenced by seasonal changes in climate. In Chapter 7, I present the results of censuses and estimate population density and biomass of the anthropoid species in the Lama Forest. In the final chapter, I explore possible ecological factors that influence the population biomass of the mona species group in West Arican forests.and summarize the conclusions made throughout this document and make a few suggestions for future investigations on *C. mona* and other members of the mona species group.

CHAPTER 2: CLIMATE

I. Introduction

Seasonal and periodic changes that occur in rainfall, daylight length, ambient temperature, humidity, and other abiotic factors (e.g., wind patterns, availability of standing water, mineral content in the soil) and biotic factors (e.g., competitors, pollinators, seed predators and dispersers) directly and indirectly regulate the growth and reproduction of plants. In particular, water stress and photoperiod are major factors (van Schaik *et al.*, 1993). Consequently, these factors largely determine the quantity, quality, and dispersion of potential foods in primate habitats (Richards, 1966; Janzen and Schoener, 1968; Frankie *et al.*, 1974; Clutton-Brock and Harvey, 1977a, b; Cant, 1980; Eisenberg, 1983; Leighton and Leighton, 1983; Terborgh, 1983, 1986a; Boinski, 1987; Oates, 1987; Boinski and Fowler, 1989; van Schaik *et al.*, 1993).

Almost all tropical forests experience some degree of seasonality with respect to rainfall, temperature, humidity, daylight and other abiotic factors. Seasonality is a pervasive phenomenon that facilitates evolutionary changes, especially changes in life-history traits in organisms (Boyce, 1979, 1988). Primate species that live in seasonal habitats tend to have higher intrinsic rates of increase than those species living in less seasonal habitats. This allows for speedy recovery if populations crash due to prolonged periods of food scarcity (Ross, 1992). Another example is the timing of conception and birth in mammals. In most mammalian species, the timing of breeding and birth seasons appear to be triggered by physiological mechanisms that have evolved through the selection pressure exerted by seasonal changes in resource availability (Butynski, 1988).

Increased levels of seasonality due to climatic changes have caused extinctions and adaptive radiations of many primate taxa. For example, increasing aridity and variability, leading to more pronounced variability in resource availability, that started occurring at the end of Miocene has been postulated as a major selection pressure that drove many species of apes, primarily ripe fruit specialists, to extinction (Jablonski, 2005). The decline of the apes was accompanied by the radiation of the Old World Monkeys that began to exploit seasonally critical food sources as they developed dietary, life history, and locomotory characteristics that are adapted to seasonal environments (Jablonski, 2005).

Such changes in climate also caused the evolution of early hominids in East Africa (Foley, 1993; Reed and Fish, 2005). The global climatic changes that started to occur at 3.2 Ma caused longer dry seasons and declines in plant primary production (Reed and Fish, 2005). This aridification may have led to the extinction of some early *Australopithecus* species. Aridification that occurred between ~2.8 Ma and the beginning of the Pleistocene Epoch (1.8 Ma) caused a decline in resource availability, but *Paranthropus* species that relied on underground storage organs continued to survive until another climatic change that occurred at ~1.0 Ma. This time, early *Homo* that relied on animal resources was able to survive (Reed and Fish, 2005).

Many West African forests along the Gulf of Guinea, whether they are rain forests or seasonally dry forests, have two wet seasons per year that are separated by two dry seasons: one long (major) and one short (minor) (Richards, 1966; Martin, 1987). The climate of seasonally dry forests such as the Lama Forest, however, differs from the rain forest climates. For example, monthly variations in rainfall, temperature, and humidity are more pronounced than in rain forests. Year-to-year variation in rainfall is also more pronounced (Murphy and Lugo, 1986). Dry seasons are also longer and drier. During the dry seasons, plant growth and germination may become depressed (Njoku, 1963, 1964; Lieberman and Lieberman, 1984; Murphy and Lugo, 1986). By and large, seasonally dry forests experience more severe moisture stress than tropical rain forests; leading to cycles of boom and bust more dramatic than those experienced by organisms living in rain forests (Medina, 1995). In this chapter, I will examine and describe the climate of the Lama Forest to better understand the extent of seasonality at my field site.

II. Methods

A rain gauge, a maximum-minimum thermometer, and a wet-and-dry bulb thermometer were placed in the weather station at the Agadjaligbo research station 2 km north of the *Noyau Central* in the Lama Forest (Fig. 1.2). Precipitation, maximum-minimum temperatures, and relative humidity were checked once a day between 06:30 and 07:30 G.M.T. from December 1995 to June 1997 by the researcher or a field assistant. Notable features of daily weather conditions were also recorded. Rainfall data measured between January 1988 and November 1995 by ONAB's Agajarigbo *Secteur de Koto* forestry station 300 m west of the research station are included to supplement my data to demonstrate the extent of interannual variation in the rainfall. Months with ≤ 100 mm are considered dry months. Climatograms were plotted following Walter and Lieth (1967). To facilitate analysis, I divided the study period into two years. The first year is defined as the period between October 1995 and September 1996 and the second year, the period between October 1996 and June 1997.

III. Results

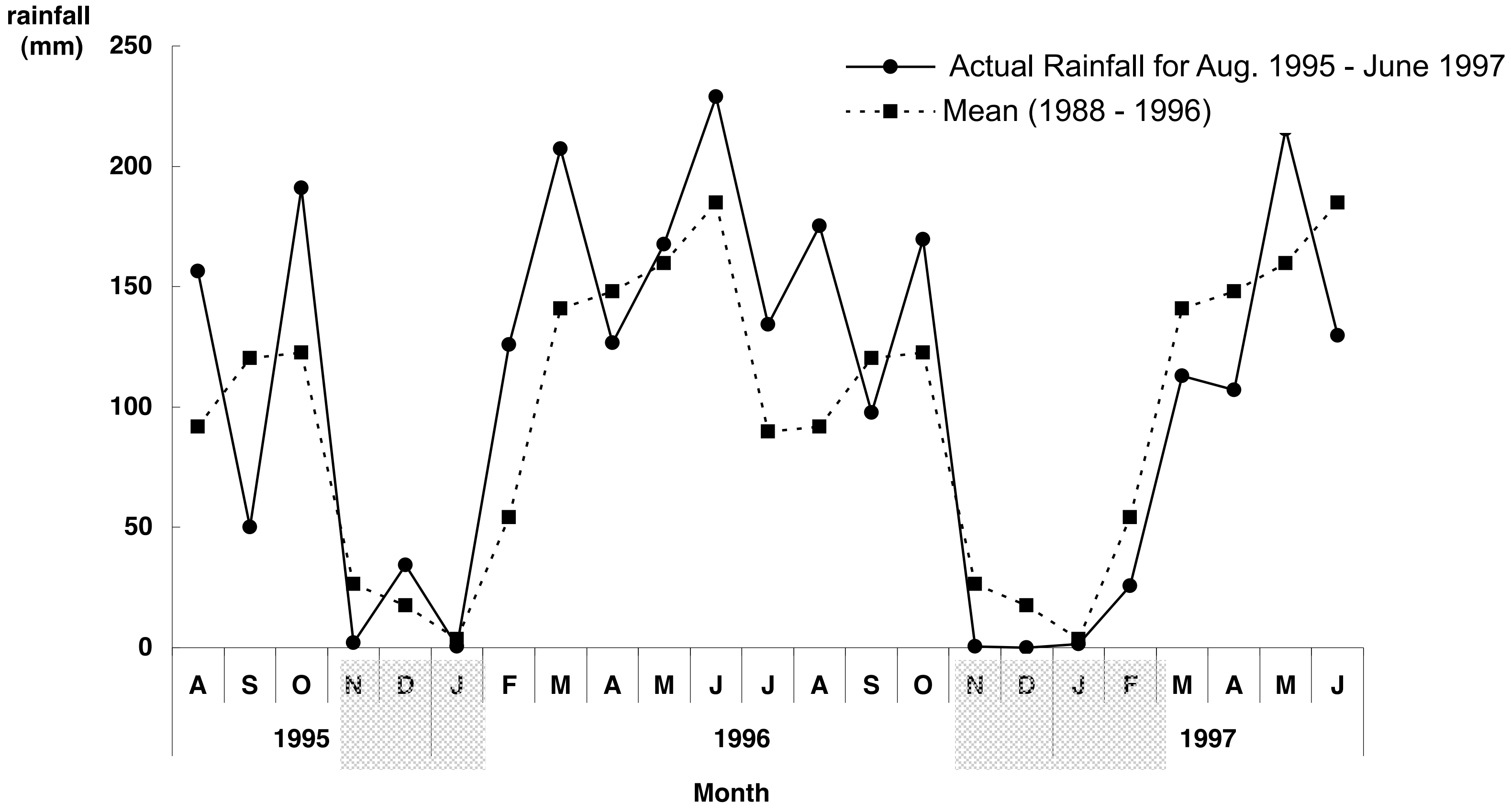
A. Rainfall

The Lama Forest data show that annually there are two dry seasons, one long and one short, with two wet seasons separating the two dry seasons. Fig. 2.1 shows the monthly rainfall recorded for the study period in contrast with the mean monthly precipitation for the period of January 1988–December 1996. The total rainfall in 1995 was 1,334 mm with the monthly mean of 111.1 mm (range: 0–306, *s.d.* = 101.1). Total 1996 rainfall was 1,434 mm with the monthly mean of 119.6 mm (min. = 0, max = 228.8, *s.d.* = 80.37). Both 1995 and 1996 were wetter than the mean ($\bar{x}$ = 1,159.8, range: 895.5–1,434.2, *s.d.* = 209.2). The 1995 rainfall, however, falls within one standard deviation and the 1996 rainfall falls within 1.5 standard deviations of the mean annual rainfall. The total rainfall for the first six months of 1997 was 592.3 mm with the monthly mean of 98.7 mm, which is about 31% less than that for the same period in the previous two years and 14% less than the average for the same period in 1988-1996.

August 1995 recorded unusually high rainfall (151 mm). At the beginning of August when I initiated this study, the forest floor was muddy, but not flooded. In a few weeks, however, many areas of the *Noyau Central* became flooded. In September, rainfall diminished to 50 mm, essentially a minor dry season ("*le petit saison séche*") and the degree of inundation decreased. In October, rainfall increased to 191 mm and the forest again became inundated. From August to mid-December, a heavy fog often enveloped the sky from dawn to about 09:00 GMT and the dew dripped from the canopy throughout the morning.

Fig. 2.1 Monthly precipitation during Aug. 1995 - June 1997 and Mean monthly precipitation during 9 years (1988 - 1996)

(Shaded months indicate major dry seasons.)



Oct. 1995 = Wet Season 1 (WS1); Nov. 1995 – Jan. 1996 = Dry Season 1 (DS1); Feb.– Apr., 1996 = Wet Season 2 (WS2); May – Jul, 1996 = Wet Season 3 (WS3); Aug.– Oct., 1996 = Wet Season 4 (WS4); Nov. 1996 – Feb., 1997 = Dry Season 2 (DS2); Mar. 1997 – Jun 1997 = Wet Season 5 (WS5).

The first major dry season started in November 1995 and lasted for three months. It was shorter than major dry seasons in previous years. At the onset of the major dry season, the northeasterly Harmattan wind carrying extremely dry, dust-laden warm air from the Sahara desert started. Due to the Harmattan, the sky was hazy during most of the day, almost every day. Visibility was limited to about 25 m, and under these conditions, observation of the monkeys was very difficult. The Harmattan continued until the end of January 1996. In February, the major wet season started and continued until August. Heavy fog enveloped the morning sky during most of this period. June received the greatest rain (228.8 mm). The minor dry season occurred later than usual in September.

October 1996, at the beginning of the second year, was a rainy month. In November, the second major dry season started and continued until February 1997. Rain started in March and continued until the end of June when this study ended.

Fig. 2.2 illustrates the annual precipitation, the monthly pattern of rainfall, and the number of dry months (defined as months with ≤ 100 mm rainfall) for Jan. 1988 – June 1995. After three dry years, 1995-1996 was a very rainy year. There is considerable interannual variation in monthly rainfall, but a bimodal rainfall pattern is apparent only in some years. March 1995 had the greatest monthly rainfall recorded since 1988, and the annual precipitation and the number of rainy days in 1996 was the maximum recorded since 1988. The number of dry months in 1995 did not significantly differ from the mean ($\bar{x}$ = 5.8, range: 4–7, *s.d.* =1.09) while the number of dry months in 1996 was much lower than the mean. Interannual variation in monthly rainfall is substantial, especially in March (*s.d.* = 108.54) and May (*s.d.* = 83.12)(Fig. 2.3). Interannual variation in the

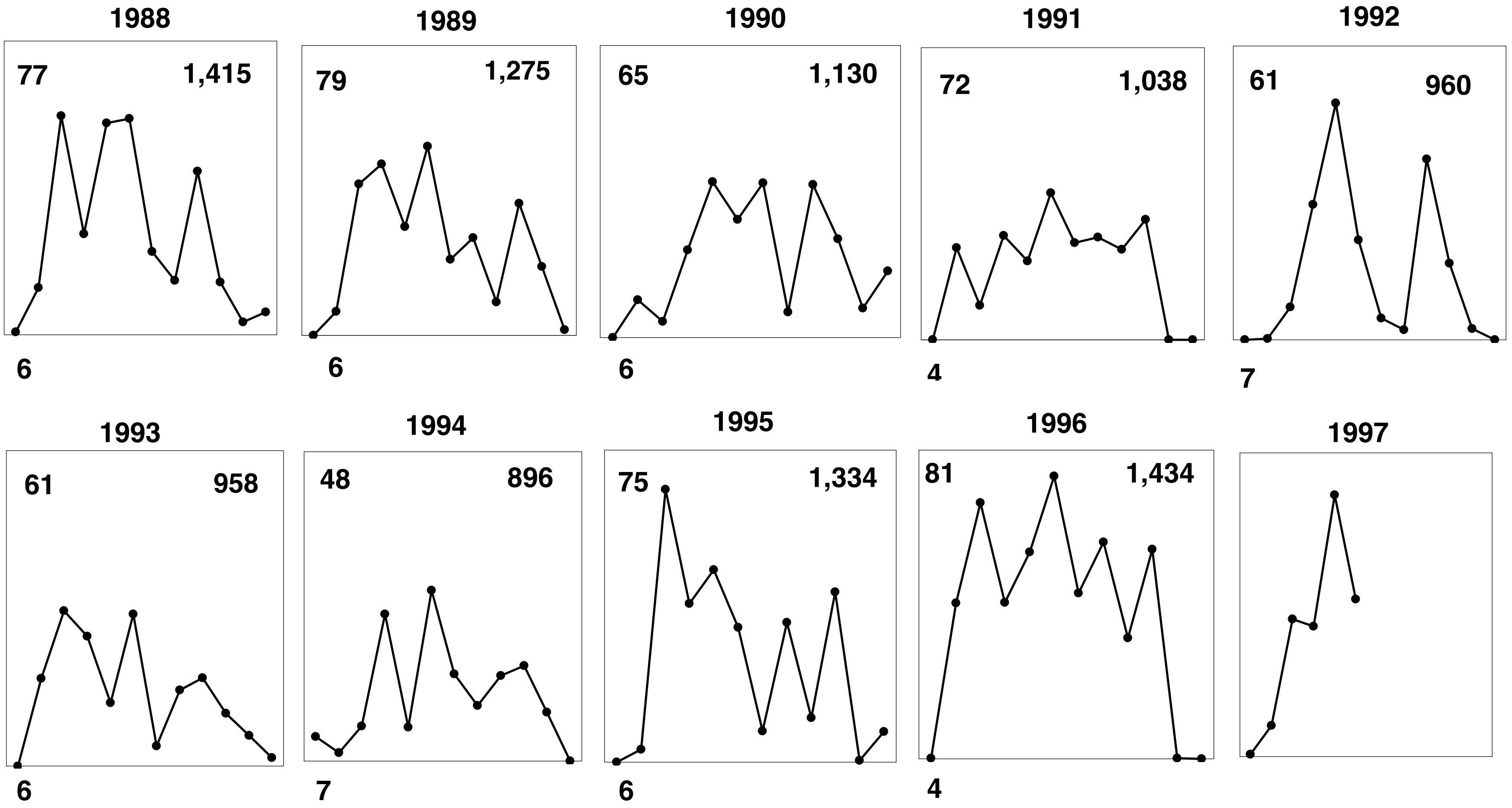


Fig. 2.2 Monthly precipitation (mm) between January 1988 - June 1997. Number of rainy days is indicated at upper left and number of dry months is indicated at lower left. Annual precipitation is indicated at upper right.

Fig. 2.3 **Interannual variation in monthly rainfall during 10 years (July 1987 – June 1997) at the Lama Forest. Shown are mean values (open circles), range (open triangles), and standard deviation (bars).**

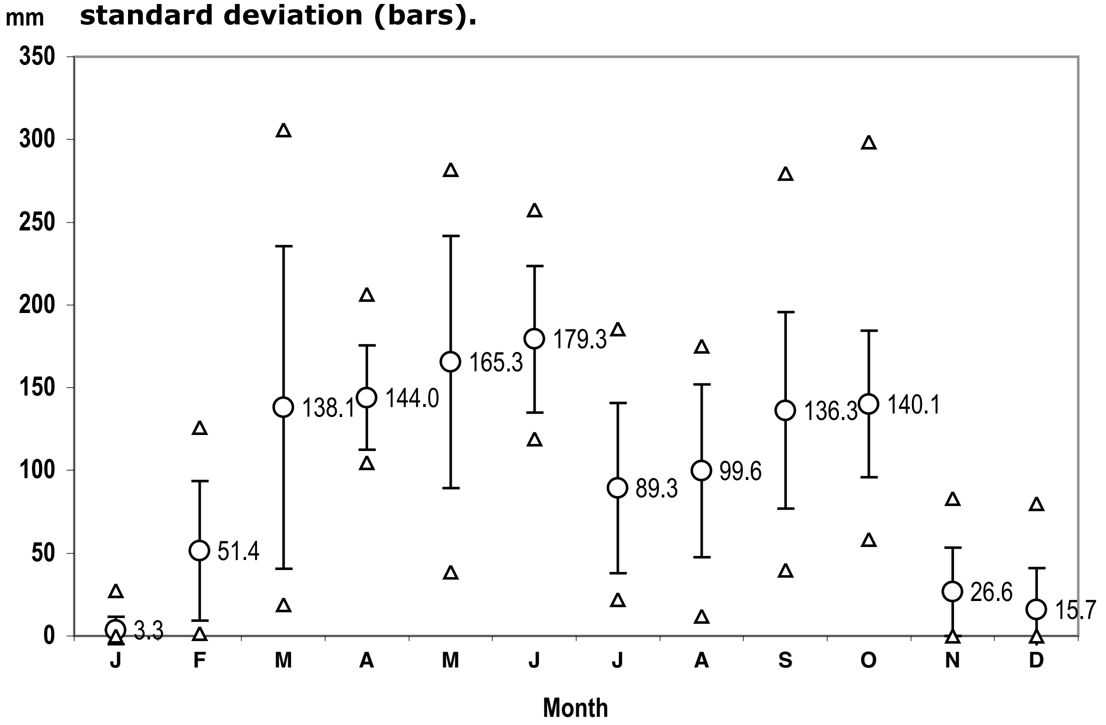
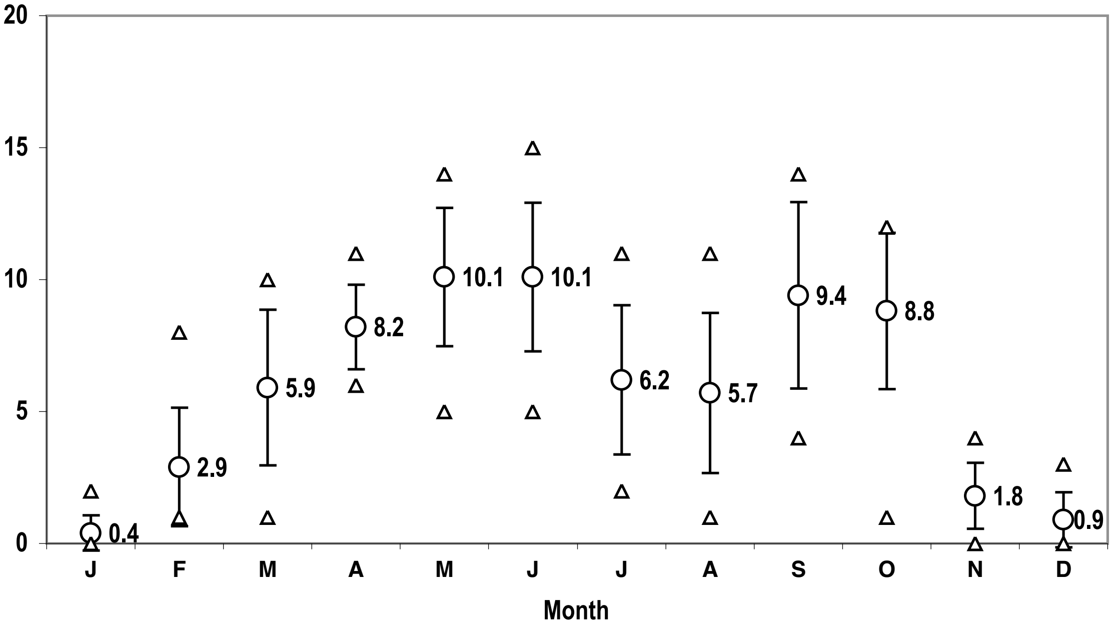


Fig. 2.4 **Interannual variation in the number of rainy days per month during 10 years (July 1987 – June 1997) at the Lama forest. Shown are mean values (open circles), range (open triangles), and standard deviation (bars).**



number of rainy days per month is also extensive, especially in October (*s.d.* = 2.96) and March (*s.d.* = 2.95)(Fig. 2.4).

B. Temperature and Relative Humidity

Fig. 2.5 shows the relative humidity, mean monthly temperatures, and mean maximum and minimum temperatures measured between December 1995 and June 1997. The mean daily temperature for the period was 27.4 ˚C. The mean maximum temperature varied between 28.3 ˚C and 37.5 ˚C and the mean minimum temperatures varied between 20.2 ˚C and 21.8 ˚C. The temperatures were highest during the dry seasons and lowest during the wet seasons. The absolute maximum temperature of 40 ˚C was recorded in April 1996 and in January 1997 and the absolute minimum temperature of 17 ˚C was recorded February 1997. The average relative humidity in the early morning ranged from 93–98%.

IV. Discussion and Conclusion

Murphy and Lugo (1986) defined tropical dry forests as forests with 250–2,000 mm of mean annual rainfall, which is distributed over 4–9 months with Temperature/Precipitation (T/P) ratios[1] that range from 4.1 x 10^{-2}°C/mm to 1.4 x 10^{2}°C/mm (least to most favorable moisture conditions). According to their definition, the mean T/P ratio of the Lama Forest, 2.4 x 10^{2}°C/mm is within this range. The moisture condition of the Lama Forest was less favorable during the driest years (e.g.,

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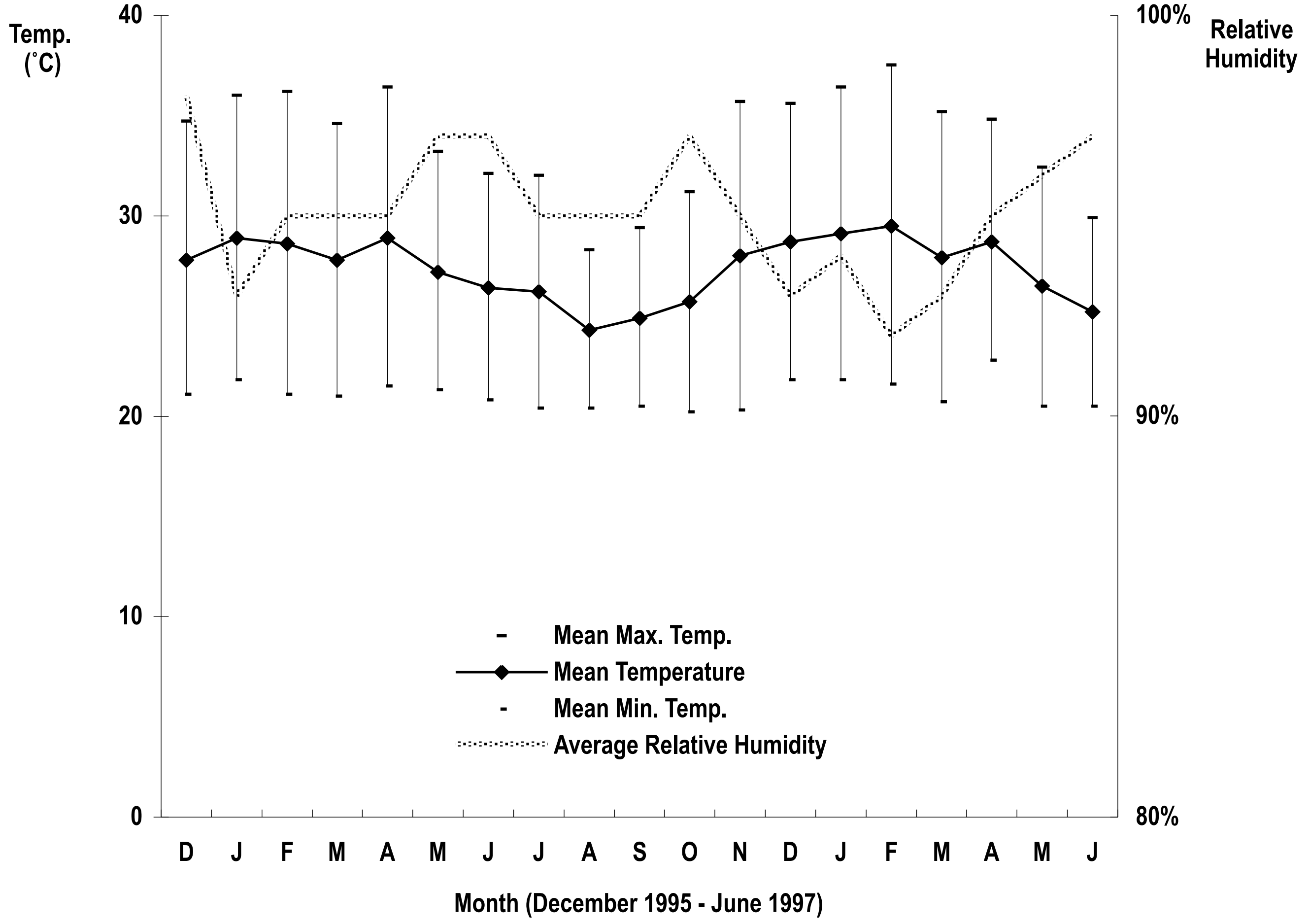
[1] A ratio of mean annual temperature (˚C) (T) to mean annual precipitation (mm) (P) x 100. Since PET /T (Potential Evapotranspiration/Temperature) ratio is not available in most forests, T/P ratio (Temperature /Precipitation) is used as a proximate measure (Murphy and Lugo, 1986).

Fig. 2.5 Relative humidity (%) and temperature (°C) in the Lama Forest



1992–1994) (2.9–3.1 x 10^{2}°C/mm) and more favorable (1.9 x 10^{-2}°C/mm) during the wettest years (e.g., 1988, 1996).

In other forests where *C. mona* has been studied or surveyed, rainfall is much greater and seasonality is much less severe than the Lama Forest. For example, the mean annual rainfall in the Mungo F.R. in Cameroon, Grand Etang F. R. in Grenada, and in the Gulf of Guinea islands of São Tomé and Príncipe were 2,613.6 mm, 4,060 mm, and ≥ 3,000 mm/year, respectively (Howard, 1972; Glenn, 1996; Glenn *et al.*, unpublished a). A major dry season occurs in December–January in the Mungo F.R. (Howard, 1977), but there is no dry season in the Grand Etang F.R. (Glenn, 1996).

This is the first study of *C. mona* conducted in a seasonally dry forest. *Cercopithecus mona* also inhabits drier habitats than the Lama Forest. For example, *C. mona* also occurs in woodlands in northern Bénin. In the Gashaka Gumti N.P. in northeastern Nigeria, *C. mona* was observed in the savanna adjacent to forest (Dunn, 1993). Many species of arboreal guenons inhabit a variety of habitats with a wide range of moisture conditions, but the behavior and ecology of guenons inhabiting seasonally dry forests have been little investigated.

CHAPTER 3: VEGETATION STRUCTURE AND TREE SPECIES COMPOSITION

I. Introduction

Tropical dry forest, also called semi-deciduous forest, mixed-deciduous forest, seasonally dry forest, or *forêt mésophile* has been described as the most threatened and vulnerable habitat type in the world (Clayton, 1958; Murphy and Lugo, 1986; Janzen, 1988; Sussman and Rakotozafy, 1994; Sánchez-Azofeifa *et al.*, 2005).

Murphy and Lugo (1986) list a number of differences that separate tropical dry forests from rain forests worldwide. Some of these differences are: (1) The number of tree species in dry forests (35–90) is half to a third less than that found in tropical rain forests (50–200). (2) The trees are shorter in stature. The range of tree heights is 5–45 m in dry forests. It is 20–84 m in rain forests. (3) Basal area of trees in dry forests is 17–40 (m^2/ha). While in rain forests, it is 20–75 (m^2/ha) (Table 3.1). Other researchers use different measures to differentiate dry forest from rain forest. Gentry (1995) for example states that tropical seasonally dry forests receive ≤ 1,600 mm/year and there are 5-6 dry months per year.

Although seasonally dry forests are ubiquitous in Africa, in particular in West Africa, our knowledge of this type of biome is still incomplete. Most research on the diversity and dispersion patterns of the vascular plants in tropical dry forests by English-speaking scientists have been conducted in Central and South America (e.g., Mexico, Costa Rica, Bolivia, Brazil, Venezuela, Peru) and Madagascar, to a lesser extent in Asia, and rarely in Africa. This is noticeable in the most recently published book on this subject, Seasonally Dry Tropical Forests, edited by S.H. Bullock, H. Mooney, and E.

Table 3.1 Characteristics of tropical dry forests

According to Murphy and Lugo (1986)	The Lama Forest
1. Rainfall 600–1800 mm/yr distributed over 4–8 mos.	1,163 mm over 9 mos.
2. Pronounced monthly variation in rainfall	Yes
3. Pronounced monthly temperature variation	Not really
4. Pronounced monthly humidity variation	Unknown
5. Pronounced Year-to-year variation in rainfall	Yes
6. Usually two dry periods	One long, one short
7. T/P ratio: 4.1 x 10^{-2} (driest) – 1.4 x 10^{-2} (moist)	2.16
8. Trees smaller in stature	11.5 m (Mean HT)
9. Tree species about 1/2 of rainforests	Probably
10. Less complex structure (strata, liana)	Yes
11. Larger proportion of root biomass	Unknown
12. Microbial activity is reduced.	Unknown
13. Fertile Soil (Conservative recycling of N, K, P)	Unknown
14. Peak fleshy fruits in wet seasons	Yes
15. Leaf fall occurs in dry seasons	Major dry seasons
16. Normally, leaf flush and flowering precedes the onset of wet seasons.	Yes
17. Easy to convert to farmland	Yes
18. Long cultivation (3.7 yr vs. 1.8 yr in moist climate)	Unknown
19. Short fallow period (7.6 yr vs. 9.9 yr in moist climate)	Unknown

Medina in 1995. It is, for now, the most comprehensive review of the state of knowledge of the tropical dry forests in the world. There are more than five chapters on the ecology of Neotropical dry forests in this book, but only one chapter by Menaut *et al.* (1995) was dedicated to the "Savannas, Woodlands and Dry Forest in Africa."

In West Africa, most data on the plant species diversity, composition, and structure of tropical forests come from forests that are located east and west of the Dahomey Gap, which is a 150 km wide lower rainfall area along the Guinea Coast that interrupts the continuous belt of closed rain forest along the West African coast. Therefore, our understanding of the tropical dry forests in the Dahomey Gap is relatively restricted (e.g., Clayton, 1958; Nye, 1958; Lawson *et al.*, 1970; Hall and Okali, 1979; Lieberman and Lieberman, 1984; Swaine *et al.*, 1990, Swaine, 1992). According to the studies conducted outside the Dahomey Gap, the species composition and structures in dry forests are different from those in wetter forests. For example, dry forests tend to have more deciduous species, and species that are typical of wetter forests are often absent. Dry forests are characterized by fewer plant species, fewer trees, and shorter trees (Clayton, 1958). Floristically and structurally, tropical dry forests are simpler than wet forests. Furthermore, growth and succession in tropical dry forests is slower than in wet forests. Once dry forests are destroyed, they may never regenerate to the original state. Richards (1996) stated that regenerating forests found in many parts of West Africa experience "deflected successions." He wrote, "Deflected successions lead to the replacement of forest by 'derived' (secondary) savannas, tracts of grassland with or without scattered trees and bushes. The development of these communities in West Africa has not been described in detail."

Many seasonally dry tropical forests are situated within or adjacent to areas of high human population density. Because they are drier than rain forests, they are more accessible, easier to exploit, and more quickly deforested for timber extraction and conversion to farmland (Janzen, 1986, 2004). The Lama Forest is no exception. It is located in southern Bénin, the region of the country where human population density is highest (> 300/km^2), and where local people are heavily dependent on forest resources for food, construction materials, firewood, charcoal, medicine, cultural artifacts, and numerous other purposes. Cattle grazing and mining also occur in the forests. The *Noyau Central* of the Lama Forest is a mosaic of habitats that are at various stages of succession, since it has been subjected to varying degrees of forest destruction and degradation at various points in time. The vegetation of the *Noyau Central* has been examined and described in at least three published reports and some unpublished GTZ internal documents (e.g., Marsch, 1976). Mondjannagni (1969) described all forest types in Bénin, but his discussion on the Lama Forest vegetation was general and limited to a list of vascular plants. Paradis and Houngnon (1977) conducted a detailed study on the vegetation and provided information regarding tree species diversity, frequencies of the trees belonging to various classes of diameter-at-breast height (hereafter DBH) by species, and a habitat-wide description of the forest at different stages of succession. Most recently, Nansen *et al.* (2001) conducted a multivariate analysis of trees enumerated in many small sample plots to determine the relationship between species composition, species density, and tree locations to elucidate a successional sequence of different habitat types from Forest Type 1 through Forest Type 5.

The main goal of this chapter is to describe and discuss the density, composition, diversity, and patterns of spatial distribution of the tree species in the Lama Forest and to examine whether the Lama Forest fits the above description of dry forests. I examine whether any changes in species composition and/or population structure have taken place between the time when Paradis and Hougnon (1977) conducted a vegetation study in 1976 and the time this study took place (Aug. 1995–Jul. 1997). Another aim is to evaluate whether there are ecological differences among sample plots. Since primate behavior is directly affected by how plant food and structural support are distributed not only in time, but also in space, an examination of some of the ecological characteristics of the sample plots may permit inferences regarding monkey preferences for specific habitat types (see Chapter 6).

II. Methods

A. Sampling Techniques

1. Enumeration Along Two Census Routes

The *Noyau Central* has nine linear trails (*Layons* 8–15) running east to west parallel to each other at 1 km intervals. The length of these one-meter wide trails varies from 2 to 7 km. The eastern 4 km section of *Layon* 14, that goes through the East Study Site, was established as primate census route A (Fig. 3.1). Census route B, also 4 km in length, which is not a straight line, was later established in the West Study Site where a grid system of one-meter wide trails had been cut. Wooden or plastic posts were pegged to demarcate 50 m intervals on both routes. These census routes were established to conduct line-transect surveys to estimate anthropoid population densities (Chapter 7).

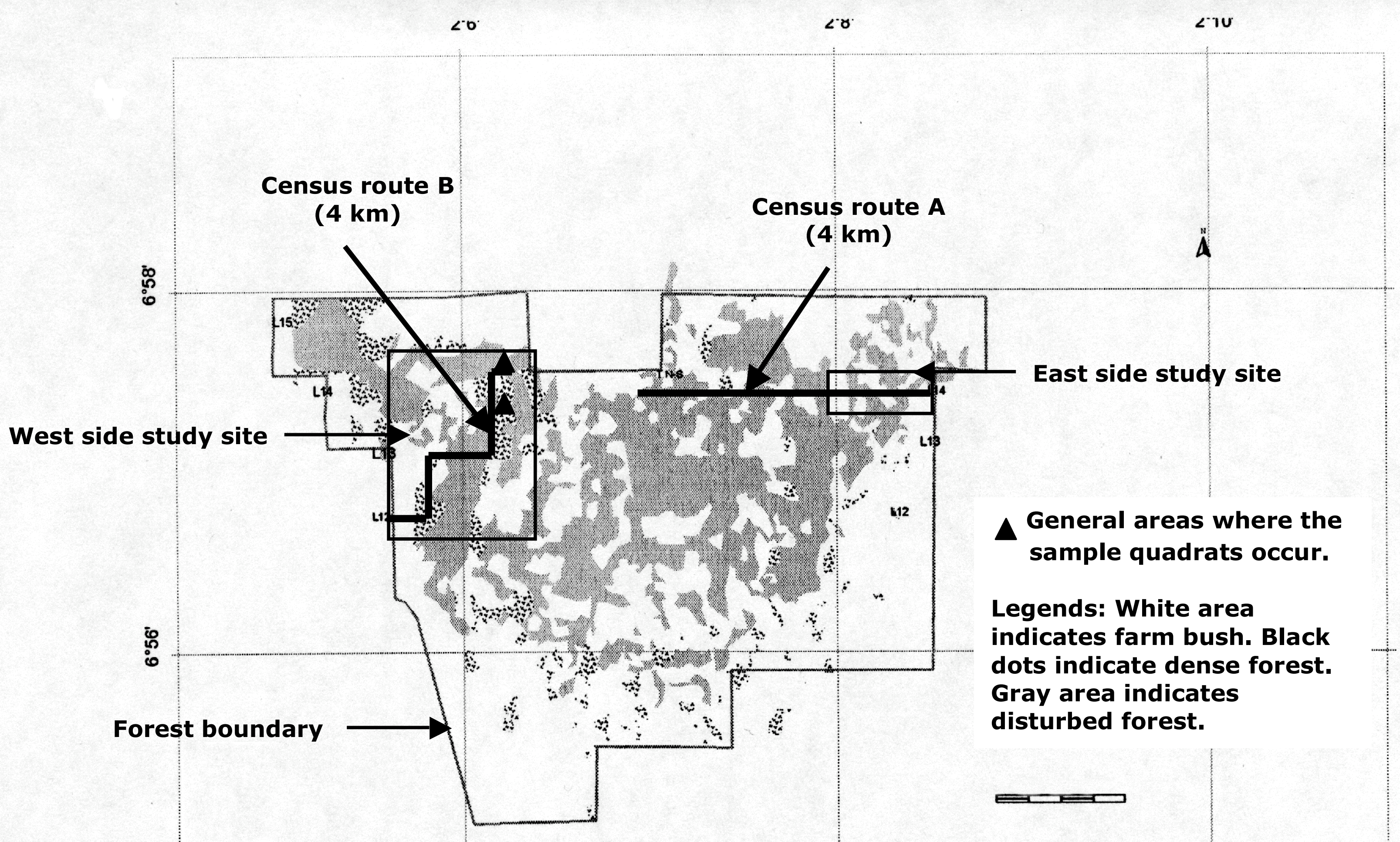


Fig. 3.1 Study sites and census routes A and B in the *Noyau Central* of the Lama Forest

For each 50 m strip, the gross habitat characteristics of the area (25 m south and 25 m north) surrounding the census routes were examined. To facilitate statistical analysis, each sample strip was subjectively categorized into one of the three vegetation types: dense forest, disturbed forest, and farm bush rather than the five to eight different forest types recognized by Nansen *et al.* (2001) and others. The actual age of the different forest types is unknown. Therefore, the three forest type categories, dense forest, disturbed forest, and farm bush, are in fact based upon the levels of disturbance they appear to have received in the past and are interchangeable with terms such as least disturbed, moderately disturbed, and most disturbed, respectively. I found that census route A passes through 2,190 m (54.8%) of dense forest, 800 m (20.0%) of disturbed forest, and 1,010 m (25.5%) of farm bush. While census route B passes through 2,000 m (50.0%) of dense forest, 1,300 m (32.5%) of disturbed forest, and 700 m (17.5%) of farm bush.

The primary goal of the enumeration along the two census routes was to measure species diversity, composition, and basal areas and later to correlate these measures with the frequency of primate sightings during the census study (Chapter 7). If significant differences in these measures between the two census routes were found, details of the primate sightings during the censuses would be expected to differ.

Along one side of each census route, all trees, shrubs, and lianas ≥ 10 cm in stem diameter at breast height (DBH) within 2 m of the trail were identified and number-tagged. For each enumerated plant, I recorded: tag number, species, location, habitat type, DBH, estimated or measured height (HT), and date of measurement. DBH was measured to the nearest 1/10 cm and HT was estimated with a Suunto clinometer or measured to the nearest 1/10 m. Notable features of the trunk (e.g., bifurcated, previously cut at certain height, partially or completely uprooted but alive), branch features (e.g., broken branches), and the health of plants (e.g., damages by folivorous insects) were also recorded. Non-woody fruit-producing plants such as mature *Elaeis guineensis* individuals were also tagged, and their position and circumference recorded.

The identification of trees and lianas was assisted by the botanical reference books, *Flora of West Tropical Africa*, vols. 1 and I2 (Hutchinson and Dalziel, 1954, 1963) and *Trees of Nigeria* (Keay, 1989). Some local field assistants were able to identify many plants in Yoruba Nagot (the local language). Mr. Houdounou, a forestry officer at the ONAB sawmill in Bohicon, verified scientific names of many plants. Some plants that were still not identified were later identified by Dr. Paul Houngnon, a botanist at the *Laboratoire de Botanique* of the *Université Nationale du Bénin*. Nevertheless, some trees remained unidentified or identified only by local names. These trees were designated with numbers.

2. *Quadrat Sampling*

Enumeration was also carried out in six 1 ha quadrats in the West Study Site (Fig. 3.1). Quadrats were selected by a random selection procedure. Sample quadrats were not chosen from plantation areas, because my observations indicated that *C. mona* and *C. erythrogaster* traveled through plantations, but did not feed there.

The six quadrats differed in terms of their level of disturbance and age of succession. Quadrats Q131 and S141 mostly consisted of dense forest. About half of the quadrat L134 contained dense forest and half contained disturbed forest. Quadrat S140 was mostly dense forest, but it also contained some areas of disturbed forest and farm bush. Quadrat UV140 consisted of mostly disturbed forest and some farm bush. About half of quadrat T140 consisted of disturbed forest, the other half, farm bush. In summary, Q131 and S141 appear to be the oldest in age. L134 and S140 appear to be somewhat younger than Q131 and S141. UV140 and T140 appeared to be the youngest.

The goal of the quadrat enumeration was similar to the enumeration conducted along the two routes: to quantify tree species diversity, composition, and basal area among the quadrats. Another goal was to find out the patterns of spatial distribution of the highest-ranking tree species (based upon basal areas) and to understand how these patterns may influence the dispersion of *C. mona* groups and individuals in the habitat.

B. Data Analysis

1. Species/Area Relationships

To examine the relationship between the areas sampled and the number of species enumerated, a species-area curve was produced by plotting the cumulative number of enumerated species as a function of the cumulative sampled quadrat area.

2. DBH, HT, and Basal Areas

Mean, minimum, maximum, and standard deviation of DBH and HT of both live and dead stems were computed for each route, each quadrat, and each tree species. Species-specific basal area (BA/ha) along each census route, each quadrat, and each species were computed using the equation:

$$\text{Basal Area (BA)} = \pi\,(\text{DBH}/2)^2 \ldots \text{(Equation 3.1)}$$

3. Species Diversity

Tree species diversity was analyzed for each route and quadrat by using two indices: Simpson's Index (*D'*) and Shannon-Wiener Index (*H'*), which are calculated by the following equations, respectively:

$$D' = 1 - \Sigma pi^2 \text{ .... (Equation 3.2)}$$

$$H' = \left| \sum_{i=i}^{c} p_i \log_2(p_i) \right| \text{ .... (Equation 3.3)}$$

where p_i = proportion of total sample belonging to the *i*th species in community *c*, which is n_i/N, where n_i = number of individuals belonging to the *i*th species and *N* = total number of individuals in a sample community. The values for both indices increase with increasing diversity.

4. Evenness Index

I also calculated the species evenness index for each quadrat. Species evenness is calculated by the equation:

$$E = S/\ln(H') \text{ .... (Equation 3.4)}$$

where *S* = number of species found in each quadrat, ln = natural logarithm, and H' = Shannon-Wiener Index. The maximum value for Evenness Index is 1.0, which indicates complete evenness. The value for Evenness Index decreases with decreasing evenness.

5. Similarity Index

Similarity Index (Krebs, 1985) examines the degree of similarities in the number of species shared between two sample plots. Similarity Index is calculated by the equation:

$$SI = (2 \text{ x } c_{1,2} / (s_1 + s_2)) \text{ x } 100 \text{ .... (Equation 3.5)}$$

where SI = Similarity Index between two plots, $c_{1,2}$ = number of species common to plot 1 and 2, S_1 = number of species in plot 1, S_2 = number of species in plot. The maximum value of SI is 100, indicating that two plots are equivalent.

6. Statistical Tests

Two-tailed Student's T tests were used to compare the mean DBH, HT, basal area, and species diversity between the two census routes. Non parametric Kolmogorov-Smirnov tests were performed for each species to find out if there are any significant differences between Paradis and Hougnon's (1977) data and my data regarding tree population structures. The confidence level was set at 95%. Most statistical tests were carried out using SPSS 11.5 (SPSS, 2002).

7. Tree Dispersion Patterns

All live stems of the five highest density species, and some selected pioneer species such as *Ceiba pentandra* and *Ficus excelsa* were plotted on the dispersion maps using X/Y coordinates and D values to discern the patterns of distribution of the tree species and the DBH size of trees in each quadrat using the rectangular coordinate system. X represents the distance of a stem from the origin (i.e., the southwestern corner of the quadrat) and Y represents the distance of the stem from the origin in each quadrat. D represents the DBH of the stem.

To compute the dispersion patterns of the five highest-ranking species in the sample quadrats, I used the quadrant count method (Upton and Fingleton, 1985; Cressie, 1993). First, appropriate quadrant size for each species in each quadrat was determined by using the following equation:

$$q = 2\frac{A}{ni} \text{ ……………….. (Equation 3.6)}$$

where q = size of quadrants appropriate for the ith species, A = the size of quadrat (in this study it is always 1 ha) and ni = the number of trees for the ith sp. in each quadrat. This procedure is necessary to compare actual tree dispersion pattern against the tree dispersion pattern that is mathematically expected, since appropriate quadrant size for a quadrat that contains 100 trees would differ from a quadrat that contains only 10 trees. Then the number of individuals of the ith species that occur in each appropriate quadrant was counted and computed for the Coefficients of Dispersion for each species, which is calculated as:

$$CD = \frac{Variance}{Mean} \text{ …………….. (Equation 3.7).}$$

If CD is significantly greater than 1.0, the ith species has a clumped dispersion pattern. If it is equal or close to 1.0, it is randomly distributed. If it is significantly less than 1.0, it has a uniform dispersion pattern. To determine whether the departures from CD = 1.0 were statisticall significant, Chi-Square Goodness of Fit Tests were used to compare observed and expected frequencies of individuals belonging to particular species in quadrants given by the Poisson series (Sokal and Rohlf, 1969; Upton and Fingleton, 1985; Cressie, 1993).

III. Results

A. Enumeration along the Two Census Routes

Table 3.2 gives a list of plant species enumerated along the two routes. In total, 847 trees were enumerated. Twenty-eight species belonging to 17 families were identified. Nine lianas belonging to *Strychnos africanus*, *Flabellaria paniculata*, *Ficus obovata* and 21 individuals of the oil palm, *Elaeis guineensis*, were also found.

Two trees along route A were not identified. Twenty species were commonly found along both routes. Seven and five species were unique to routes A and B, respectively. Along both routes, *Dialium guineensis* had the highest density of live stems. *Dialium guineensis* represented 36.6% and 32.8% of the total live stems along routes A and B, respectively. The second most frequently occurring species was *Drypetes floribunda* (*n* = 74, 16.4%) and *Celtis brownii* (*n* = 57, 14.4%) along routes A and B, respectively. *Drypetes floribunda* is a short slanted tree that produces cauliflorous fleshy fruits. *Celtis brownii* is also a short tree that produces small amounts of fruits all year long. Route A included 54 more trees than route B. Pioneer tree species such as *Ficus sur*, *Ficus excelsa*, *Diospyros ferra,* and *Lonchocarpus sericeus* were more abundant along route A than route B, but *Anogeissus leiocarpus* and *Ceiba pentandra*, were more abundant along route B than route A. There were no *Afzelia africana* trees along route B. Species diversity measured by the Shannon-Wiener Index was only slightly greater along route B (H'= 0.946) than along route A (H'= 0.926).

Fig. 3.2 and Fig. 3.3 summarize the trees enumerated along the two routes by DBH size classes. The smallest size class dominates the live trees (A: 274, 60.5%; B: 243, 58.2%). The mean DBH of live trees along the two routes was almost identical (A:

Table 3.2 List of plant species enumerated along census routes A and B

Family*	Scientific Name	Abbrev.	Route A	RD*	Rank	Route B	RD	Rank	Total	RD	Rank
			Monocot								
Palm											
Arecaceae	*Elaeis guineensis*	ELGU	20			1			21		
			Dicot								
Lianas											
Loganiaceae	*Strychnos africanus*	STAF	5			0			5		
Malpighiaceae	*Flabellaria paniculata*	FLPA	4			1			5		
Moraceae	*Ficus obovata*	FIOB	0			1			1		
	Total		9			2			11		
Trees and Shrubs											
Caesalpinioideae	*Dialium guineense*	DIGU	165	36.6	1	130	32.8	1	295	34.8	1
Ebenaceae	*Diospyros mespiliformis*	DIME	64	14.2	3	55	13.9	3	119	14.0	2
Euphorbiaceae	*Drypetes floribunda*	DRFL	74	16.4	2	22	5.6	6	96	11.3	3
Ulmaceae	*Celtis brownii*	CEBR	23	5.1	5	57	14.4	2	80	9.4	4
Sapotaceae	*Mimusopus andongensis*	MIAN	33	7.3	4	34	8.6	5	67	7.9	5
Bombacaceae	*Ceiba pentandra*	CEPE	14	3.1	6	35	8.8	4	49	5.8	6
Combretaceae	*Anogeissus leiocarpus*	ANLE	5	1.1	13	21	5.3	7	26	3.1	7
Moraceae	*Ficus sur*	FISU	14	3.1	6	10	2.5	8	24	2.8	8
Moraceae	*Ficus excelsa*	FIEX	12	2.7	8	4	1.0	10	16	1.9	9
Papilionoideae	*Lonchocarpus sericeus*	LOSE	7	1.6	10	5	1.3	9	12	1.4	10
Ebenaceae	*Diospyros ferrea*	DIFE	9	2.0	9	0	–	–	9	1.1	11
Caesalpinioideae	*Afzelia africana*	AFAF	6	1.3	11	0	–	–	6	0.7	12
Unknown	Unidentified Sp. 2	UND2	6	1.3	11	0	–	–	6	0.7	12
Anacardiaceae	*Lannea nigritana*	LANI	4	0.9	14	2	0.5	15	6	0.7	12
Sapindaceae	*Lecaniodiscus cupanioide*	LECU	3	0.7	15	3	0.8	11	6	0.7	12
Euphorbiaceae	*Margaritaria discoidea*	MADI	3	0.7	15	1	0.3	19	4	0.5	16
Mimosoideae	*Albizia zygia*	ALZY	1	0.2	19	3	0.8	11	4	0.5	16
Rhizophoraceae	*Cassipourea congoensis*	CACO	1	0.2	19	3	0.8	11	4	0.5	16
Sapindaceae	*Pancovia bijuga*	PABI	2	0.4	17	1	0.3	19	3	0.4	19
Sapotaceae	*Malacantha alnifolia*	MAAL	1	0.2	19	2	0.5	15	3	0.4	19
Moraceae	*Milicia excelsa*	MIEX	0	–	–	3	0.8	11	3	0.4	19
Sterculiaceae	*Sterculia tragacantha*	STTR	2	0.4	17	0	–	–	2	0.2	22
Apocynaceae	*Holarrhena floribunda*	HOFL	0	–	–	2	0.5	15	2	0.2	22
Mimosoideae	*Tetrapleura tetraptera*	TETE	0	–	–	2	0.5	15	2	0.2	22
Asteraceae	*Vernonia colorata*	VECO	1	0.2	19	0	–	–	1	0.1	25
Unknown	Unidentified Sp. 1	UND1	1	0.2	19	0	–	–	1	0.1	25
Mimosoideae	*Albizia ferruginea*	ALFE	0	–	–	1	0.3	19	1	0.1	25
	Total		451	100		396	100		847	100	

*For Leguminosae, subfamilies are listed.

** RD = Relative Density = Number of *i* th species/Total number of individuals x 100

Fig. 3.2 Five most commonly occurring fleshy fruit producing tree species classified by DBH (cm) Size (Total number of enumerated trees is indicated in the parentheses) along routes A and B. Individuals of *Diospyros mespiliformis* and *Mimusops andongens* are represented by several DBH classes, but the smallest DBH class overwhelmingly dominates *Drypetes floribunda, Celtis brownii* , and *Ficus sur.*

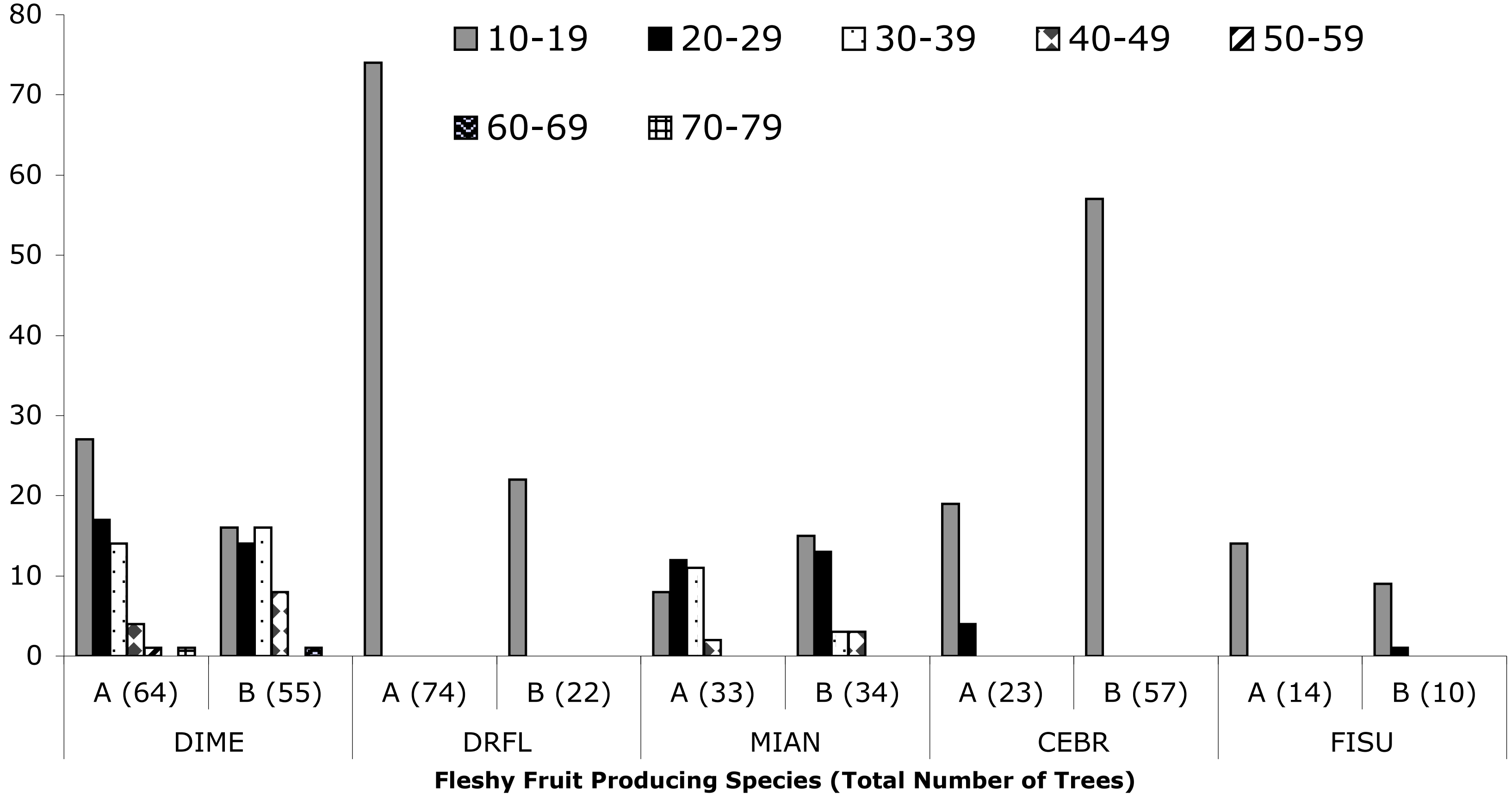
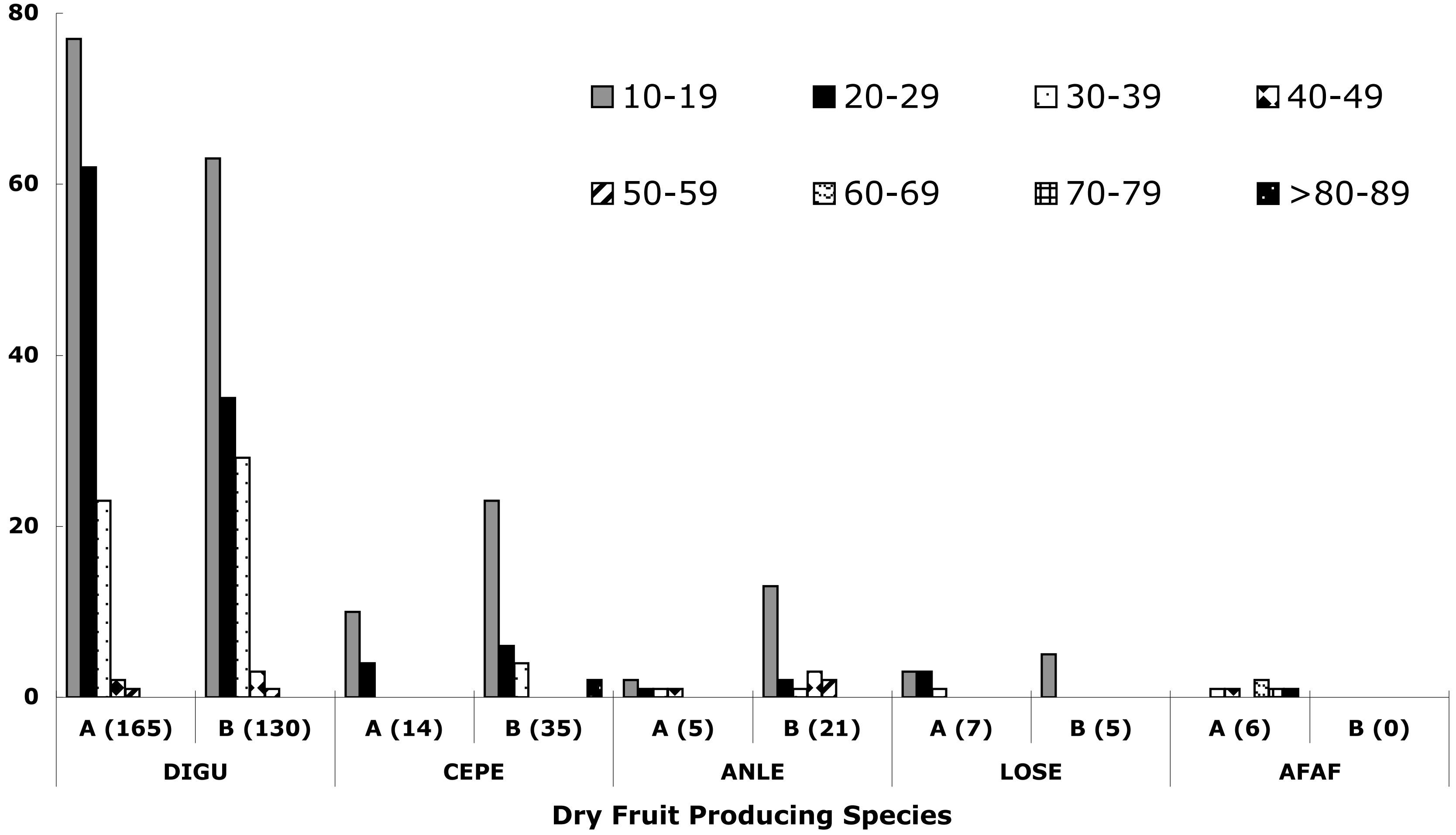


Fig. 3.3 Five most commonly cccurring dry fruit producing tree species classified by DBH (cm) Size (Total number of enumerated trees is indicated in the parentheses). *Dialium guineense* is the dominant dry fruit producing species and most species are dominated by individuals that belong to the 10 -19 cm DBH class.



$\bar{x} = 20.4$, $n = 451$, *s.d.* = 11.1; B: $\bar{x} = 20.6$, $n = 397$, *s.d.* = 11.7), but the HT of the trees along route B ($\bar{x} = 12.0$ m, range: 1.9–28.1, $n = 397$, *s.d.* = 5.43) was slightly greater than that along route A ($\bar{x} = 10.8$ m, range: 1.1–28.8, *s.d.* = 5.43).

Route B (2,176.6 cm^2/ha) has a larger total tree basal area than route A (2,059.9 cm^2/ha) (Table 3.3). BA/ha for shared species were not significantly different between the two routes (Wilcoxon Signed Rank: $z = -0.229$, $p = 0.819$). The differences between BA/ha of early and late successional species between the two routes were also not significantly different (Wilcoxon Signed Rank: early: $z = -0.804$, $p = 0.422$; later: $z = -0.706$, $p = 0.480$).

B. Quadrat Enumeration

1. Species/Area Relationships

The species-area curve shows that the rate of increase was zero to one species per hectare after the first quadrat (Fig. 3.4).

2. Tree Species Composition

The total number of live trees enumerated in the six quadrats was 2,024 (Table 3.4). In addition to the trees, 26 lianas and 86 individuals of *Elaeis guineensis* were also found. Thirty-seven species belonging to 21 families were identified. Three trees and two lianas remained unidentified. The five most frequently occurring species in all quadrats were: *Dialium guineense* ($n = 635$, 29.7%), *Drypetes floribunda* ($n = 317$), *Celtis brownii* ($n = 218$), and *Diospyros mespiliformis* ($n = 214$), and *Mimusops andongensis* ($n = 168$)(Table 3.5).

Table 3.3 Per hectare basal area of all tree species enumerated along census routes A and B: classified according to successional stages

The BA/ha of *Ceiba pentandra* and *Anogeissus leiocarpus* along route B are much greater than those along route A, but the differences between the two routes are not statistically significant.

Successional Stages	Species	Abbrev.	Route A (cm^2/ha)	Route B (cm^2/ha)
Early	*Ceiba pentandra*	CEPE	46.6	351.0
	Anogeissus leiocarpus	ANLE	45.1	157.1
	Lonchocarpus sericeus	LOSE	31.7	9.5
	Ficus sur	FISU	22.8	20.4
	Diospyros ferrea	DIFE	21.7	0.0
	Ficus excelsa	FIEX	17.0	10.7
	Lannea nigritana	LANI	11.4	11.4
	Vernonia colorata	VECO	1.0	0.0
	Albizia ferruginea	ALFE	0.0	4.6
	Albizia zygia	ALZY	0.0	5.7
	Ficus spp.	FI SP.	0.0	4.8
	Zanthozylum xanthoxyoides	ZAXA	0.0	4.3
	Holarrhena floribunda	HOFL	0.0	8.1
Subtotal			197.3	587.7
Late	*Dialium guineense*	DIGU	916.7	738.0
	Diospyros mespiliformis	DIME	485.5	493.1
	Mimusops andongens	MIAN	257.7	203.6
	Drypetes floribunda	DRFL	105.5	39.2
	Celtis brownii	CEBR	55.1	85.1
	Sterculia tragacantha	STTR	12.1	0.0
	Malacantha alnifolia	MAAL	4.3	4.0
	Pancovia bijuga	PABI	4.3	1.2
	Lecaniodiscus cupanioides	LECU	4.2	6.6
	Margaritaria discoidea	MADI	3.5	1.2
	Milicia excelsa	MIEX	0.0	9.3
	Tetrapleura tetraptera	TETE	0.0	7.7
Subtotal			1848.9	1588.9
Unknown	Unknown spp. #1	UNI1	1.4	0.0
	Unknown Spp. #2	UNI2	12.3	0.0
Grand Total			2059.9	2176.6

Fig. 3.4 Cumulative number of species-area relationship in six quadrats
After six hectares of sampling, the curve has not reached a plateau. It indicates that more sampling is needed to find the diversity of species that occur in the Lama Forest.

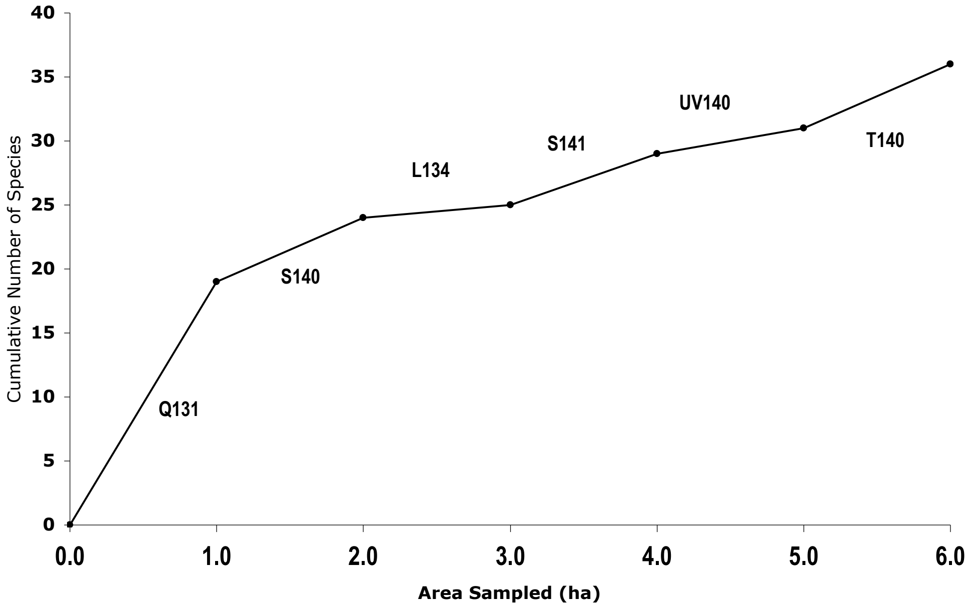


Table 3.4 Total numbers of enumerated trees, lianas, and oil palms in six quadrats

Quadrat	Trees		Lianas		Palms		Total	
	Freq.	%	Freq.	%	Freq.	%	Freq.	%
L134	418	20.7	3	11.5	40	46.5	461	21.6
S140	360	17.8	7	26.9	5	5.8	372	17.5
Q131	353	17.4	5	19.2	15	17.4	373	17.4
S141	340	16.8	7	26.9	7	8.1	354	16.5
UV140	278	13.7	3	11.5	5	5.8	286	13.4
T140	275	13.6	1	3.8	14	16.3	290	13.6
Total	2024	100.0	26	100.0	86	100.0	2136	100

Table 3.5 Frequency of trees enumerated in six quadrats

Rank	Species	S141	S140	L134	T140	Q131	UV140	TTL	RD	# of Quadrat Occurrence
1	DIGU	116	122	165	40	123	69	635	31.37	6
2	DRFL	78	82	49	41	10	57	317	15.66	6
3	CEBR	33	40	50	17	51	26	217	10.72	6
4	DIME	25	29	65	8	55	32	214	10.57	6
5	MIAN	30	31	40	5	47	15	168	8.30	6
6	CEPE	8	7	5	50	9	25	104	5.14	6
7	FISU	2	0	0	48	5	12	67	3.31	4
8	ANLE	0	0	15	0	24	1	40	1.98	3
9	LANI	6	6	7	6	7	2	34	1.68	6
10	LOSE	3	6	4	7	4	8	32	1.58	6
11	AFAF	6	3	6	3	3	9	30	1.48	6
12	FIEX	2	0	0	22	1	4	29	1.43	4
13	ALZY	3	4	0	7	3	3	20	0.99	5
14	LECU	5	7	1	0	4	2	19	0.94	5
15	CACO	6	6	2	1	2	0	17	0.84	5
16	MADI	0	3	0	6	0	4	13	0.64	3
17	HOFL	3	0	4	1	1	4	13	0.64	5
18	PABI	3	6	1	1	0	0	11	0.54	4
19	MIEX	0	1	3	2	1	3	10	0.49	5
20	ANTO	4	1	0	1	0	0	6	0.30	3
21	MAAL	1	5	0	0	0	0	6	0.30	2
22	FINA	3	0	0	0	0	0	3	0.15	1
22	NALA	0	0	0	3	0	0	3	0.15	1
24	ALFE	0	0	0	2	0	0	2	0.10	1
24	SPMO	0	0	0	0	2	0	2	0.10	1
24	ZAXA	0	0	0	1	0	1	2	0.10	2
27	ANDJ	0	0	0	0	0	1	1	0.05	1
27	DIFE	0	0	0	1	0	0	1	0.05	1
27	GATR	1	0	0	0	0	0	1	0.05	1
27	SPDI	0	0	0	1	0	0	1	0.05	1
27	OCME	1	0	0	0	0	0	1	0.05	1
27	PSGU	0	0	0	0	1	0	1	0.05	1
27	STTR	0	1	0	0	0	0	1	0.05	1
27	VECO	0	0	1	0	0	0	1	0.05	1
27	UNID1	0	0	0	1	0	0	1	0.05	1
27	UNID2	1	0	0	0	0	0	1	0.05	1
Total		340	360	418	275	353	278	2024	100.00	

RD = Relative Density

Table 3.6 shows two indices of species diversity and evenness values as well as tree density, frequency of tree species, basal areas, and approximate percentage of each forest type for each quadrat. The indices of species diversity and evenness indicate that the quadrat that contains half dense forest and half disturbed forest (L134) is least diverse with the greatest evenness and fewer numbers of species and the quadrats that contain no dense forest (UV140 and T140) show the greatest and second greatest diversity and least evenness. The matrix of Similarity Index (Table 3.7) among six quadrats shows a complex picture of similarities among quadrats. For example, although S141 shares the greatest similarities with S140, S140 shows more similarities with L134 than with S141.

3. Tree Density

The mean tree density was 337 individuals/ha (range: 275–418, $n = 6$, *s.d.* = 49.3) (Table 3.6). The highest tree density was found in Quadrat L134, which contained about 50% dense forest and 50% disturbed forest. Quadrat S140 that contained mostly dense forest with some areas of disturbed forest and farm bush had the second highest density (Table 3.6).

4. Mean DBH and HT

The mean DBH of the trees were significantly different among quadrats ($F = 7.05$, *d.f.* = 5, $p < 0.01$) and among species ($F = 32.286$, *d.f.* = 36, $p < 0.01$). The largest mean DBH was found in L134 ($\bar{x} = 22.2$, range: 10–130, $n = 418$, *s.d.* = 13.71) and the smallest mean was found in T140 ($\bar{x} = 16.9$, range: 10–83.9, $n = 275$, *s.d.* = 9.36). The smallest size class dominates the trees in all quadrats ($n = 1{,}306$, 64.5%).

Table 3.6 A comparison of various measurements in six quadrats

Sample Quadrat	Spp.	Tree Species Diversity & Evenness Index						Tree Freq.				Mean				Total Basal Area (cm^3)	% of Forest Type*		
		D'	Rank	H'	Rank	E	Rank	Live	%	Dead	%	DBH	s.d.	HT	s.d		DF	df	FB
T140	24	0.879	1	2.42	1	0.76	5	275	96.8	9	3.2	16.9	9.37	7.7	3.86	802	0	50	50
UV140	19	0.860	2	2.28	2	0.78	6	278	95.5	13	4.5	22.2	14.72	11.5	6.05	1656	0	80	20
Q131	19	0.809	3	2.03	5	0.69	3	353	84.7	64	15.3	21	12.03	13	5.09	1638	100	0	0
S141	22	0.807	4	2.11	3	0.68	2	340	91.6	31	8.4	20	13.60	11.4	5.12	1591	100	0	0
S140	18	0.806	5	2.04	4	0.71	4	360	96.0	15	4.0	20.9	13.44	11.7	5.12	1754	80	10	10
L134	16	0.781	6	1.88	6	0.68	1	418	88.0	57	12.0	22.2	13.70	12.6	5.65	2237	50	50	0
Mean	20	0.824	–	2.13	–	0.72	–	337	91.5	32	8.5	20.7	5.50	11.5	5.50	1210	55	32	13

Spp. = # of identified species
D' = Simpson's Index
H' = Shannon-Wiener Index
E = Evenness Index
*= Approximation

DF = Dense forest
df = Disturbed forest
FB = Farmbush

Table 3.7 Similarity index (SI) of six quadrats (Highlighted values indicate the greatest similarity between the quadrat above and the quadrat at left.)

Quadrat	S141		S140		L134		T140		Q131		UV140	
	SI	Rank	SI	Rank	SI	Rank	SI	Rank	SI	Rank	SI	Rank
S141			75.0	2	63.2	5	69.6	4	73.2	3	68.3	5
S140	75.0	1			76.5	2	71.4	2	70.3	4	70.3	4
L134	63.2	5	76.5	1			65.0	5	80.0	2	74.3	3
T140	69.6	3	71.4	3	65.0	4			69.8	5	74.4	2
Q131	73.2	2	70.3	4	80.0	1	69.8	3			84.2	1
UV140	68.3	4	70.3	4	74.3	3	74.4	1	84.2	1		

The mean tree HT in all quadrats was 11.5 m (range: 0.8–30.1, *n* = 2,022, *s.d.* = 5.51) (Table 3.6). The mean tree HT was significantly different among quadrats (*F* = 38.168¸, *d.f.* = 5, p < 0.01) and among species (*F* = 43.269, *d.f.* = 36, *p* < 0.01).

C. Basal Areas

Table 3.8 shows basal areas of all 43 species in each quadrat. The five highest-ranking species were *Dialium guineense* (554.3 cm^2/ha, 34.4%), *Diospyros mespiliformis* (290.2 cm^2/ha, 18.0%), *Ceiba pentandra* (218.6 cm^2/ha, 13.6%), *Afzelia africana* (165.3 cm^2/ha, 10.3%), and *Mimusops andongensis* (87.2 cm^2/ha, 5.4%). The five highest-ranking families (or subfamilies) were: Caesalpinioideae (44.6%), Ebenaceae (18.0%), Bombacaceae (13.6%), Sapotaceae (5.6%), and Euphorbiaceae (4.7%)(Table 3.9).

L134 has the greatest basal area of trees and T140 has an exceptionally low basal area. The mean basal area in all quadrats was 1210 cm^2/ha (range: 802–2237 cm^2/ha, *s.d.* = 498, *n* = 6) (Table 3.6).

D. Dispersion Patterns

Table 3.10 shows the CD (Coefficients of Variation) and the results of the Chi-Square Goodness of Fit Tests for each species in each quadrat. In almost all quadrats, CDs of all species except *Mimusops andongensis* were ≥ 1, indicating that the trees were distributed in clumps. Nevertheless, the null hypothesis that the sampled trees were distributed randomly could not be rejected in many species due to the results of the Chi-Square Goodness of Fit Tests. For example, even though the CDs of *Diospyros mespiliformis* in all quadrats were >1.0, the null hypothesis could be rejected in only one quadrat, while the null hypothesis was rejected in four and three quadrats in *Dialium guineense* and *Drypetes floribunda*, respectively. Random distribution could not be

Table 3.8 Basal areas of enumerated live trees and lianas in six quadrats

Species	S141	Q131	S140	L134	T140	UV140	Total	%	Mean BA(cm^2)/ha
DIGU	545.4	592.6	688.3	800.8	245.1	453.6	3325.8	34.36%	554.3
DIME	263.3	466.7	281.5	382.0	75.7	271.9	1741.0	17.99%	290.2
CEPE	211.2	68.7	319.3	338.5	100.1	273.7	1311.5	13.55%	218.6
AFAF	203.1	109.5	109.0	171.6	100.0	298.6	991.8	10.25%	165.3
MIAN	81.6	158.9	85.4	116.8	26.8	53.4	523.0	5.40%	87.2
DRFL	111.2	16.0	109.3	56.7	57.3	85.1	435.7	4.50%	72.6
ANLE	0.0	76.8	0.0	219.2	0.0	2.5	298.5	3.08%	49.8
CEBR	48.2	63.3	52.2	63.5	23.1	43.3	293.6	3.03%	48.9
MIEX	0.0	18.9	7.2	34.6	13.4	72.0	146.1	1.51%	24.3
FISU	2.0	6.0	0.0	0.0	65.3	16.1	89.4	0.92%	14.9
LANI	19.0	22.8	14.7	21.1	16.1	0.0	93.7	0.97%	15.6
LOSE	9.3	5.4	14.5	6.4	12.3	15.1	63.0	0.65%	10.5
FIEX	2.3	0.8	0.0	0.0	27.6	7.0	37.7	0.39%	6.3
LECU	13.2	8.1	19.2	4.3	0.0	0.0	44.8	0.46%	7.5
ALZY	6.2	4.4	5.1	0.0	10.3	13.9	39.8	0.41%	6.6
HOFL	12.9	2.2	0.0	14.0	1.8	6.0	37.1	0.38%	6.2
FITH*	20.9	3.5	0.8	0.0	0.0	15.0	40.3	0.42%	6.7
CACO	6.9	3.1	8.9	3.0	1.0	0.0	22.8	0.24%	3.8
FLPA	6.3	4.0	3.4	0.0	0.0	6.2	19.9	0.21%	3.3
MAAL	1.7	0.0	18.3	0.0	0.0	0.0	20.0	0.21%	3.3
DIFE	0.0	0.0	0.0	0.0	1.2	0.0	1.2	0.01%	0.2
MADI	0.0	0.0	4.0	0.0	9.0	5.1	18.1	0.19%	3.0
ZAXA	0.0	0.0	0.0	0.0	1.4	13.4	14.8	0.15%	2.5
STAF**	3.5	0.0	2.7	1.8	0.8	3.2	12.0	0.12%	2.0
PABI	3.8	0.0	6.3	1.1	0.8	0.0	12.0	0.12%	2.0
STTR	0.0	0.0	2.4	0.0	0.0	0.0	2.4	0.02%	0.4
ANTO	12.1	0.0	1.0	0.0	0.8	0.0	13.9	0.14%	2.3
ALFE	0.0	0.0	0.0	0.0	5.4	0.0	5.4	0.06%	0.9
UNID 4*	0.0	2.7	0.8	0.8	1.8	0.0	6.1	0.06%	1.0
FINA	3.8	0.0	0.0	0.0	0.0	0.0	3.8	0.04%	0.6
NALA	0.0	0.0	0.0	0.0	3.1	0.0	3.1	0.03%	0.5
SPMO	0.0	2.4	0.0	0.0	0.0	0.0	2.4	0.02%	0.4
UNID 5*	0.0	0.0	0.0	0.0	2.1	0.0	2.1	0.02%	0.3
VECO	0.0	0.0	0.0	0.9	0.0	0.0	0.9	0.01%	0.2
UNID 2	1.0	0.0	0.0	0.0	0.0	0.0	1.0	0.01%	0.2
PSGU	0.0	1.0	0.0	0.0	0.0	0.0	1.0	0.01%	0.2
OCME	1.0	0.0	0.0	0.0	0.0	0.0	1.0	0.01%	0.2
GATR	0.9	0.0	0.0	0.0	0.0	0.0	0.9	0.01%	0.2
ANDJ	0.0	0.0	0.0	0.0	0.0	0.8	0.8	0.01%	0.1
Total	1590.9	1637.9	1754.3	2237.0	802.4	1655.9	9678.4	100.00%	1613.1

**** BA/ha for the liana species was calculated by using the same equation that calculates the BA/ha of trees. Therefore, actual BA/ha of lianas is probably underestimated.**

Table 3.9 Basal areas (cm^2/ha) of tree families in six quadrats

* Family Leguminosae (subfamilies Caesalpinioideae, Papilionioideae, Mimosoideae) comprises 45.8% of the total BA/ha.

Family	BA (cm^2/ha)	%
Caesalpinioideae*	**719.6**	**44.6%**
Ebenaceae	**290.4**	**18.0%**
Bombacaceae	**218.6**	**13.6%**
Sapotaceae	**90.5**	**5.6%**
Euphorbiaceae	**75.6**	**4.7%**
Moraceae	**55.2**	**3.4%**
Combretaceae	**49.8**	**3.1%**
Ulmaceae	**48.9**	**3.0%**
Anacardiaceae	**16.0**	**1.0%**
Papilionioideae*	**10.5**	**0.7%**
Sapindaceae	**9.6**	**0.6%**
Mimosoideae*	**7.5**	**0.5%**
Apocynaceae	**6.2**	**0.4%**
Rhizophoraceae	**3.8**	**0.2%**
Malpighiaceae	**3.3**	**0.2%**
Rutaceae	**2.5**	**0.2%**
Loganiaceae	**2.1**	**0.1%**
Other Families	**2.9**	**0.2%**
Total	**1613.1**	**100.0%**

Table 3.10 Coefficients of variatiion (CD) and Chi-square values of spatial distribution of the five highest-ranking species.

According to the CD, all species except MIAN in amost all quadrats show contagious distribution; however, Chi-sq. tests confirmed contagious distribution in DRFL, DIME, and DIGU in 1-4 quadrats out of 6 (shown in Bold types).

Species / Quadrat	CEBR				DRFL				DIME				DIGU				MIAN			
	CD	x^2	d.f.	H^*	CD	x^2	d.f.	H^*	CD	x^2	d.f.	H^*	CD	x^2	d.f.	H^*	CD	x^2	d.f.	H^*
L134	2.87	6.37	6	H^0	1.57	5.86	8	H^0	1.73	6.92	9	H^0	**1.21**	**16.44**	**7**	**H^1**	0.63	2.49	4	H^0
S140	1.21	4.28	6	H^0	2.53	5.15	11	H^0	2.48	5.15	6	H^0	**1.82**	**12.35**	**7**	**H^1**	0.51	4.16	5	H^0
Q131	1.78	5.10	9	H^0	0.67	4.43	4	H^0	**1.52**	**11.51**	**7**	**H^1**	**2.17**	**21.20**	**10**	**H^1**	0.90	3.36	6	H^0
UV140	2.78	13.50	6	H^0	**3.16**	**19.97**	**9**	**H^1**	1.62	2.98	6	H^0	2.39	7.42	8	H^0	1.49	2.77	4	H^0
S141	1.65	4.36	9	H^0	**4.15**	**54.44**	**7**	**H^1**	1.70	1.16	7	H^0	**3.13**	**64.45**	**7**	**H^1**	0.56	2.56	4	H^0
T140	4.70	8.95	9	H^0	**6.35**	**48.34**	**10**	**H^1**	3.19	3.29	6	H^0	3.75	9.26	8	H^0	1.80	N/A#		

CD = Coefficients of Dispersion

* H = Hypothesis testing results, H^0 = Null hypothesis cannot be rejected. H^1 = Null hypothesis should be rejected.

\# The X^2 was not calculated due to rarity.

rejected for *Celtis brownii* in all quadrats and *Mimusops andongensis* in five quadrats; however, these species occur infrequently in the forest, indicating that interindividual distance of these species is great.

Dispersion maps of all live stems of all five highest-ranking species, *Ceiba pentandra, Afzelia africana,* and some pioneer species are shown in Appendix D (Figs. D.1–11). Although *Ceiba pentandra* and *Afzelia africana* did not make the five top species' rank in terms of their frequencies, they are the two high-ranking species in terms of BA/ha (Table 3.8). They are also among *C. mona*'s most important food species (see Chapter 5). Therefore, these two species were included in the dispersion maps. Dispersion maps of some pioneer species were also made, because *C. mona* feeds on them.

Tree dispersion patterns seen in the maps partly reflect the history of human use (i.e., cultivation, human habitation) and regeneration patterns.

IV. Discussion and Conclusion

A. Species Composition

In this study, I found that Caesalpinioideae trees that produce dry fruits make up 34 % of all trees (≥ 10 cm DBH) that were enumerated in six 1 ha sample quadrats in the Lama Forest. In comparison, Glenn (1996) found that the five commonest species at Grand Etang, *Licania ternatensis* (Chrysobalanaceae), *Dacryodes excelsa* (Burseraceae), *Prestoea montana* (Palmae), *Sloanea caribaea* (Elaeocarpaceae), and *Cassine xylocarpa* (Celastraceae) (≥2.5 cm DBH), are fleshy-fruit producing plants. At Mungo, the five most frequenty occurring and species-rich tree families were Caesalpinioideae, Flacourtiaceae, Moraceae, Euphorbiaceae, and Annonaceae (≥ 46 cm DBH) (Howard, 1977). Howard (1977) did not present data on the biomass of these families.

Tree species composition also differs among forests where other members of the mona species group have been studied in the past. The five most common tree species in the main tract of the Boabeng-Fiema Monkey Sanctuary, Ghana were *Cola gigantea* (Sterculiaceae), *Anogeissus leiocarpus* (Combretaceae), *Monodora myristica* (Annonaceae), *Myrianthus arboreus* (Cecropiaceae), and *Holarrhena floribunda* (Apocynaceae). These species – all except *Anogeissus* produce fleshy fruits – account for 43 % of all trees surveyed (Saj. *et al.*, 2005). At Taï, *Diospyros sanza-minika* (Ebenaceae), *Strombosia glaucescens* (Olacaceae), *Corynanthe pachyceras* (Rubiaceae), *Dialium aubrevillei* (Caesalpinioideae), *Pycnanthus angolensis* (Myristicaceae) are listed as dominant (Galat and Galat-Luong, 1979). All but *Dialium* are fleshy fruit producing species. At Makandé, Gabon where *C. pogonias* was studied by French researchers, Caesalpinioideae (23.9%), Burseraceae (13.6%), Ebenaceae (4.9%), and Olacaceae (4.8%) were dominant families (≥ 10 cm DBH) (Maisels and Gautier-Hion, 1994; Brugière *et al.* 2002). Similarly, at Salonga, DRC, where the diet of *C. pogonias wolfi* has been studied, Caesalpinioideae (45.6%, ≥ 16 cm DBH) is the dominant family, followed by Annonaceae, Euphorbiaceae, Burseraceae, and Olacaceae (Maisels *et al.*, 1994). As in the Lama Forest, Caesalpinioideae is dominant at Makandé and Salonga.

The above survey of the species composition in forests where mona species group has been studies shows that this species group was studied in both fleshy fruit dominating forests and dry fruit dominating forests.

B. Species Richness

In this study, 16–24 species per hectare were found. In total, 43 species were enumerated. Since a species-area curve of my data did not reach a plateau after sampling six quadrats, my sampling almost certainly does not reveal the full tree species richness of the the Lama Forest. During the course of this study, ≥ 50 additional species of small shrubs and climbers (≤ 10 cm DBH) were also identified (see Appendix C).

A floristic inventory of the Lama Forest vegetation taken by Paradis and Houngnon (1977) listed 97 vascular plant species, which included 20 common species, but it is not clear how many tree species per hectare were found. According to a more recent floristic inventory made by Emlich *et al.* (1999) (cited in Nansen *et al.*, 2001), 173 species belonging to 67 families were reported to occur in the Lama Forest, but these numbers included all types of vascular plants. More recently, Nansen *et al.* (2001, pers. comm.) identified more than twice as many species (47 spp. in 69 x 225 m^2 sample plots,≥ 10 cm DBH) as my study (16–24 spp./ha) (Nansen, pers. comm.).

In comparison with other forests where *C. mona* and other members of the mona species group have been studied, the Lama Forest appears to be species depauperate, especially with regard to fleshy fruit species. However, not all studies have used 10 cm DBH as a criterion, therefore a direct comparison is not always possible. For example, Glenn (1996) found 41 species (≥ 3 cm DBH) in 20 1^{-1} ha plots in the evergreen forest of Grand Etang. In the Douala-Edéa F.R. Cameroon, Whitesides (1981) enumerated 48 species in five 1 ha quadrats (>10 cm DBH). At Makokou, there were 95 fruiting species in 0.4 ha plots (≥ 5 cm DBH) (Maisels and Gautier-Hion, 1994). At Tiwai, Oates *et al.* (1990) found 133 species (≥ 5 cm DBH) in 112 small old secondary forest plots (total area sampled = 0.56 ha) and Fimbel (1992) reportred 86 species (≥ 2.5 cm DBH) in young secondary forest plots (total area sampled = 0.62 ha). At the Boabeng-Fiema Monkey Sanctuary, where *C. campbelli* and *C. vellerosus* are considered sacred and protected, with a similar climate as the Lama Forest, 69 tree species were found in 9 x 0.025 ha plots (≥ 40 cm DBH)(Teichroeb *et al.*, 2003; Saj *et al.*, 2005).

C. Species Diversity

Tree species diversity in the Lama Forest is low. Actual age or years that lapsed since disturbance last took place in the sample quadrats is unknown. The fact that people were living in the forest until 1984 and disturbance occurred continuously until then indicates that many parts of the forests are at early stages of regeneration and may appear to be young.

In the Lama Forest, tree species diversity was significantly different among the sample quadrats. The quadrats that appeared to be most disturbed with the youngest vegetation had the greatest species diversity. These quadrats had more gaps and exposed edges that provide a favorable environment for light-demanding species than other quadrats. The quadrats that consist of dense forest, disturbed forest, and farm bush, appearing to be intermediate in the degree of disturbance, had intermediate species diversities. The quadrats that appeared to be least disturbed and oldest had least species diversity.

Most botanical studies that examine tree species diversity in regenerating forests in various parts of the world have been conducted on local or regional scales. Therefore, direct comparisons cannot be made easily. However, most agree that older forests tend to have greater species diversity and there is a strong trend of declining tree diversity with increasing dryness (Hall and Swain, 1976).

Ashton (1978) stated that species diversity is lowest in the earliest stage of succession and that it steadily increases as the forest becomes mature. In a study of primate abundance, Sorensen and Fedigan (2000) examined tree species diversity in 14 sites in Santa Rosa National Park (SRNP), a regenerating dry forest in Costa Rica. These sites had varying ages of regeneration and disturbance histories. Species diversity (H'= 0–5.22) varied depending on the age of the forest. It was higher (H'= 4.55–5.22) in older forests (60-180-year-old), intermediate (H'= 3.89–4.14) in middle age forests (14–30-year-old), and least (H'= 0–2.15) in the youngest forests (0-10-year-old) (Sorensen and Fedigan, 2000). Fimbel (1992) also found that old secondary forests had higher species diversity in an inventory of all ≥ 2.5 cm DBH trees in old and young secondary forests in Tiwai, a semi-deciduous lowland moist forest in Sierra Leone. The pattern found in these forests by both Sorensen and Fedigan (2000) and Fimbel (1992) (i.e, more diversity in older forests than younger forests) is just the opposite of what I found in the Lama Forest. This is because even the dense forest in the Lama Forest is a relatively disturbed forest that is also relatively young in the context of regeneration. Horn (1974), however, suggested that forests at intermediate successional stages have higher species diversity than either early or late stage plots.

D. Tree Heights

The mean height of the trees at Lama was relatively short ($\bar{x}$ =11.5 ± 5.5 m). There were only a few emergent trees along the two census routes and in the sample quadrats. Within the six quadrats sampled, only one *Ceiba pentandra* tree exceeded 30 m in height. The tree height observed at Lama is comparable with that observed in some seasonally dry forests (Murphy and Lugo, 1986). For example, the mean tree height in Chiquitanía, a dry forest in Santa Cruz, Bolivia, was 12.01 ± 6.67 m (Killeen *et al.*, 1998). The highest canopy of the Santa Genebra Forest in Brazil (rainfall 1,366 mm/yr), a Caesalpinioideae dominant forest, was 15–20 m. The mean tree height in Santa Rosa National Park was also short (3.9-10.3 m) (Sorensen and Fedigan, 2000). In the Boabeng-Fiema Monkey Sanctuary, a semi-deciduous forest in Ghana, some *Anogeissus leiocarpus* trees reached the height of 25 m (Fargey, 1992). At Lama, the tallest trees of *Anogeissus leiocarpus* had similar heights (23–28.8 m, $n = 3$). Trees at Pinkwae, one of the driest forests in the Accra Plain, Ghana, in the western most area of the Dahomey Gap, were even shorter than at Lama. The mean canopy height at Pinkwae was 6–10 m and emergent trees reached only 12-14 m, and the mean height of trees in gap regrowth was 3–5m (Lieberman, 1982). Trees are taller in other dry forests. For example, trees at the dry Guana Casta Forest in Costa Rica (rainfall 1,533 mm/yr) reach 20-25 m in height and some emergents reach 35 m in height. Swaine (1992) stated that in semi-deciduous forests in Casamance and Senegal, tallest trees can exceed 40 m in height; however, such tall trees are rare even in wetter forests (J.F. Oates, pers. comm.).

E. Tree Basal Areas

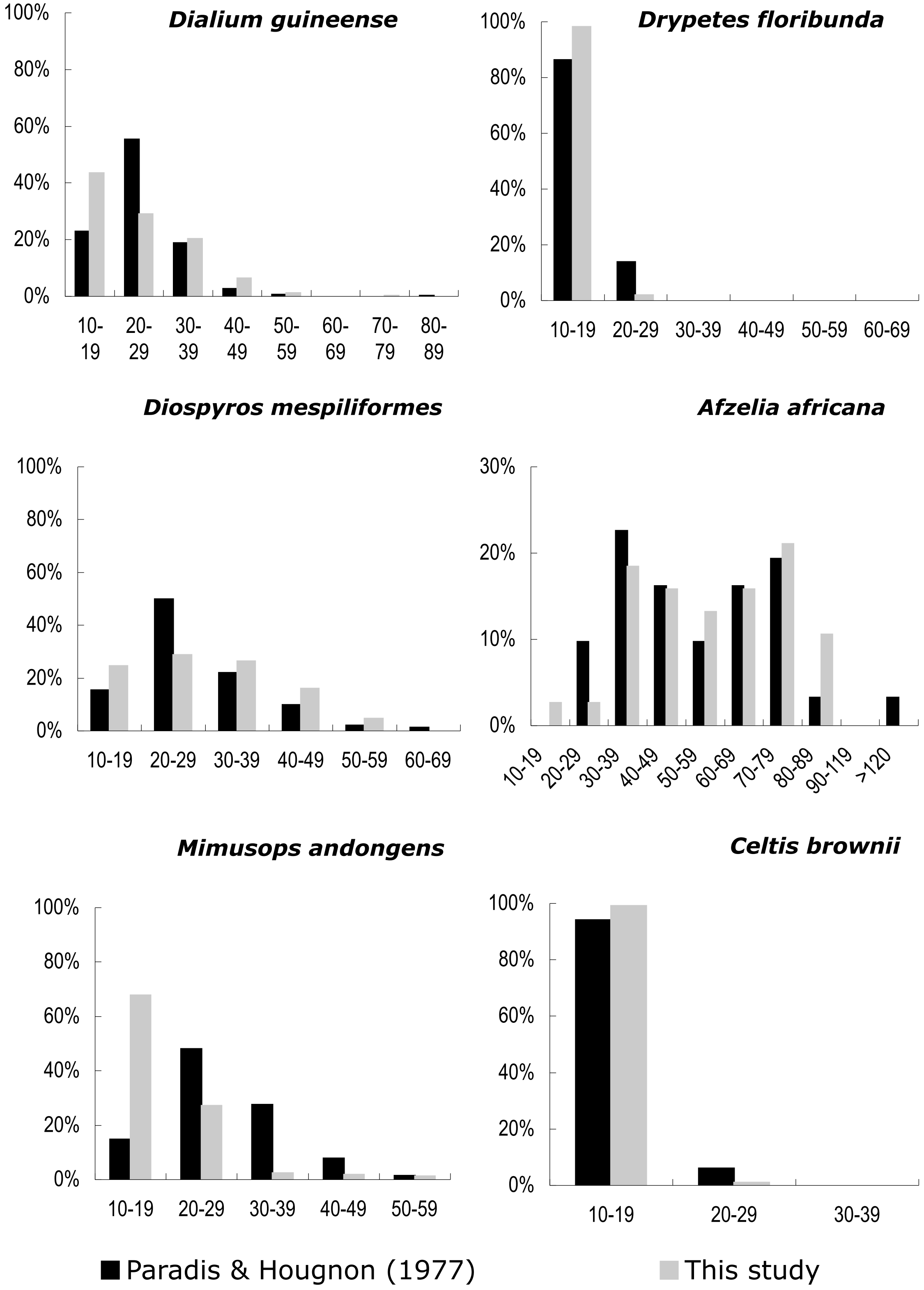
The mean per hectare basal area of trees found in this study included only trees that were ≥ 10 cm DBH ($\bar{x} = 18 \pm 4.98$ m^2/ha). Therefore, total plant biomass is underestimated by this figure. Among many studies that studied or surveyed members of the mona species group, only a few studies have reported tree biomass data in their habitats. For example, Whitesides (1991) and Fimbel (1992) reported tree biomass in old and young secondary forest plots at Tiwai were 203.3 m^2/ha (40 cm DBH) and 106.4 m^2/ha (62 0.01 ha plots), respectively. At Grand Etang, mean basal areas of trees that are ≥ 3 cm DBH in primary forest, secondary forest, and palm brake were 100.3, 80.4, 26.8 m^2/ha, respectively (total sample area = 0.2 ha). In comparison with these wetter forests, tree BA/ha values in the Lama Forest are much lower.

F. Tree Population Structures: 20 Years Ago vs. Present Day

In 1976, Paradis and Houngnon (1977) enumerated ≥ 20 cm DBH trees of nine common species in 269 25 m^2 plots, and all species that were ≥ 10 cm DBH in 21 625 m^2 plots in the Lama Forest. Fig. 3.5 shows a comparison of DBH classes of the seven highest-ranking tree species in their study and this study. Population structures of these species slightly differ between the two studies. In almost all species, there were greater percentages of individuals belonging to larger DBH size classes in the earlier study. In *Mimusops andongensis*, larger size classes had the higher percentages (85.2%) in the 1976 study, while the two smallest size classes had the highest percentages (84.7%) in this study. In *Drypetes floribunda*, the smallest size class had the highest relative density in both studies (1976 study = 0.86, this study = 0.98), but the next size class had higher percentages in the earlier study. In *Diospyros mespiliformis* and *Dialium guineense*, there were greater percentages of individuals belonging to smaller DBH size classes than to larger DBH size classes in the 1976 study. The differences between the two studies were not statistically significant in all species, however.

Although the discrepancies found in the two studies were not statistically significant, I examined only tree population structure. Therefore, my results should be taken as provisional. Comparisons of tree mortality rates and biomass should be

**Fig. 3.5 Comparison of tree enumeration:
Paradis & Hougnon (1977) vs. this study**



conducted to verify this result. Given the fact that an extensive fragmentation and destruction of many parts of the forests has taken place in the last 20 years, it is somewhat surprising to find that little change in tree population structure has taken place. In wetter forests in Africa, there is accumulating evidence that a time lapse of > 15 years can bring about slight to significant changes in forest structure, composition, tree recruitment rate, and mortality rate (e.g., Kade Forest, Ghana, Swaine *et al.*, 1987; Kibale Forest, Uganda: Lwanga *et al.*, 2000; Mpanga Forest, Uganda, Taylor *et al.*, 1996).

G. Monodominance of Caesalpinioideae in the Lama Forest

According to Richards (1966), single-dominant communities occur either at: (1) sites that are sometimes flooded with poor drainage, where the soil is poorly aerated; or (2) *terra firme* sites with white sands and other non-kaolisols. These unfavorable soil conditions can lead to single-species dominance. The Lama Forest belongs to the first category.

The monodominance of Caesalpinioideae in some Neotropical forests has been attributed, at least partially, to seasonal flooding (Torti *et al.*, 2001). It appears that trees belonging to family Caesalpinioideae better tolerate the stressful conditions that flooding imposes on them than the trees belonging to other families. Lopez and Kursur (1999), however, recently conducted a flooding experiment on the saplings of species that commonly occur in *terra firme* forests in comparison with species that commonly occur in seasonally flooded forests to examine the root growth, leaf area growth, and the biomass response in the Barro Colorado Island (BCI) in Panama. They found that there were some negative effects on the saplings in both *terra firme* species and species that occur in flooded forests, but there was little difference in flood response between the two.

They concluded that equally important to flood tolerance is the plants' response to post-flooding events such as drought.

The predominance of Caesalpinioideae in some African forests, however, cannot be attributed solely to seasonal flooding, since not all of them are subject to seasonal flooding (Hart *et al.*, 1989). Connell and Lowman (1989) explored a possible mechanism that maintains single-species dominance and single-family dominance in tropical forests. They found that a majority of monodominant trees possesses ecotomycorrhizae (EM) and urged testing the "mycorrhiza hypothesis," which states that the possession of an EM association by host plants gives a competitive edge over vesicular-arbucular mycorrhizae (VAM) associations, because EM are more efficient in uptaking minerals and nutrients from the soil. Ecotomycorrhizae also provide an excellent protection from natural enemies and better deal with stressful physical conditions. Torti and Coley (1999) recently examined the hypothesis in the *Gilbertiodendron dewevri* (Caesalpinioideae) monodominant forest at the Okapi Wildlife Reserve in the Ituri Forest (DRC) and found that host-plant-mycorrhizae associations are more complex than Connell and Lowman (1989) had suggested. More recently, Torti *et al.* (2001) studied the characteristics of the juvenile trees of *Gilbertiodendron*, *Julbernardia*, and *Cynometra* (all belong to Caesalpinioideae) in the Ituri Forest and found that seeds and the juvenile trees of these species possess a suite of characteristics that allows them to grow under stressful understory conditions created by adult trees. Some of these characteristics are: (1) masting and satiation of predators increases aveage survivoship of seeds (satiation hypothesis, Janzen, 1974); (2) saplings survive long periods to capitalize on gaps; (3) leaves of juveniles trees survive and grow better because they suffer low leaf damage;

leaves have high-efficiency use of carbon and nitrogen that would lead to high survivorship.

We currently have little data on the factors for the dominance of Caesalpinioideae in a majority of mixed forests, including the Lama Forest. The findings of above studies give some directions in understanding the possible factors for the Caesalpinioideae's dominance.

A feature that is shared by monodominant forests is low species diversity. The low species diversity found in the Lama forest is more comparable with single-species forests than with other mixed dry forests. Mast fruiting by the dominant species, which may have supra-annual flowering and fruiting cycles, is also a shared character (Hart, 1995). In this study, mast fruiting in *Dialium guineense* was observed in 1997 (see Chapter 4). Based upon the fact that the above key features of single-species dominant forests are also found at Lama, I speculate that the Lama Forest once might have been an undisturbed single-species dominant climax forest or a *Dialium-Diospyros* (or *Dialium-Drypetes*) co-dominant forest. Co-dominance is more common in semi-deciduous forests than in rain forests (e.g., *Cynometra-Celtis* forests in Uganda) (Richards, 1966).

H. Tree Dispersion Patterns

In tropical forests, species are often clumped in their spatial distribution (Richards, 1966; Hubbell, 1979). Hubbell (1979) found that adult individuals (≥ 10 cm DBH) of 44 out of 61 species that included trees, shrubs, and vines in the Guana Caste National Park in Costa Rica were distributed in clumps. When juvenile individuals were included, 102 out of 114 species were significantly clumped. Richards (1966) stated that in West Africa, trees of Caesalpinioideae, as well as of other families, tend to grow in clumps.

My study also found that *Dialium guineense*, a caesalpinioid species, had clumped distributions in four out of six quadrats and *Drypetes floribunda* (Euphobiaceae) had clumped distributions in three out of six qauadrats. For other highest-ranking species, Coefficients of Dispersion indicate clumped distributions, however, chi-square values could not rule out random distributions of these species. Rigorous statistical tests may be able to clarify the patterns of dispersion in these species.

When the dispersion patterns of some high-ranking species were compared with those of pioneer species, their complementary relationships become obvious. For example, in quadrat S141, where *Drypetes floribunda* and *Dialium guineense* do not occur, the pioneer species such as *Albizia zygia*, *Lannea nigritana*, *Ficus* spp. and *Elaeis guineensis* occur (Fig. D.4). According to Nansen *et al.*'s (2001) succession scheme, Type 3 Forest, a woodland type habitat becomes like a thicket type habitat (Type 4 Forest) when *Drypetes floribunda* and *Dialium guineense* become established by replacing the above pioneer species. Such succession may be occurring in quadrat S141.

The composite maps of the locations of *Celtis brownii*, *Mimusops andongensis*, *Dialium guineense* and *Diospyros mespiliformis* in contrast with *Ceiba pentandra* in T140 and UV140 also indicate a complimentary relationship between these species and *Ceiba pentandra*. Lieberman (1982) listed *Ceiba pentandra* as a thicket species in the Pinkwae Forest in Ghana. According to Nansen *et al.* (2001), Type 2 Forest, a type of forest that occurs in formerly cultivated areas, is characterized by the dominance of *Ceiba pentandra* and *Ficus sur*. According to Nansen *et al.* (2001), succession from Type 2 to Type 3 occurs when *Afzelia africana*, *Celtis brownii*, *Mimusops andongensis*, *Dialium* *guineense*, and *Diospyros mespiliformis* replace *Ceiba pentandra* and *Ficus sur*. Such succession may be taking place in quadrats T140 and UV140.

The fact that trees of the most common species occur only in specific areas in quadrats T140 and UV140 and trees of *Dialium guineense* and *Drypetes floribunda* occurred only in specific area in quadrat S141 appears to reflect the historical use of the forest. It is not certain whether these areas were clear-cut, farmed, or supported human habitation in the past. Further investigation is needed to find out the reasons for the rarity of trees in these areas.

CHAPTER 4: PHENOLOGY

I. Introduction

Phenology can be defined as the study of recurring natural phenomena that take place in the environment in relation to climate (Deshmukh, 1986; van Schaik *et al.*, 1993; van Schaik and Brockman, 2005). Generalizing the complex phenological patterns in tropical forests is extremely difficult. In wetter forests, seasonal peaks and troughs of fruit abundance as well as of flowers and new leaves tend to be correlated with rainfall (Janzen and Schoener, 1968; Janzen 1973a, b; Fleming *et al.*, 1987, Whitesides, 1991). Fruiting peaks tend to occur during high rainfall periods and fruit scarcity tends to occur at the end of rainy seasons or the beginning of dry seasons (Fleming *et al.,* 1987). These trends were obvious in the Pinkwae Forest, a dry forest in Ghana (Lieberman, 1982; Lieberman and Lieberman 1984). In contrast, flowering peaks occurred in the middle of the long dry season and leaf flush and fruiting peaks occurred at the end of the long dry season to the beginning of the rainy season in a dry forest in Guanacaste National Park, Costa Rica (Daubenmire, 1972; Frankie *et al.*, 1974). Such contrasting results show the phenological complexity that involves factors other than rainfall in dry forests.

Seasonal changes in the availabilities of food in primate habitats have been shown to influence many aspects of feeding, reproductive, and ranging behavior in primates (e.g., Gautier-Hion *et al.*, 1985; Baranga, 1986; Oates, 1987; Beeson, 1989; Beeson and Lea, 1994; Boinski and Fowler, 1989; M. Mitani, 1989; Lucas and Corlett, 1991; Kinnaird, 1992; Dasilva, 1994; Peres, 1994b; White, 1994a; Tutin *et al.*, 1997a; Conkin-Brittain *et al.*, 1988; Wrangham *et al.*, 1998; Yamakoshi, 1998; Heymann, 2001; Tweheyo and Obua, 2001; Brugière, *et al.*, 2002; Fairgrieve and Muhumuza, 2003). Some studies have found that primates and other animals also adjust their metabolism, physiology, and digestive system in relation with the fluctuation in food types and abundance (Lambert, 1998; Ganzhorn *et al.*, 2003; Starck, 2003). There is also accumulating evidence that certain abundant foods have supra-annual periodicity (Kaplin *et al.*, 1998; Chapman *et al.*, 2002; Brugière *et al.*, 2002). Therefore, primates must adjust their feeding behavior in accordance with the abundance and scarcity of potential foods that occur beyond seasonal periodicity (Kaplin *et al.*, 1998; Brugière *et al.*, 2002).

To accurately grasp the quantity, quality, and types of food that are potentially available for a study subject through space and different seasons, collecting data on phenological changes that take place in its habitat is indispensable. In Chapter 3, I examined the abundance of trees and their spatial dispersion patterns. In this chapter, I quantify the temporal food availability to identify the periods of food abundance and scarcity by using two methods: visual observation by binoculars and a trail survey of fruits. I used the fruit trail method (also known as the raked-fruit survey method) in addition to the visual observation method, which captures phenophases of leaves, floral parts, and fruits, because I was interested in finding out whether the two different methods yielded different results in the timing and extent of fruit productivity and if so, why. Some ecological studies have found that different methods yield different results in plant phenophases (Fimbel, 1992; Chapman *et al.*, 1994; Zhang and Wang, 1995). I will test a hypothesis that fleshy fruits are mainly abundant during wet seasons and dry fruits are available in dry seasons. I will examine whether there are any similarities and differences in the patterns of phenophases in the Lama Forest in comparison with other seasonally dry forests. Finally, I will consider some advantages and disadvantages of phenology methods that are frequently used in primate studies.

II. Visual Observation of Plant Phenophases

A. Method

My assistants and I carried out 36 periodic visual observations of the phenophases of selected tree and liana species in the West Study Site (see Fig. 3.1). Observations were conducted monthly during the first six months, beginning on October 15, 1995 (Phenological or Pheno Period 1– 6); thereafter, semimonthly. We began observing 11 species that included 10 out of 20 highest-ranking BA/ha species (hereafter "highest-ranking species") in the dense forest (Table 4.1). These species, which account for 81.9% of the total BA/ha, were selected partially based upon the preliminary observations of *C. mona*'s food recorded during the August 1994 reconnaissance trip and upon field assistants' knowledge of *C. mona* food species. Each month, the number of species for observation was increased to examine the extent of non-common tree species' contribution to resource production. The number of species monitored was increased to 54 by April 1, 1996 and to 79 by Sept. 15, 1996. We also began observing trees in disturbed forest and farm bush on April 1, 1996 to find out if there is any variability in plant phenophases among habitat types.

The observation of plant phenophases was carried out over 2–3 days per Pheno Period when the forest floor was dry and over 3–4 days when the forest floor was muddy or inundated. The mean interval between two consecutive semimonthly Pheno Periods was 15 days. Sampled individuals, randomly selected within the West Study Site, had no

Table 4.1 79 species sampled for direct observation of phenophases

Scientific name	Local name	Abbrev.	Growth form	Fruit type	E/D^	Sample Size^^		
						DF^1	df^2	FB^3
Anacardiaceae								
Lannea nigritana*	Arekan	LANI	tree	fleshy	D	9		
Sorindeia warneckei	Babaokun	SOWA	shrub	fleshy	D			3
Spondias mombin	Ekan	SPMO	tree	fleshy	D			1
Annonaceae								
Artabotrys velutinus	Okouigbo	ARVE	climber	fleshy	D	1		
Dennettia tripetala	Eweigbo	DETR	climber	fleshy	D	1		
Apocynaceae								
Carissa edulis	Agobai	CAED	climber	fleshy	D			1
Holarrhena floribunda*	Iré	HOFL	tree	dry	D	10		
Landolphia spp.	Assan-Igbo-dudu	LASP	liana	fleshy	D	1	1	
Saba senegalensis	Assan-Igbo-Koupa	SASE	liana	fleshy	(E)	1		
Asclepiadaceae								
Parquetina nigrescens	Orobi-Ogbon	PANI	climber	fleshy	D		1	
Bignoniaceae								
Spathodea campanulata	Oshiri	SPCA	tree	dry	D		1	
Bombacaceae								
Ceiba pentandra*	Angou	CEPE	tree	dry	D	9		3
Cappariaceae								
Capparis thonningii	Achoumchoun	CATH	climber	fleshy	D	1	1	
Combretaceae								
Anogeissus leiocarpus*	Ayin	ANLE	tree	dry	D	2	2	4
Combretum hispidum	Ogan	COHI	climber	dry	D	1		
Combretum obanense	Sagado	COOB	climber	dry	D	1		
Aristolochiaceae								
Pararistolochia triactina	Iton-Ogbin	PATR	climber	fleshy	D	1		1
Ebenaceae								
Agelaea obliqua	Abpavadja doudou	AGOB	climber	fleshy	D	1		
Diospyros ferrea **	Akolemadu	DIFE	shrub	fleshy	(E)	1		
Diospyros mespiliformis*	Adou	DIME	tree	fleshy	D	9	1	
Diospyros monbuttensis	Okocho	DIMO	tree	fleshy	D	4	2	6
Vernonia colorata **	Anokoro	VECO	tree	dry	D	2		2
Euphobiaceae								
Bridelia ferruginea	Erra	BRFE	shrub	fleshy	D		1	
Drypetes floribunda* *	Tagbesso	DRFL	tree	fleshy	SE	6	9	
Mallotus oppositifolius	Eïdja	MAOP	shrub	fleshy	D	2	4	1
Margaritaria discoidea **	Awewe	MADI	shrub	fleshy	D	2	3	4
Flacourtiaceae								
Flacourtia flavescens	Elegègé	FLFL	shrub	fleshy	D	2	2	
Hippocrateaceae								
Salacia lomensis	Egba	SALO	liana	fleshy	D	5	1	
Icacinaceae								
Neostachyanthus occidentalis	Aromishai	NEOC	climber	fleshy	D	1		
Leguminosae - Caesalpinioideae								
Afzelia africana* *	Akpa	AFAF	tree	dry	D	11		
Dialium guineense*	Aïran	DIGU	tree	dry	D	9	11	
Mezoneuron benthamianum	Ikakun	MEBE	liana	dry	D	2	1	

(cont'd from previous page)

Scientific name	Local name	Abbrev.	Growth form	Fruit type	E/D$^{\wedge}$	Sample Size$^{\wedge\wedge}$		
						DF^1	df^2	FB^3
Leguminosae - Mimosoideae								
Acacia caffra	Edén	ACCA	tree	dry	D			1
Albizia ferruginea **	Ayorè ogo	ALFE	tree	dry	D	2	3	
Albizia zygia **	Ayorè	ALZY	tree	dry	D	2	7	2
Dalbergia afzeliana	Aragba	DAAF	liana	dry	D	4	2	2
Entada mannii	Ahimaga	ENMA	climber	fleshy	D			2
Tetrapleura tetraptera **	Oridan	TETE	tree	fleshy	D	1		1
Leguminosae - Papilionoideae								
Lonchocarpus cyanescens		LOCY	shrub	dry	D			1
Lonchocarpus sericeus **	Akpo	LOSE	tree	dry	D	4	2	6
Loganiaceae								
Anthocleista djalonensis	Okpo	ANDJ	tree	fleshy	D		1	
Strychnos afzelii **	Gbelé	STAF	liana	fleshy	D	10	1	
Malpighiaceae								
Flabellaria paniculata **	Iférin	FLPA	climber	dry	D	2	1	
Melastomataceae								
Memecylon dinklagei	Eweikpa	MEDI	shrub	fleshy	D	1	3	1
Menispermaceae								
Chasmanthera dependens		CHDE	liana	dry	D		1	
Moraceae								
Antiaris toxicaria **	Oro	ANTO	tree	fleshy	D	2	2	
Ficus excelsa **	Ikpin	FIEX	tree	fleshy	D	1	5	7
Ficus natalensis **	Abadan	FINA	tree	fleshy	D	2	1	
Ficus obovata	Aba (II)	FIOB	liana	fleshy	D	1		
Ficus sagittifolia **	Aba (III)	FISA	liana	fleshy	E	2	1	
Ficus sur **	Okpoto	FISU	tree	fleshy	D			17
Ficus thonningii **	Abairo or Aba (IV)	FITH	tree	fleshy	D	8	4	1
Milicia excelsa *	Iroko	MIEX	tree	fleshy	D	9	1	
Myrtaceae								
Psidium guineense **	Yagarou	PSGU	tree	fleshy	D	1		4
Ochnaceae								
Ochna membranacea **	Gbadu	OCME	tree	dry	D	13		
Passifloraceae								
Adenia lobata	Elemin	ADLO	climber	fleshy	D	1	1	
Rhizophoraceae								
Cassipourea congoensis **	Issilo	CACO	tree	fleshy	D	13		
Rubiaceae								
Canthium multiflorum		CAMU	shrub	fleshy	D	1		
Canthium vulgare	comme Elégégé	CAVU	shrub	fleshy	D	1		
Gardenia triacantha **	Awobalé	GATR	tree	dry	D	9	1	
Morinda lucida	Howo-igbo	MOLU	tree	fleshy	D	1	1	
Nauclea latifolia **	Agbossi	NALA	tree	fleshy	D		7	3
Pouchetia africana		POAF	tree	fleshy	D	1		
Psychotria latifolia	Okpaoro	PSLA	shrub	fleshy	D	1	1	
Rytigynia senegalensis	comme Elègègè	RYSE	climber	unknown	D			1
Vangueria sp.		VASP	climber	unknown	D		1	

(cont'd from previous page)

Scientific name	Local name	Abbrev.	Growth form	Fruit type	E/D^	Sample Size^^		
						DF[1]	df[2]	FB[3]
Sapindaceae								
Allophylus africanus	Idjéyé	ALAF	shrub	fleshy	D		2	2
Lecaniodiscus cupanioides **	Ayikka	LECU	tree	fleshy	D	6	3	
Pancovia bijuga **	Eheï	PABI	tree	fleshy	E (DF) D (df)	7	4	
Paullinia pinnata	Owoiya	PAPI	climber	fleshy	D	1	1	
Sapotaceae								
*Malcantha alnifolia**	Akkala	MAAL	tree	fleshy	D	4	1	
*Mimusops andongensis** BA	Ochedo	MIAN	tree	fleshy	SE	7	3	
Sterculiaceae								
Sterculia tragacantha **	Oshunshun	STTR	tree	fleshy	D	2	1	
Tiliaceae								
Grewia carpinifolia	comme Afé	GRCA	liana	fleshy	D	1		1
Grewia mollis	Afé	GRMO	shrub	fleshy	D	1	1	
Ulmaceae								
*Celtis brownii**	Amako	CEBR	tree	fleshy	D	8	6	
Vitaceae								
Cissus spp.	Affala	CISP	climber	fleshy	D		1	
Total Sample Size						225	111	78

* = species that included in PI computation between Oct. 1995 and March 1996.
** = species that were included in PI computation since Apr. 1996.
^: E = evergreen, SE = semievergreen, (E) = evergreen, but inconclusive due to small sample size; D = Deciduous
^^: This indicates the location of the samples. It does not indicate that the samples occur only in the particular habitats
DF = Dense Forest, df = Disturbed Forest

obvious signs of disease or structural damage. Their crowns were easily and clearly viewable from the trail (Struhsaker, 1981; Whitesides, 1991).

The number of sampled individuals per species varied between 1 and 20 ($\bar{x}$ = 6.4, *s.d.* = 4.91), but at least five individuals per species were observed for the 15 highest-ranking species. The sampled trees belonging to the 15 highest-ranking species were always ≥ 10 cm DBH, but sampled shrubs and climbers included individuals with ≤ 10 cm DBH. On average, phenophases of 355 individual plants (range: 285–381, *s.d.* = 32.89) were checked at each Pheno Period.

During each Pheno Period, we scanned the crown of tagged trees, lianas, and shrubs with a pair of 10 x 42 binoculars and scored the relative abundance of three vegetative parts (mature leaves, young leaves, leaf buds) and four reproductive parts (floral buds, flowers, ripe fruits, unripe fruits) in terms of the estimated percentage of maximum production. The maximum production for each part was considered 100% and estimated percentages were rounded to the nearest 5%. For cauliflorous species (i.e., *Drypetes floribunda*, *Ficus sur*), the entire trunk was observed for reproductive parts. To minimize interindividual errors, assistant's records were randomly checked. If there were large discrepancies, entire records were verified.

Fruits were further distinguished as ripe or unripe by color and size. Leaf buds, young leaves, and mature leaves were scored based on their percentages of an estimated total maximum crown volume. I distinguished young leaves from mature leaves by size, color, and texture, but for some species, these criteria were not sufficient. In this study, I have defined the period between October 1995 and September 1996 as the "first year" and the period between October 1996 and June 1997 as the "second year." To facilitate statistical analysis, I also defined Oct. 1995 as Wet Season 1 (WS1), Nov. 1995–Jan. 1996 as Dry Season 1 (DS1), Feb.–Apr., 1996 as Wet Season 2 (WS2), May–Jul, 1996 as Wet Season 3 (WS3), Aug.–Oct., 1996 as Wet Season 4 (WS4), Nov. 1996–Feb., 1997 as Dry Season 2 (DS2), and Mar. 1997–Jun 1997 as Wet Season 5 (WS5). Furthermore, I defined evergreen species as those species in which all individuals retained at least 50% of the maximum production of total leaf parts (i.e., the total of mature leaves, young leaves, and leaf buds) throughout the study period in each habitat. If all but one individual of a species retained ≥ 50% of total leaf parts at all but one consecutive Pheno Period, I defined it as a semi-evergreen species.

If ≥ 90 % of the sampled individuals of a species had lost ≥ 50 % leaves, I considered that the species had lost ≥ 50 % of leaves. If ≥ 90 % of individuals had lost all leaves, I considered that the species has lost all leaves. If < 90 % and ≥ 50 % of individuals had lost all leaves, I considered that the species had lost ≥ 50 % leaves.

B. Data Analysis

Each score obtained for vegetative and reproductive parts was summed and averaged for each species per Pheno Period. To calculate the Productivity Index for each part of each species, the average score was multiplied by the relative abundance of each species represented by the percentage contribution of its BA/ha to total tree basal area at the study site (see Chapter 3) (Fimbel, 1992). The rationale for the use of percentage contribution of BA/ha of each species is that a number of studies have found that the DBH of trees (Leighton and Leighton, 1982; Symington, 1988; Mitani, 1989; Chapman *et al.*, 1992, 1994) and tree density x DBH (Miller and Dietz, 2004) are effective indicators of plant productivities.

Species that normally do not attain ≥10 cm DBH, as well as small trees with unknown BA/ha contribution and climbers, were eliminated from the Productivity Index computation. Consequently, the computation of Productivity Index during the first six months was limited to the following nine species that accounted for 81.1% of total BA/ha in the forest: *Anogeissus leiocarpus*, *Celtis brownii*, *Dialium guineense*, *Diospyros mespiliformis*, *Holarrhena floribunda*, *Lannea nigritana*, *Malacantha alnifolia*, *Mimusops andongensis*. Thereafter, the Productivity Index was calculated for 35 species that accounted for 99.7% of the total BA/ha (Table 4.2).

I focus on the Productivity Index of young leaf parts, floral parts, and fruits, since these parts rather than mature leaves are probably more important to the diet of *C. mona* that is examined in the following chapter. I also examine the Productivity Index of unripe and ripe fruits more thoroughly than other plant parts because the study subject, *C. mona* is a frugivore. Spearman's Correlation Coefficients between monthly Productivity Indices for young leaf parts, floral parts, and fruits and rainfall were examined. I also examined correlation between rainfall and monthly summed Productivity Index for each of the following three plant categories: deciduous dry fruit producing species (e.g., pods, capsules, winged-fruits), deciduous fleshy fruit producing species (e.g., species that produce drupes, berries, fruits with arillate seeds), and evergreen and semi-evergreen fleshy fruit producing species (Brugière *et al.*, 2002). Furthermore, to find out whether there are any differences in the timing of phenophases in vegetative and reproductive parts in different habitat types, Spearman's Correlation Coefficients were examined for summed Productivity Index of young leaf parts, flower parts, and fruits among habitats for Pheno Periods 7–36.

Table 4.2 Number of species and BA/ha % included in the Productivity Index computation

Pheno Period 1-6	Fleshy Spp.		Dry Spp.		Total	
	N	BA/ha %	N	BA/ha %	N	BA/ha %
Evergreen and Semi-evergreenspp.	1	6.9	1	34.9	2	41.8
Deciduous spp.	5	24.2	3	15.8	8	40.1
Total	6	31.1	4	50.8	10	81.9

Pheno Period 7-38	Fleshy Spp.		Dry Spp.		Total	
	N	BA/ha %	N	BA/ha %	N	BA/ha %
Evergreen and Semi-evergreenspp.	7	11.9	1	34.9	8	46.8
Deciduous spp.	14	26.3	13	26.5	27	52.9
Total	21	38.2	14	61.5	35	99.6

C. Results

1. Evergreen, Semi-Evergreen, and Deciduous Species

Ficus sagittifolia was definitely evergreen. *Saba senegalensis*, and *Diospyros ferra* also appeared to be evergreen species. *Drypetes floribunda* and *Mimusops andongensis* were semi-evergreen species. *Pancovia bijuga*, an understory trees, behaved as if it is an evergreen species in dense forest, but it was deciduous in disturbed forest. Therefore, it is considered a deciduous species. All other species were deciduous.

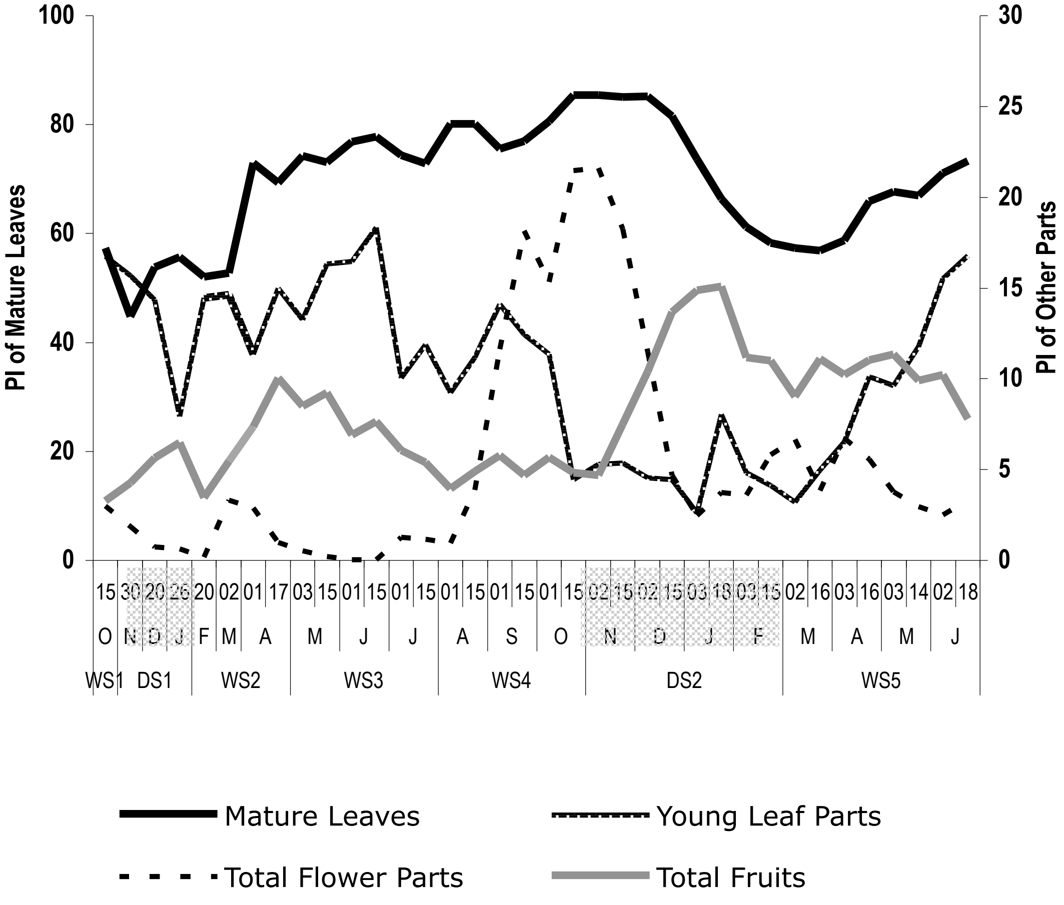
2. General Patterns

Vegetative Parts: The phenological paterns observed were distinctly seasonal. The peak of mature leaves occurred during the major dry seasons. Leaf flush occurred mostly in wet seasons, but it also occurred to a much lesser degree in dry seasons (Fig. 4.1). The production of young leaf parts was correlated with rainfall ($r_s = 0.538$, $p = 0.012$).

Fig. 4.2 shows percentage of species that lost ≥ 50% and all of their leaves during this study. The peak percentage of species without any leaves occurred at the beginning of wet seasons following the major dry seasons. The percentage of species that lost ≥ 50% leaves was negatively correlated with monthly rainfall ($r_s = -0.620$, $p = 0.003$), but the percentage of species that became entirely leafless was negatively correlated with rainfall from previous month only ($r_s = -0.553$, $p = 0.009$). It appeared that there was a delayed effect of rainfall.

At the height of the first major dry season, the percentage of species that lost ≥ 50% of their leaves was 37% and the percentage of species that lost all of their leaves was 11%. During the second major dry season, however, the percentage of species that

Fig. 4.1 Summed Productivity Indices of reproductive and vegetative parts* of all fleshy and dry fruit species combined
The peak of mature leaves occurred during the second major dry season. Leaf flush occurred mostly, but not only in wet seasons. Flowering peaked in a wet season during the first year and in the major dry season in the second year. Fruiting peak also occurred in a wet season in the first year, but in the major dry season in the second year.



* PI computation was limited to nine species that accounted for 81.9% of total BA/ha% during the first six months. Thereafter, 35 species that accounted for 99.7% of total BA/ha% were included in the computation.

Fig. 4.2 Percentages of observed species that have shed at least 50% leaves or all leaves Shaded months indicate major dry seasons. (If all or all but one individual of a species have lost ≥ 50% or 100% leaves, the species was considered to have lost ≥ 50 % or 100 % leaves.)

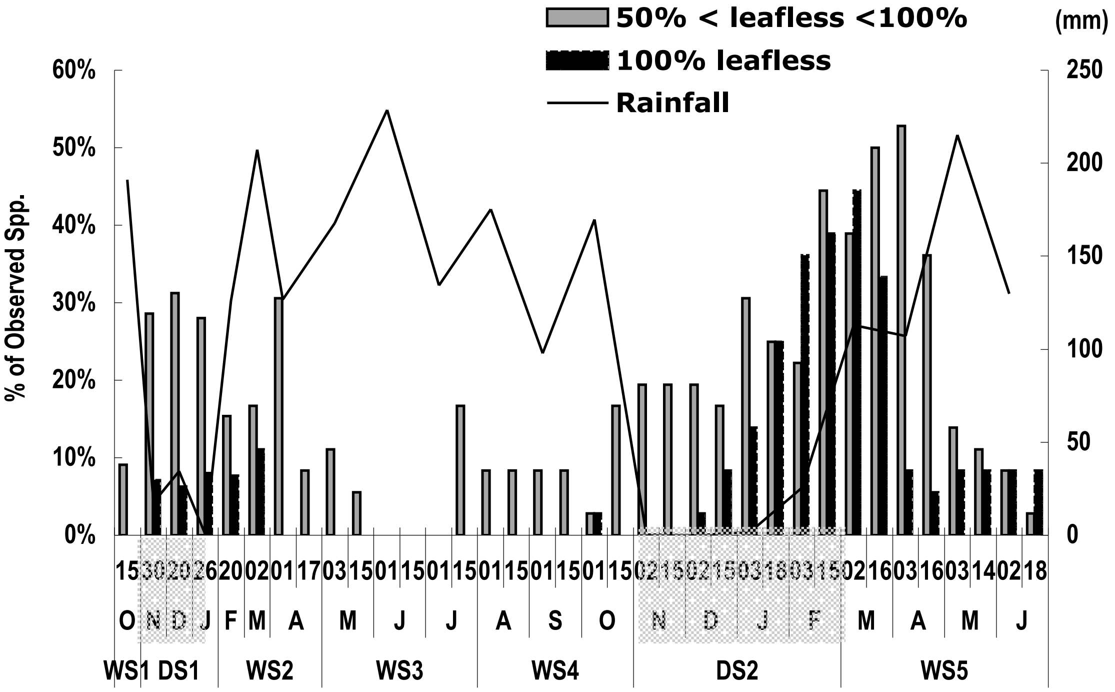
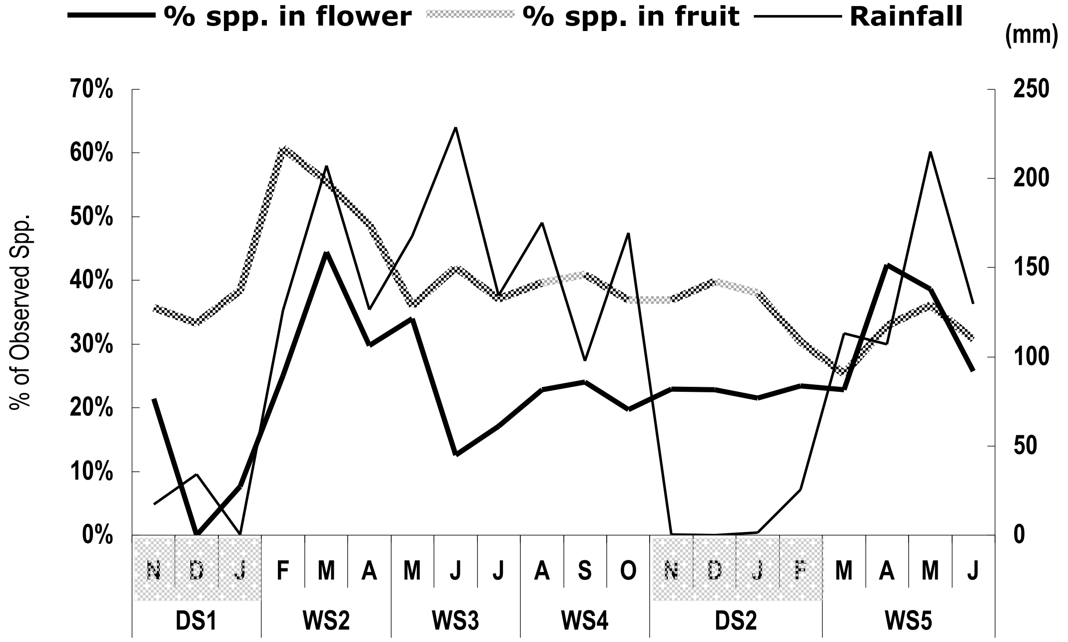


Fig. 4.3 Percentages of observed species in flower and in fruit Shaded months indicate major dry seasons.



lost ≥ 50% of leaves was 83% and the percentage of species that lost 100 % leaves was 44%. More than twice as many species lost ≥ 50% of their leaves, and four times more species were leafless in the second major dry season than in the first major dry season.

Reproductive Parts: The peaks of floral parts occurred in March during the first year and in November during the second year. As for fruits, minor peaks occurred in April during the first year and January in second year (Fig. 4.1). Many species had flowers when they were partially or entirely leafless. The seasonal patterns of the percentages of the number of species in flower and fruits are shown in Fig. 4.3. The peak of the percentage of observed species in fruit occurred at the beginning of the wet season (WS2) that immediately followed the major dry season in the first year, but it occurred during the major dry season in the second year, earlier than the first year.

3. Differences Among Plant Categories

The above general pattern of plant phenophases masks striking differences that mainly distinguish dry fruit species from fleshy fruit species (Fig. 4.4–9).

Leaf Parts: All plant categories had their peaks of leaf loss (Fig. 4.4) in major dry seasons and young leaf (Fig. 4.5) production mainly in wet seasons, although the precise peaks differed among the plant categories. Some dry fruit species such as *Ceiba pentandra, Afzelia africana*, *Albizia ferruginea,* and fleshy fruit species such as *Milicia excelsa* shed their leaves during the major dry seasons and had leaf flush almost simultaneously even before the onset of rain. In some species, leaf fall began during the major dry seasons, but the peak leaf fall and subsequent leaf flush did not occur until the onset of rain. These species included *Anogeissus leiocarpus*, *Antiaris toxicaria*, *Celtis brownii*, *Diospyros mespiliformis*, *Ficus natalensis*, *Flabellaria paniculata*, *Holarrhena*

Fig. 4.4 Summed Productivity Indices of mature leaves by plant categories (Shaded months indicate major dry seasons.) As in many tropical forests, productivity of mature leaves in the Lama Forest is depressed during major dry seaons.

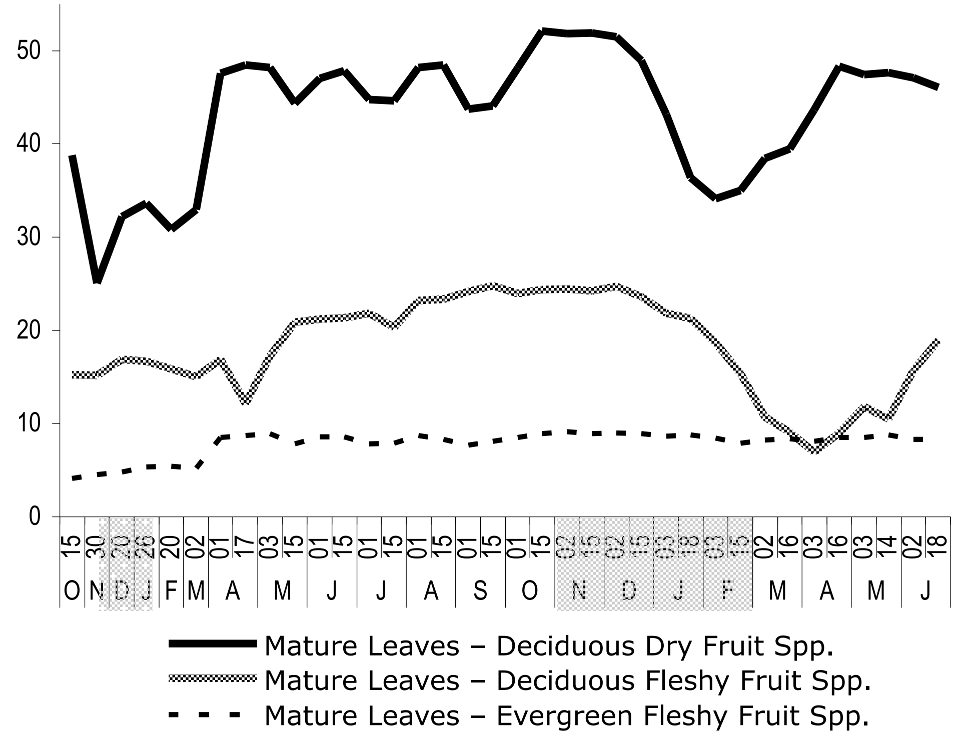
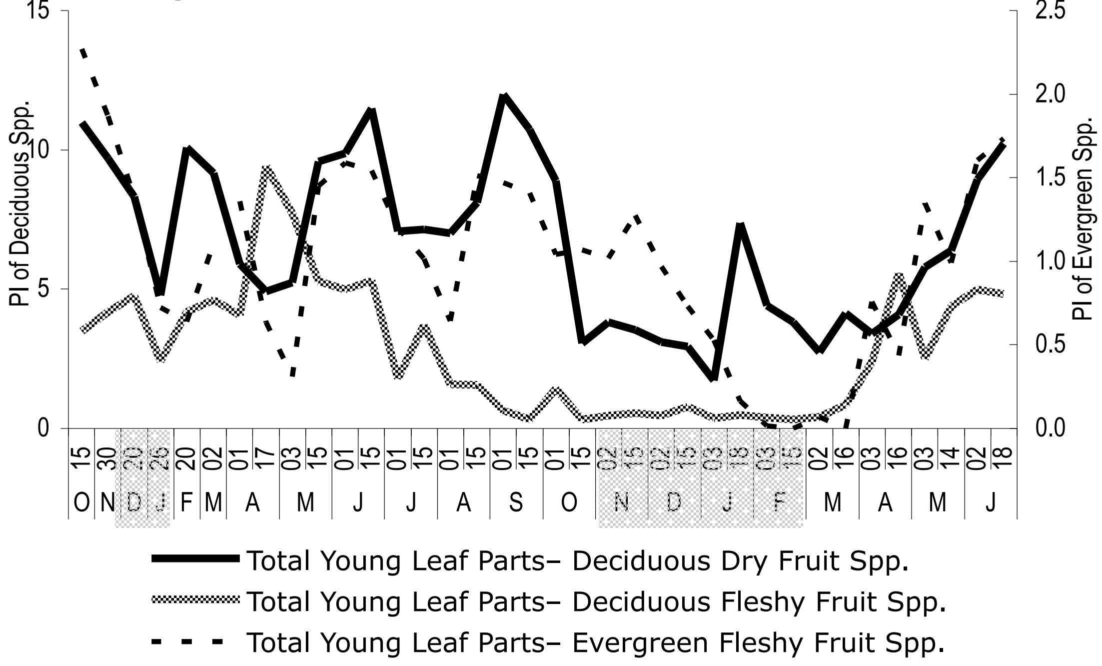


Fig. 4.5 Summed Productivity Indices of young leaf parts by plant categories (Shaded months indicate major dry seasons.) As in many tropical forests, leaf flush in the Lama Forest mostly occurs in wet seasons.



floribunda, *Lannea nigritana*, *Lonchocarpus sericeus*, *Malacantha alnifolia*, *Sterculia tragacantha*, and *Tetrapleura tetraptera*.

Floral parts: In dry fruit species, there was no discernible peak during the first year, but a peak occurred during the transitional period from a wet season to a major dry season. In deciduous fleshy fruit species, there was no discernible peak in 1996, but in 1997, a peak occurred in a wet season. In evergreen/semi-evergreen species, peaks occurred in wet seasons (Fig. 4.6).

Total Fruits: Dry fruits had peaks in January in both years, but the second year's peak was much greater than the first. All fleshy fruits peaked in April 1996 during the first year. During the second year, the peaks of fleshy fruits occurred in November for deciduous species and June for evergreen/semi-evergreen species (Fig. 4.7).

Unripe Fruits: The peaks of dry fruits and deciduous fleshy fruits occurred in January and November in both years, respectively. Evergreen/semi-evergreen fruits had a greater peak in April 1996 and a smaller peak in June 1997 (Fig. 4.8).

Ripe Fruits: Dry fruits had a small peak from March to May 1996 and a greater peak from February to May 1997. In comparison, deciduous fleshy fruits had a peak in April 1996 and February 1997. Evergreen/semi-evergreen species had a smaller peak in April 1996 and a greater peak in September 1996 (Fig. 4.9).

Fig. 4.10 shows the Productivity Index of *Dialium guineense* fruits, other dry fruits, and fleshy fruits. If I define a season of scarcity for *C. mona* as a period when fleshy fruits are scarce, the major dry season (Nov. – Mar.) fits this definition. If I define it as the period when the Productivity Indices of all fruits are lowest, October 1995, February 1996, and August 1996 become periods of scarcity. The details of the scarcity

Fig. 4.6 Summed Productivity Indices of flower parts by plant categories, showing a highly seasonal pattern of flower production. Flowering in dry fruits peaked in the major dry season, but flowering in fleshy fruits peaked in wet seasons.

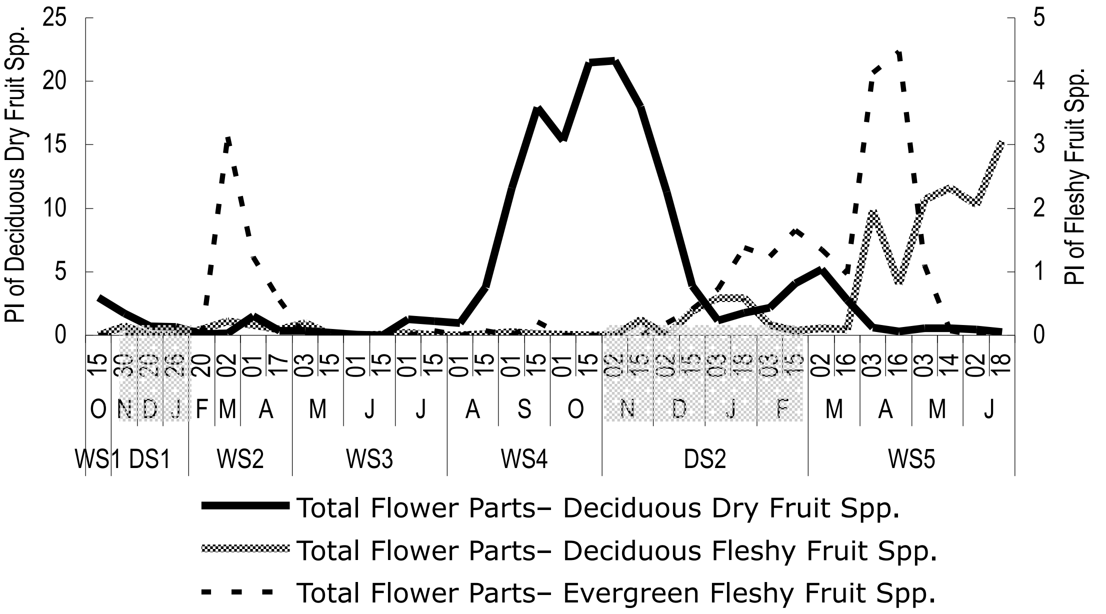


Fig. 4.7 Summed Productivity Indices of fruits by plant categories. In the first year, deciduous fleshy fruits peaked in a wet season, but in the second year, it peaked from the end of a wet season to the beginning of the major dry season. Evergreen fleshy fruits peaked in wet seasons. Dry fruits peaked in the major dry seasons.

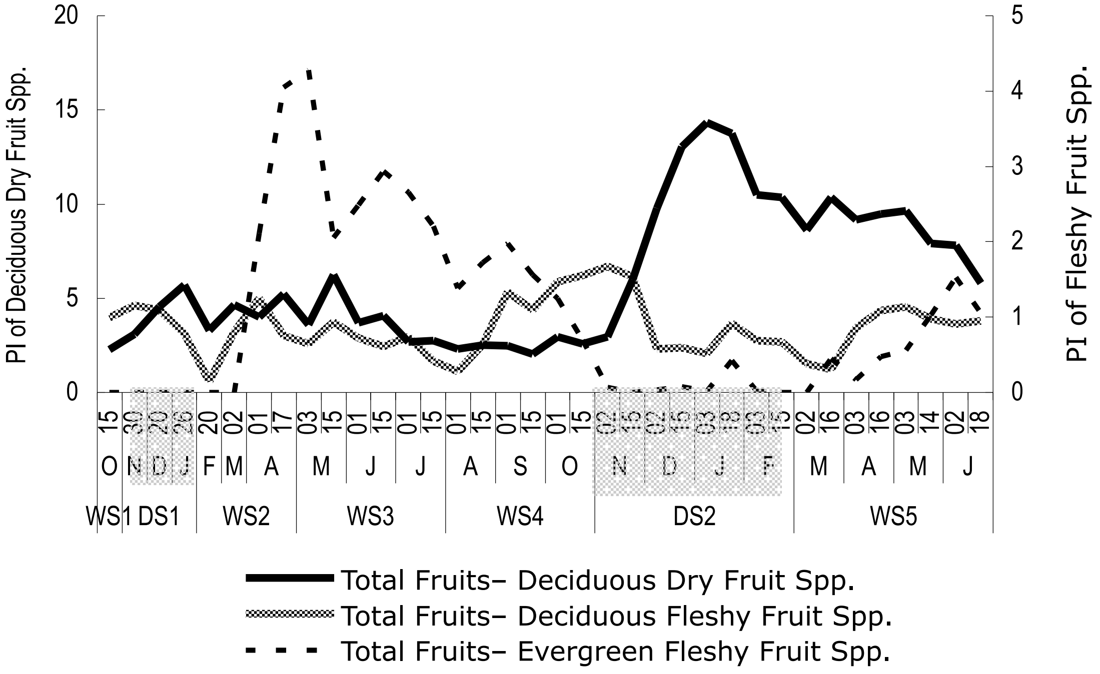


Fig. 4.8 Summed Productivity Indices of unripe fruits by plant categories. Unripe dry fruits are available in major dry seasons and unripe fleshy fruits are mainly available in wet seasons.

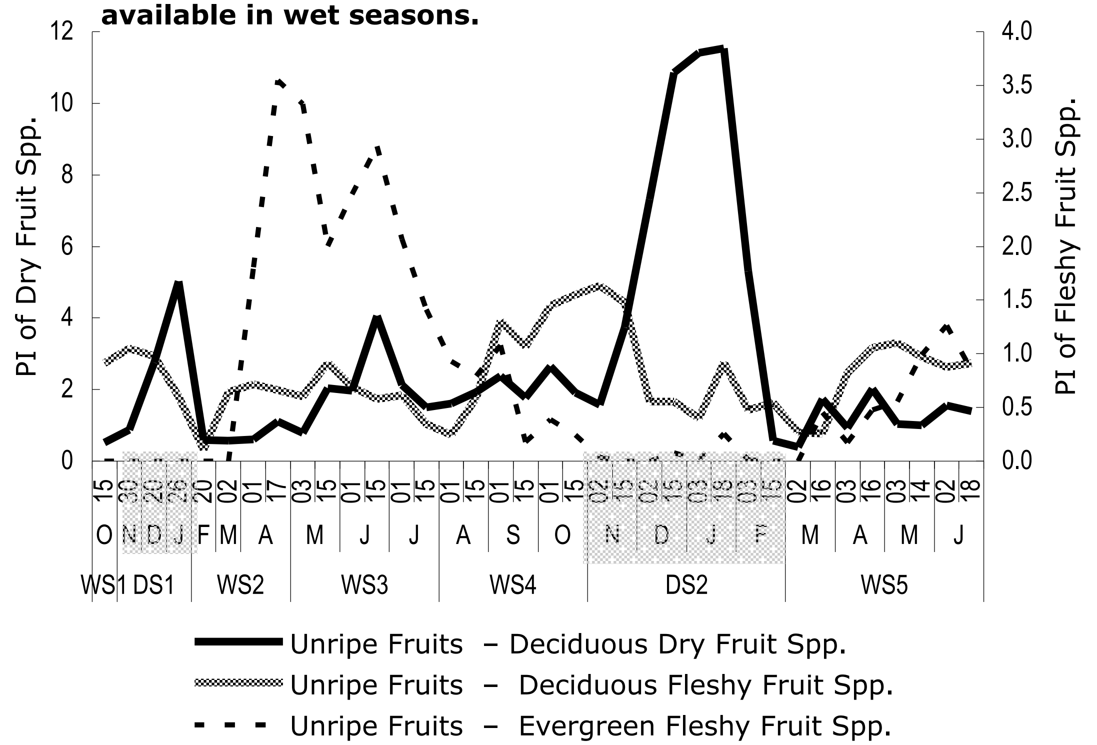


Fig. 4.9 Summed Productivity Indices of ripe fruits by plant categories. Ripe dry fruits and fleshy fruits are mostly available in wet seasons.

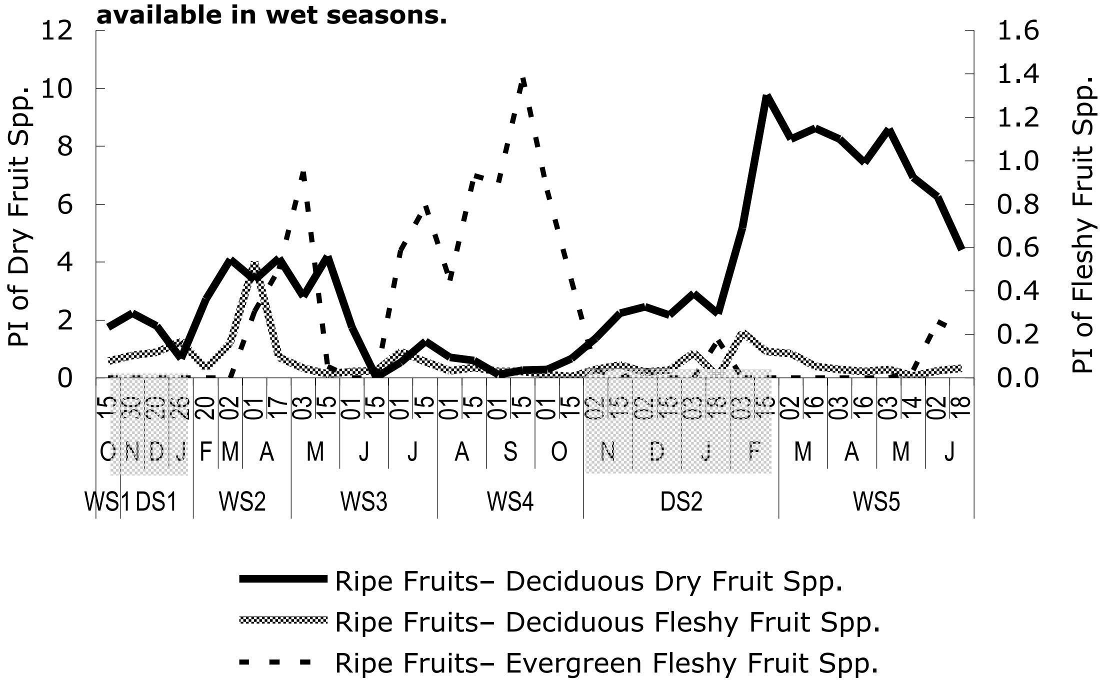
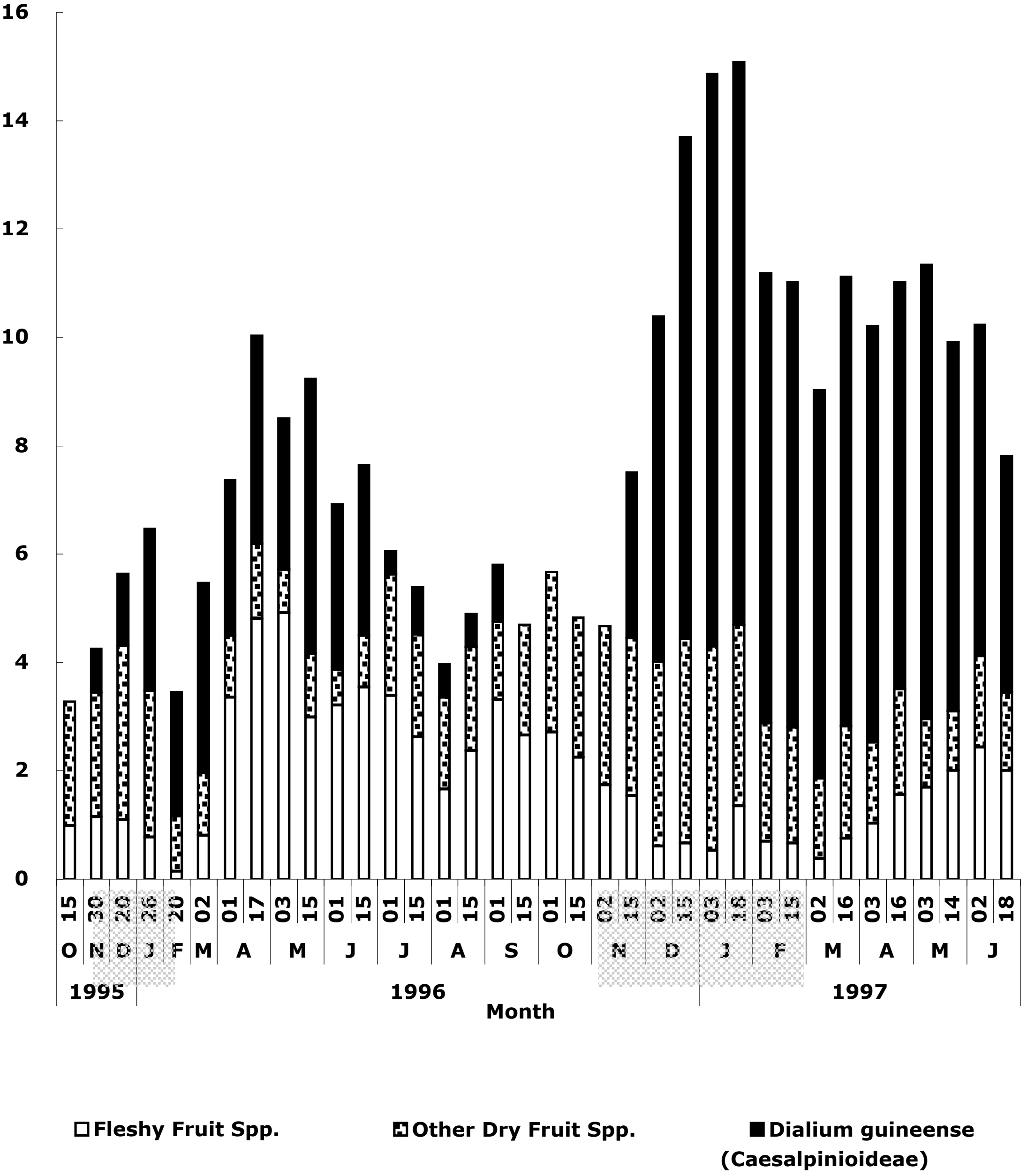


Fig. 4.10 Productivity Indices of *Dialium guineense* (Caesalpinioideae) fruits, other dry fruits, and fleshy fruits (Shaded months indicate major dry seasons.)



during these periods, however, differed. In October 1995 (WS1) and August 1996 (WS4), there were little or no *Dialium guineense* fruits, but other dry fruits and fleshy fruits were available. In February 1996 (DS1), fleshy fruits were scarce, but *Dialium guineense* fruits and other dry fruits were available.

The Productivity Index of deciduous fleshy fruits at Lama fluctuated erratically at intervals of about 1–2 months throughout the study period; however, such a phenomenon was not observed in dry fruit species.

4. Habitat Differences

Leaves: In all plant categories, the seasonal production of mature leaves was similar in all habitats for fleshy fruit species, but the production of mature leaves in the dry fruit species was more seasonal in dense forest than in disturbed forest or farmbush (Fig. 4.11A). As for young leaf parts, the patterns of production in all plant categories were more seasonal in disturbed forest than in dense forest (Fig. 4.11B).

Floral parts: In dry fruit species, the production of floral parts was correlated between dense forest and disturbed forest ($r_s = 0.571, p < 0.001$) and between disturbed forest and farm bush ($r_s = 0.676, p < 0.001$) (Fig. 4.12). The peak flowering in dry fruit species in farm bush occurred 1.1/2 months earlier than that occurred in dense forest and disturbed forest. In deciduous fleshy fruit species, the production of floral parts in dense and disturbed forests was much lower in the first year than in the second year, but in farm bush it was higher in the first year than the second year. In evergreen/semi-evergreen fleshy fruit species, the Productivity Index was highly correlated between dense forest and disturbed forest ($r_s = 0.839, p < 0.001$).

Fig. 4.11A Productivity Indices (PI) of leaves in three habitats: mature Leaves

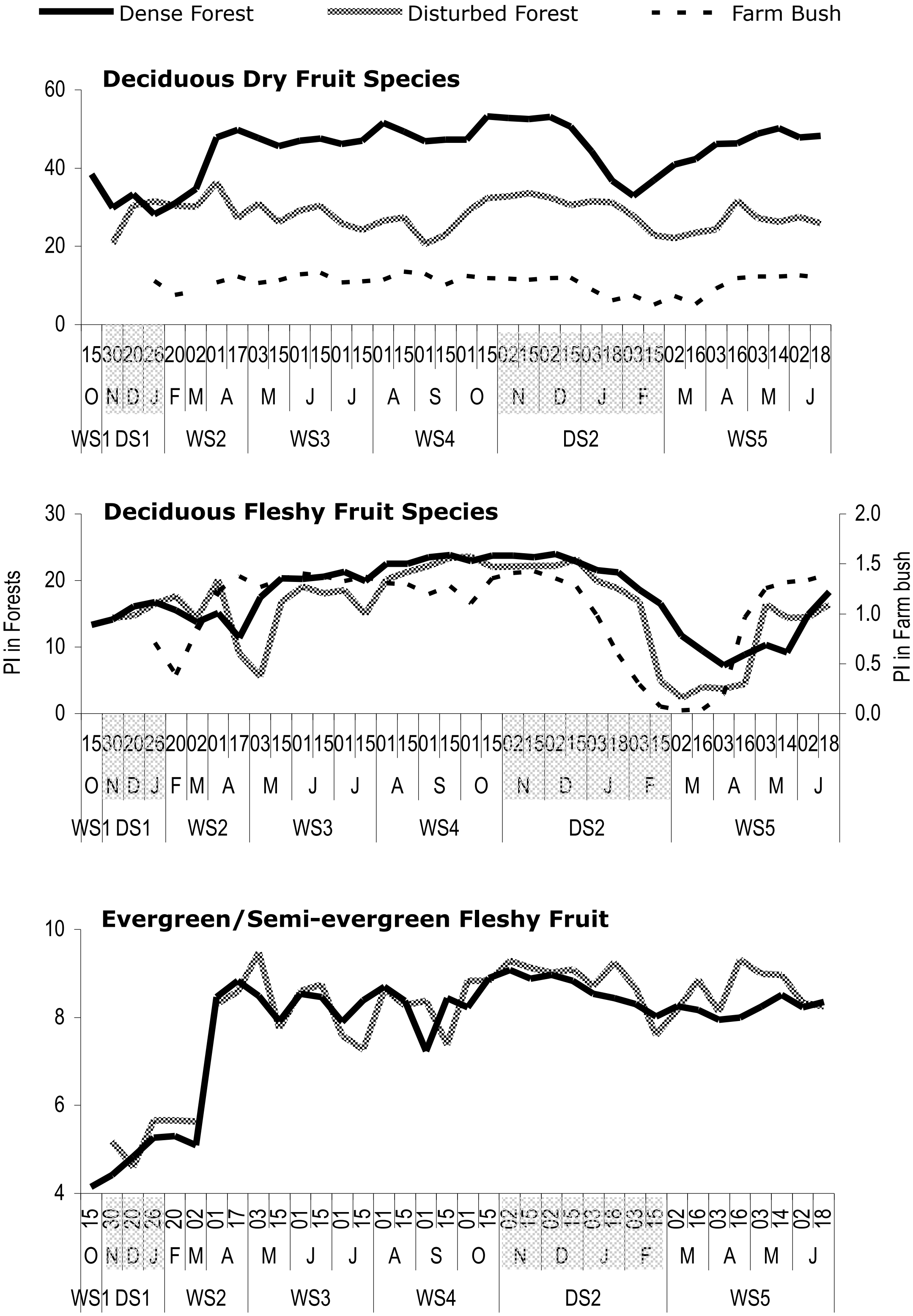
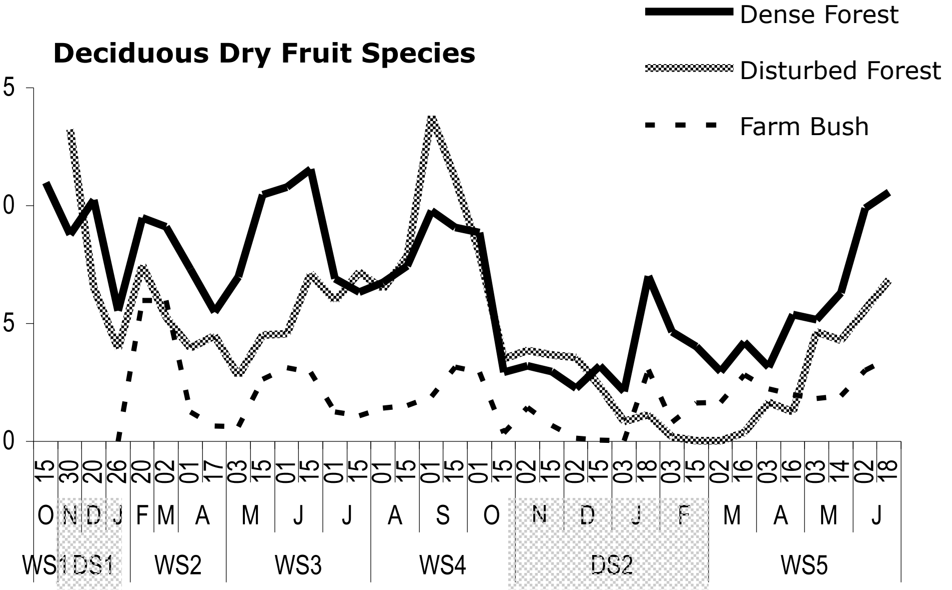
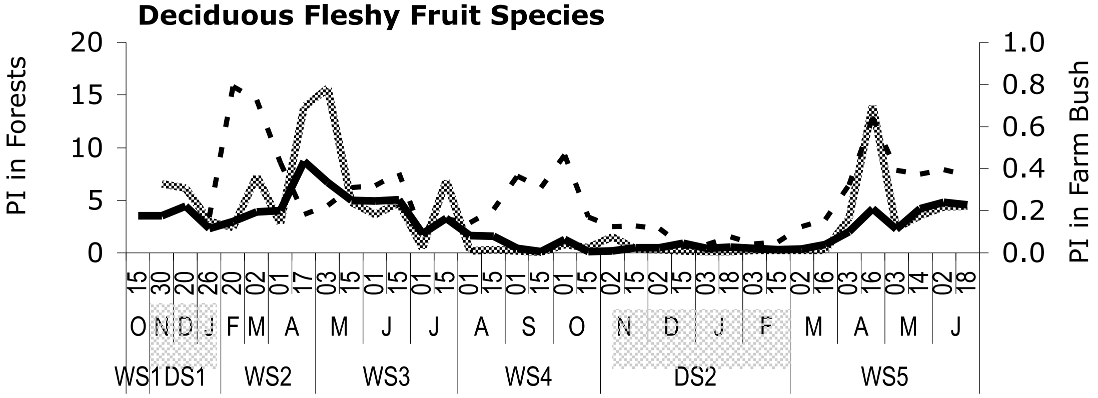


Fig. 4.11B Productivity Indices (PI) of leaves in three habitats: young leaf parts


Deciduous Dry Fruit Species


Deciduous Fleshy Fruit Species

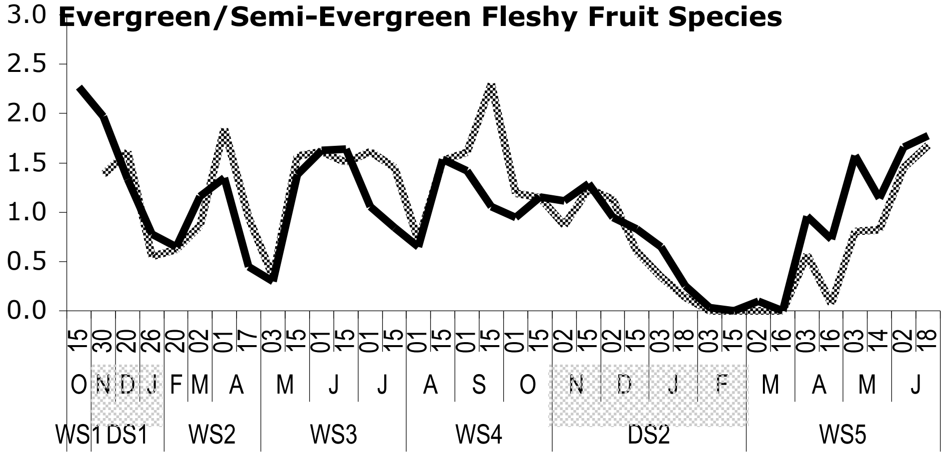
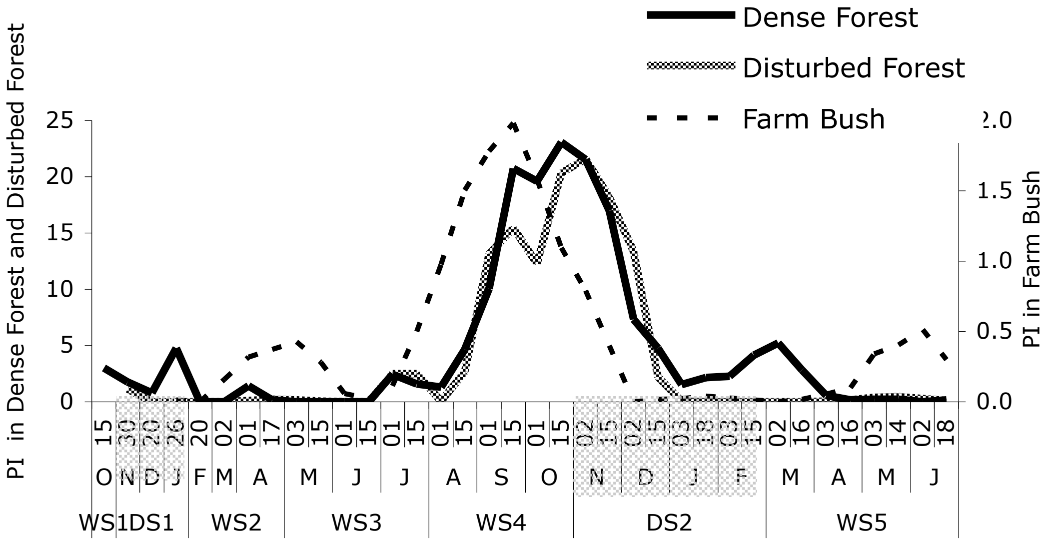
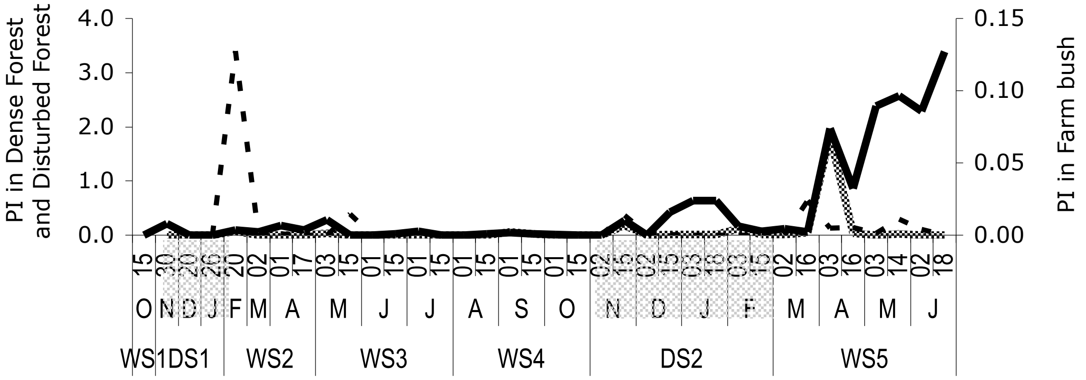

Evergreen/Semi-Evergreen Fleshy Fruit Species

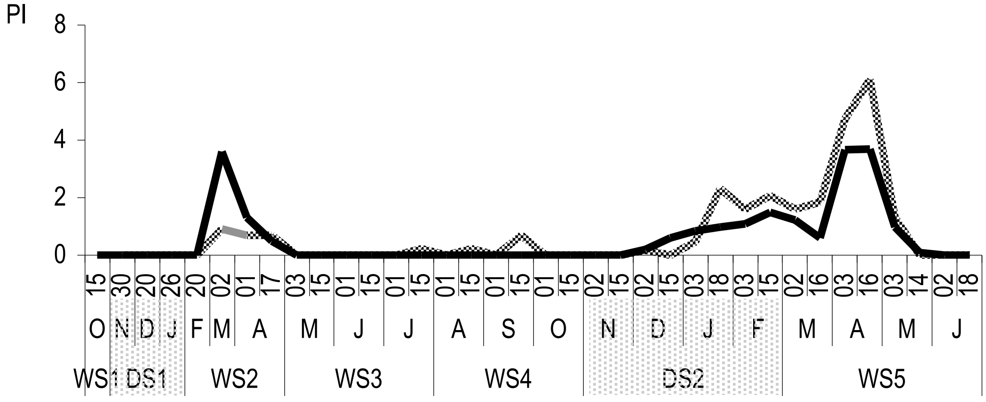
Fig. 4.12 Productivity Indices of flower parts in three habitats. Productivity in farmbush is about 1/10 or less than that in Dense Forest or Disturbed Forest.



Deciduous Dry Fruit Species



Deciduous Fleshy Fruit Species



Evergreen/Semi-Evergreen Fleshy Fruit Species

Fruits: The Productivity Index of deciduous fleshy fruit species fluctuates irregularly in dense forest while its fluctuation in disturbed forest is more equable (Fig. 4.13). Such a difference is not evident in dry fruit species and evergreen/semi-evergreen fleshy fruit species. Fruit productivities in dense and disturbed forests were more highly correlated in dry fruit species ($r_s = 0.791, p < 0.001$) and in evergreen/semi-evergreen fleshy fruit species ($r_s = 0.809, p < 0.001$) than in deciduous fleshy fruit species ($r_s = 0.381, p = 0.024$).

5. Intraspecific and Interannual Variations

There was intraspecific variation in the patterns of phenophases in many species. For example, Fig. 4.14 shows that only one out of five *Ceiba* trees monitored for phenophases produced fruits during the second dry season and the timing of flowering, fruiting, and leaf flush was asynchronous. In contrast, the timing of flowering, fruiting, and leaf flush was synchronized in *Afzelia africana*, although the peak fruiting periods differed (Fig. 4.14). In *Diospyros mespiliformis*, flowering and fruiting occurred in less than half of sampled individuals in both years. Fig. 4.15 shows that two *Diospyros* trees produced fruits in 1996, but two others did not. It also shows the variability in the production of floral parts in *Milicia* trees during the second major dry season.

The patterns of leaf fall and leaf flush over a 15–17 month period in some fleshy and dry fruit species are shown in Fig. 4.16 and Fig. 4.17, respectively. Although only nine species were observed at the beginning of the first major dry season, the figures show that the patterns of mature leaf and young leaf production in deciduous fleshy fruit species (e.g., *Ficus thoningii, Diospyros mespiliformis, Antiaris africana, Ficus excelsa, Celtis brownii*) differed more between the first and second years than dry fruit species.

Fig. 4.13 Productivity Indices of fruits in three habitats

Productivity in Farmbush is 1/8 or less than that of the productivities in Dense Forest or Disturbed Forest.

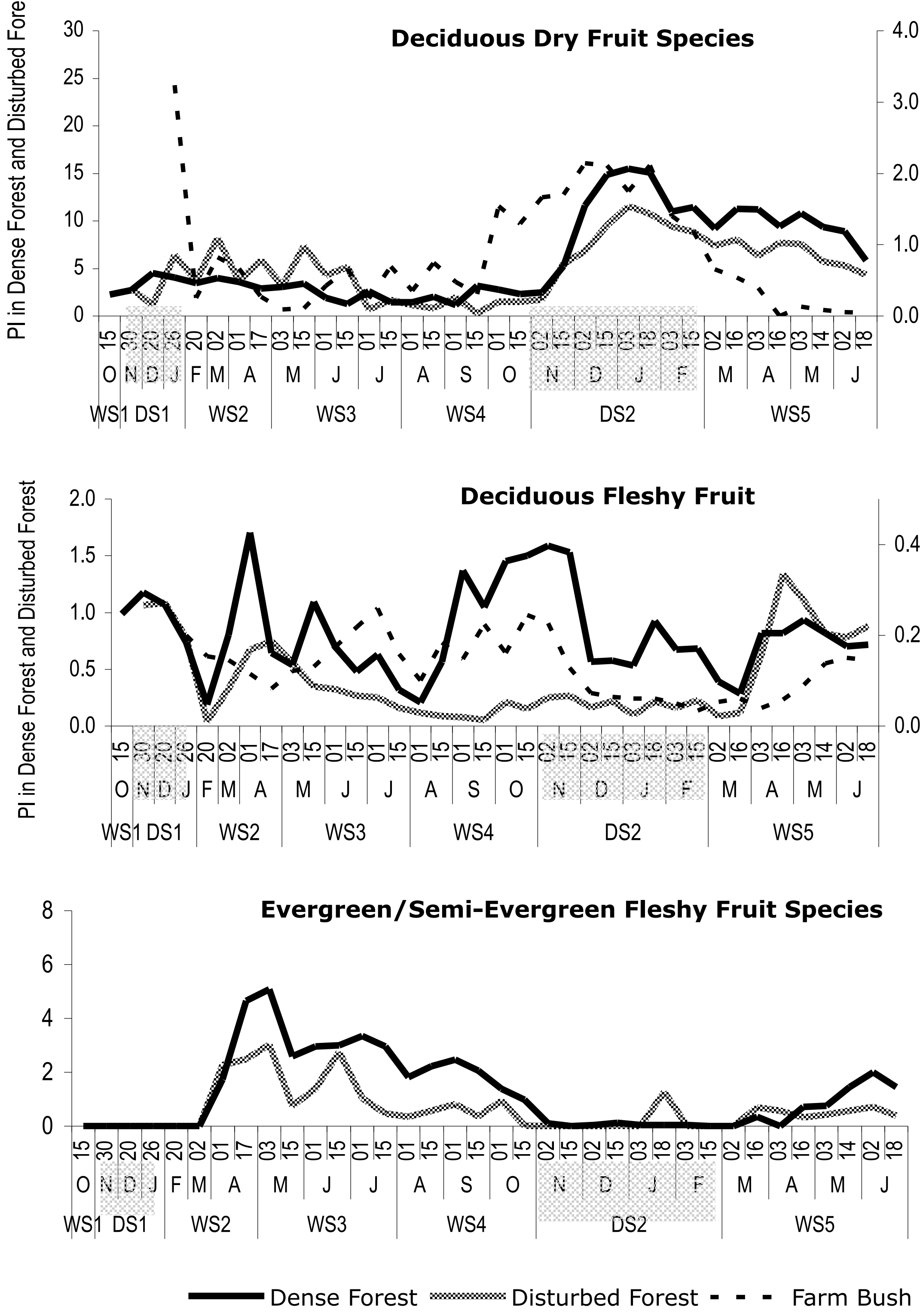


Fig. 4.14 Interindividual variation in the leaf phenophases in *Ceiba pentandra* (CEPE) and *Afzelia africana* (AFAF)

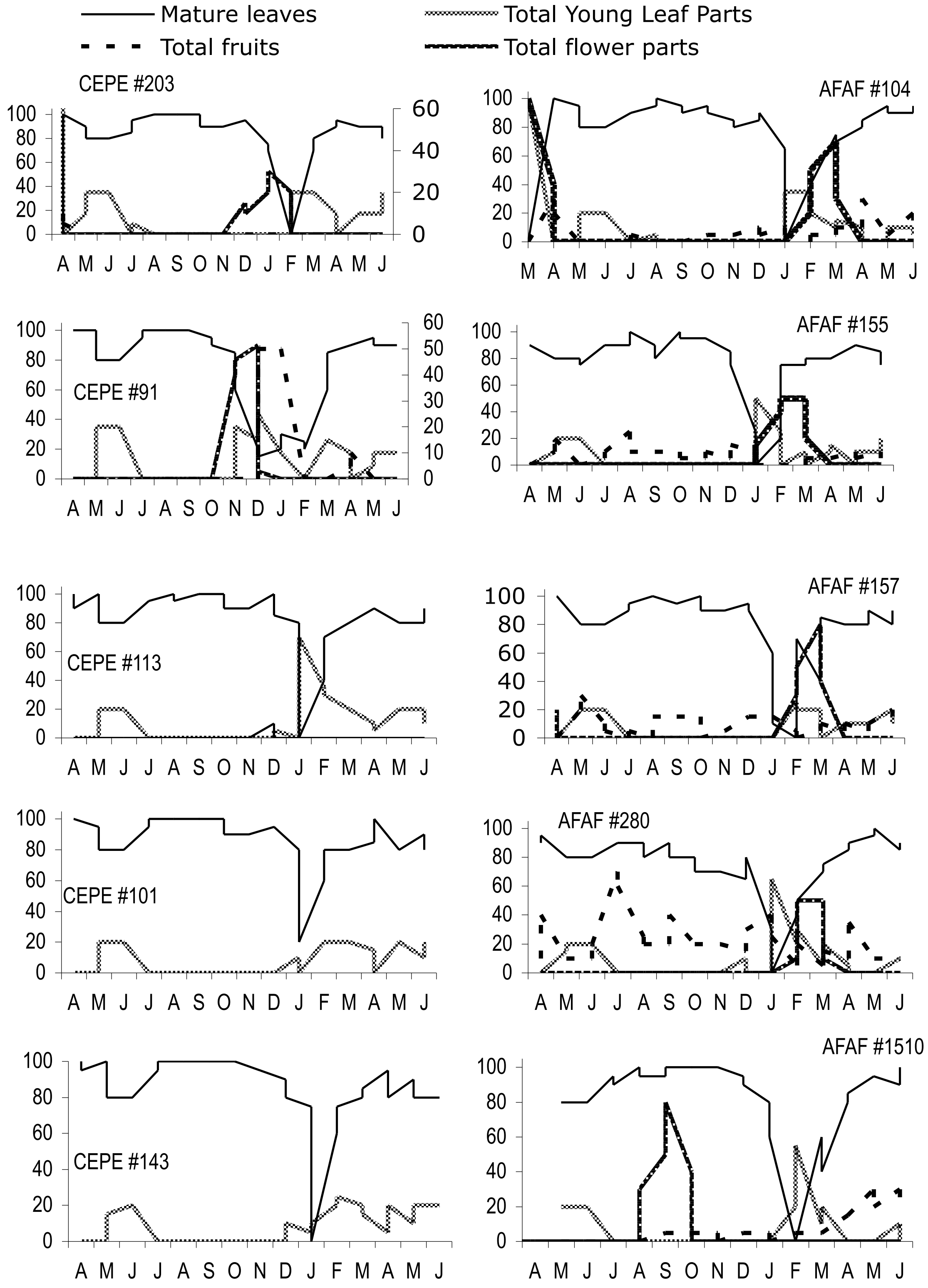


Fig. 4.15 Intraspecific variation in phenophases in *Diospyros mespiliformes* and *Milicia excelsa*

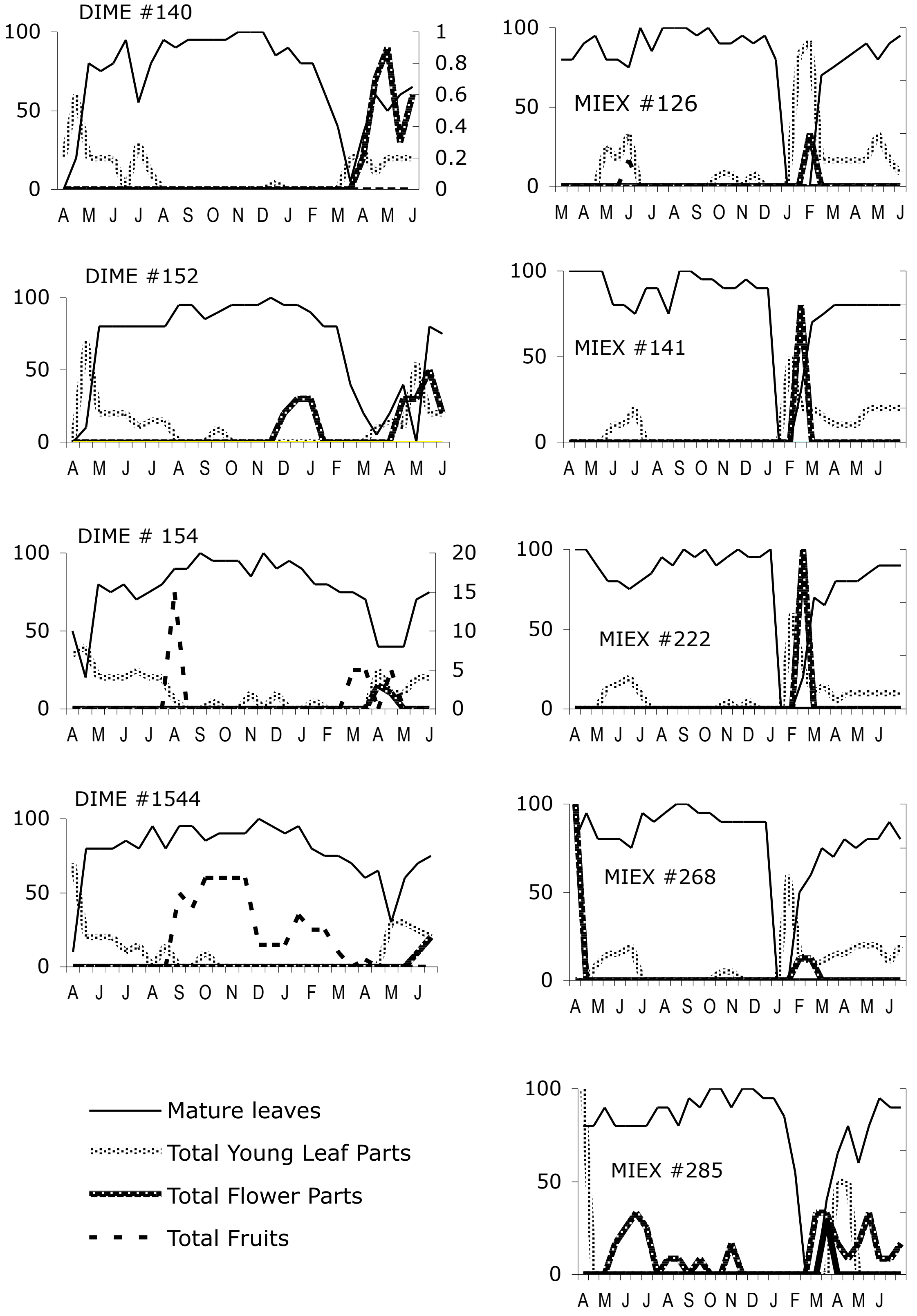
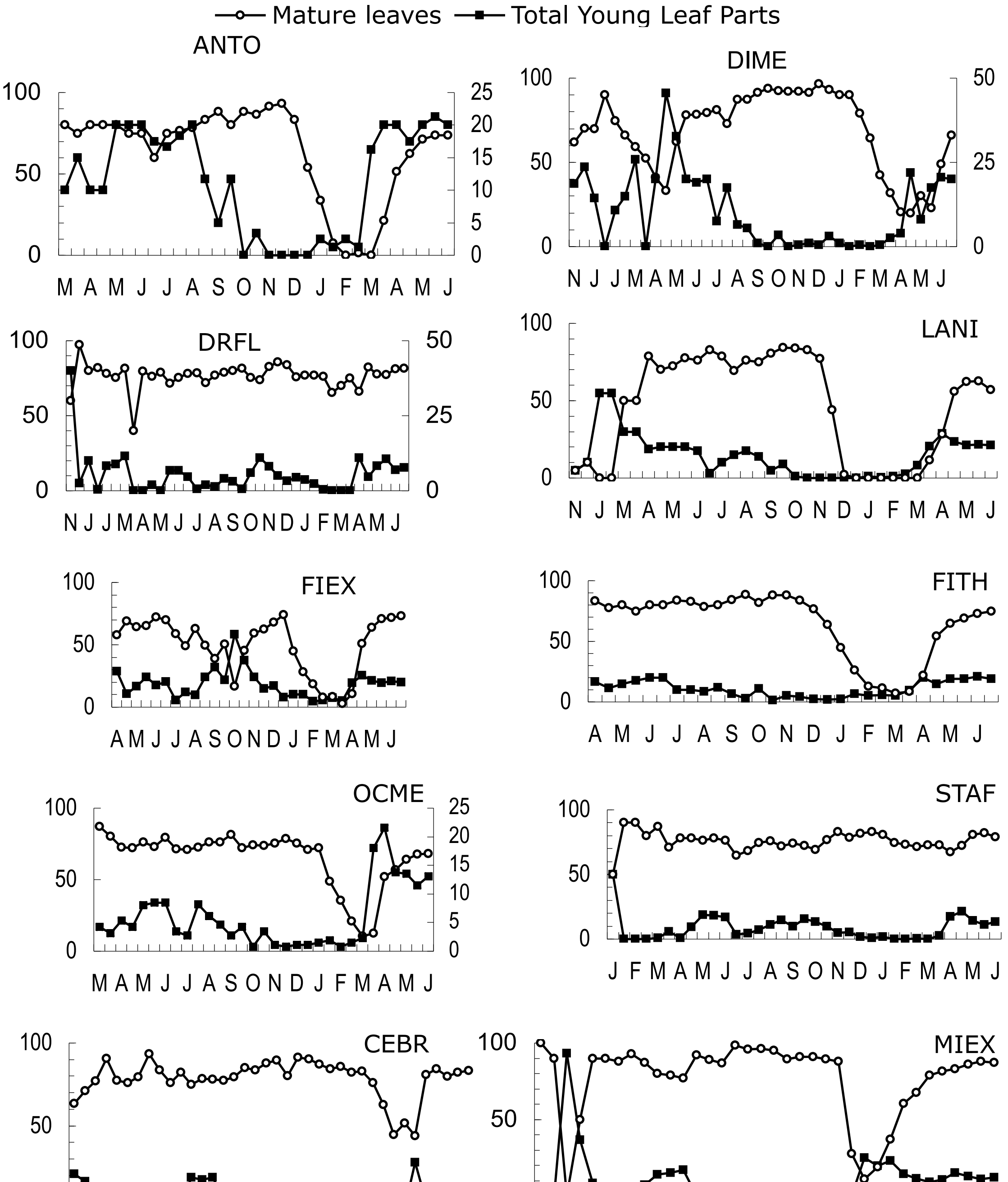
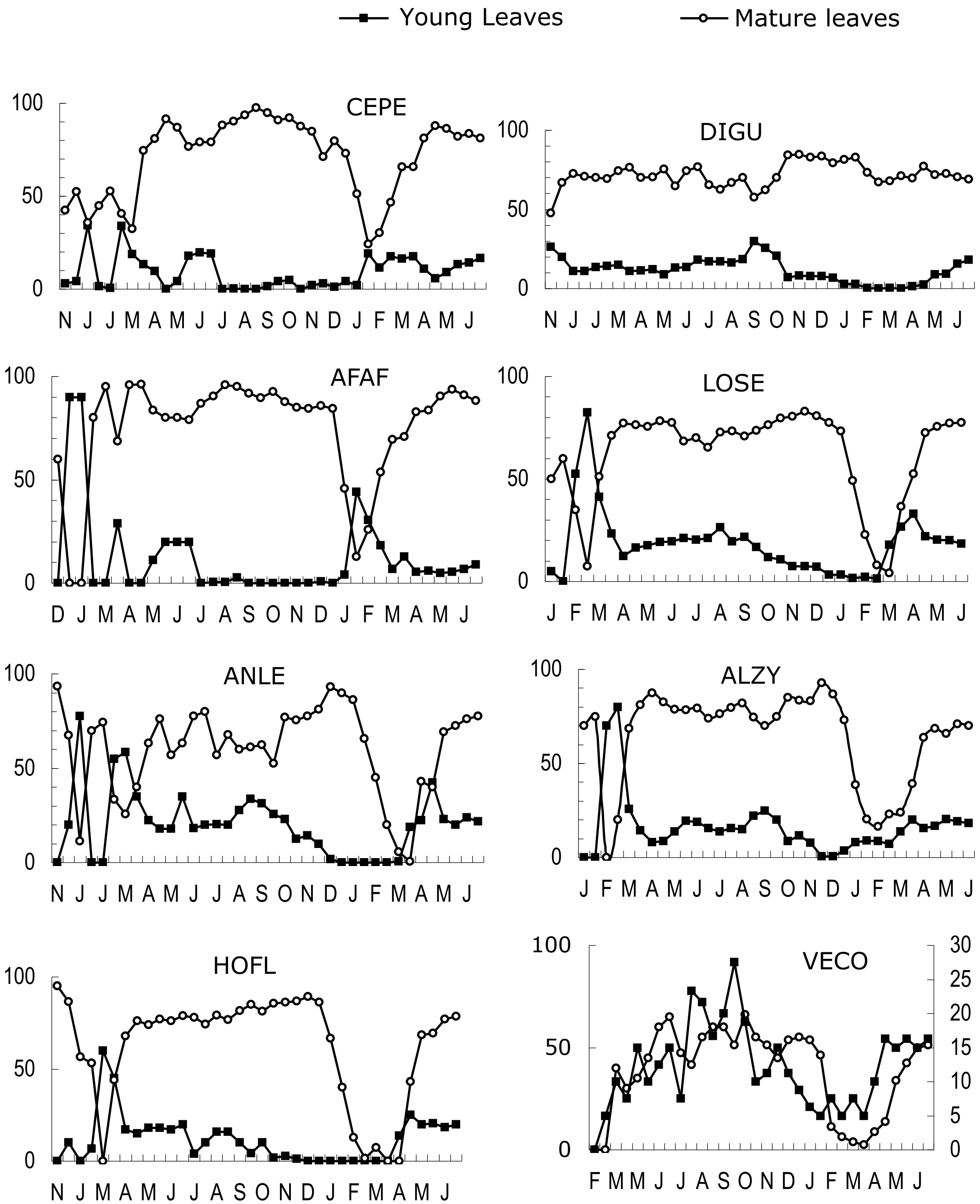


Fig. 4.16 Leaf phenophases in selected fleshy fruit species



Note: The secondary y-axis for some species is for young leaf parts.

Fig. 4.17 Leaf phenophases in selected dry fruit species



Note: The secondary y-axis for VECO is for young leaf parts.

Fig. 4.18 shows the patterns of flowering and fruiting over a 15–17 month period in some fleshy fruit species. *Antiaris africana* produced no flowers in 1996. *Drypetes floribunda* flowered extensively in the first year, but many fewer floral parts were produced in the second year. Similarly, *Lannea nigritana* produced many more flowers in the first year than the second year. *Celtis brownii* produced more ripe fruits in the first year than the comparable period in the second year. Similar interannual variation is also evident in dry fruit species (e.g., *Ceiba pentandra*, *Dialium guineense*, *Afzelia africana*) (Fig. 4.19).

III. Trail Survey of Fallen Fruits

A. Method

In addition to the direct observation of plant phenophases, I also conducted trail surveys of fallen fruits on two census routes to quantify fruit productivities. The trail survey method is also termed the raked-trail survey, but it does not use a rake to collect fruits (Zhang and Wang, 1995). I began collecting fruits in plastic bags on the 1m-width 2.5 km census route A on Oct. 15, 1995. This distance was increased to 4 km in mid-January 1996 when I also began collecting fruits on the equidistant census route B. The fruit-trail surveys were conducted monthly during the first six months, thereafter, semimonthly except the period between June 1 and September 1, 1996 when the survey was conducted once a month due to deep inundation. All unripe and ripe intact fruits, which were not rotten or partially eaten, were collected in plastic bags and identified by species, counted, and grouped into one of the two fruit categories: fleshy or dry fruits (Sabatier, 1985; Sourd and Gautier-Hion, 1986; Butynski, 1990; White, 1994b; Brugière

Fig. 4.18 Interannual variation in phenophases of flower parts and fruits in fleshy fruit species

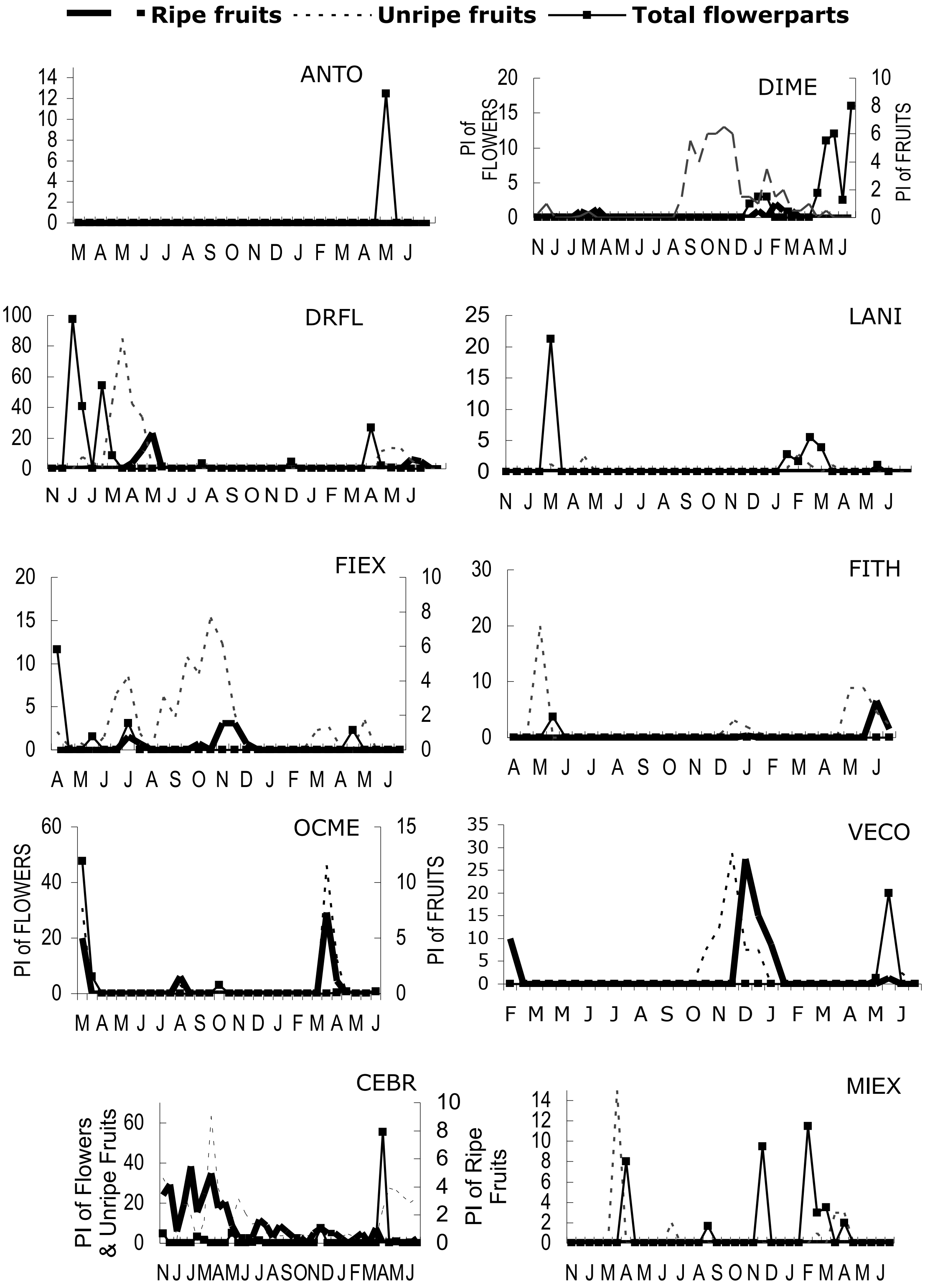
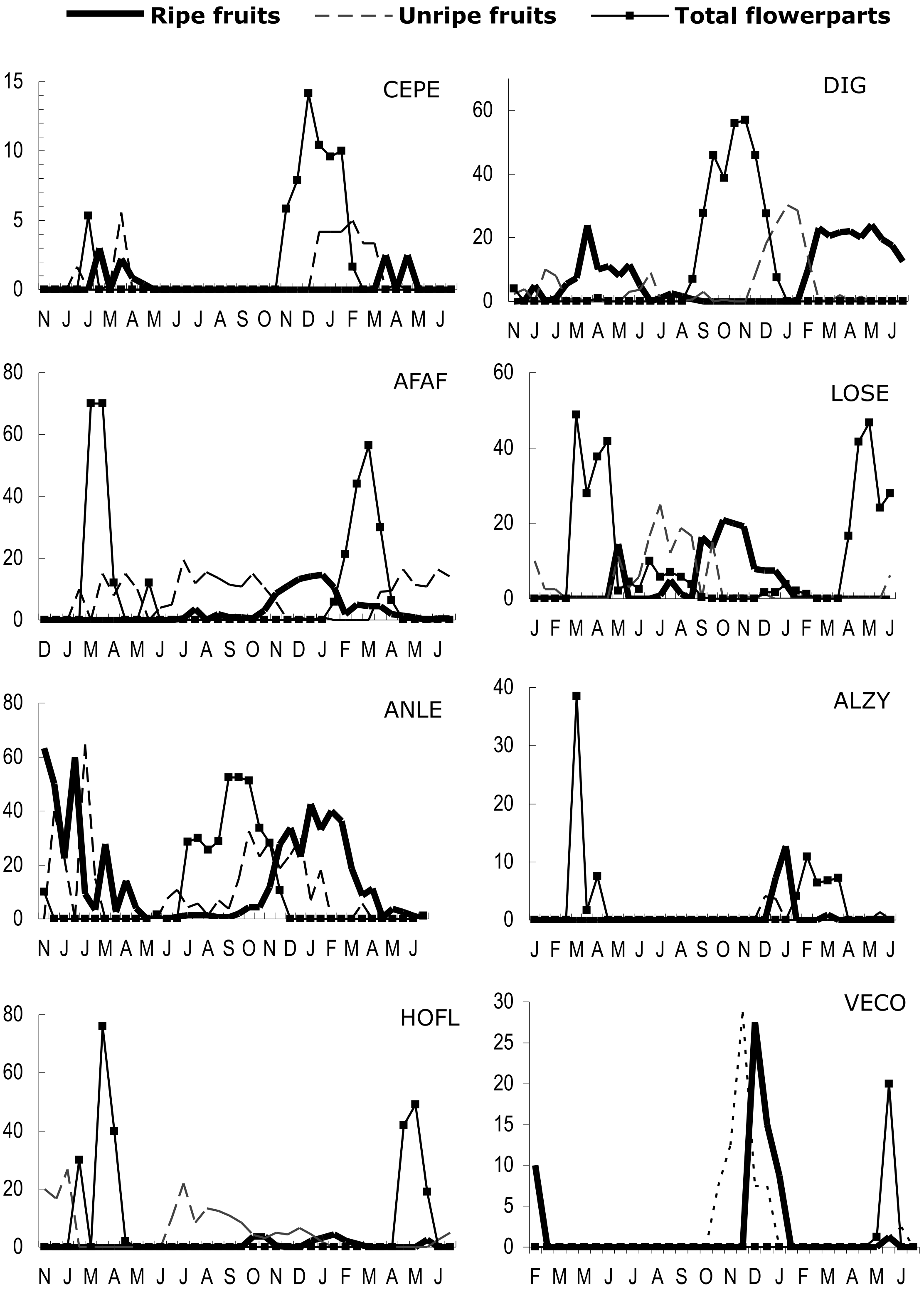


Fig. 4.19 Interannual variation in phenophases of fruits and flower parts in dry fruit species



et al., 2002; Poulsen *et al.*, 2001a). After recording these data, collected fruits were put back off the trail to prevent re-sampling in subsequent sample periods. The fruit-trail survey was conducted a few days after the direct observation of plant phenophases at each Pheno Period.

B. Data Analysis

The comparison of the trail-survyed data between the two routes was limited to the periods in which both routes were sampled. I produced histograms of total numbers of fleshy and dry fruit species to identify the periods of high and low abundance.

Species diversity was computed by the Shannon-Wiener Index. Spearman's Rank Correlation Coefficients were calculated to examine the relationships between the relative contribution of the fruit categories and rainfall. Wilcoxon Signed Ranks Tests were conducted to find out if there are significant differences in the total species-specific number of fruits, total number of dry fruits, and total number of fleshy fruits between the two routes. I used the Spearman's Rank Correlation Coefficients (r_s) to correlate the seasonal Productivity Index of plant parts and quantities of collected fleshy and dry fruits.

C. Results

The quantity of dry and fleshy fruits that were trail-surveyed along the two routes are shown in Tables 4.3. *Dialium guineense* accounted for 47.9% and 35.1% of all fruits collected along routes A and B, respectively. The second and third most abundant fruits along route A were *Mimusops andongensis* (10.9%) and *Drypetes floribunda* (9.3%), respectively. The second and third most abundant fruits along route B were *Drypetes*

Table 4.3 Trail-surveyed dry fruits and fleshy fruits along census routes A and B

Fruits were collected 33 times (3 on 2.5 km, 30 on 4km) on census route A and 32 times (4 km) on census route B. The census routes are 1-m wide. Shaded areas indicate ten most frequently collected fruits.

Species	**Abbrev.**	**A**			**B**			**Total**		
Dry Fruit Species		**freq.**	**%* (D)**	**%** (D&F)**	**freq.**	**% (D)**	**% (D&F)**	**freq.**	**% (D)**	**% (D&F)**
Dialium guinnense	DIGU	14185	82.02	47.93	10992	74.08	35.09	25177	78.35	41.33
Flabellaria paniculata	FLPA	596	3.45	2.01	1258	8.48	4.02	1854	5.77	3.04
Spathodea dinklagei	SPDI	1124	6.50	3.80	496	3.34	1.58	1620	5.04	2.66
Elaeis guinnensis	ELGU	114	0.66	0.39	593	4.00	1.89	707	2.20	1.16
Ceiba pentandra	CEPE	110	0.64	0.37	442	2.98	1.41	552	1.72	0.91
Anogeissus leiocarpus	ANLE	225	1.30	0.76	281	1.89	0.90	506	1.57	0.83
Dalbergia afzeliana	DAAF	309	1.79	1.04	43	0.29	0.14	352	1.10	0.58
Afzelia africana	AFAF	76	0.44	0.26	268	1.81	0.86	344	1.07	0.56
Combretum sp.	CDSP	292	1.69	0.99	0	0.00	0.00	292	0.91	0.48
Combretum paniculatum	COPA	71	0.41	0.24	107	0.72	0.34	178	0.55	0.29
Holarrhena floribunda	HOFL	90	0.52	0.30	85	0.57	0.27	175	0.54	0.29
Lonchocarpus cyanscens	LOCY	0	0.00	0.00	152	1.02	0.49	152	0.47	0.25
Lonchocarpus sericeus	LOSE	41	0.24	0.14	46	0.31	0.15	87	0.27	0.14
Indigofera tinctoria	INTI	3	0.02	0.01	46	0.31	0.15	49	0.15	0.08
Nauclea latifolia	NALA	6	0.03	0.02	17	0.11	0.05	23	0.07	0.04
Akparown igbo	#403*	16	0.09	0.05	0	0.00	0.00	16	0.05	0.03
Awaigbo	Awai	14	0.08	0.05	0	0.00	0.00	14	0.04	0.02
Chasmanthera dependens	CHDE	8	0.05	0.03	1	0.01	0.00	9	0.03	0.01
Ouratea flava	OUFL	0	0.00	0.00	7	0.05	0.02	7	0.02	0.01
Gardenia triacantha	GATR	4	0.02	0.01	2	0.01	0.01	6	0.02	0.01
Cynometra megalophylla	CYME	6	0.03	0.02	0	0.00	0.00	6	0.02	0.01
Albizia zygia	ALZY	2	0.01	0.01	0	0.00	0.00	2	0.01	0.00
Daniella oliveri	DAOL	2	0.01	0.01	0	0.00	0.00	2	0.01	0.00
Ocna membranacea	OCME	0	0.00	0.00	2	0.01	0.01	2	0.01	0.00
Albizia ferruginea	ALFE	1	0.01	0.00	0	0.00	0.00	1	0.00	0.00
Total Dry Fruits		17295	100	58.44	14838	100	47.36	32133	100	52.74

* the tree number observed in the direct observation method. %(D) = % of all dry fruits; %(F) = % of all fleshy fruits; %(D+F) = % of all fruits

(Trable 4.3 cont'd)

Species	Abbrev.	A			B			Total		
Fleshy Fruit Species		**Freq.**	**% (F)**	**% (D&F)**	**Freq.**	**% (F)**	**% (D&F)**	**Freq.**	**% (F)**	**% (D&F)**
Drypetes floribunda	DRFL	2746	22.32	9.28	5396	32.72	17.22	8142	0.28	13.36
Mimusops andogensis	MIAN	3235	26.30	10.93	2880	17.47	9.19	6115	0.21	10.04
Margaritaria discoidea	MADI	248	2.02	0.84	2482	15.05	7.92	2730	0.09	4.48
Strychnos afzelii	STAF	1024	8.32	3.46	1024	6.21	3.27	2048	0.07	3.36
Celtis brownii	CEBR	1420	11.54	4.80	538	3.26	1.72	1958	0.07	3.21
Neostachyanthus occidenta	NEOC	878	7.14	2.97	1060	6.43	3.38	1938	0.07	3.18
Mallotus oppositifolius	MAOP	564	4.58	1.91	1031	6.25	3.29	1595	0.06	2.62
Cremaspora triflora	CRTR	450	3.66	1.52	256	1.55	0.82	706	0.02	1.16
Ficus sur	FISU	192	1.56	0.65	291	1.76	0.93	483	0.02	0.79
Parquetina nigrescens	PANI	161	1.31	0.54	252	1.53	0.80	413	0.01	0.68
Diospyros mespiliformis	DIME	322	2.62	1.09	76	0.46	0.24	398	0.01	0.65
Paullinia pinnata	PAPI	131	1.06	0.44	240	1.46	0.77	371	0.01	0.61
Allophylus africanus	ALAF	21	0.17	0.07	243	1.47	0.78	264	0.01	0.43
Cissus aralioides	CISP	168	1.37	0.57	40	0.24	0.13	208	0.01	0.34
Psychotria latistipula	PSLA	139	1.13	0.47	54	0.33	0.17	193	0.01	0.32
Pancovia bijuga	PABI	149	1.21	0.50	13	0.08	0.04	162	0.01	0.27
Psidium guajava	PSGU	60	0.49	0.20	94	0.57	0.30	154	0.01	0.25
Adenia lobata	ADLO	31	0.25	0.10	93	0.56	0.30	124	0.00	0.20
Sorindeia warneckei	SOWE	47	0.38	0.16	47	0.29	0.15	94	0.00	0.15
Deinbollia pinnata	DEPI	56	0.46	0.19	32	0.19	0.10	88	0.00	0.14
Ficus natalensis	FINA	41	0.33	0.14	38	0.23	0.12	79	0.00	0.13
Ficus exasperata	FIEX	16	0.13	0.05	52	0.32	0.17	68	0.00	0.11
Dracaena sp.	DRSP	18	0.15	0.06	46	0.28	0.15	64	0.00	0.11
Cassipourea congoensis	CACO	0	0.00	0.00	46	0.28	0.15	46	0.00	0.08
Entada manniI	ENMA	18	0.15	0.06	16	0.10	0.05	34	0.00	0.06
Culcasia angolensis	CUAN	33	0.27	0.11	0	0.00	0.00	33	0.00	0.05
Spondias mombin	SPMO	16	0.13	0.05	16	0.10	0.05	32	0.00	0.05
UNID 4	UNI4	14	0.11	0.05	14	0.08	0.04	28	0.00	0.05
Landolphia sp.	LASP	0	0.00	0.00	20	0.12	0.06	20	0.00	0.03

(Trable 4.3 cont'd)

Species	**Abbrev.**	**A**			**B**			**Total**		
Fleshy Fruit Species		**Freq.**	**% (F)**	**% (D&F)**	**Freq.**	**% (F)**	**% (D&F)**	**Freq.**	**% (F)**	**% (D&F)**
Milicia excelsa	MIEX	0	0.00	0.00	20	0.12	0.06	20	0.00	0.03
Lecaniodiscus cupanioides	LECU	0	0.00	0.00	18	0.11	0.06	18	0.00	0.03
Mussaenda elgans	MUEL	3	0.02	0.01	15	0.09	0.05	18	0.00	0.03
UNID 8	UNI8	9	0.07	0.03	9	0.05	0.03	18	0.00	0.03
Canthium multiflorum	CAMU	12	0.10	0.04	0	0.00	0.00	12	0.00	0.02
Dioscorea cayennensis	DICA	8	0.07	0.03	4	0.02	0.01	12	0.00	0.02
Dioscorea sp.	DISP	11	0.09	0.04	0	0.00	0.00	11	0.00	0.02
Diospyros monbuttensis	DIMO	11	0.09	0.04	0	0.00	0.00	11	0.00	0.02
Grewia pubescens	GRPU	4	0.03	0.01	7	0.04	0.02	11	0.00	0.02
Culcasia saxatilis	CUSA	10	0.08	0.03	0	0.00	0.00	10	0.00	0.02
Pouchetia africana	POAF	8	0.07	0.03	1	0.01	0.00	9	0.00	0.01
Gudugudu	Gudu	7	0.06	0.02	1	0.01	0.00	8	0.00	0.01
UNID 7	UNI7	4	0.03	0.01	4	0.02	0.01	8	0.00	0.01
Agouechan	Agou	0	0.00	0.00	6	0.04	0.02	6	0.00	0.01
UNID 10	UN10	3	0.02	0.01	3	0.02	0.01	6	0.00	0.01
Malacantha alnifolia	MAAL	5	0.04	0.02	0	0.00	0.00	5	0.00	0.01
Vangueriopsis nigerica	VANI	0	0.00	0.00	5	0.03	0.02	5	0.00	0.01
Syzygium guineense	SYGU	1	0.01	0.00	3	0.02	0.01	4	0.00	0.01
UNID 9	UNI9	2	0.02	0.01	2	0.01	0.01	4	0.00	0.01
Oncoba sp.	ONSP	2	0.02	0.01	0	0.00	0.00	2	0.00	0.00
UNID 3	UNI3	1	0.01	0.00	1	0.01	0.00	2	0.00	0.00
Agelaea obliqua	AGOB	1	0.01	0.00	0	0.00	0.00	1	0.00	0.00
Grewia mollis	GRMO	1	0.01	0.00	0	0.00	0.00	1	0.00	0.00
Pararistolochia triactina	PATR	0	0.00	0.00	1	0.01	0.00	1	0.00	0.00
Total Fleshy Fruits		**12301**	**100**	**41.56**	**16490**	**100**	**52.64**	**28791**	**100**	**100**
Total All Fruits		**29596**	**100**	**100**	**31328**	**100**	**100**	**60924**	**100**	

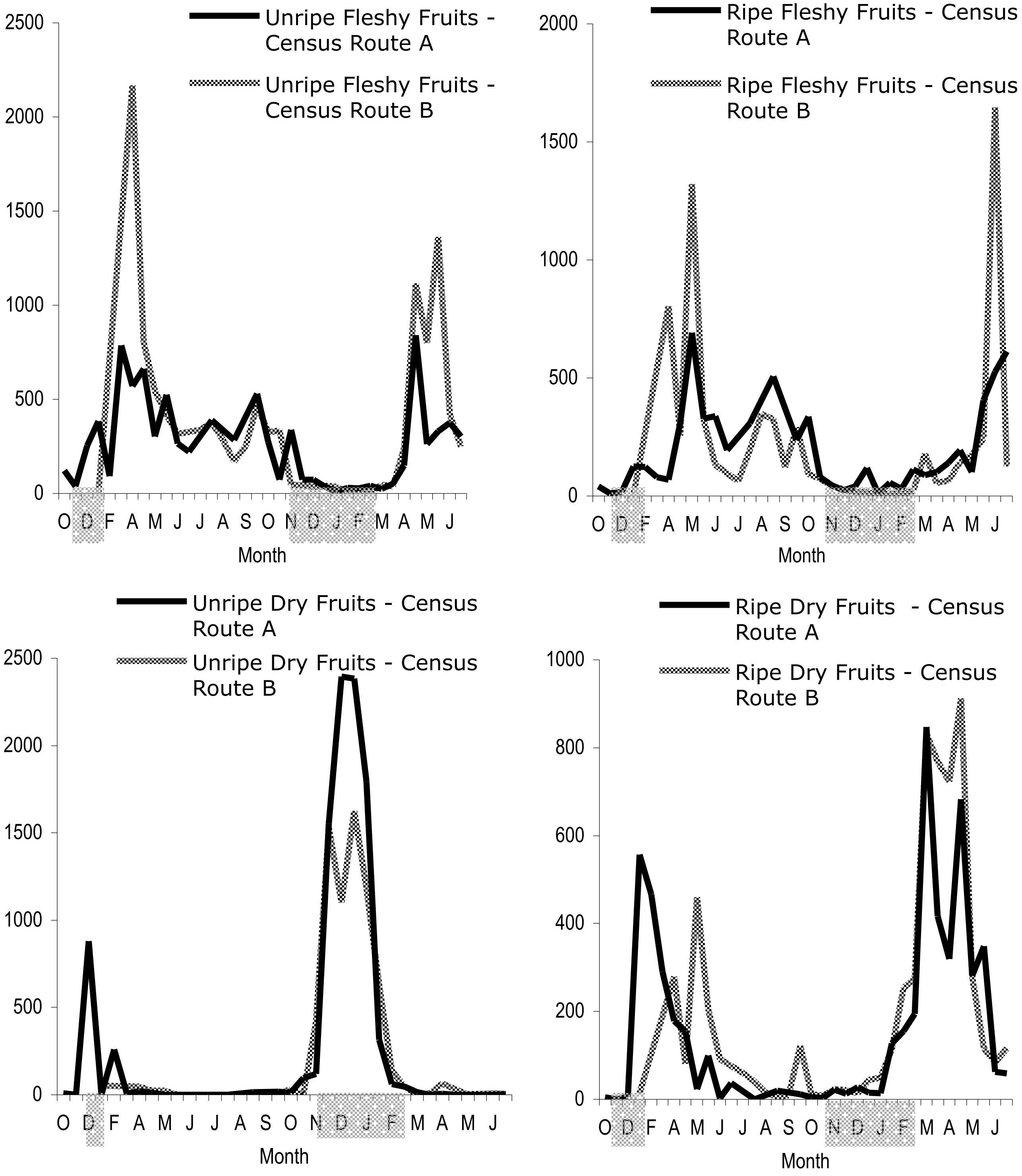
floribunda (17.2%) and *Mimusops andongensis* (9.2%), respectively. In total, 20 dry and 47 fleshy fruit species were identified. Twenty-two species that were collected (5 dry fruit spp. and 17 fleshy fruit spp.) had not been included in the visual observation of phenology. Most of these species were small climbers and herbs. Among the 79 species directly observed for phenophases, 23 species were not collected either along route A or B. Fleshy fruits ($r_s = 0.709$, $n = 53$, $p < 0.001$) co-occurred on the two routes more frequently than dry fruits ($r_s = 0.587$, $n = 25$, $p = 0.002$). Table 4.4 shows the families of fruits that were collected along the two routes. The most, second most, and third most collected families were Leguminosae (43.1 %), Euphorbiaceae (20.5 %), and Sapotaceae (10.0 %), respectively. Within the Leguminosae, Caesalpinioideae fruits (41.9 % of all fruits) made up the majority of the trail-surveyed fruits (Table 4.4). Shannon-Wiener Indices for species diversity along route B ($H' = 2.374$) was slightly higher than along route A ($H' = 2.138$), but it was not significantly different ($z = -0.993$, $p = 0.321$). The number of dry fruits collected along routes A and B was significantly different ($z = -2.146$, $p = 0.032$), but the difference in the numbers of fleshy fruits collected along routes A and B was not significant ($z = -1.344$, $p = 0.179$). Rainfall and monthly quantity of trail-surveyed fleshy fruits were correlated along route A for ripe fruits ($r_s = 0.526$, $p = 0.014$) and along route B for both ripe ($r_s = 0.603$, $p = 0.013$) and unripe fruits ($r_s = 0.543$, $p = 0.03$). Rainfall and monthly quantity of trail-surveyed unripe dry fruits were negatively correlated (route A: $r_s = -0.464$, $p = 0.034$; route B: $r_s = -0.745$, $p = 0.001$).

Fig. 4.20 shows the seasonal changes in the quantities of trail-surveyed fruits. Fleshy fruits were most abundant during the first part of wet seasons and the lowest point occurred during the major dry seasons when dry fruits were most abundant. There were

Table 4.4 Quantities of trail-surveyed fruits along census routes A and B: categorised by tree family

Rank	Family	A		B		Total	
		N	%	N	%	N	%
1	**Leguminosae**	**14673**	**49.6**	**11563**	**36.9**	**26236**	**43.1**
	Caesalpinioideae	14269	48.2	11260	35.9	25529	41.9
	Mimosoideae	363	1.2	105	0.3	468	0.8
	Papilionioideae	41	0.1	198	0.6	239	0.4
2	**Euphorbiaceae**	**3558**	**12.0**	**8909**	**28.4**	**12467**	**20.5**
3	**Sapotaceae**	**3240**	**10.9**	**2880**	**9.2**	**6120**	**10.0**
4	**Loganiaceae**	**1024**	**3.5**	**1024**	**3.3**	**2048**	**3.4**
5	**Ulmaceae**	**1420**	**4.8**	**538**	**1.7**	**1958**	**3.2**
6	**Icacinaceae**	**878**	**3.0**	**1060**	**3.4**	**1938**	**3.2**
7	**Malpighiaceae**	**596**	**2.0**	**1258**	**4.0**	**1854**	**3.0**
8	**Melastomataceae**	**1124**	**3.8**	**496**	**1.6**	**1620**	**2.7**
9	**Combretaceae**	**588**	**2.0**	**388**	**1.2**	**976**	**1.6**
10	**Rubiaceae**	**622**	**2.1**	**350**	**1.1**	**972**	**1.6**

Fig. 4.20 Fluctuations in the quantities of trail-surveyed fruits (Shaded months indicate major dry seasons.)

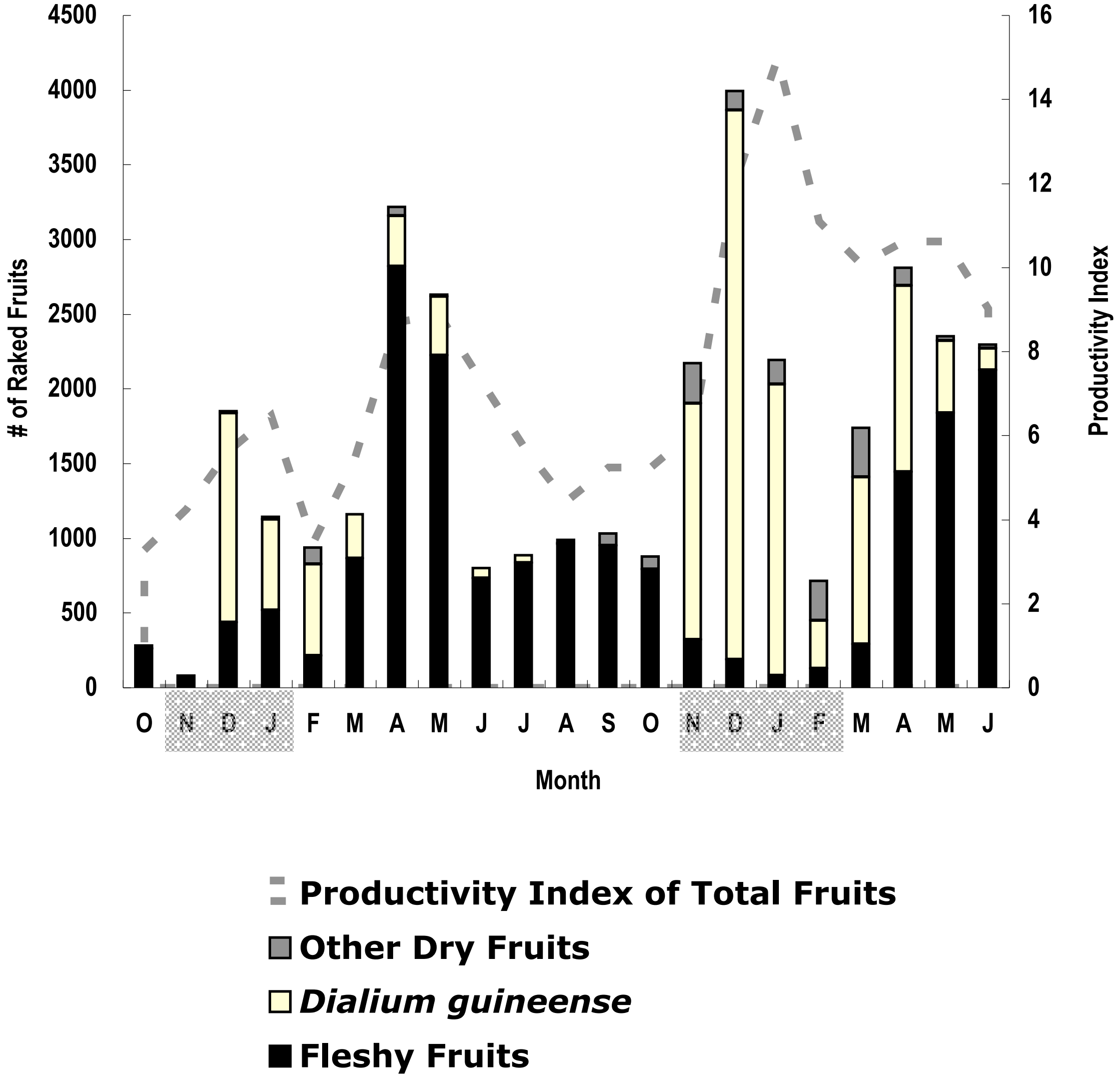


three major differences that relate to fleshy fruits between the two routes: (1) The quantities of trail-surveyed unripe fleshy fruits along route B were about three times and twice as many as those along route A at their first and second year peaks, respectively. (2) During the first year, the peaks of unripe fleshy fruits along both routes occurred in May, but the second year peak occurred one month later along route B than route A. (3) The quantities of trail-surveyed ripe fleshy fruits along route B were twice and three times as many as those along route A at their first and second year peaks, respectively.

The quantity of trail-surveyed unripe dry fruits at their peak was much lower in the first year than during the second year, especially along census route B. In 1997, the peaks of unripe dry fruits along both routes occurred in January and route A had many more fruits than route B. In the first year, the peak of ripe dry fruits along route A occurred three months earlier than that along route B. The second year peaks along routes A and B occurred in March and April 1997, respectively.

Fig. 4.21 shows a comparison between trail-surveyed fruits of *Dialium guineense*, other dry fruits, and fleshy fruits and the productivity index of all fruits as determined by the visual observation method. The peaks and troughs of collected-fruits corresponded well with those of Productivity Index of fruits. The monthly average of trail-surveyed fruits and monthly average Productivity Index was correlated only along route A ($r_s = 0.538$, $n = 16$, $p = 0047$), but it was highly correlated with the monthly average Productivity Index from the succeeding month (A: $r_s = 0.777$, $n = 13$, $p = 0002$; B: $r_s = 0.758$, $n = 13$, $p = 0003$). The complementary relationship between the periods of abundance and scarcity in fleshy and dry fruit observed visually is again obvious in the survey of fruits.

Fig. 4.21 Monthly average number of trail-surveyed fruits of *Dialium guineense* , other dry fruits, fleshy fruits in comparison with the Productivity Index of total fruits (Shaded months indicate major dry seasons.)



IV. Discussion and Conclusion

A. Plant Phenophases in the Lama Forest

1. General Patterns Observed in the Direct Observation Method

The phenology patterns observed in this study were distinctly seasonal and individuals of some of the most common tree species showed different phenological patterns between the first and second years of my study (Fig. 4.14–16). In particular, the extent of interindividual variation for reproductive parts was more extensive than the variation observed in vegetative parts (Fig. 4.14, 4.15).

Some of the interannual variation in phenophases observed in many species is undoubtedly related to the interannual variation in rainfall. For example, more species lost 50% and all leaves during the second major dry season than in the first major dry season (Fig. 4.2) and the productivity of dry fruits was less in the first year than that in the second year (Fig. 4.13).

Factors other than rainfall (e.g., temperature, predation) also influence variation in phenophases between years. For example, on the average, there were fewer *Diospyros* fruits in the second year than the first year (Fig. 4.15) and this could have been been influenced by an extensive defoliation of the young leaves caused by insect larvae.

Intraspecific and interannual variations in phenophases are more widespread in dry forests than in rain forests. In Pinkwae, Ghana, *Antiaris africana*, *Lannea nigritana*, *Drypetes abyssinica*, and *Drypetes floribunda* showed extensive individual variation in leaf fall and leaf flush (Lieberman, 1982). The importance of interannual variations in phenophases in influencing primates' food choice appears to have only recently been recognized among guenon researchers (Chapman *et al.*, 2002). Interannual variation in phenophases pertaining to primate food selection has been reported in some primate species and will be discussed in the next chapter.

2. Plant Category Differences

In both vegetative and reproductive parts, dry fruit producing species and fleshy fruit producing species had distinct phenophases. In seasonally dry forests, such a clear pattern separating dry fruit producing species and fleshy fruit producing species seems common (Lieberman, 1982; Lieberman and Lieberman, 1984).

3. Habitat Differences

The timing of leaf fall and leaf flush, the duration of flowering, and fruiting periods were also different among the three habitat types in the Lama Forest. Several studies have examined the relationship between fruit productivity and habitat characteristics, but most have been on regional scale. Therefore, a direct comparison with these studies is not possible. One study that has compared plant food productivity in different habitat types within a forest is the study conducted by Fimbel (1992) in young secondary forest (YSF) and old secondary forest (OSF) plots in Tiwai Island, Sierra Leone, a semi-deciduous lowland moist forest. Fimbel (1992) found that the availability of mature and young leaves was more seasonal in YSF than in OSF. This study, however, found that the productivities of mature leaves in fleshy fruit species were similar, but the productivityof mature leaves in dry fruit species was more seasonal in dense forest than in disturbed forest and farmbush. As for young leaf parts (in dry fruit species and deciduous fleshy fruit species), productivities were more seasonal in disturbed forest than in dense forest (Fig. 4.11A, B).

In the Lama Forest, flowering in dry fruit species began a month earlier in farm bush than in disturbed forest or dense forest, but flowering in disturbed forest and dense forest occurred about the same time (Fig. 4.12). Similarly, Fimbel (1992) found that flowering periods of YSF species occurred earlier than in OSF. As for fruits, the availability of dry fruits in dense forest and disturbed forests in the Lama Forest were similar, but the availability of fleshy fruits fluctuated more in dense forest than in disturbed forests (Fig. 4.13). Similarly, Fimbel (1992) reported that the availability of fruits in OSF fluctuated erratically, but it was more equitable in YSF.

Many factors probably influence the habitat differences in phenophases described above. Moisture in the deep soil, lighting conditions, and the extent of edge effects in microhabitats are some of the factors, but without gathering relevant ecological data, it is uncertain which factors are more important.

B. Fruit-Trail Survey: Comparison between the Two Routes

The quantitiy of fruits that were surveyed along the two routes differed. Some of the differences that were found in the quantities of surveyed fruit between the two routes reflect the tree BA/ha differences found between the routes (Table 3.2 and 4.3). For example, more fruits of *Dialium guineense, Pancovia bijuga*, and *Mimusops andongensis* were collected along route A than route B (Table 4.3). The BA/ha of *Dialium*, *Pancovia*, and *Mimusops* are greater along route A (916.7 cm^2/ha, 4.3 cm^2/ha, 257.7 cm^2/ha, respectively) than route B (738.0 cm^2/ha, 1.2 cm^2/ha, 203.6 cm^2/ha, respectively) (Table 3.3), corresponding well with the differences in the fruit quantities. Similarly, more fruits of *Ceiba pentandra* were collected along route B ($N = 442$) than route A ($N = 110$), corresponding well with greater BA/ha of this species along route B (351.0 cm^2/ha) than route A (46.6 cm^2/ha) (Table 3.3).

A corresponding relationship between the number of collected-fruits and tree BA/ha was not found in some early successional species such as *Ficus sur*, *Ficus exasperata, Lonchocarpus sericeus*. In these species, more fruits were collected along route B than route A (Table 4.3) despite the fact that BA/ha of these species were greater along route A (*Ficus sur*, 22.8 cm^2/ha; *Ficus exasperata,* cm^2/ha; *Lonchocarpus,* 31.7 cm^2/ha) than route B (*Ficus sur*, 20.4 cm^2/ha; *Ficus exasperata,* 10.7 cm^2/ha; *Lonchocarpus,* 9.5 cm^2/ha)(Table 3.3). The following factors might have contributed to this:

(1) All trees of the two *Ficus* species along route A were < 20 cm DBH, but a few 20–29 cm DBH fig trees were found along route B (Fig. 3.2). Thus, although total BA/ha of *Ficus* spp. was greater along route A (Table 3.2), the larger trees along route B may have produced proportionally more fruits than smaller trees.

(2) Route A may be more accessible than route B to terrestrial frugivorous animals such as *Chlorocebus aethiops* (that favor savanna-woodland habitats), since it is closer to the laterite road. Fruit-trail surveys amass residual fallen fruits that were first harvested in tree crowns by frugivores (Chapman *et al.*, 1994). Even if more fruits had been produced along route A than route B, fewer fruits would remain on the ground if terrestrial, aerial, or other arboreal frugivores had fed on the fruits.

(3) Disturbed forest may have higher fruit productivity of pioneer species than dense forest and farm bush irrespective of the size of trees (Fimbel, 1992). Although route B contains fewer farm bush blocks, it had more disturbed forest blocks. Regardless

of the Basal Area of the species, more fruits might have been produced along B than along A.

Other differences also warrant some scrutiny. For example, more than three times as many fruits of *Afzelia africana* were collected along route A than route B. Along route A, however, no *Afzelia africana* trees were enumerated, although at least three *Afzelia africana* trees occur beyond the sampled area, not directly on the route. Mature tall *A. africana* trees extend their crown to 30–50 m radius from the trunk. The seedpods of *Afzelia africana* fall onto the forest floor from where the branches spread out. Furthermore, when *Afzelia africana* seedpods dehisce, they could fly away a few hundred meters. *Cercopithecus mona* was also observed removing seedpods from the branches and processing the seeds away from the tree. For these reasons, it is not surprising to find no relationship between the number of collected *Afzelia africana* fruits and the BA/ha of *Afzelia africana*.

The fact that more than twice as many *Drypetes floribunda* fruits were collected along route B than route A also cannot be explained by the differences in BA/ha, since the BA/ha of *Drypetes floribunda* along route A (105.5 cm^2/ha) is overwhelmingly greater than that along route B (39.2 cm^2/ha)(see Table 3.3). During the first year, 1,318 and 4,578 fruits were collected along routes A and B, respectively. In the second year, 1,428 and 818 fruits were collected, respectively. It is possible that the production of *Drypetes floribunda* fruits along route B in the second year was simply delayed or significant amounts of fruits may have been eaten by frugivores. A more likely explanation is that *Drypetes floribunda* has supra-annual or asynchronous fruiting cycles. The data obtained from direct observation provides some evidence for this conjecture. In the first year, all sampled *Drypetes floribunda* trees produced fruits (see Fig. 4.18). In the second year, three out of nine trees produced only 5–10% fruits (100% is considered maximum production) and four out of nine trees in disturbed forest did not produce fruits after flowering in April 1997 (Fig. 4.18). In dense forest, one out of six trees (17%) set fruits. Lieberman (1982) also reported a supra-annual fruiting periodicity in *Drypetes floribunda* in the Pinkwae Forest, Ghana. Similarly, the fact that more fruits of *Diospyros mespiliformis* were collected along route A ($N = 322$) than route B ($N = 76$), but route B (493.1 cm^2/ha) has a greater basal area than route A (485.5 cm^2/ha) may indicate that there is interannual variation in fruiting behavior among individuals.

C. Comparison between the Two Methods Used in this Study

The patterns of fruit abundance and scarcity found by direct observation and fruit-trail survey were not in precise agreement, but the general patterns were similar. Both methods showed that the peaks of dry fruits occurred during the major dry seasons and the peaks of fleshy fruits occurred during the wet seasons. There are some differences, however. For example, summed collected dry and fleshy fruits were similar in quantity (Fig. 4.20), but the Productivity Index of fleshy fruits was only 1/4 of the Productivity Index of dry fruits at the peak points. The use of the Productivity Index is more representative of the contribution made by each fruit type to frugivores' food supply than the quantity of fallen fruits, since tree BA/ha in the forest (calculated from measured DBH and density of each species) is taken into account. The number of fruits as a unit of study cannot accurately reflect the availability of the fruits to frugivores, since the area where the fruits come from cannot be estimated. Furthermore, since the fruit-trail survey was conducted semi-monthly, fruits that have short highly-synchronized fruiting durations were probably missed (White, 1994b). The fruit-trail survey method used in this study equates the value of each fruit, ignoring tremendous variations that exist in many aspects of fruits (e.g., size, volume, weight, softness of pulp, moisture content, nutritional contents, hardness of seeds) (Gautier-Hion *et al.,* 1985; Worman and Chapman, 2005). For this reason, many ecological studies have measured the dry weight of the fruit rather than simply counting the number of fruits (e.g., Chapman *et al.,* 1992; Fimbel, 1992). In future studies, measuring the dry weight and analyzing nutritional contents of the fruits in addition to counting the number of fruits could provide more useful information in regard to the availability of fruit resources.

D. Comparison with Other Forests

In this study, 94.9% of the species directly observed for phenophases were deciduous. In the semi-deciduous forest zones in Ghana (rainfall 750–1,000 mm/yr), 46–74% of the species in drier forests were deciduous, while 33–37% of the species in wetter forests (rainfall > 1,000 mm/yr) were deciduous species (Hall and Swaine, 1976). In the Comelco Forest (rainfall 1,533 mm/yr) in Costa Rica, 75.2% (85/113 spp.) of the species monitored for phenophases were deciduous (Frankie *et al.*, 1974). In Trinidad, over two thirds of the upper canopy consists of obligate deciduous trees (Richards, 1966). This short list supports the statement made by Richards (1966) and Murphy and Lugo (1986) that the number of deciduous species in dry forests increases as the moisture stress increases (Richards, 1966; Murphy and Lugo, 1986).

In many seasonally dry forests, many deciduous species start shedding their leaves before moisture stress develops and leaf flush usually occurs before the onset of the first rain and flowering occurs almost simultaneously (van Schaik *et al.*, 1993). Such a pattern was not observed in the Lama Forest. At Lama, many deciduous trees began shedding their leaves after the dry season started (see Figs. 4.4–5 & Fig. 4.14–16); however, leaf flush and almost simultaneous flowering indeed occurred before the onset of first rain in many fleshy fruit species such as *Milicia excelsa* (Fig. 4.16) and dry fruit producing species such as *Ceiba pentandra, Afzelia africana*, and *Albizia ferruginea* (Fig. 4.17). In other dry forests, leaf flush occurs synchronously after the start of the rain season (e.g., Pinkwae Forest, Ghana: Lieberman, 1982; Chamela Forest, Mexico: Bullock and Solis-Magalianes, 1990). De Bie *et al.* (1998) stated that for deciduous species, there are two strategies to avoid drought damage. One strategy is to maintain leaves throughout the dry season, but avoid water loss through scleromorphic (i.e., strongly veined with few stomata) features. Another strategy is to shed leaves at the start of the dry season. At Lama, a majority of the tree species shed leaves during dry seasons.

The Pinkwae Forest in the Accra Plain in Ghana is climatically similar to Lama. Pinkwae receives an annual rainfall of 1,100 mm that falls between March and June and between August and November. Common tree species such as *Lannea nigritana*, *Ceiba pentandra*, *Dialium guineense*, *Vernonia colorata*, *Diospyros mespiliformis,* and *Drypetes floribunda* that occur at Lama also occur at Pinkwae, but the majority of forest species are fleshy fruit species and *Dialium guineense* is not an abundant species at Pinkwae (Lieberman, 1982; Lieberman and Lieberman, 1984). There are similarities and differences in plant phenophases between the two forests. For example, in Pinkwae, regardless of fruit categories, leaf flush was entirely limited to wet seasons. In the Lama Forest, the majority of fleshy fruit species had flowers and fruits in wet seasons, but dry fruit species had flowers and fruits in major dry seasons (see Figs. 4.6, 4.7). In Pinkwae, most species had flowers and fruits during the periods of high rainfall. The patterns of phenophases observed in the Lama Forest also share some similarities with some semi-deciduous forests in South America (Frankie *et al.*, 1974; Bullock and Solis-Magallanes, 1990; Galetti and Pedroni, 1994). For example, in Santa Genebra Reserve in southeast Brazil, the peak flowering occurred during the dry season throughout the beginning of the wet season, and fleshy fruits were lowest in dry seasons, but dry fruits were highest during the transitional season and dry season (Galetti and Pedroni, 1994). In many seasonally dry forests, the peak of flowering tends to occur at the end of the dry or at the beginning of the wet season. Therefore, flowering and fruiting peaks are close to each other (Frankie *et al.*, 1974; Murphy and Lugo, 1986; van Schaik *et al.*, 1993).

The duration of leaflessness in some deciduous tree species appears to be related to the duration of dry seasons (Eggeling, 1947; Paradis and Houngnon, 1977). In my study, the second major dry season was longer and drier than the first major dry season (see Fig. 2.1). For many species, this difference directly affected the durations of the leafless period. For example, the mean duration of leaflessness in *Ceiba pentandra* during the first major dry season was about 15 days, but it was about twice as long during the second major dry season. Paradis and Houngnon (1977) also had reported that *Ceiba pentandra*, *Antiaris toxicaria*, and *Milicia excelsa* never lost leaves in 1975–1976, but in 1976–1977, which was much drier than the previous year, they were leafless for about three months.

E. Advantages and Disadvantages of Different Phenological Methods

The two methods that I used identified the same seasonal peaks and troughs of resource availability, and those of fruits in particular, but each method has some advantages and disadvantages. Some advantages of the direct observation method are the following:

(1) It is cost effective, since the only required tools are a pair of binoculars and data sheets.

(2) It is time efficient.

(3) If scoring is done by a single observer, potential errors are consistent throughout the study period.

Some disadvantages are the following:

(1) If scoring is done by a number of observers, potential inter-individual errors are great, since estimating the maximum productivity of vegetative or reproductive parts in a crown or on a trunk is a subjective exercise. Personnel training may alleviate such problems. In this study, efforts were made to minimize potential errors by random examination of observation records by multiple observers.

(2) Identifying the age or maturity of leaves and fruits is sometimes difficult, especially when environmental conditions are unfavorable (e.g., during the period of Harmattan, heavy rain, multi-layer crowns).

(3) Persistent fruits that hang onto branches can lead to rescoring in consecutive periods (Struhsaker, 1979). In this study, fruits of some species (e.g., *Ficus sur)* fell off easily even when they were still unripe, but fruits of other species (e.g., *Diospyros mespiliformis*, *Dialium guineense*) continued to hang on even after they become fully ripe and started to rot. These fruits may have been repeatedly scored, leading to an overestimation of fruits. Since there is no easy way to distinguish new fruits from old

fruits, there is a need to develop a method that can distinguish newly produced fruits from preexisting ones.

Some advantages of the fruit-trail survey are the following:

(1) It is useful in gaining information regarding the seasonality of non-tree fruit species that are inconspicuous and overlooked by visual observation (Poulsen *et al.*, 2001a). Zhang and Wang (1995), however, found lower numbers of species in the fruit-trail survey than the fruit trap method (discussed below) or the platform observation method (see Zhang and Wang, 1995 for the detail of the method). Zhang and Wang (1995) found that among 665 woody species listed in their study area, the numbers of species that were recorded in one year using platform observation, a fruit-trail survey, and fruit-traps were 91, 44, and 64, respectively. In this study, the fruit-trail survey method was able to quantify the number of fruits of many climber species that were not directly observed or excluded from the Productivity Index computation.

(2) Inter-observer variation is non-existent or minimal.

(3) It is simple, time-efficient, and cost-effective, since the only materials required are plastic bags.

Some disadvantages of fruit-trail survey are the following:

(1) The quantity of fallen-fruits does not accurately reflect the total fruit biomass produced, since it only included the residual fruits after arboreal and terrestrial frugivores have had access to the fruits. Short fruit-survey intervals (< 2 week) may somewhat compensate for this shortcoming, but not entirely.

(2) The quantity of fruits on the ground cannot accurately reflect the productivity of fruits that persist on branches.

(3) Certain environmental conditions (e.g., heavy rain, inundation) can disrupt fruit-trail survey in some seasons. In this study, monthly rather than semimonthly surveys were conducted between June and September 1996, due to deep inundation on the census routes.

(4) There may be a delay in the timing of peaks and troughs of fruit productivity (Zhang and Wang, 1995). Zhang and Wang (1995) found that the fruit-trail method as well as the fruit-trap method (discussed below) recorded fruits about one month later than direct observation from the platforms.

Another widely used phenological method is the fruit-trap method. Prior to setting up fruit traps, the size, shape, material, and the number of traps must be decided. There is also a need to decide where (e.g., height and location) to place traps, how frequently the content of traps needs to be collected, and the method of estimating fruit biomass. Some advantages of the fruit-trap method are the following.

(1) Fruit traps may catch rare fruits, which are important for study subjects during the time of fruit scarcity, that may not be sampled by direct observation or fruit-trail surveys (Fimbel, 1992).

(2) There is little inter-observer variation, because trapped fruits are directly quantified, rather than subjectively estimated (Howe, 1992).

Some disadvantages of this method are the following.

(1) Traps only catch the fruits that fall from trees. The productivities of the fruits that persist onto branches are underestimated.

(2) Sesamoid fruits are not easily trapped, because they are easily blown away by wind.

(3) Heavy rain may wash out the contents of traps and fragile fruits may disintegrate between two collection periods.

(4) It is more time-consuming than direct observation or fruit-trail survey (Chapman *et al.,* 1994). The set up of fruit traps involves multi-faceted procedures: preparation and set-up of traps and collecting fruits take a long time.

(5) It cannot accurately measure fruit biomass, since there is no direct relationship between the summed area of the traps and the size of the forest (Fimbel, 1992; Chapman *et al.,* 1994).

Many factors, such as duration, budget, and the goal of a research, and presence or absence of qualified assistants, can influence the decision by a researcher to use one or more methods. If the aim of a research project is simply to find the seasonal peaks and troughs of fruit availability, the fruit-trail survey is an easy method that can also be used in the absence of principal researchers, especially if the research spans many years. If the aim of a study is to monitor seasonality of fruit production and measure fruit biomass as closely as possible, a combination of direct observation and fruit-trail survey at shorter intervals (e.g., weekly) can better monitor fruit productivities in a forest.

CHAPTER 5: FEEDING ECOLOGY

I. Introduction

More often than not, seasonality produces a cycle of boom and bust in primate habitats. Even forests with high rainfall experience periodic fluctuations in food abundance and quality (Fleming *et al.*, 1987; Oates, 1987). During crunch periods, animals' cognitive and biological limits are often challenged. Non-human primates must be flexible and deal with such challenges in a variety of ways. They must mitigate the demands of fluctuations in the availability of resources with physiological, behavioral, and social mechanisms, or they face serious consequences. In the long run, failure to meet such demands could lead to disease, stunted skeletal growth, delayed sexual development, failure to reproduce, or even death.

Terborgh (1986b) has defined a frugivorous mammal as one whose diet consists of 50% fleshy fruits, although this definition certainly is not universally applied and is impractical at times. Davies *et al.* (1999) considered that seed-eating is a type of frugivory, but Lambert (2005) defined frugivory as "pulp-eating." Fruits vary in shape, size, hardness, attractiveness, and nutritional content in time and space, so affecting fruit feeding, fruit processing, and patterns of fruit preferences among frugivores (Lambert, 1997; Norconk and Conklin-Brittain, 2004). Frugivores are a dominant group of vertebrates in tropical forests (White, 1994b) and some, but not all, are important seed-dispersal agents (Lieberman and Lieberman, 1986; Rowell and Mitchell, 1991; Norconk *et al.*, 1998; Lambert, 2001, 2005; Poulsen *et al.*, 2001a; Norconk and Conklin-Brittain, 2004). White (1994b) estimated that in Gabon, 53 % of mammals are primary consumers and 85 % of these mammals feed on fruits and seeds. Strier (2003) stated that most primates ingest some fruits. According to Harding (1981), however, only about half of all primate species are categorized as frugivores, feeding primarily on fruits (including seeds). In comparison, about one quarter of the primate species consume mainly insects, and another quarter, leaves. Only a few primate species specialize on gum and nectar.

Some of the morphological characteristics that have been ascribed to frugivorous primates are: intermediate body size (approx. 1.5–6 kg), relatively large incisors, simple low-cusped molar teeth, and a lack of elaboration in the stomach or large intestine (Martin, 1990; Fleagle, 1999).

Behaviorally, frugivores tend to travel further, have relatively larger home range size and shorter resting time than sympatric folivorous primates. Guenons are classically considered typical frugivorous primates, and they have been characterized as unspecialized frugivores in regard to their digestive morphology, contrasting with anatomically specialized and more folivorous colobines (Oates, 1994b; Conkin-Brittain *et al.*, 1998; Fleagle, 1999).

For frugivorous primates, the hardest time of year is when fleshy fruits are in short supply, because given a choice they generally prefer fleshy fruits. Finding suitable fruits in a primate's home range during a season of scarcity may be a bigger problem than finding leaves, since fruits are distributed more in clumps than other foods (Oates, 1987; van Schaik and van Noordwijk, 1988; Isbell, 1991).

When pulpy fruits are scarce, one strategy used by frugivores is emigration from their usual home ranges (van Schaik *et al.*, 1993). This has been observed in primates (e.g., *Cercopithecus mitis*: Beeson, 1989; *Lagothrix lagotricha*: Peres, 1994a; *Eulemur fulvus*: Overdorff, 1993; *Pan troglodytes*: Tweheyo and Lye, 2005) and in other frugivorous mammals (Foster, 1982; Eisenberg, 1983; Leighton and Leighton, 1983). For primates living in forest fragments, such as the Lama Forest, this may not be a viable option. They are forced to adjust their diets, daily foraging, ranging, and social behavior within their home ranges (Terborgh, 1983; Gautier-Hion, 1988; Galetti and Pedroni, 1994).

One potential foraging strategy that can be adopted by primates living in forest fragments is to continue feeding on scarce fruits, but to increase foraging time and search areas (Schoener, 1971; Clutton-Brock, 1977a; Pyke *et al.*, 1991). Fruit specialists that maintain a high proportion of ripe fruits in their diet all year round appear to use this strategy (e.g., *Saimiri oerstedi*: Boinski, 1987; *Ateles paniscus*, *Ateles belzebuth*, *Cebus olivaceus*: Robinson and Janson, 1987; *Cercocebus galeritus*, *Lophocebus albigena*: Waser, 1977, 1984; *Pan troglodytes*, *Pan paniscus*: White and Wrangham, 1988; *Varecia variegata*: H. Morland, pers. comm.). When fruits are scarce, these primates increase the time spent feeding or foraging, and traveling; they may concentrate on a few keystone species or food items (e.g., figs, palm nuts, nectar), range further, and spend less time in any one area of their home ranges (*Cebus albifrons, Cebus apella*: Terborgh, 1983; *Cercocebus galeritus*: Waser, 1984). Although other factors also influence fission-fusion sociality in some platyrrhine species and chimpanzees, the availability and dispersion of ripe fruits is the primary factor causing that these species to adjust their foraging group size (Freese, 1976; Chapman, 1990; Symington; 1990; Chapman *et al.*, 1994; reviewed for platyrrhines in Kinzey and Cunningham, 1994).

An alternate strategy is to increase the proportion of non-fruit foods in the diet (Schoener, 1971; Clutton-Brock, 1977a; Pyke *et al.*, 1991). Frugivorous primates following this strategy increase the amount of and time spent feeding on leaves, arthropods, and/or seeds, and decrease the amount and time spent feeding on fruits. They reduce overall time spent feeding and shorten day range length (e.g., *Pongo pygmaeus*: Leighton and Leighton, 1993; *Symphalangus syndactylus*: Chivers, 1977). These species seem to cut back on energy expenditures when their preferred food is scarce (Clutton-Brock and Harvey, 1977a, b).

The above two strategies are at the opposite ends of a continuum. Whether primates use one strategy or the other, or elements of both, depends on many factors such as cyclic availabilities of alternative foods, spatial distribution of foods, competition over foods within a group, the diet of sympatric primates, and population density (Garber, 1987; Oates, 1987; Chapman *et al.*, 2002).

For most of the medium-sized rain forest-living guenons studied so far, fruits, especially sugar-rich pulpy fruits, are preferred foods and the most important dietary items (reviewed in Gautier-Hion, 1988 and Chapman *et al.*, 2002). Seeds as an independent source of food, not as an incidental source of food ingested along with the pulp of fruits, also appear to be an important food for guenons and other frugivorous primates, but because seed-eating is often difficult to distinguish from pulp-eating, seeds are often included with fruits as a dietary item (Happel, 1988; Chapman *et al.*, 2002). Other important foods for guenons are: arthropods, leaves (especially young leaves), leaf petioles, flowers, nectar (Jones, 1970; Struhsaker, 1980; Sourd and Gautier-Hion, 1986; Cords, 1986, 1987a, b; Gautier-Hion, 1988; Happel, 1988; Butynski, 1990; Gautier-Hion and Maisels, 1994; Tutin *et al.*, 1997a, b; Chapman *et al.*, 2002; Curtin, 2002; Buzzard, 2004; Porter, 2005), and small vertebrates such as bats and birds (Fairgrieve, 1997;

Matsuda Goodwin, pers. obs.). On an annual basis, fruit consumption by medium-sized guenons in rain forests shows a bimodal tendency that appears to be correlated with rainfall seasonality.

In previous studies of *Cercopithecus mona*, fruits have been found to be the most important food (Howard, 1977; Glenn, 1992). Glenn (1996) reported that *C. mona* in Grand Etang F.R., where pulpy fruits were available throughout the year, ate ripe fruits all year round. In mainland Africa, however, there is little information regarding the seasonality of *C. mona*'s food (Booth, 1956; Gartlan and Struhsaker, 1972; Howard, 1977). Howard (1977) reported the diet of *Cercopithecus mona*, but he stated that food does not become seasonally critical at Mungo.

The quantity, quality, and types of food resources available for frugivorous monkeys living in drier forests are expected to fluctuate more than for those in wetter forests. Therefore, it is expected that in a seasonal forest such as Lama, *C. mona* will incorporate a large proportion of fruits in its diet on an annual basis, but shift to alternative foods when pulpy fruits become seasonally scarce. In the previous chapter, I showed that the availabilities of *C. mona*'s potential foods fluctuate from season to season. In this chapter, I examine the seasonality of *C. mona*'s diet and relate it to the temporal changes in food availabilities identified in the previous chapter. I examine whether there are any similarities and differences in their diet in comparison with the diets of *C. mona* in other forests, members of *mona* species group, and other arboreal guenons.

II. Methods

A. Data Collection

Because *C. mona* maintained a flight distance of ≥ 50 m at the beginning of the study, locating specific groups and constantly following them was only occasionally possible. To compensate for this constraint, I used two methods to locate groups: systematic walks and censuses.

(1) **Systematic walk**: I systematically walked on the trails in the West and East Study Sites for 5–10 days per month between December 1995 and June 1997 (no data were collected in May 1996). When a monkey group was encountered, I followed it as long as possible to observe feeding behavior. When I lost sight of the group, I looked for it for 15 minutes. After 15 minutes, if it could not be located, I began looking for another group. I scored an observation as feeding when an individual picked a food item and placed it in its mouth.

I used the frequency method to collect feeding records. When a solitary individual or a member of a group was observed picking a plant part of a particular species, or ingesting it, during a particular 15-minute sample interval, one point would be recorded for that plant part of the particular species. An additional point would be recorded for the particular food when an individual ingested the same item during the next 15-minute interval. More often than not, I was unable to observe any behavior at specified points in time. Therefore, the 15-minute interval was used as a guideline, rather than a rule. When an individul or a group of individuals was feeding on a food item at a sample period, I recorded one point for the plant part of the particular food item irrespective of the number of individuals seen feeding on that particular food item. In practice, I observed only one or a few individuals feeding during the great majority of samples. I did not record multiple food items at any sample period.

(2) **Censuses**: I also recorded details of feeding episodes during the semi-monthly censuses between October 1995 and June 1997 (see Chapter 7). During a group or solitary sighting in a census, if an individual was seen picking or ingesting a food item of a particular species, one point was recorded for the plant part-species per sighting that lasted ≤ 10 min.

I identified plant parts eaten as leaves, fruits, floral parts, arils, immature seeds, mature seeds, nectar, others, and unknown parts. When possible, leaves were further divided into the finer categories of young leaves, mature leaves, leaf buds, and leaf petioles. When monkeys fed on floral parts and fruits, fine distinctions between flowers and floral buds and between unripe and ripe fruits were made when possible. Sometimes, when a monkey's face was buried in a flower, it was difficult to ascertain whether it was licking the nectar or feeding on the reproductive parts (e.g., pollen, anther, stigma, styles). The food was identified as nectar only when the monkey was obviously feeding on nectar. When an individual was clearly feeding on immature or mature seeds by removing and discarding the pulp of the fruit, it was recorded as "immature seeds" or "mature seeds". Otherwise, it was recorded as "unripe fruits" or "ripe fruits." When the plant part eaten was known, but species not identified, I recorded the plant part of "unknown species." When a monkey ate an unidentified plant part of a known species, it was recorded as an unidentified plant part of *xyz* species.

B. Data Analysis

All feeding records from the walk and censuses were combined for each month and season, because the number of feeding records per day was low ($\bar{x}$ = 3.4, range = 1–13, *s.d.* = 2.31). Due to small sample size, feeding records were transformed into monthly percentages and these were grouped into six seasonal data sets (DS1, WS2, WS3, WS4, DS2, WS5). The data from October 1995 were eliminated from the analysis, because of small sample size (*n* = 17). The Productivity Indices of all plant parts except mature leaves were transformed into monthly average scores that were summed into seasonal groups. Similarly, monthly average quantities of collected fruits were computed and summed up for each season. I used the Shannon-Wiener Index (*H'*) to measure the diversity of species consumed for each season (Krebs, 1999). I used the Spearman's Rank Correlation Coefficients (r_s) to correlate the amount of particular food items consumed with the seasonal Productivity Index of plant parts and seasonal quantities of collected fleshy and dry fruits.

III. Results

A. Diet Composition

I collected 566 *Cercopithecus mona* feeding records. Table 5.1 lists the reproductive and vegetative parts of 37 identified species belonging to 24 families of plants ingested by the monkeys. Table 5.2 and Table 5.3 show the 10 commonest plant foods and species eaten by *C. mona*. They show that almost 40% of the feeding records came from just two species, *Dialium guineense* and *Diospyros mespiliformis*. Another 40% came from the following species (descending order of importance): *Ceiba*

Table 5.1 A list of *C. mona* 's plant food

Family (or Subfamily)	Species	Plant Parts Eaten*				Fruit type
		Leaves	Flower Parts	Fruits	Seeds	
Ampelidaceae	*Cissus aralioides*		NC	RF		Fleshy
	Cissus sp.	YL	NC	RF		Fleshy
Anacardiaceae	*Sorindeia warneckei*			FR		Fleshy
	Spondias mombin			FR		Fleshy
Apocynaceae	*Landolphia owariensis*		NC	URF, RF		Fleshy
Arecaceae	*Elaeis guinnensis*			RF		Dry
Bombacaceae	*Ceiba pentandra*	YLP	FL, NC	URF	IMSD	Dry
Caesalpinioideae	*Afzelia africana*	YL, YLP	FL		SA	Dry
	Dialium guinnense	YL, YLP	FL, NC	RF	IMSD	Dry
Combretaceae	*Anogeissus leiocarpus*	YL		RF, URF		Dry
Ebenaceae	*Diospyros mespiliformis*	YL	FL		IMSD	Fleshy
Euphorbiaceae	*Drypetes floribunda*	YL			IMSD	Fleshy
Hippocrateaceae	*Salacia lomensis*	FR				Fleshy
Loganiaceae	*Strychnos afzelii*		FL	URF, RF	IMSD	Fleshy
Malpighiaceae	*Flabellaria paniculata*	FL				Fleshy
Mimosoideae	*Albizia zygia*				IMSD	Dry
	Entada manni				IMSD	Fleshy
Moraceae	*Ficus exasperata*			FR		Fleshy
	Ficus natalensis			FR		Fleshy
	Ficus sur	YL		RF		Fleshy

(Table 5.1 cont'd from previous page)

Family (or Subfamily)	Species	Plant Parts Eaten*				Fruit type
		Leaves	Flower Parts	Fruits	Seeds	
Moraceae	*Ficus thonningii*			FR		Fleshy
	Milicia excelsa			RF		Fleshy
Myrtaceae	*Psidium guajava*			RF, URF		Fleshy
	Sterculia tragacantha	YL				Fleshy
Papilionoideae	*Dalbergia afzelia*			RF		Dry
	Lonchocarpus sericeus	LV	FL			Dry
Passifloraceae	*Abrus precatorius*	YLP				Fleshy
Rubiaceae	*Canthium multiflorum*			RF		Fleshy
	Mussaenda elegans		NC	FR, RF		Fleshy
	Vangueriopsis nigerica			RF, URF		Fleshy
Sapindaceae	*Deinbollia pinnata*			FR		Fleshy
	Lecaniodiscus cupanioides			RF		Fleshy
	Pancovia bijuga			RF		Fleshy
	Paullinia pinnata			FR		Fleshy
Sapotaceae	*Mimusops andongensis*	YLP, YL		RF, URF	IMSD	Fleshy
Tiliaceae	*Grewia carpinifolia*			FR		Fleshy
Ulmaceae	*Celtis brownii*	YL	NC	RF, URF		Fleshy

* YL = young leaves; YLP = petiole of young leaves; LV = leaves of unknown maturity; NC = nectar; FL= flower parts; FR = Fruits of unknown maturity, RF = ripe Fruits; URF = unripe fruits; IMSD = unripe seeds; SA = arils.

Table 5.2 10 commonest plant foods eaten by *C. mona*

Species	% of Feeding Records	Parts Eaten	% of Feeding Records	Cumulative % of Feeding Records
Dialium guineense	17.6	Ripe Fruits	9.2	17.6
		Immature Seeds	8.4	
Diospyros mespiliformis	18.8	Immature Seeds	4.2	36.4
		Young Leaves	6.4	
		Ripe Fruits	6.0	
		Fruits	2.2	
Ceiba pentandra	9.2	Flower Parts	6.2	45.6
		Immature Seeds	3.0	
Afzelia africana	6.2	Seed Arils	6.2	51.8
Strychnos afzelii	5	Ripe Fruits	5.0	56.8
Total	56.8			

Table 5.3 ***C. mona*** **'s seasonal top five foods**

DS1 (11)*	%	N (30)	WS2 (32)*	%	N (111)	WS3 (22)	%	N (38)	WS4 (36)	%	N (69)	DS2 (39)	%	N (183)	WS5 (30)	%	N (116)
CEPE (FL)	25	8	AFAF (SA)	11	10	DIGU (RF)	18	7	DIGU (IMSD)	9	6	AFAF (SA)	15	26	DIGU (RF)	19	22
DIGU (IMSD)	13	4	DIGU (RF)	10	9	MIAN (RF)	16	6	DIME (IMSD)	9	6	DIGU (IMSD)	14	25	DIME (YL)	14	16
DIME (RF)	13	4	DIME (RF)	10	9	DIME (RF)	8	3	DIGU (RF)	7	5	CEPE (FL)	11	20	STAF (RF)	13	15
AFAF (SP)	6	2	DIME (YL)	10	9	CEBR (RF)	5	2	DIME (RF)	6	4	CEPE (IMSD)	7	13	CEBR (URF)	4	5
STAF (RF)	6	2	STAF (RF)	9	8	DIME (ARTH)	5	2	MIAN (RF)	6	4	DIME (IMSD)	7	13	DIME (RF)	3	4

* It indicates the number of species-plant categories ingested by *C. mona*

SA = Seed Arils; RF = Ripe Fruits; URF = Unripe Fruits; YL = Young Leaves and Leaf Petioles; FR = Fruits of Unknown Maturity; IMSD = Immature Seeds; ARTH = Arthropods; FL = Nectar and Flower Parts *pentandra, Afzelia africana, Strychnos afzelii, Mimusops andongensis, Celtis brownii, Ficus sur, Anogeissus leiocarpus,* and *Drypetes floribunda*. The average number of plant species consumed was 9.3 spp./month (range: 6–14).

B. Seasonal Changes in Feeding Behavior

When fleshy fruits became scarce during the first major dry season, *C. mona* consumed more dry fruits and increased the consumption of nectar, floral parts, seeds and seed arils. In December 1995, when many *Ceiba pentandra* trees began blooming, *C. mona* buried their faces in the flowers and licked the nectar and ate the stigma and styles of the flowers while discarding the petals. *Cercopithecus mona* also fed on immature seeds of *Dialium guineense* and ripe fruits of *Diospyros mespiliformis*. The pedicels of immature green pods of *Afzelia africana* were also eaten during the first dry season (DS1). By the end of DS1, the seedpods of *Afzelia africana* became hard and developed and *C. mona* began feeding on the seed arils by striking the mature hard seedpods against large tree branches and extracting the arils that cover the seeds, and discarding the seeds. Ripe fruits of *Dialium guineense* and ripe fruits and young leaves of *Diospyros mespiliformis* were also important food items during the Wet Season 2 (WS2). During Wet Sesason 3, ripe fruits of *Dialium guineense*, *Mimusops andongense*, and *Diospyros mespiliformis* were favored over other foods, but feeding records were few (N = 38) for this season. Heavy rain and deep inundation made observations difficult during this season. In Wet Season 4, especially between September and October 1996, *C. mona* avidly fed on the immature seeds of unripe *Diospyros mespiliformis* and *Dialium guineense* fruits. At the beginning of the second major dry season (DS2), there were few ripe fleshy fruits in the forest. *Cercopithecus mona* began feeding on the seed arils of

Afzelia legumes and continued to feed on immature *Dialium* seeds. As in the first major dry season, *C. mona* was also observed feeding on the nectar and flower parts of *Ceiba pentandra*. Ripe fleshy fruits were scarce until the beginning of March 1997. In Wet Season 5, *C. mona* preferentially fed on the ripe fruits of *Dialium*, young leaf parts of *Diospyros*, and ripe fruits of *Strychnos africana*. As the fruits of *Diospyros* were becoming ripe at the end of Dry Season 2, *C. mona* examined the fruits and either ate them or rejected them. It selectively rejected the fruits with developed hard seeds, but it also rejected the fruits that were still not fully ripe to eat. When *Diospyros* fruits became fully ripe again around April 1997, *C. mona* began feeding on only the pulp. To do this, the monkeys first rolled the fruit back and forth with both hands on a branch to split it into two halves. Then, they bit into the fruit, dug out and threw away the seeds with their fingers or mouth, and then bit into the pulp, spitting out the skin.

I observed *C. mona* pouncing upon leaping arthropods and cupping them with one or both hands on tree stems to catch them. To capture slow-moving prey, the monkeys put their mouth directly on the stem. They inspected the inside of curled-up dry leaves by opening them. They also turned over leaves to find arthropods on the back of leaves. Furthermore, they obtained wood-boring insects by digging up the interior of dead-but-standing *Dialium guineense* trees.

C. Quantitative Comparison of Seasonal Diets

Cercopithecus mona fed on fewer food species in the second major dry season[*] (8.3 spp./month, *s.d.* = 1.707) than wet seasons (9.0 spp. month, *s.d.* = 2.449).[**] Fig. 5.1

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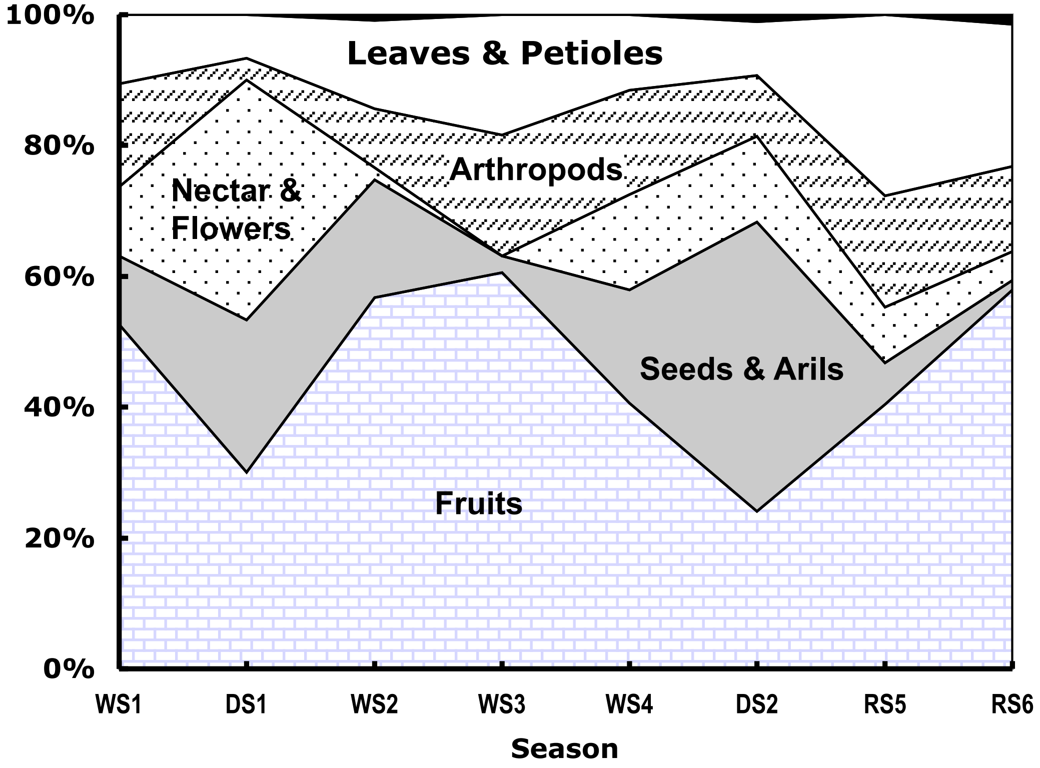
[*] Oct. 1995 = Wet Season 1 (WS1); Nov. 1995–Jan. 1996 = Dry Season 1 (DS1); Feb.–Apr., 1996 = Wet Season 2 (WS2); May–Jul, 1996 = Wet Season 3 (WS3); Aug.–Oct., 1996 = Wet Season 4 (WS4); Nov. 1996–Feb., 1997 = Dry Season 2 (DS2); Mar. 1997–Jun 1997 = Wet Season 5 (WS5).

shows the seasonality of percentages of food categories eaten by *C. mona*. Fruits were the main food during all seasons except the major dry seasons. Fruits made up 24.0% (DS2) to 60.5% (WS3) of the diet. Fruit consumption was highly correlated with the consumption of leaf parts ($r_s = 0.829$, $p = 0.042$, $N = 6$) and negatively correlated with the consumption of seeds ($r_s = -0.899$, $p = 0.015$) and floral parts ($r_s = -0.829$, $p = 0.042$). Fruit consumption was also correlated with the quantity of collected fleshy fruits ($r_s = 0.771$, $p = 0.036$). The consumption of seeds and seed arils was lowest during the wet seasons and the highest during the major dry seasons when *C. mona* consumed more seeds (DS1 = 23.3%, DS2 = 44.3%) than fruits. It was negatively correlated with the Productivity Index of fleshy fruits ($r_s = -0.841$, $p = 0.036$), with collected fleshy fruits ($r_s = -0.783$, $p = 0.033$), and with the consumption of leaves ($r_s = -0.928$, $p = 0.004$). Nectar and floral parts were important during the first major dry season (36.7%), but in other seasons, their consumption varied from 1.8% (WS2) to 14.5% (WS4). The consumption of foliage was highest in WS2 and WS5 and lowest during the major dry seasons and it was highly correlated with the Productivity Index of young leaf parts ($r_s = 0.886$, $p = 0.009$). The consumption of arthropods was highest in wet seasons (17-18.4%) and lowest in major dry seasons (3.3–9.3%).

Cercopithecus mona consumed more arthropods in WS3 (18.4%) and WS5 (17%) and the fewest arthropods in the major dry seasons. Eighty percent of the trees where they obtained arthropods belonged to five species (*Diospyros mespiliformis, 28%; Dialium guineense, 21%; Afzelia africana, 14%; Ceiba pentandra, 9%; Mimusops andongensis, 8%).*

[**] The significance cannot be tested due to small sample size.

Fig. 5.1 Types of food consumed by *C. mona*



In this study, fruits were the main food for *C. mona*, as expected. When ripe fleshy fruits were not available, the monkeys fed on immature seeds. *Cercopithecus mona* used both reproductive and vegetative parts of the most abundant tree species, *Dialium guineense* and *Diospyros mespiliformis*, especially the fruits at different developmental stages, as seasons changed. *Cercopithecus mona* ingested fruits, seeds and arils, young leaves, petioles, flowers, and nectar from these species along with arthropods that occurred on them.

IV. Discussion and Conclusion

A. Comparison with Other Populations

The results of this study show that *Cercopithecus mona* incorporates alternative foods when fleshy fruits become scarce. In comparison, *C. mona* in Grand Etang feed on mostly ripe fruits of 21 species all year round (Glenn, 1992). This is not surprising since there was little seasonality of fruit production at Grand Etang. Glenn (1996) found that monthly numbers of fruiting food trees and the mona's use of primary forest and palm brake were correlated, but monthly numbers of fruiting food trees and *C. mona*'s use of secondary forest were not correlated with each other. She suggested that this was because fruits in secondary forests tend to be lower in nutritional value than fruits in primary forests and palm brake. In addition to forest food resources, the Grenada monas fed on various cultivars. In Sào Tomé and Príncipe monas also feed on food crops (Glenn *et al.*, unpublished a).

Fruits were the main food for *Cercopithecus mona* in Mungo F.R., Cameroon (Howard, 1977). In Mungo F.R., *C. mona* fed on 20 species of fruit, 17 species of young leaves and other plant foods. *Cercopithecus mona* obtained six plant food species from primary forest and 41 species from secondary forest. In comparison, *C. erythrotis* and *C. nictitans* at Mungo each obtained 11 species of plant foods from the primary forest, and 19 and 20 plant food species from the secondary forest, respectively. Seeds of *Julbernardia seretii* eaten by *C. mona* were not eaten by *C. erythrotis* or *C. nictitans*. In addition to forest plant foods, *C. mona* at Mungo fed on a number of cultivated foods in a nearby farm where *C. nictitans* and *C. erythrotis* never fed (Howard, 1977). In addition, *C. mona* at Mungo F.R. spent a lot of time feeding on arthropods. Between May and October was the season of abundance during which new leaves, flowers, and fruits become plentiful, but Howard (1977) noted that food scarcity does not seem to occur in the Mungo F.R.

B. Comparison with Other Members of Mona Species Group

In the Dja Reserve, Cameroon, 17% and 55% of sampled *C. pogonias'* feces contained pieces of seeds and entire plant seeds, respectively (Poulsen *et al.*, 2001a). In comparison, broken seeds were found in 6% and 1%, and whole seeds in 37% and 43% of sampled *C. cephus* and *C. nictitans'* feces, respectively (Poulsen *et al.*, 2001a). These data indicate that at Dja, *C. pogonias* feeds on more seeds than two other sympatric guenons. Based on an analysis of stomach contents, Gautier-Hion (1980) found that *C. pogonias*, *C. nictitans*, and *C. cephus* at Makokou, Gabon all preferred ripe soft fruits (epicarp and mesocarp), but *C. pogonias* was the most frugivorous and insectivorous, and least folivorous of all guenons. At Lopé, during the major dry season, *C. pogonias* in Makokou mainly fed on Myristicaceae arils and increased its consumption of animal matter while other monkeys fed on mature leaves (Tutin *et al.*, 1997a). Leaves of four

Marantaceae herb species were one of *C. nictitans* and *C. cephus*' 12 keystone species-food items. These species-food item were not important food sources for *C. pogonias* at Lopé (Tutin *et al.*, 1997a).

The diets of *C. pogonias pogonias* in Makandé, Gabon and *C. pogonias wolfi* in Salonga, Democratic Republic of Congo (DRC) were seasonally and interannually variable (Gautier-Hion *et al.*, 1993; Brugière *et al.*, 2002). In Makandé, *C. pogonias* as well as *Lophocebus albigena*, *C. nictitans*, and *Colobus satanas* derived nearly 50% of their annual diets from Caesalpinioideae seeds. The numbers increased to 60–80% during the dry seasons. During the 1993 dry season in Makandé, there were few *Dialium* fruits, but *Pterocarpus soyauxii* (Papilionoideae) flowers were abundant. *Cercopithecus pogonias* increased its feeding on these flowers during that season. In the 1994 dry season, when fleshy fruits became scarce, 50% of *C. pogonias*' diet came from seeds of two *Dialium* species. In Salonga, the main foods of *C. p. wolfi* were leaves in January (76%), flowers (51% in March), arils (70% in May and 43% in July), and legume pods (about 60% in Aug.–Nov.) (Gautier-Hion *et al.,* 1993). Fruit consumption was always low (max = 10%). The availability of fruits, measured by the monthly number of fruiting species and fruiting sites, was significantly higher in Makokou than in Makandé. Fruit consumption was related to the number of fruiting species in Makokou. In Makandé, the availability of fleshy fruits and the consumption of fleshy fruits were low. The monthly consumption of fleshy fruits was correlated with the monthly availability of fleshy fruit species and sites. In addition, the monthly consumption of legume seeds was correlated with the monthly availability of legume fruits and sites. In Makandé, *C. pogonias* fed on most commonly available foods at each season. Brugière *et al.* (2002) suggested that at both Makandé and Salonga, a combination of Caesalpinioideae predominance, mature leaves of low quality due to poor sandy soil, low fleshy fruit diversity, and a lack of secondary vegetation brings about irregular resource bottlenecks that force primates to feed on seeds when other alternative foods such as flowers are not available.

In Taï Forest, Buzzard (2004) found that *C. campbelli* most frequently fed on fruits (46.3% of all dietary items). In this forest, fleshy fruits are abundant and do not become scarce even during the short dry season (June–August). The top ten ranked species-specific plant items eaten by *C. campbelli* included three species of *Diospyros* fruits (fleshy fruits). The second most important foods of *C. campbelli* in Taï Forest were arthropods (33.1%). Taï Campbell's monkeys were the most insectivorous and least folivorous of the three guenons studied (*C. campbelli*, *C. petaurista*, and *C. diana*). Leaf consumption was limited to 8.4% of all dietary items and floral parts were little eaten (1%). Fruit consumption was highest during the periods of fruit abundance and when the availability of fruits became lower, *C. campbelli* incorporated more arthropods and somewhat more foliage (Buzzard, 2004).

In the Boabeng-Fiema Monkey Sanctuary in Ghana, Porter (2005) found that arthropods and cultivated foods made up ≥ 50% and 25% of *C. campbelli*'s diet during two wet seasons. Fruits composed of ≤ 10% of *C. campbelli*'s diet and leaves were little eaten.

C. Comparison with Larger and Smaller Guenons

A majority of arboreal guenons so far studied in rain forests also employs the "alternative foods" strategy, although the degree of flexibility in incorporating alternative foods varies among species (Whitesides, 1991; Rudran, 1978; Struhsaker, 1980, Cords, 1986). For example, Gartlan and Brain (1968) observed that *C. mitis* in an evergreen forest in Zimbabwe fed on significant amount of leaflets of large trees of *Albizia gummifera* (Mimosoideae) at the end of the dry season. When fruits were scarce at Makokou (rainfall 1,755 mm/yr), the stomach contents of *C. cephus*, *C. nictitans*, and *C. neglectus* showed increased proportions of leaves, especially mature leaves (Gautier-Hion, 1978, 1980, 1988). When fruits were scarce in the Kibale Forest, a semi-evergreen medium-altitude moist forest, and Kakamega Forest (rainfall approx. 2,000 mm/yr), *C. mitis* became more folivorous and *C. ascanius* more insectivorous (Rudran, 1978; Cords, 1986). In a forest fragment at Lopé Reserve in Gabon (rainfall 1,548 mm/yr), when fruits became scarce, *C. cephus* fed on more insects (80%) and flowers (Tutin, 1999).

All species groups in the Cercopithecini contain at least one species that inhabits seasonally dry forests, but the dietary data on the arboreal guenons that inhabit such habitats are rare (Cords, 1987a). *Cercopithecus mitis* is probably the only species that has been studied in a wide variety of habitats that include rain forests (e.g., Kibale Forest, Uganda: Butynski, 1990; Budongo Forest, Uganda: Fairgrieve and Muhumuza, 2003; Kakamega Forest, Kenya: Cords, 1986), montane and bamboo forests (Zomba Plateau, Malawi: Beeson, 1989; Beeson *et al.*, 1996; Nyungwe Forest Reserve, Rwanda: Kaplin, 2001; Kaplin and Moremond, 1998, 2000) and dry forests (Cape Vidal Forest: South Africa: Lawes *et al.*, 1990; Lawes, 2002). *Cercopithecus mitis labiatus* in Cape Vidal, a dry forest with 6–7 dry mos. per year, fed on a large portion of leaves when fleshy fruits were unavailable (Lawes *et al.*, 1990; Lawes, 2002). *Cercopithecus mitis* is well adapted to low-quality folivorous diet. Because of this dietary flexibility, Lawes (2002) stated, “The competitive advantage that folivory confers on an essentially frugivorous primate has allowed the *Cercopithecus mitis* species group to become almost exempt from climatic seasonality and food restriction."

In Nyungwe Forest Reserve, a tropical montane forest in Rwanda (rainfall 1,744 mm/yr), *C. mitis* responded differently in two dry seasons (Kaplin *et al.*, 1998). In the 1991 dry season, *C. mitis* increased the proportion of leaves, but in the 1992 dry season, *C. mitis* increased the consumption of seeds, especially those of *Macaranga neomildbraediana* (Euphorbiaceae)(Kaplin *et al.*, 1998). Their study has illustrated that interannual variation in plant seasonality has a profound influence on determining what foods are consumed by primates. Whether primates play a role as seed dispersers or destroyers depends on the availability of particular food sources at a particular time (Chapman *et al.*, 2002).

Cercopithecus diana is more folivorous than sympatric guenons on Tiwai Island, Sierra Leone and Taï Forest, Côte d'Ivoire (Whitesides, 1989). However, *Cercopithecus diana* in Bia National Park in Ghana, a moist semi-deciduous forest, incorporated 24.3% seeds (ripe and unripe) during an exceptionally dry year (Nov. 1976 – Jul. 1977)(938 mm rainfall vs. 1,441 mm of rain in the previous year) in its diet (Whitesides, 1989, 1991; Curtin, 2002). It appears that *C. diana* incorporated seeds in its diet due to a lack of palatable leaves in its habitat during the dry year. *Cercopithecus nictitans* in Makandé and Lopé also fed on a significant amount of seeds, but its favorite alternative foods are leaves.

The above brief survey of guenons' use of alternative seasonal foods suggests that members of the mona species group tend to shift to either seeds or insects, smaller-bodied guenons tend to shift more to insectivory (and to a lesser extent young-leaf feeding), and larger-bodied guenons tend to shift more towards folivory. There has been no report of members of the mona species group supplementing their diets with significant amounts of leaves in their diets when pulpy foods are scarce.

D. Semivory

Seeds, as an independent food source, not as an unintended consequence of pulp eating, play a significant role in the diets of both folivorous primates (e.g., *Colobus satanas*: McKey, 1978; Gautier-Hion *et al.*, 1997; Brugière *et al.*, 2002; *Procolobus badius, Colobus angolensis*: Maisels *et al.*, 1984; *Procolobus verus*: Oates, 1988b; *Colobus polykomos*: Dasilva, 1994; *Presbytis melalophos*, *Presbytis rubicunda*: Davies, 1991) and frugivorous primates (e.g., *Chiropotes chiropotes*: van Roosmalen *et al.*, 1988; *Pithecia pithecia*: Kinzey and Norconk, 1990; *Cacajao melanocephalus*: Barnett and Castilho, 2000; *Cebus apella*: Struhsaker and Leland, 1977; Terborgh, 1986a; van Roosemalen *et al.*, 1988; Lambert *et al.*, 2004; Terborgh, 1983; Peres, 1991; *Cebus albifrons*: Terborgh, 1986a; *Lophocebus albigena*: Lambert *et al.*, 2004; *C. diana*: Curtin, 2002; *C. nictitans*: *C. pogonias*: Brugière *et al.*, 2002). Seeds are generally high in proteins and lipids or starch (non-structural carbohydrates) and often more nutritious than leaves (Davies *et al.*, 1999; Norconk and Conklin-Brittain, 2004). Lipids and nitrogen are high in some legume seeds (Kinzey and Norconk, 1990; Waterman and Kool, 1994; Lambert, 1998; Janson and Chapman, 1999).

Seed eating, whether seeds are soft or hard, by the primates is accomplished via a variety of mechanisms. Saki-uakaris (genera *Pithecia*, *Chiropotes*, and *Cacajao*) are well known seed-predators (Boubli, 1999). They possess robust canines, laterally divergent incisors that are adapted for opening tough exocarp, and quadritubercular molars (low flat molar teeth) that are adapted for crushing seeds (Kinzey and Norconk, 1990). Their forestomach is small, but their enlarged hindgut allows caeco-colic fermentation of structural carbohydrates (van Roosemalen, *et al.*, 1988; Norconk *et al.*, 2002). *Cebus apella* possesses some of the thickest molar enamel of all extant primates and is known for its excellent manual dexterity (Struhsaker and Leland, 1977; van Roosemalen *et al.*, 1988; Peres, 1991). In Cocha Cashu, Manu N.P. in Peru, *C. apella* obtained the mesocarp of the *Astrocaryum* palm nuts by bashing two nuts against each other or using one as a mallet and bashing it to another (Terborgh, 1983).

Mangabeys (genus *Lophocebus* and *Cercocebus*) are also known to possess some of the thickest-enameled molar teeth (Fleagle, 1999). *Lophocebus albigena* feed on a significant amount of seeds (29% of annual diet) in the Dja Forest, Cameroon (Poulsen *et al.,* 2001b, 2002) and at Lopé, Gabon (Ham, 1994 cited in Poulsen *et al.*, 2001b). In the Kibale Forest, however, seeds consisted of a small portion (8%) of *L. albigena*'s annual fruit feeding (Wallis, 1979 cited in Poulsen *et al.*, 2001b).

Colobines, with their large sacculated forestomachs and large (relative to body size) higher-crowned thin-enameled molar teeth, are well equipped to ingest and digest high fiber foods (Chivers, 1994; Kay and Davies, 1994; Lucas and Teaford, 1994). Among the colobines, *C. satanas* is best known to feed on a significant amount of seeds, in particular Caesalpinioideae seeds, in Douala-Edéa and Lopé (Oates, 1994). *Colobus guereza* feeds on a significant amount of young leaves in the Kibale Forest (Oates, 1977). In Douala-Edéa, nutritious Caesalpinioideae seeds are abundant, but leaves are poor in quality. In contrast, digestible foliage is abundant, while edible legume seeds are scarce in Kibale. *Colobus satanas*, however, feeds on more seeds in Lopé than in Douala-Edéa, even though high-quality young leaves are available in Lopé. Thus, Oates (1994b) suggests that the difference in the diets of *C. guereza* and *C. satanas* cannot be solely explained by the abundance or scarcity of palatable leaves or seeds in these forests; he suggests that the propensity for *C. satanas* to incorporate legume seeds is an evolved system, more than a proximate mechanism. *Colobus polykomos* in Tiwai, Sierra Leone also feeds on a significant amount of legume seeds (Dasilva, 1994). Oates (1994b) has suggested that the dental, oral, and jaw morphology of *C. satanas* and *C. polykomos* are better adapted to semivory than *Procolobus* spp.. Daegling and McGraw (2001) took a large number of linear and areal measurements of the mandibles from wild caught individuals in sympatric *C. polykomos*, *P. verus* and *P. badius* populations in the Taï region in Côte d'Ivoire and Sierra Leone, West Africa to examine if mandibular morphology corresponds with feeding behavior among the three taxa. They found little congruence. However, other variables such as the size, morphology, orientations of the canines and incisors, and frequency of chewing would likely influence the biomechanics of chewing and other functional demands that the mandible must fulfill act as a noise that obscures the direct relationship between the jaw morphology and diet. Therefore, these issues need to be taken into account and examined before a definite conclusion can be drawn (Daegling and McGraw, 2001).

There is evidence that guenons as well as other cercopithecines are also able to process seeds with their blunt low cusped molars that can work as mortars and pestles in pounding hard objects such as seeds (Hill, 1966; Happel, 1988; Maisels, 1993; Chivers, 1994; Lucas and Teaford, 1994; Lambert, 1998, 2005). Lucas and Teaford (1994) present evidence that colobines have an advantage over cercopithecines in processing leaves and large hard seeds that are covered with thin flexible coats. It appears, however, that cercopithecines may have an advantage over colobines in processing certain types of seeds (immature seeds for example). Guenons' long gut passage rates (GPR) coupled with their small-body size perhaps allow them to ferment structural carbohydrates, detoxify chemical deterrents faster, and to efficiently absorb nutrients (Maisels, 1993; Lambert, 1998; Lambert *et al.*, 2004).

There is tremendous variation in patterns of primate seed eating, since the structure, texture, hardness, morphology, size, chemistry, and nutritional content of seeds are extremely variable within individuals, species, and between seasons (Kinzey and Norconk, 1990; Kaplin and Moermond, 1998; Norconk and Conklin-Brittain, 2004). Since the chemistry of fruits changes rapidly as they ripen, the palatability of the seed decreases as the palatability of the pulp increases. Therefore, colobines often prefer to feed on immature seeds that are usually softer and moister than mature seeds, but immature seeds often contain more secondary metabolites than mature ones (Davies *et al.*, 1999; Lucas and Teaford, 1994; Lambert, 2005).

Lucas and Teaford (1994) drew attention to the fact that some mechanical properties of seeds can determine seed preferences in closely related colobine species. They observed both *Presbytis melalophos* and *Presbytis rubicunda* feeding on seeds (unlignified testa) of *Millettia atropurpurea* (Papilionideae) that were encased in a thin seed coat (0.5 mm thickness), but these species did not feed on the seeds of *Mezzetia parviflora* (Annonaceae) that were encased in a 3–4 mm thick hard shell, which was 10 times harder than *M. atropurpurea.* In the Lama Forest, most of the seeds consumed by *C. mona* were immature seeds. Kibale guenons tend to visit fruiting sites before the chimpanzees arrive, often feeding on fruits that contain immature seeds (J. Lambert, pers. comm.).

Manual and behavioral dexterity can compensate for their lack of significant anatomical specialization. *Cercopithecus mona* in the Lama Forest exhibited behavioral dexterity to obtain seed arils of *Afzelia africana*.

E. Determinants of Semivory in Frugivorous Primates

In the Lama Forest, a majority of seeds *C. mona* fed on were immature seeds of *Dialium guineense* (Caesalpinioideae). *Cercopithecus mona* also favored seed arils of *Afzelia africana* (Caesalpinioideae). Semivory by the members of mona species group and other guenons is often prevalent in seasonal forests or seasonally inundated forests where Caesalpinioideae trees are dominant and fleshy fruit species are poor, as long as the legume seeds are available during critical times (e.g., Salonga, DRC; *Forêt des Abeilles*, Gabon, Maisels and Gautier-Hion, 1994; Brugière *et al.*, 2002; Gautier-Hion, unpub. data, cited in Chapman *et al.*, 2002, and this study) (Fig. 5.2). Leaves of Caesalpinioideae are difficult to digest due to high contents of phenolics and fiber (Maisels and Gautier-Hion, 1994). Maisels and Gautier-Hion (1994) found that monkeys tend to turn to seeds in forests that are dominated by Caesalpinioideae trees. Soil quality influences the quality of leaves in the forests and Caesalpinioideae trees are often abundant in poor soil, but the relationship between poor soil quality and an abundance of Caesalpinioideae trees is not strong (Maisels and Gautier-Hion, 1994). In Central Africa, they suggest that the degree of inundation has an influence on the abundance of Caesalpinioideae trees.

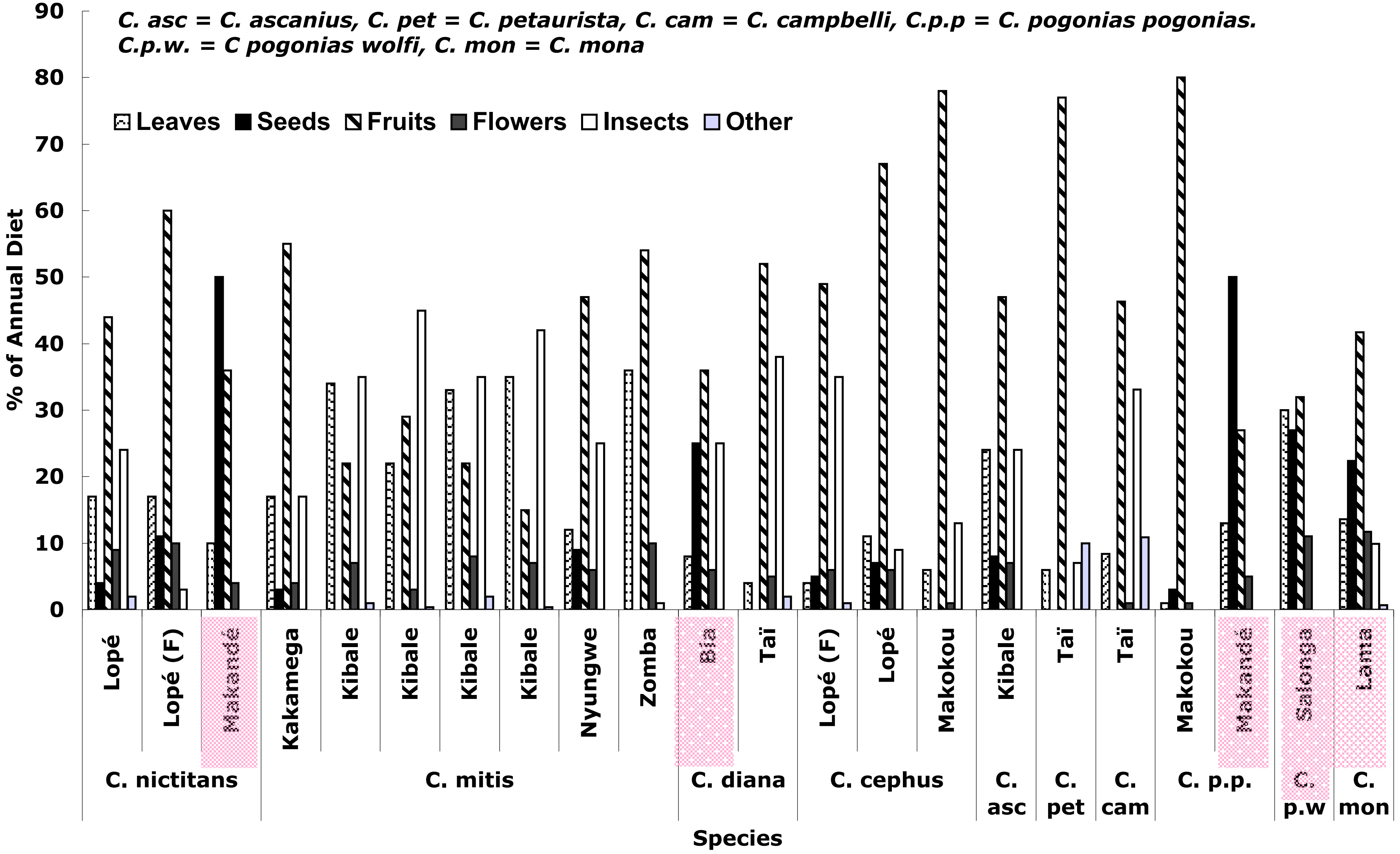


Fig. 5.2 A comparison of guenon annual diets Shaded areas show forests in which Caesalpinioideae is the dominant family. Semivory is often prevalent in these forests.

C. asc = C. ascanius, C. pet = C. petaurista, C. cam = C. campbelli, C.p.p = C. pogonias pogonias. C.p.w. = C pogonias wolfi, C. mon = C. mona

Other frugivorous primates also consume seeds in forests that are often dominated by Caesalpinioideae trees. For example, *Cebus apella* in the Santa Genebra Reserve in Brazil fed on more seeds (about 30%), especially seeds of dry fruit species during the dry season when the lowest availability of freshly fruits occurred (Galetti and Pedroni, 1994). Capuchins ate more pulp in the wet season (68.8%) than in the dry season (53.3%). There was a negative correlation between fruit availability and pulp consumption by capuchins, but there was no correlation between fleshy fruit availability and pulp consumption (Galetti and Pedroni, 1994).

The Venezuelan white-faced saki (*Pithecia pithecia*) that lives on Isla Redonda (Round Island) in Lago Guri is widely known as a seed predator. Caesalpinioideae trees are dominant (29.4%, ≥ 10 cm DBH) (Parolin, 1992). The seeds of *Connarus venezuelanus* (Connaraceae), the fourth highest-ranking species, were *P. pithecia*'s most eaten food item. The saki's two most important foods were fruits and seeds (88.3% ± 6.9%). The monthly consumption of seeds of any kind (excluding seeds eaten together with the pulp) was 63.2% ± 32.7%. The sakis' diet contained 33.8% legume seeds during the early dry season. Norconk and Conklin-Brittain (2004) chemically analyzed *P. pithecia*'s eaten and uneaten plant items and found that the amounts of crude protein, free simple sugars, and tannins were not significantly different between the two, but the amounts of lipids, non-structural carbohydrates, and fibers were higher in eaten items. They suggested that the saki's food selection was a trade-off: obtaining high lipid foods that incidentally contained high fibers and condensed tannins. In comparison with the Venezuelan saki, *P. pithecia* that lives in Central Amazon, 80 km north of Manaus in Brazil, fed on less unripe fruits and seeds (26–31% of diet) (Setz, 1994).

In the Lama Forest, the availability of fleshy fruits including those of secondary vegetation was depressed during major dry seasons. Therefore, fruits of secondary vegetation were unreliable food sources for *C. mona*. In disturbed or regenerating areas of wet forests such as Tiwai, however, fleshy fruit producing pioneer trees are abundant (Fimbel, 1992). The basal areas of fleshy fruit producing species such as *Nauclea latifolia* and *Musanga cecropioides* in young secondary forest at Tiwai were 8,857.4 cm^2/ha and 4,170.6 cm^2/ha, respectively. In young secondary forest, *Cercopithecus campbelli* was often observed feeding on these pioneer fruits. In contrast, the basal area of a fleshy fruit producing species, *Ficus sur*, that is common in farm bush areas of the Lama Forest was 1,659 cm^2/ha. Fruits of pioneer species are able to provide foods for frugivorous primates in wetter forests, but in seasonal forests like Lama, they are not sufficient to provide daily sustenance. In the Lama Forest, factors such as intense seasonality, the abundance of Caesalpinioideae trees, a lack of fleshy fruits in disturbed and dense forests, and perhaps the superior nutritional quality of seeds in the forest, are guiding *C. mona* to seek seeds as alternative foods that they can rely on during the periods of low ripe fleshy fruits.

Guenons, however, also feed on seeds of other types of fruits (Curtin, 2002; Lambert. 2001, 2005; Poulsen *et al.*, 2002). In addition to Caesalpinioideae seeds, *C. mona* in the Lama Forest also fed on immature seeds of non-leguminous trees, such as *Diospyros mespiliformis* and *Strychnos afzelii*, when legume seeds and ripe fleshy fruits were not available. In the Bia National Park, Ghana, where Caesalpinioideae trees comprise approximately 24% of the BA/ha in the park (Martin, 1987), *C. diana* incorporated a lot of seeds in its diet, but it fed on mostly non-legume seeds (Curtin, 2002). This indicates that a relationship between the abundance of Caesalpinioideae trees and semivory suggested above is not a tight one and needs to be further investigated.

CHAPTER 6: GROUP STRUCTURE, SOCIAL BEHAVIOR, AND REPRODUCTIVE BEHAVIOR

I. Introduction

The social behavior of cercopithecins has been contrasted with that of papionins. Rowell (1988) noted that: (1) cercopithecins use subtle communication systems to maintain group cohesion, but papionins extensively use obvious gestures and noise to communicate with each other; (2) cercopithecins are mostly territorial as long as population densities are high, but papionins are not territorial, since they occupy home ranges that are too large to defend; (3) in the presence of females, adult male cercopithecins are intolerant of other males, but papionin males are usually tolerant of each other and may cooperate with each other[*]; (4) cercopithecin males seldom interact with non-receptive females, but papionin males maintain affiliative bonds with females even when the females are not in estrus and females are therefore more integrated into the group.

Studies conducted on guenons in the last 20 years or so have revealed that the differences between papionins and cercopithecins are not clear-cut (Newton and Dunbar, 1994; Cords, 1988, 2000, 2002; Isbell *et al.*, 2002). There are variations in regard to female-female relationships (Rowell *et al.*, 1991; Cords, 1987a, 2001; McGraw *et al.*, 2002; Payne *et al.,* 2003; Pazol and Cords, 2005) as well as male-male relationships among guenon species (Cords, 2000). Furthermore, in some guenon species, adult females in social groups are more involved in territorial defense, while in other species,

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[*] There is an exception to this. Male gelada baboons, *Theropithecus gelada*, are intolerant of each other.

males are more involved. For example, Buzzard (2004) reported that in the Taï Forest, *Cercopithecus diana* females are active defenders of group territories, while in *C. campbelli* and *C. petaurista*, males are more involved. At Grand Etang, Glenn (1996) reported that males belonging to all-male groups of *C. mona* are friendly to each other.

Regarding male residency, the one-male group is the usual pattern in many guenons (e.g., *C. mitis, C. diana, C. nictitans, C. ascanius*, *C. patas. C. cephus, C. petaurista*, *C. erythrotis, C. erythrogaster*) (Chism and Rowell, 1988; Cords, 1997a, 2000; Buzzard, 2004). In blue, redtail, and patas monkeys, the one-male group structure breaks down during multi-male influxes that occur in some years. In blue and redtail monkeys, during multi-male influxes, multiple males sometimes form loose associations. During mating seasons, male patas monkeys sometimes form all-male groups in which males frequently interact. After entering into a group of females, however, one male usually evicts extra males from his new group, sometimes inflicting fatal wounds to them (Isbell, 2002).

Unlike the modally one-male group pattern seen in blue, redtail, and patas monkeys, the talapoins and Allen's swamp monkey form large multi-male groups. Vervets (*Chlorocebus aethiops*) form facultatively multi-male groups (Isbell *et al.*, 2002). In most field sites, vervets form multi-male groups, but in some areas such as in Barbados, vervets are territorial and form one-male groups (Isbell *et al.*, 2002). During breeding seasons, solitary males may form all-male groups in which males are gregarious (Fedigan and Fedigan, 1988).

Previous research has shown that there is a variation in the group structure of *C. mona*. In Grand Etang F.R. in Grenada, mixed-sex groups contain only one male.

Outside mixed-sex groups, multiple males may form all-male groups all year round (Glenn, 1996). In these all-male groups, males are friendly towards each other. In Mungo F.R. and Douala-Edéa, Cameroon, some groups contain more than one-male all year round, but no all-male groups were reported there (Howard, 1977; Whitesides, 1981). Other aspects of *C. mona*'s social system are still poorly known, because the study subjects at Grand Etang and Mungo were never fully habituated. To obtain detailed information regarding "who does what to whom how often (Rowell, 1988)," individuals need to be recognized and the visibility in the forest must be excellent. Without these conditions, observations are intermittent and samples are potentially skewed. Because I had a similar habituation problem as the two previous long-term studies, I resorted to obtaining data on *C. mona*'s social and reproductive behavior from about eight unhabituated groups. Some individuals in two of these groups were recognizable, but these two groups were not always found. Therefore, observations were often intermittent and sample size is small. Nevertheless, a preliminary sketch of *mona* social and reproductive behavior is presented here and needs to be corroborated by further studies. I describe the social structure in *C. mona* in the Lama Forest and examine some factors that may influence the intersite variation in male numbers. I describe affiliative behaviour, vocal behavior, behavior displayed during inter-group encounters, and reproductive behavior of *C. mona* in the Lama Forest. These data are compared with the data obtained in previous studies and surveys on this species and I attempt to examine the reasons for similarities and differences that occur between the sites.

I also examine how changes in rainfall and food availability may have an influence on certain aspects of *C. mona*'s social and reproductive behavior. Butynski

(1988) has shown a strong correlation between birth seasons in a large number of guenon species and the period of high rainfall and food abundance. I examine whether *C. mona* in the Lama Forest follows this pattern.

II. Methods

A. Data Collection Procedures

I gathered data on group structures and social and reproductive behavior from systematic walks, censuses, and *ad libitum* samplings.

(1) **Systematic walks**: I systematically walked the trails established in the East and West Study Sites for 5–10 days per month between Aug. 1995 and June 1997 (data were not collected in May 1996). When a group was encountered, I followed it as long as possible, recording any visible behavior. When individuals went out of sight, I looked for them for 15 minutes. If the individuals were not found, I began looking for another group on the same trail.

(2) **Censuses**: During the semi-monthly census, I recorded *C. mona*'s behavioral data. Group composition data obtained through censuses are reported here.

(3) ***Ad libitum* sampling**: During the period between Oct. 1995 and Jan. 1996, I attempted to habituate a group of *C. mona* by making myself visible to the monkeys. During this period, I collected a few data by using the *ad libitum* sampling method. I also used this method to collect behavioral data while conducting tree enumeration (Chapter 3) and phenology observation (Chapter 4). This method was also used to collect data during some intergroup encounters.

B. Focal Animal Sampling

I defined a primate encounter as the "continuous or intermittent behavioral observation of an individual (or individuals) belonging to the same group" and a behavioral record as a "focal animal sampling of behavior during a primate encounter." When monkeys were encountered, I began recording their behavior. Some encounters were brief, as the monkeys simply fled after the initial contact of the encounter, especially during the first seven months while I was trying to habituate a group. Many encounters, however, had a long contact duration. When it was ascertained that monkeys were not fleeing, I looked around the group to find any visible individual, and I recorded the behavior of this individual at 3-minute intervals. The following information was recorded: time of initial contact, quadrat position, age-sex class of individual, behavior (e.g., feed, roage, rest, locomote, sit, sleep, flee, groom, supplant, copulate, etc.), height of the individual in a tree, substrate species, group type, group size, group composition, and end time of encounter. Recorded behavior was categoried into gross behavioral categories. Close proximity (≤ 1 m distance) interactions between individuals (e.g., coming to sit in close proximity, coming to feed in close proximity, grooming, touching, playing) were considered as affiliative behavior. Threats, attacks, hair pulling, and scratching were recorded as aggressive behavior. The number of individuals in a group was counted or estimated during most primate encounters. A primate encounter ends when a group or individuals under observation become out of sight for more than 15 minutes.

When calls were given, I recorded date, time, location, call type (e.g., contact call, high hack, loud call, etc.), age-sex category of the caller, social features of the caller if possible (e.g., resident male, non-resident male), and substrate. Additionally, for loud calls, possible auditory or physical triggers or cues (e.g., tree fall, thunder) that immediately (≤ 10 sec.) preceded the calls were recorded. Many calls were also tape-recorded using a Sony TCM Mono tape recorder and a Sennheiser directional microphone for future sound analysis.

C. Data Analysis

To find out how frequently behavioral records were obtained during each primate encounter, I calculated the ratio of the number of behavioral records (B) to the contact duration (D)(min.) (B/D) for all encounters that lasted > 1 minute. For example, if five records were collected during a 20-minute encounter, the ratio is 5/20 = 0.25. The greater ratio indicates more records per encounter. The mean ratio per month was calculated to examine if observation was becoming easier (or partial habituation was taking place) as the study progressed.

All behavioral records were pooled from all collection methods and combined for each season. Data from Wet Season 1 (WS1) (Oct. 1995) and Dry Season 1 (DS1) (Nov. 1995 – Jan. 1996) were eliminated from statistical analysis because of an incompleteness of records and small sample size. Spearman's Correlation Coefficients between the relative scores for each activity, rainfall, and calls (corrected for the summed observation hours) were computed. Confidence level was set at 95% and all tests were two-tail tests.

III. Results

A. Primate Encounters and Behavioral Records

I obtained 2,006 behavioral records from 499 primate encounters (Table 6.1). The vast majority of primate encounters involved *C. mona*[*] ($n = 416$, 83%). The mean monthly number of records that involved *C. mona* was 95 (range: 22-403, *s.d.* = 86.717). The mean contact duration was 63 minutes (range: 1–538 min., *s.d.* = 104.18, $n = 389$), which gradually increased as this study progressed. The contact duration was highly correlated with cumulative hours of observation ($r_s = 0.893$, $p = 0.007$) (Fig. 6.1).

B. Group Size and Structure

1. Group Types

I observed two types of *C. mona* social groups: mixed-sex groups and all-male groups, which differed both in the number of individuals and in composition. Table 6.2 shows the number of group sightings and sightings of solitaries during the censuses. Among the 470 *C. mona* group sightings, 181 were mixed-sex groups (88 one-male groups, 45 multi-male groups, 48 groups with unclear male number) and 46 were all-male groups that contained 2–5 males ($\bar{x} = 2.8$, *s.d.* = 0.87, $n = 35$). The structure and composition of 243 *C. mona* groups were undetermined. Mean group size of mixed-sex groups was 13.3 (*s.d.* = 0.87, $n = 181$). Mixed-sex groups contained 1–4 males ($\bar{x} = 3.2$, s.d. = 0.93, $n = 68$), females, and juveniles. The mean group size of one-male groups ($\bar{x} = 11.2$, s.d. = 3.96, $n = 33$) was smaller than the mean group size of multi-male groups

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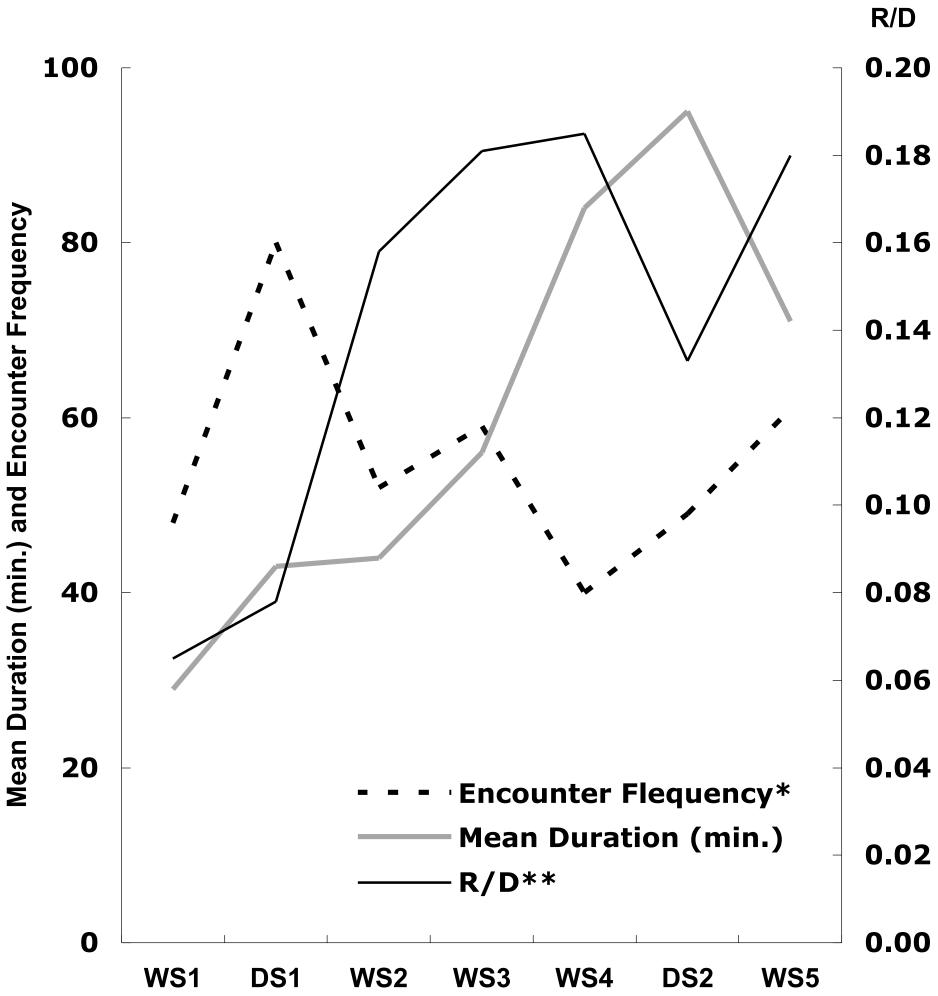
[*] The high percentage of *C. mona* group sightings is partly because I was intentionally looking for this species rather than other species. This number, however, would probably not differ too much even if I looked for other primate species, since the population density of *C. mona* is much higher than that of other species (see Chapter 7).

Table 6.1 Frequency of primate encounters

Species	Freq.	%
C. mona	351	70.3
C. mona & C. erythrogaster	62	12.4
C. erythrogaster	64	12.8
C. mona & Procolobus verus	1	0.2
C. mona, P. verus & C. erythrogaster	1	0.2
Chlorocebus aethiops	17	3.4
Galagoides demidovii	3	0.6
Total	499	100.0

Fig. 6.1 Encounter frequency, contact duration, and the ratio of focal animal sampling records to contact duration.

As the study progressed, the mean duration per primate encounter increased and the frequency of samples also increased.



*Only those encounters that lasted > 1 min were included in the analysis.
** R/D = Frequency of Focal Animal Sampling Records/Contact Duration

Table 6.2 Sightings of *C. mona* groups and solitaries during censuses, systematic walks, and ad lib sampling

Group Types		Number of Group Sightings	Group Size				N*
			mean	min.	max.	s.d.	
Mixed-Sex	One-male	88	11.2	5	25	3.96	33
	Multi-male	45	15.6	5	35	8.69	27
	Male number Unclear	48	15	10	20	3.53	4
	Total	181	13.3	2	35	6.73	64
All-male		46	2.8	2	5	0.87	46
Uncertain Group Type		243	13.1	3	40	6.51	198
Total Group Sightings		651					
Solitaries		24					

** The N of group size and N of group sightings do not match, because I focused on discerning the number of adult males in social groups and estimating group size was not always successfully made.

($\bar{x}$ = 15.6, s.d. = 8.69, n = 27) and the difference was significant (t = -2.333, *d.f.* = 25, p = 0.028). The mean number of all-male groups observed per month was 4.8 (range: 1–10, *s.d.* = 2.4). All-male group size varied between two and five ($\bar{x}$ = 3.4, *s.d.* = 0.9741, n = 35). I observed all-male groups containing a juvenile and groups that contained a *C. erythrogaster* male twice. The sightings of all-male groups occurred throughout the study period, but it was weakly negatively correlated with rainfall (r_s = -0.548, p = 0.028). A few all-male groups, recognizable due to distinguishing physical characteristics of certain males, appeared to change in size within one day and between days.

2. Foraging Subgroups

I observed on seven occasions some females and subadults moving ≥ 100 m away from a mixed-sex group. For example, at 11:35 GMT on Apr. 12, 1996, I observed four females of a *C. mona* group of about 10 individuals moving about 100 m to the north while other individuals (females and juvenile) of the group moved off south and disappeared in the forest. Although these individuals were far from the rest of the group, they maintained contacts by exchanging soft contact calls. In many instances (n = 86 encounters), a group appeared to be spread out in wider than a 2 ha area. I also observed an adult male of a mixed-sex group moving away from the group five times.

C. Behavioral Repertoire and Seasonality of Behavior

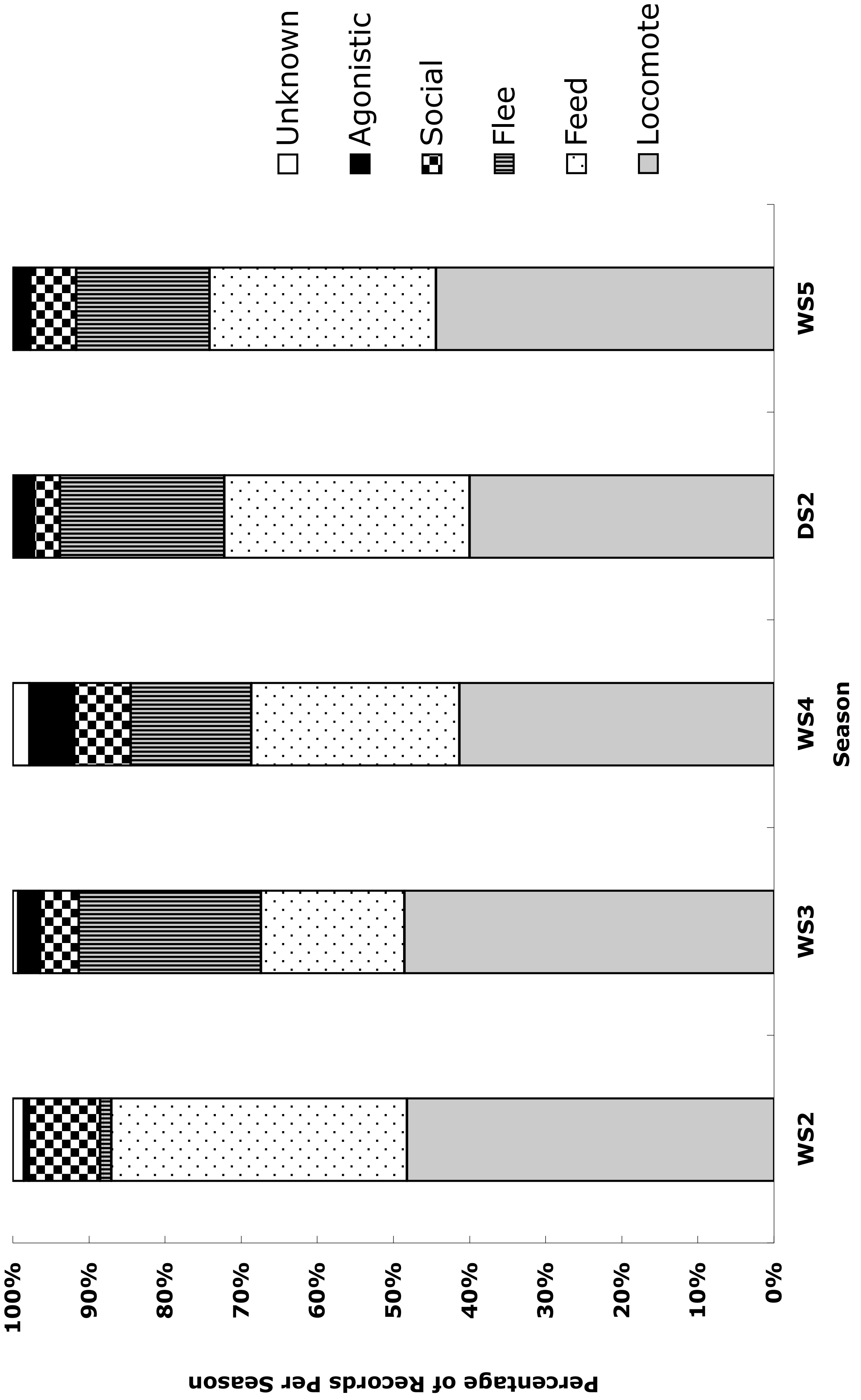
All observed behavioral categories are described in Table 6.3. The most frequently observed behavior was “locomote” (38.4%), followed by “feed” (24.6%), “flee” (16.4%), and “sit/rest” (14.7%). Seasonality of the frequency of these behavioral categories is shown in Fig. 6.2. Large differences in the frequency of behavioral categories were not found among seasons.

Table 6.3 Behavior recorded during focal animal sampling on *Cercopithecus mona* and behavioral categories used in analysis

Behavioral Category	Behavior Recorded	Description
Locomote	walk, jump, climb	An individual moves from one place to another by walking, jumping, descending, and climbing.
Feed/Forage	Forage	An individual moves around looking for a food item to feed.
	Feed	An individual uses its fingers to pluck food items from a vegetation and/or just places a food item in its mouth and may start chew ing.
Flee/Hide	Flee	An individual quickly moves away from a position after noticing the observer(s).
	Hide	An individual quickly moves behind a vegetation presumably because of the individual's fear towards humans.
Sit/Rest	Sit	An individual is sitting down on its buttocks.
	Rest	An individual is sitting quietly with its eyes closed on a branch with or without its legs hanging.
	lie down	An individual is lying down on its back or on the side.
Affiliative	Groom	An individual uses its hands or mouth to remove particles from another individual's fur.
	Solicit Grooming	An individual demands being groomed by thrusting its entire or a part of its body against the potential groomer.
	Play	At least two individuals engage in a joyful chase-after-one-another game.
	Sit together*	An individual comes close to an individual and sit near(≤ 1 m) the individual.
	Cling	An individual attaches itself onto another individual's fur.
Agonistic	Supplant	An individual takes another individual's position by having another individual move from its position.
	Head-bob	An individual moves its head up and down or side to side, showing it off to a targeted individual(s).
	Squabble	At least two individual engage in a loud vocal exchanges that may involve some close physical interactions.
	Branch Shake	An individual grasps a branch and shakes it with a force.
	Chase	An individual quickly goes after another individual.
	Bite	An individual uses its teeth to physically inflict wounds to another individual's body.
	Fight	At least two individuals engage in physically aggressive interactions.
Copulate/ Mount	Mount	An individual mounts on the rear of another individual.
	Copulate	A male individual mounts on the rear of a female individual and copulate.
Unknown		Undetermined behavior.

* I considered this behavior a type of affiliative behavior. When this happened, an individual appeared to have an intention to sit close to a targeted individual rather than randomly finding a place to sit.

Fig. 6.2 Seasonality of behavioral categories



D. Social Behavior

1. Affiliative Behavior

I collected 40 grooming episodes (Table 6.4). Adult females groomed most (42.5%) and adult males received the most grooming (32.5%). In two episodes, an adult male *C. erythrogaster* groomed a juvenile *C. mona* who several minutes later reciprocated. Self-grooming behavior in *C. mona* was observed 20 times (adult male, 35%; subadult male, 30%; adult female, 20%; juvenile, 15%).

I observed affiliative behavior between adult males in multi-male groups 121 times. The most frequent affiliative behaviors between these males were sitting in close proximity (59%), grooming (25.6%), and feeding in close proximity (18%).

Behaviors of individuals within all-male groups were recorded 120 times. Locomoting (45%), feeding (23%), sitting (10%), and grooming (7%) were most frequently observed. I did not observe any mounting behavior in all-male groups. Members of all-male groups exchanged characteristic soft contact calls while they were traveling.

2. Agonistic Behavior

Agonistic behavior within social groups was recorded 73 times: 2 in mixed-sex groups and 71 times during intergroup encounters (see below). All agonistic behavior occurred during intergroup encounters were among adult or subadult males belonging to different groups. There were frequent instances of agonistic behavior that were not recorded, since they occurred while I was recording other behavior.

Table 6.4 Matrix of grooming records in mixed-sex groups

Groomee* / Groomer*	Adult Female	Adult Male	Juvenile	Subadult	Adult Male *Ce*	UNID	Total	%
Adult Female	4	7	3			3	17	42.5%
Adult Male	1	3	1			1	6	15.0%
Juvenile	1	2			1		4	10.0%
Subadult		1				1	2	5.0%
Adult Male *Ce*			2				2	5.0%
UNID						9	9	22.5%
Total	6	13	6	0	1	14	40	100.0%
%	15.0%	32.5%	15.0%	0.0%	2.5%	35.0%	100%	

* There may have been switches between groomers and groomees during each grooming session, but I observed and noted only the initial direction of grooming during each session. *Ce* = *C. erythrogaster* ; UNID = Unidentified.

E. Mating Behavior and Observations of Newborns and Infants

Copulations and mounting behavior were observed 13 times. All but two of these episodes occurred between September and March in both years. It is not certain whether all copulations were terminated in male ejaculation. Only once, I observed an adult couple copulating and giving copulation calls. Other copulation calls were not associated with visual observation; therefore, whether copulation calls were always associated with actual copulation or whether copulation calls were given out only by adults or also by subadults cannot be determined. In one episode, an adult male groomed a female for a few minutes after copulating with her. Two episodes of mounting behavior appeared to have no reproductive function. In both cases, a subadult male briefly perched on the rear of an adult female, but neither thrusting nor copulation calls accompanied the mounts.

I observed a black newborn carried by a female with large nipples on March 14, 1996. Clinging infants were observed only from April–September 1996 and April–June 1997, when my study ended.

F. Intergroup Encounters and Agonistic Behavior

I observed 49 intergroup encounters. Intergroup encounters were characterized by male behavior that included head bobbing, branch shaking, chases, squabbles, and physical aggression such as hair pulling, biting, scratching, and wrestling. Agonistic behavior was recorded 71 times. One male had an atrophied forelimb. Another male had a torn earlobe. Although the former case may have resulted from a fall from a tree, the latter case has probably resulted from a male-male fight. Aggressive behavior among males, especially between males that belong to different mixed-sex groups, was common. Some males that participated in intergroup encounters belonged to all-male groups.

During intergroup encounters, males gave out a series of loud calls. Ten encounters were accompanied by copulation calls. During intergroup encounters, females and juveniles usually gave high hacks, but most of the time they did not engage in overt aggressive behavior. They appeared to continue with their normal behavior.

G. Vocalizations

Cercopithecus mona has a wide repertoire of calls that are emitted in different situations (see extensive descriptions in Struhsaker, 1970 and Glenn, 1996). Some of these are: two types of male loud calls, double boom calls and low hacks, high hacks that are given out by females, subadult males, and juveniles during alarming situations, male alarm barks, male chortle (a characteristic call given out during intergroup encounters), soft grunts, and the copulation warbles and grunts (Struhsaker, 1970; Glenn, 1996). Below, I describe the male loud calls and copulation calls.

1. Male Loud Calls

The low frequency (0.1–0.2 kHz) loud double boom given out by adult males is the most prominent call given by any *C. mona* individual. It can be heard from ≥ 2 km distance (Struhsaker, 1970). I heard 995 double boom calls between August 1995 and June 1997 (Table 6.5). Double booms were given out singly (26.4%), two in a row (60.7%), three in a row (8.1%), or four in a row (0.3%) by the same individuals. The number of double booms was uncertain for 44 calls (4.4%). The combination of the double booms and low hacks can be considered a complete loud call series. On 79.5% of occasions, the double booms were followed by low hacks. The low hack series (also known as “rapid hacks” or “low sneezes”)(1-2.5 kHz, Glenn, 1996) were heard 1,231

Table 6.5 Double booms and low hacks given out by male *C. mona*

No. of Double Booms		Frequency	%
Double Booms not Followed by Low Hack Series	1	76	7.60%
	2	115	11.60%
	3	13	1.30%
	4	0	0.00%
	Undetermined	0	0.00%
	Subtotal	204	20.50%
Double Booms Followed by Low Hack Series	1	187	18.80%
	2	489	49.10%
	3	68	6.80%
	4	3	0.30%
	Undetermined	44	4.40%
	Subtotal	791	79.50%
Total Booms		995	100.00%

times. Among these, 791 series (64.3%) were preceded by boom calls. The mean number of the low hacks that occurred as a series was 31.6 (range: 4–122, *s.d.* 26.5).

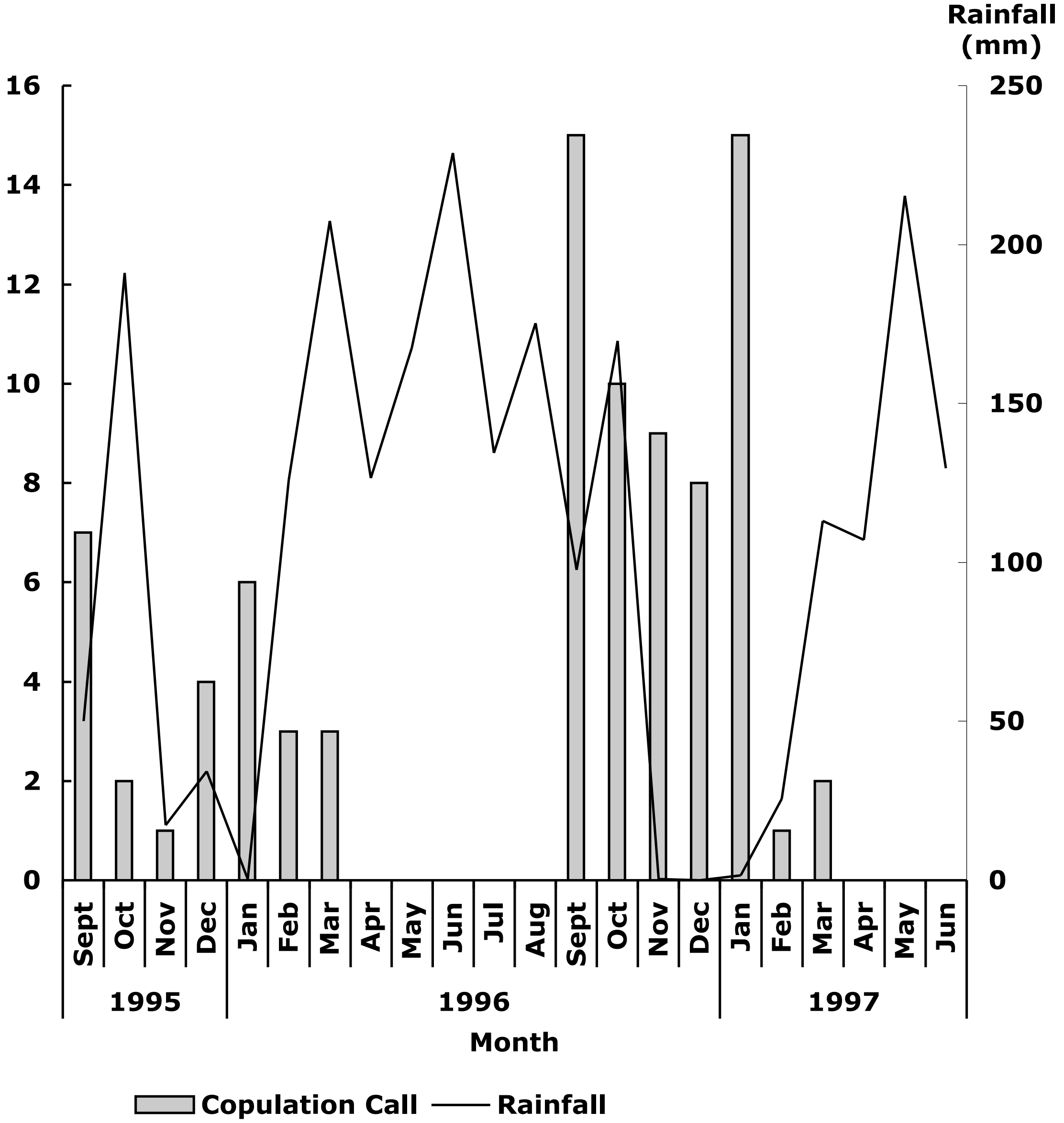
Thirteen percent of *C. mona* loud calls were followed by the loud call (low frequency guttural croaks) given out by an adult male *C. erythrogaster* (Oates, 1985). Male *C. erythrogaster*'s "gekko" calls (the first part of the complete series of the loud call) preceded 2.8% of C. *mona's* loud calls. At dawn and dusk, contagious loud calls by *C. mona* males were common. I heard male *C. erythrogaster,* emitting loud calls 321 times.

2. Copulation Calls

The copulation call series consists of two distinct calls, warbles and grunts, which appear to be given out by females and males, respectively (Glenn, 1996). Warbles are a continuous whining, which erratically rises and falls in pitch. Grunts are choppy, low-toned calls that are rapidly repeated. Warbles and grunts are given out simultaneously, alternately, or singly during a call series. Both calls are loud and can be heard > 200 m away. I heard 86 copulation calls during my study. Among these, 43 calls (50%) were a complete series, 19 (22%) were warbles only, and 24 (28%) were grunts only. On 9% of occasions, male loud calls were heard shortly before or after (within 10-minutes) the copulation calls given.

Copulation calls were heard between September and March (that include major dry season months) in both years (Fig. 6.3). The monthly number of copulation calls was negatively correlated with monthly rainfall ($r_s = -0.546$, $p = 0.013$).

Fig. 6.3 Relationship between the frequency of copulation calls and monthly rainfall



IV. Discussion and Conclusion

A. Group Size and Structure

The average group size of 13.3 estimated for mixed-sex groups is within the range of variation documented by previous researchers (Table 6.6). A smaller group size of eight was reported by Kassa (2001) for *C. mona* in the Lama Forest. P. Bekhuis (unpublished) conducted a short-term survey in several sites in Bénin, Togbota (6°41'N, 2 25'W), Dasso/Houanvé (6°41'N, 2 25'W), Gnanhouizoume (6°41'N, 2 25'W), and the Lama Forest between February 13 and March 1, 2000 and from her observations estimated 25 individuals per group, much larger than the estimate made in this study. One reason for the larger group size reported by Bekhuis (unpublished) may be small sample size (N < 3), but Kassa's (2001) estimate is probably an underestimate or perhaps he was observing foraging groups. At each group sighting, he probably missed many individuals that silently hid in the vegetation upon detecting humans. Sinsin and Assogbadjo (2002) reported a group size of 13 for *C. mona* in the Lokoli Forest in Bénin, similar to my estimate for monas in Lama. At other field sites, average *C. mona* group size varies between 8.8 and 19 (range: 4-47).

At Lama, 10.7% of all group sightings consisted of all male groups. In comparison, 8.4% of the group sightings during Glenn's (1996) regular trail surveys in Grand Etang, Grenada contained all-male groups. The size of all-male groups during my study is only slightly larger than what Glenn (1996, 1997) reported for habituated all-male groups ($\bar{x} = 2.4$, range = 2–4, *s.d.* = 0.6) and for wild all-male groups ($\bar{x} = 2.2$, range = 2–3, *s.d.* = 0.4, $n = 26$) in Grenada. Kassa (2001) did not report the group type and structure of *C. mona* in the Lama Forest.

Table 6.6 Comparison of *C. mona* group size

Research Site		Mean	Min.	Max.	N	*N.B.*	Ref.
Cameroon	Douala-Edéa	8.8	3	13	6	Actual counts	Struhsaker 1969
		10.8	2.5	20	7	Estimated counts	
		20	12	17 (30)	2	Multi-male groups observed	Whitesides 1981
	Mungo	19	4	47	4	Groups contained one or more males	Howard 1977
	Gashaka-Gumti	25	20	30	N/A	N/A	Dunn 1993
Grenada	Grand Etang	18	5	32	206	No multi-male groups observed	Glenn 1996
Bénin	Togbota, Dasso/Houanvé, Gnanhouizoume	25	Not reported			Survey only; no line transect method used	Bekhuis Unpublished
	Lama	13.3	2	35	51	Census & Systematic walk	This Study
		8.8	No data provided			N/A	Kassa 2001
	Lokoli	13	N/A	46	N/A	N/A	Assagbadjo & Sinsin 2000

The variation found in *C. mona* group size is similar to what has been reported in other members of the mona species group. In Côte d'Ivoire, Adiopodoumé *C. campbelli* group contained 8-13 individuals (*n* = 1) (Bourlière *et al.*, 1970) and Taï *C. campbelli* groups contained 9-10 (*n* = 3)(Buzzard, 2004). A larger group size was reported for a *C. campbelli* group (33 individuals) at the Boabeng-Fiema Monkey Sanctuary in Ghana (Porter, 2005). At Adiopodoumé, there were more than one male in a group (Bourlière *et al.*, 1970). The group sizes of *C. pogonias* at Beringa, Ebieng, and Makokou in northeastern Gabon were 12 (*n* = 1), 11 (*n* = 1), and 13-18 (*n* = 1), respectively (Gautier and Gautier-Hion, 1969, 1974). Recently, Gautier-Hion *et al.* (1999) reported that the mean group size of *C. pogonias* in Central African Countries (Cameroon, Equatorial Guinea, Gabon, PRC, CAR, DRC) is 20 and usually there is only one male per group. Group sizes of *C. pogonias wolfi* in Salonga N.P. and Lomako in DRC were 15–25 and 10, respectively (Gautier-Hion *et al.*, 1999).

B. Factors that Influence Multi-Male Sociality

1. Intraspecific Variation in Male Numbers

In the Lama Forest, I found that mixed-sex groups contained either one or more than one male. Whitesides (1981) reported that some *C. mona* groups in Douala-Edéa contained more than one adult male. In the Mungo F.R., three out of four Howard's (1977) study groups contained 2-4 adult males all year round. In comparison, all mixed-sex groups of *C. mona* in Grenada contained only one male, but Glenn (1996) suggested that some mixed-sex groups might have contained more than one adult male. If not, some multi-male influxes were taking place, since she heard more than one male giving copulation calls at the same time.

What are possible factors that cause more than one male to reside in mixed-sex groups of the mona monkeys in the Lama Forest and Mungo Forest? Why do most (if not all) *C. mona* mixed-sex groups in Grenada contain only one male? Are there any differences in certain ecological factors between Grenada and mainland Africa that cause differences in male numbers?

In the vervets, talapoins, and Allen's swamp monkeys, the presence of multiple males in mixed-sex groups is the norm. In contrast, male blue, redtail, and patas monkeys associate only during male influxes and take-overs. Males temporarily enter into groups of females and the frequency of male influx and the composition of male membership is variable between years in these species (Cords, 2000).

A number of factors, such as predation (Stanford, 1998; Hill and Lee, 1998), phylogenetic inertia (Struhsaker, 1969), female defensibility (Mitani *et al.*, 1996; Cords, 2000), cooperative defense of home range (Wrangham, 1980), cooperative defense of females (Isbell *et al.*, 1991; Mitani *et al.*, 1996), and limited dispersal (Isbell *et al.*, 2002) have been proposed as a major factor that influences the presence of multiple males in primate groups (Isbell *et al.*, 2002). Although data are severely limited, below I examine whether some of these factors may limit or determine male numbers in mixed-sex groups in the mona monkey.

2. Potentially Important Factors Considered

Predation: In mainland Africa, raptors prey upon *C. mona*. Pythons and leopards may also be significant predators for *C. mona*, since I observed that *C. mona* tends to be active at low tree heights and on the forest floor. In Grenada, aside from human hunters, *C. mona* lacks natural predators and sympatric primate species. Another difference could be the openness of the vegetation in the forests. An assumption has been made that in open habitats, primates are easier prey to predators than in forests. The Mungo F.R. and Lama Forest appear to have more open areas than the evergreen forest in Grenada. Thus, there is greater predation pressure in mainland Africa than in Grenada. However, if we assume that a lower predation rate had changed the social structure in mixed-sex groups in Grenada, we must explain why it had not influenced the structure of all-male groups there.

Limited Dispersal: Isbell *et al.* (2002) proposed that the social system of vervet monkeys (*C. aethiops*) is facultatively multi-male due to the configuration of its habitats and high costs of dispersal. They proposed that a home range of a vervet group must contain a source of water and there are high costs of dispersal associated with male transfer. Therefore, a vervet male typically disperses into a neighboring group in which genetic relatedness between him and members of his new group would be high. Under these circumstances, infanticide would not be a viable reproductive strategy for the immigrating male, because committing infanticide would decrease his inclusive fitness. Only when these constraints are relaxed (i.e., lower dispersal costs, larger area for dispersal), infanticide becomes viable and monopolization of females by one male could occur. Isbell *et al.* (2002) tested this and other hypotheses using data from many *Chlorocebus aethiops* populations and found that their limited dispersal hypothesis better explains why the social system of *C. aethiops* is facultatively multi-male. For example, a one-male group is a typical pattern for the green monkeys in Barbados. Gene flow among the green monkeys is relatively unrestricted throughout the island and the green monkeys lack natural predators there. Therefore, for the Barbados green monkey, the costs of long-range dispersal appear to be low. Isbell *et al.* (2002) explain that these ecological factors set the stage for an increased male monopolizability for females, leading to the one-male grouping pattern. The estimated rate of infanticide among the green monkey is higher (4.5 infanticide per 100 immigration events) than the rates of infanticide in other *C. aethiops* populations (e.g., in Amboseli, 0.03 infanticide per 100 immigration events).

Although we lack data on the costs of dispersal by *C. mona* males and the rates of infanticides in *C. mona*'s habitats, the limited dispersal hypothesis may well be able to explain why mona monkey groups in Grenada form one-male groups. *Cercopithecus mona* in Grenada lacks natural predators. Dispersal costs in Grenada appears to be low and habitat quality is high with little seasonality. Habitat characteristics of Grand Etang are similar to those in Barbados. As for *C. mona* in mainland Africa, mixed-sex groups contain either one or more than one male. The Mungo Forest, situated along the Mungo River, is surrounded by farms. The Lama Forest *Noyau Central* is a mosaic of dense forest, disturbed forest, and farmbush. Forest patches are often fragmented and separated by a wide area of farmbush and the entire perimeter of the *Noyau Central* is surrounded by the farms. Thus, the costs of dispersal may be high and dispersal may be restricted to neighboring areas at both Mungo and Lama. If we assume that these factors make male dispersals difficult and decrease male monas' ability to monopolize females, we must be able to answer why same factors do not seem to influence the grouping patterns in sympatric guenons (*C. nictitans* and *C. erythrotis* at Mungo; *C. erythrogaster* at Lama). The limited dispersal hypothesis, therefore, cannot explain why many mixed-sex groups of *C. mona* in mainland Africa contain more than one male.

Spatial Defensibility of Females: An ability to monopolize females in estrus may be limited by not only the temporal distribution of females, but also the spatial distribution of foods and females that pursue the foods. Primate females distribute themselves in accordance with how high-quality food patches are distributed in time and space and males distribute themselves in accordance with the distribution of females (Wrangham, 1980; Oates, 1987). My limited data indicate that *C. mona* females often disperse widely (100–200 m) during foraging and form small feeding parties. Fission-fusion sociality is an important coping mechanism in relation to within-group scramble competition in multi-male groups of cebids, atelines, and *Pan* spp. (Kinzey and Cunningham, 1994; Strier, 1989, Boesch, 2002). It has been shown that seasonal changes in the availability of ripe fruits have a profound influence on the fission-fusion sociality in *Pan* species and spider monkeys, especially (Hemingway and Bynum, 2006). Data are scarce, but the fission-fusion sociality has been suggested in frugivorous guenons that incorporate significant amounts of insects in their diets (e.g. *C. ascanius*, Struhsaker, pers. comm.). For example, *C. ascanius* groups in Bangui split into subgroups by day and night (Galat-Luong, 1975). Quris *et al.* (1981) also reported that some females of a *C. cephus* group in Makokou went off about 150-200 m away from the group three times during their five-week study. In *Allenopithecus nigroviridis*, large multi-male groups often split into two or three sub groups (Gautier-Hion *et al.*, 1999).

It is possible that in the Lama Forest, females disperse into feeding parties due to the distribution patterns of seasonally important foods and each food patch size may be too small to provide food for an entire group. Tree dispersion patterns in the Lama Forest indicate that *Dialium guineense* trees (the most important food for Lama mona monkeys,

Table 5.2; see Appendix D, Fig. D.1) and *Drypetes floribunda* (another important food, Table 5.2) are distributed in clumps in 50–67% of the quadrats examined (Table 3.6, see Appendix D, Fig. D.2). Other important fleshy fruit producing trees (e.g., *Diospyros mespiliformis*, *Mimusops andongensis*, *Celtis brownii*) that mainly produce fleshy fruits in wet seasons are sparsely distributed (see Appendix D, Figs. D.1, D.3). These data suggest that *C. mona*'s foods occur patchily in space even without considering the effect of seasons. Furthermore, in the Lama Forest, a majority of fruit producing trees belongs to the smallest DBH class (64.5 % of sampled quadrats) (see Figs. 3.2, 3.3, & 3.5) and the tree HT in the sampled quadrats was short ($\bar{x}$ = 11.6 m). The DBH and HT of a tree are indicative of food patch size (Chapman *et al.,* 1994; Miller and Dietz, 2004). Thus, in the Lama Forest, it appears that small food trees occur in clumps, influencing females to spread out in large areas in small feeding parties and that negatively influences male defendability of multiple females in estrus. This suggestion should be corroborated in future studies that examine the relationship between seasonality of the spatial distributions of food trees and female dispersion.

The number of females per group: Cords (2000) provided evidence that the number of males per group in *Chlorocebus aethiops* and *Miopithecus talapoin*, multimale species, is a function of the number of females per group. She found that on average, *C. aethiops* and *M. talapoin* groups contain more females per group than typically one-male guenon species such as *C. mitis* and *C. ascanius*. I do not have data on the number of females per mixed-sex group, but the group size in multi-male groups ($\bar{x}$ = 15.6) was significantly larger than that in one-male groups ($\bar{x}$ = 11.2) (see Table 6.2), suggesting that there are more females in multi-male groups than in one-male groups. In the Mungo

F.R., there was a variation in both male ($N = 0$–4) and female numbers (0–16) in Howard's (1977) study groups. The largest group contained 16 females and four males and the smallest group contained six females and two adult males. In Grand Etang, where a one-male group was a usual pattern, the number of females per group was small ($N = 3$). These data lend support to the idea that the number of adult males in a *C. mona* group is at least partially related to the number of adult females in a group.

Other factors are probably also involved (e.g., length of breeding season, home range defense, population density, phylogeny) and several factors likely interplay and shape the social structure of *C. mona.* Data such as the costs of dispersal, immigration rates, number of females in estrus per day, genetic relatedness of immigrant males and females, and the seasonality of the spatial distribution of females in relation to foods in a habituated mona population need to be obtained to tease apart which factors are more important than others.

C. Occurrence of All-Male Groups

At Grand Etang, Glenn (1996) observed 18 males (8 adult, a subadult and two juvenile monkeys) belonging to one or more of 33 different semi-habituated all-male groups (Glenn, 1996). She observed these semi-habituated all-male groups 1,164 times during her study. The groups consisted of 2–4 males ($\bar{x} = 2.4$, *s.d.* = 0.6). Groups of three individuals were most common. She reported that these individuals were never observed in mixed-sex groups at any time. Several male pairs were seen together for more than one or two years (Glenn *et al.*, 2002). In addition, she reported that 8.4% of 308 sightings of wild unhabituated monkeys were all-male groups that consisted of 2–3 males ($\bar{x} = 2.2$, *s.d.* = 0.4). Two-male groups of subadult/subadult pairs were most commonly seen. She observed solitary individuals nine times, but these individuals were also seen in all-male groups at one time or another.

On São Tomé and Príncipe and in the Bimbia Bonadikombo Community F.R. in Cameroon, however, all-male groups and solitary individuals were not observed (Glenn *et al.*, unpublished *a, b*). Previously, because the sightings of all-male groups occurred only in the Grenada population, some researchers may consider that it is an aberrant behavior. The present study now confirms that the presence of all-male groups in *C. mona* is not unique to the Grenada population and most likely is species-specific. The lack of observation of all-male groups in São Tomé and Príncipe is probably related to the short duration of their survey.

As for other species in the *mona* species group, *C. campbelli* is so far the only species that has been reported to form all-male groups (Bourlière *et al.*, 1970; Buzzard, 2004). In Taï Forest, in Cote d'Ivoire, Buzzard (2004) observed at least two all-male groups of *C. campbelli*, each of which shared its home range with a particular *C. diana* group. One all-male group contained 2-4 adult males and a large juvenile male. Another all-male group contained two adult males. Buzzard's field assistants have reported that one all-male group of *C. campbelli* was apparently attached to a particular *C. diana* group for at least 10 years. Whether this represented a series of different all-male groups or different individuals was not certain. Among males within all-male groups, friendly interactions such as grooming and aggressive behavior such as threats towards adult males of mixed-sex groups were frequently seen. Hunkeler *et al.* (1970) had also reported that males in all-male *C. campbelli* groups at Adiopodoumé, Côte d'Ivoire were friendly towards each other. In comparison with *C. mona* and *C. campbelli*, sightings of all-male groups have not been reported in *C. pogonias*.

Outside the *mona* species group, *C. mitis* (Tsingalia and Rowell, 1984) and *C. neglectus* (Chism and Cords, 1997/1998) are the only other forest-dwelling guenons that have been reported to form clusters of male individuals. Males loosely associate only during multi-male influxes that generally last several months; therefore, male membership in such associations is temporary and interactions are infrequent (Cords, 2000). In the savannah/woodland, maturing male *Chlorocebus patas* and *Chlorocebus aethiops* may briefly join temporary associations of males (Chism, 1999). Buzzard (2004) proposed that vulnerability to predation in terrestrial habitats is associated with the formation of all-male social groups. He found that all-male groups are commonly found in terrestrial Hanuman langurs (*Semnopithecus entellus*) and patas monkeys (*C. patas*). *Cercopithecus campbelli* in the Taï Forest also uses lower strata more frequently than the higher strata. I also found that *C. mona* uses lower strata more frequently. Whether a causal relationship exists between the use of low tree strata and the existence of all-male groups remains to be corroborated.

One major social advantage of males joining other males that are not associated with females is the more likely successful takeover of mixed-sex groups. There is accumulating evidence that takeovers of one-male groups (e.g., *Semnopithecus entellus*: Hrdy, 1974, Newton, 1992; *Alouatta seniculus*: Crockett and Sekulic, 1984) and multi-male groups (*Papio anubis*, *Papio cynocephalus*, *Papio ursinus*: Collins *et al.*, 1984; *Procolobus badius*, Struhsaker and Leland, 1985; Starin, 1994; *Alouatta* spp.; Clarke, 1983; *Pan troglodytes*: Goodall, 1977, 1984) are more successful when multiple non-resident males form coalitions against resident males than when one male does it alone. Although there have been many reports of male takeovers in guenon groups, group takeovers by multiple males in a coalition have been reported only in *C. mitis* in Natal (Henzi and Lawes, 1987).

D. Affiliative Behavior among Males

In this study, affiliative behavior between adult males in multi-male groups was frequent. In particular, adult males initiated grooming in some cases and females groomed adult males. At Grand Etang, male monas were also friendly to each other. As for other members of the mona species group, adult male *C. campbelli* in Adiopodoumé was often groomed by three adult females. He also groomed these females, although less frequently (Bourlière *et al.,* 1969). Buzzard (2004) found that although the rates of grooming among members of *C. diana*, *C. petaurista*, and *C. campbelli* groups were similar, adult males were involved in grooming only in *C. campbelli* and *C. petaurista.* Grooming by adult males in *C. diana* and *C. mitis* is rare (Cords, 2001). Boulière et al. (1967) also reported that males and females frequently interact, males groom other group individuals, and engaged in interactions with infants.

E. Aggressive Behavior and Male-Male Relationships

Aggressive behavior among males was common in *C. mona* in the Lama Forest. In Grenada, many wild-caught males had extensive scars and flesh wounds presumably caused by aggressive encounters with other males; one male died of wounds sustained during a fight with another male in an all-male group (Glenn, 1996). In contrast, Howard (1977) found no evidence of male aggression at Mungo, Cameroon, although he saw 17 intense agonistic encounters among groups in one year. He reported that the lead male in mixed-sex groups of *C. mona* was located away from the center of intergroup encounters and never participated in intergroup aggression, although these males would give loud calls during the encounters. Seven agonistic encounters involved physical contacts such as hair pulling, wrestling, and biting between two groups. In the Mungo F.R., each *C. mona* group used a home range that extensively overlapped with home ranges of other groups, but each group defended its well-defined core area (Howard, 1977). Howard's (1977) largest study group (*n* = 35) had the largest area of overlap with all three other groups, that contained three adult males was most frequently involved in inter-group fights (13/17); 10 of which were directed towards a group with four adult males, but the smallest group did not enter into other groups' ranges. Inter-group conflicts were common among his study groups.

Howard (1977) nevertheless implied that these agonistic encounters only involved females. The data from the Lama Forest and Grand Etang that male *C. mona* was aggressive are in contrast with the data from the Mungo Forest. With currently available data, it is difficult to reconcile why there is such intraspecific variation in male behavior.

As for other members of *mona* species group, adult males of *C. campbelli* in Adiopodoumé are more aggressive towards each other during months of sexual activity (Juy – September) (Bourlière *et al.,* 1969; Hunkeler *et al.*, 1972). In the Taï Forest, during infrequent intergroup encounters, *C. campbelli* males were much more aggressive than females (Buzzard, 2004). Buzzard (2004) noted that the low frequency of intergroup encounters might have been due to unhabituated neighboring groups. Outside his study area, he often observed two or three *C. campbelli* groups interacting as males were giving loud calls. Infanticides by non-resident males have been suspected in Taï *C. campbelli* (Galat-Luong and Galat, 1979). In contrast with *C. mona* and *C. campbelli*, *C. pogonias* males in Makokou did not appear to be aggressive during intergroup encounters: they only seem to squabble (Gautier-Hion *et al.*, 1983). Buzzard (2004) also reported that *C. petaurista* males were much more involved in between-group interactions than females.

In patas monkeys, males are more active in intergroup encounters than females (Chism, 1999). Violent male aggression during intergroup encounters and with neighboring *C. cephus* groups has also been reported in *C. solatus* in Gabon (Gautier-Hion *et al.*, 1999).

In other arboreal guenons, females are usually more active in territorial defense than males and use threats and force towards females and males of other groups (Cords, 1987a). Female samangos (*C. mitis*) in Cape Vidal are known to kill non-resident females (Payne *et al.*, 2003) and female diana monkeys (*C. diana*) in Taï Forest had higher rates of aggressive encounters with other groups and with sympatric species than *C. campbelli* or *C. petaurista* females. One Diana female was reported to have killed another female. Males' role during intergroup encounters in Taï Forest *C. diana* was mostly vocal (Buzzard, 2004). Female *C. diana* monkeys at Tiwai also engage in physical fights with intruding group members (Hill, 1994). In these species, male aggression occurs mostly during male-influxes during mating seasons (Cords, 1987a). Infanticides by non-resident males have been also reported in Kibale *C. ascanius* (Struhsaker, 1977). Butynski (1992) also reported a series of multi-male influxes that occurred in a group of *C. mitis* in Kibale and many incidences of infanticide committed by invading males (Butynski, pers. comm. cited in Struhsaker, 1988).

In contrast to unfriendly males within social groups in the above species, *C. mona* males are friendly to each other and group membership appeared to be more permanent. Male *C. mona* also participates in territorial defense; while male *C. mitis* and *C. diana* are not active participants in territorial defense. In sum, male relationships in *C. mona* appear to be similar to that of *C. campbelli* and differ from that of *C. mitis* or *C. diana*.

F. Morphological Evidence for Intense Intrasexual Selection

Aggressive behavior exhibited by male *C. mona* during intergroup encounters suggests that male *C. mona* engages in intense intrasexual competition. Some morphological features that indicate strong intrasexual competition in primates are sexual dimorphism in body weight, body size, and canine tooth size. Large testicular volume in relation to male body weight is also indicative of intense sperm competition (Harcourt *et al.*, 1981). Although a number of factors (e.g., food competition, predation, degree of arboreality, seasonality, diet) besides male-male competition also influence morphological sexual dimorphism and testicular size in primates, intrasexal competition is the primary driving force (Cheney and Wrangham, 1987; Harcourt *et al.*, 1995).

I surveyed published data on the body weight and testicular size of some guenon species to examine if there is any morphological evidence that indicates intense intra-sexual competiton in *C. mona* (Table 6.7). According to Plavcan and van Schaik's (1992) measurements, canine tooth size dimorphism in *C. mona* is more extensive than in similar sized or larger arboreal *Cercopithecus* species. Recent published data on male and female body weight of 11 *Cercopithecus* species that inhabit Central African

Table 6.7 Sexual dimorphism in body weight and relative testicular volume of guenons (Shaded areas show the mona species group.)

Sexual dimorphism in body weight in *C. mona* is somewhat pronounced. *Cercopithecus mona* 's testicular volume is more pronounced than other species compared, but a lack of data from other arboreal species precludes making a definitive statement regarding this issue.

Species	M Wgt	N	F Wgt	N	SD	M Wgt	N	F Wgt	N	SD	M Wgt	N	F Wgt	N	SD	Rel. Tes. Wgt^	M ‡ Wgt	F ‡ Wgt	SD	M Wgt	F Wgt	SD
C. ascanius						3700	69	2924	242	0.24						0.56§	4.2	2.9	0.37			
C. cephus	4087	8	2882	10	0.35	4132	29	2839	30	0.38							4.1	2.9	0.35		2312	
C. nictitans	6600	16	4216	9	0.45	6715	56	4092	48	0.50							6.6	4.2	0.45		3800	
C. mitis						5849	41	3929	94	0.40							7.6	4.4	0.55			
C. dryas						3000	1	2250	1	0.29												
C. lhoesti						5966	19	3505	112	0.53							8.5	4.7	0.59			
C. p. pogonias	4500	4	3025	6	0.40	4442	6	2940	10	0.41							4.5	3	0.41	3215	2127.3	0.41
C. p. wolfi						3909	17	2866	120	0.31												
C. mona											5067	6	3000	3	0.52	3.4#	4.4	2.5	0.57			
C. campbelli																	3.6	3.6	0.00			
C. hamlyni st						5486	11	3361	9	0.49												
C. neglectus st	7000	4	3960	4	0.57	6384	8	3572	71	0.58							7	4	0.57		3927.5	
C. aethiops t																2.63§						
C. patas t																0.72§						
Study Site	Makokou, Gabon					Central African countries					Grand Etang F.R., Grenada						In Captivity			Equatorial Guinea		
Ref.	Gautier-Hion & Gautier (1975)"					Gautier-Hion, Colyn, and Gautier (1999)"					# Glenn (1996) §Harcourt (1991, 1995)						Clutton-Brock & Harvey (1985)≠			Jones (1970)		

Note: st = Semi-terrestrial; t = Terrestrial; SD = sexual dimorphism = Log Natural(Male Wgt/Female Wgt); " = wgt. in grams; ‡ = weight in Kg; only wild specimens are included in the analysis.; ^ Rel. Tes. wgt. = Relative Testicular Weight = Testicular wgt./Body wgt.

countries (Cameroon, Gabon, Equatorial-Guinea, PRC, DRC, CAR) show a wide range of variation in body weight dimorphism. Body weight dimorphism is most pronounced in terrestrial species (e.g., *Chlorocebus solatus*) (Gautier-Hion *et al.*, 1999). The degree of body weight dimorphism in *C. mona* is as pronounced as in *C. nictitans* and *C. mitis* and slightly more pronounced than the smaller-bodied cephus group (Table 6.7) (Gautier-Hion *et al.*, 1999).

In regard to testicular volume, Glenn (1996) stated, "monas have extremely small testicles," but this conclusion was based upon a sample that contained juvenile males and clearly malnourished captive adult males. When these males are excluded, the mean testicular weight of adult male *C. mona* becomes 17.4 g (*n* = 5, *s.d.* = 2.208) and the relative testicular weight becomes 3.44[*]. When this is compared with Harcourt's (1995) data on the relative testicular weight of *C. ascanius* (0.56), *C. aethiops* (2.63), and *C. patas* (0.72), it becomes apparent that *C. mona*'s relative testicular weight is much more pronounced than any of the above species. Data from other arboreal guenons are needed to confirm whether *C. mona*'s testicular weight is more pronounded than other arboreal guenons. In summary, although sexual dimorphism in body weight is only slightly pronounced in *C. mona*, but the large testicular weight in male *C. mona* indicates a considerable degree of sperm competition that is consistent with the observed pattern of multi-male sociality in *C. mona* in mainland Africa and the presumed occurrence of multi-male influx in Grenada.

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[*] Testicular volume was converted to weight using Harcourt's (1995) equation, testicular weight (g) = testicular volume (cm^2) x 2 x 1.1. The relative testicular weight or the ratio of the testicular weight (g) to the body weight (kg) in Grenada *C. mona* then becomes 17.4/5.1 = 3.44.

G. Vocalizations

1. Intraspecific Variation in the Loud Call

Many aspects of the *C. mona* loud call differ among three field sites. For example, there was variation in the frequency of mona double booms and low hacks. More male loud calls (1,435 calls) were heard during my 17-month study period in the Lama Forest than by Howard (1977) in the Mungo F.R. (> 1,000) during a two-year period, or by Glenn (1996) in her 18 months of study in Grenada (669 calls). The lower frequency of the loud calls heard at Grand Etang may be related to the fact that all mixed-sex groups in Grand Etang were one-male groups. The fact that there is no sympatric primate species on Grenada may also be a factor. Struhsaker (1970) stated that the rates of frequencies of calls are influenced by population density and sampling time. He demonstrated that higher population densities at Obenika and Boa than at Idenau in Cameroon were responsible for higher rates of loud calls per sample duration at Obenika and Boa than at Idenau. Data on the rate of loud calls are not available from all sites, but a crude comparison of the frequency of the loud call heard during the study periods at Mungo, Grenada, and Lama indicates that there is no positive relationship between the number of calls and *C. mona* population density.

In the Mungo F.R., only one adult male gave loud calls even when more than one adult male was present in the three study groups (Howard, 1977). Similarly, in Grand Etang, only one male in mixed-sex group emitted the loud call at any time. In contrast, in the Lama Forest two or more adult males in mixed-sex groups often gave loud calls in sequence.

The number of low hacks given out by the male also varied (range: 4–122, Lama, this study; Cameroon, 7–107, Struhsaker, 1970; 15-113; Glenn, 1996; 36–54, Howard, 1977).

2. Functions of the Loud Calls

There are several hypotheses that attempt to explain the function of male loud calls in primates. Male loud calls: (1) are a component of intra-sexual competition for mates (the mate defense hypothesis); (2) attract mates (the mate attraction hypothesis); (3) serve to protect a territory for females (the resource defense hypothesis); (4) function as an anti-predation strategy; (5) function to facilitate subgroup reaggregation (Wich and Nunn, 2002). Wich and Nunn (2002) examined the relationship between hypotheses 1–3 and various aspects of primate biology (e.g., body mass dimorphism, male canine size, socionomic sex ratio), social organization (e.g., presence or absence of female transfer), and habitat use (e.g., territoriality, home range size). Wich and Nunn's (2002) analysis showed that there was some support for the mate attraction and resource defense hypotheses, but no support for the mate defense hypothesis. They concluded that although data are still lacking from many species, the functions of male loud calls are multifaceted (Waser, 1977; Whitehead, 1987). Furthermore, most researchers agree that primate vocalization is conservative in primate phylogeny and male loud calls are particularly informative in understanding evolutionary relationships among primate species (Struhsaker, 1970, 1987; Gautier, 1988).

The contagious and simultaneous loud calls emitted by *C. mona* in the Lama Forest resemble the loud calls given by black-and-white colobus monkeys (Oates, 1977, 1994; Dasilva, 1989) and howler monkeys (*Alouatta palliata*)(Whitehead, 1987). In

Colobus polykomos, more than one male in a multi-male group typically produced loud calls at the same time (Oates, 1994b). Dasilva (1989) found that the more adult males in a group of *C. polykomos* at Tiwai, the more successful the outcome of intergroup aggression. She suggested that the male loud calls provided clues to males' physical strength and health; therefore, they are elements of male-male competitive behavior. Although I do not have data on the outcome of intergroup encounters, judging from the frequent occurrences of the loud calls during intergroup encounters, at least one of their functions appears to be related to male-male competition over access to scarce resources (e.g., females, foods, territory)(Marler, 1969; Struhsaker, 1969).

Researchers have noted that the loud call in *C. mona* has a variety of functions, and that these depend upon the situation: alarm call, spacing mechanism, signaling the location of the group to other groups, and signaling the caller's location to females (Howard, 1977; Struhsaker, 1970; Glenn, 2002).

Male *C. pogonias* and *C. campbelli* emit single-unit booms (Struhsaker, 1970). Gautier-Hion *et al.* (1999) proposed that the loud call in *C. pogonias* functions as a warning of eagle predation and that other arboreal guenons benefit from joining mixed-species groups with this species.

3. Implication of Copulation Calls and Reproductive Behavior

In the Lama Forest, 82 observed copulation calls and all but two copulations and mounting behavior were heard or observed between September and March in both study years. In the Mungo F.R., Cameroon, Howard (1977) heard ≥ 2,102 copulation calls (more than 20 times of the frequency of the calls heard at the Lama Forest) throughout the year, but the peak occurred during September–October, the rainiest months (300–400 mm/month) of the year. Rainfall in November was somewhat reduced (150 mm) and the major dry season started in December. There was a significant difference in the frequency of calls between the high (July–December, 29.3 calls/hr) and low months (February–June, 1.2 calls/hr). He also observed 72 copulations. Almost all observed copulations that occurred between adult pairs or juvenile-adult pairs were accompanied by copulation calls.

Glenn (1996) heard 104 copulation calls in 18 months at Grand Etang. Fifty percent of these calls consisted of both warbles and grunts, 45% consisted of only warbles, and 5% were just grunts. The calls were heard year round, with the peak occurring in October, which is the third rainiest month (400 mm). She observed 37 copulations; three of them were accompanied by copulation calls. She noted that local hunters in Grenada specifically associated the calls with male-female copulation. Males mounting males in all-male groups did not vocalize. In Sào Tomé and Príncipe, however, no copulation calls were heard (Glenn *et al.*, unpublished *a*). In the Bimbia Bonadikombo Community Forest in Cameroon, only one copulation call was heard in a 5-month survey (Glenn *et al.*, 2002). Although the magnitude of the variation in the frequency of the copulation call heard among sites is enormous and the reason for this is unknown, it is remarkable that at all sites the copulation calls peaked in September or October.

In a seasonal habitat, there are usually discreet mating and birth seasons in primates (Lindburg, 1987). Butynski (1988) found a strong correlation between guenons' birth seasons and periods of high rainfall and fruit abundance. Does the birth season in *C. mona* also coincide with periods of high rainfall and fruit abundance? If one assumes that *C. mona*'s breeding season in the Lama Forest is restricted to September–March and the gestation length is similar to that of captive *C. mona*[*] and *C. pogonias* (5.6 months), then March–August becomes the birth season (Gautier-Hion and Gautier, 1976). In the Lama Forest, a newborn was observed in March 1996 and clinging infants were observed only from April–September 1996 and April–June 1997. Howard (1977) reported that black newborns were observed between April and August in Mungo F.R. It makes sound ecological sense for newborns to arrive between March and August, when fleshy fruits are readily available during higher rainfall months (Butynski, 1988). Lactating females must be able to meet the high demand of maternal nutritional needs.

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[*] At the Japan Monkey Centre, a 4-yr-old female and a 7-yr-old male *C. mona* of unknown origins mated sometime between December 1960 and January 1961. The female gave birth on June 8, 1961 (Takeshita, 1962). Calculating from these dates, the gestation length for this female would be between 128 and 187 days (median 158).

CHAPTER 7: ANTHROPOID POPULATION DENSITY AND BIOMASS ESTIMATION

I. Introduction

Finding out the density and abundance of animal populations and biomass in a habitat is important because it shows how the animal community is structured. Periodic censuses of animal populations are also important in assessing the relative efficacy of conservation efforts implemented in the forest and permit monitoring of population dynamics (Plumptre, 2000). In the Lama Forest, no mammalian population densities had been estimated prior to this study.

In Chapter 3, I examined tree species diversity, composition, and spatial distribution in the *Noyau Central*. In this chapter, I estimate the population density and size of *C. mona*, *C. erythrogaster*, and *Procolobus verus* in the *Noyau Central* and examine whether there is any variation in the population density of these species across habitat types. To estimate the population density of these monkeys, I conducted a systematic diurnal census study using a modified line-transect survey technique. Because we lack *a priori* knowledge of the home range size and overlap for the Lama Forest primates, it is not possible to ascertain which analytical methods estimate densities most accurately (Fashing and Cords, 2000). Among many methods used by researchers, I chose the method of Whitesides *et al.* (1980), because it has a record of more reliable estimates of many arboreal species than other methods (Brugière and Fleury, 2000; Fashing and Cords, 2000).

Among the anthropoid species that occur in the Lama Forest, population densities of *C. mona* and *C. erythrogaster* can be relatively well estimated. The population density and biomass of the olive colobus monkey (*Procolobus verus*) could be only crudely estimated due to very few sightings of this species. *Procolobus verus* was not seen in the farm bush or plantation areas; therefore, it was assumed that it occurs only in dense and disturbed forests. Although colobines generally occur at low densities in disturbed and hunted habitats, rare *P. verus* sightings obtained in this study may not reflect the actual population density of this species. *Procolobus verus* is inconspicuous because of its suite of behavioral and physical characteristics that tend to conceal its presence (e.g., olive green pelage, quiet and cryptic behavior, preference for liana tangles and low growth) and make sightings extremely difficult (Oates, 1988b; Fimbel, 1992). The population density of *Colobus vellerosus* is not estimated, since it was never clearly observed. The population density of *Chlorocebus aethiops* was also not estimated, because of few sightings of this species within the forest. During the study period, *C. aethiops* was mainly found on the laterite road that surrounds the entire perimeter of the *Noyau Central*. The few sightings of this species in the *Noyau Central*, however, may not be indicative of its actual population size in the Lama Forest as a whole.

The results of this study provide information that can aid the formation of conservation plans, and serve as a basis for comparisons with future periodic censuses. For example, after the termination of this study, Kassa (2001) conducted a diurnal and nocturnal census study of the mammalian species that included primates and antelopes, using the line-transect and point count sampling methods and estimated the population densities by the use of DISTANCE software (Burnham *et al.*, 1980). The population densities of *C. mona* and *C. erythrogaster* estimated in the two studies are compared, and the possible causes of differences in the findings of the two studies examined.

I also briefly discuss some advantages and disadvantages of methods used in estimating primate population densities in forest habitats.

II. Methods

A. Line Transect Sampling

The two 4-km census routes described in a preceding chapter (Chapter 3) to examine vegetation were used to conduct a line-transect survey (Fig. 3.1). Two-tailed Wilcoxon Signed Rank tests have determined that the BA/ha of tree species enumerated along the two census routes was not significantly different in both early-successional species and late-successional species (early successional species: $z = -0.804$, $p = 0.422$; late successional species: $z = -0.706$, $p = 0.480$). Therefore, the two census routes are considered ecologically similar and sighting frequencies of all anthropoid species between the two routes were not expected to differ.

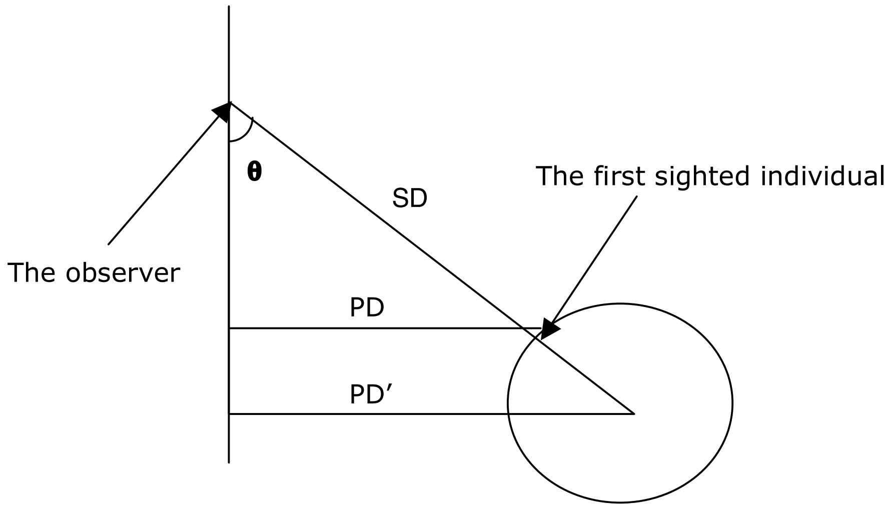
I used a modified line-transect sampling technique to conduct censuses (Struhsaker, 1972, 1981; Whitesides *et al.*, 1988). I conducted morning censuses on the two census routes twice a month ($\bar{x} = 1.9$, *s.d.* = 1.6, $n = 44$) between August 21, 1995 and June 18, 1997 (data were not collected in February 1996, May–Aug. 1996, and May 1997). The morning census began between 07:00–08:00 GMT. The direction of the walk was alternated each time. I also conducted afternoon censuses on the same routes twice a month ($\bar{x} = 2.8$, *s.d.* = 1.4, $n = 29$) between September 10, 1996 and June 11, 1997 (data were not collected in May 1997). Afternoon censuses, which began between 13:00–14:00 GMT, were conducted on the same route along which morning censuses had taken place on the same day, with a reversed walking direction. The mean census duration was 251.2 min. (range: 220–279, *s.d.* = 14.45, *n* = 73).

One or two field assistants usually accompanied the researcher during the censuses. No consultation between the observers regarding the content of primate sightings took place until after we left the position of each encounter with primates (Struhsaker, 1972). Censuses were conducted only when the weather condition at start time was appropriate. During a wet season in 1996, a census was terminated because of the overgrown undergrowth that made walking extremely difficult. Another census was terminated due to heavy rain that started only after the census began, and one was terminated after it began due to the loud noise of teak-harvest activities by ONAB foresters' in the plantation plots adjacent to the eastern end of census route A.

On census routes, I slowly and quietly walked at 1–1.5 km/hr speed, scanning all strata of the forest. When monkeys were detected, I stopped and waited for up to 10 minutes to determine their presence and to record the following information: time and mode of sighting, location, habitat type (i.e., dense forest, disturbed forest, farm bush), primate species, height of the first monkey detected, substrate, perpendicular distance (PD) (transect to first-seen animal distance) from the transect to the first seen individual, sighting distance (SD) (observer to first-seen animal distance) (Fig. 7.1), number of individuals counted, estimated group size, activity of the first seen individual, and the end time of the encounter. Determination of age/sex classes was established based upon descriptions for *C. mona* (Howard, 1977, Glenn, 1996) and *C. campbelli* (Bourlière *et al.*, 1970, Hunkeler *et al.*, 1972) as well as my preliminary observations of *C. mona*. Although individuals were classified into five categories: adult male, adult female, sub-

Fig. 7.1 Measurements recorded during line transect sampling

PD = Perpendicular Distance from the transect to the first sighted individual
PD′ = Perpendicular Distance plus 1/2 of average group spread
SD = Sighting Distance from the transect to the first sighted individual



adult male, juvenile, and infant, assessing the number of individuals beyond adult males was extremely difficult. Sex of immature individuals was noted when it could be ascertained. If age and sex classes were not determined, I noted “undetermined.”

Group members of *C. mona* in the Lama Forest were spread out across an area with a radius of 50–100 m while they foraged and progressed. Therefore, a group was defined as a cluster of individuals in which members were separated by no more than 100 m. If a monkey was sighted alone or was separated by more than 100 m from a cluster of individuals, this individual was defined as solitary (Whitesides *et al.*, 1988). This varies from Glenn’s (1996) definition of a group. She defined a group as a cluster of individuals in which members are separated by no more than 50 m.

To estimate primate population densities using the census technique used here, it is necessary to accurately estimate the average group size of each species. Due to the wariness of the monkeys and limited visibility, however, complete counts of group members, especially when the group was mixed-species group, were not always possible. Visibility at eye level was especially limited in farm bush areas due to the predominance of *Chromolaena odorata*. Counting the number of adult males and sub-adults was more successful, because males were more conspicuous and vocal than other group members. Because of these caveats, group size at each primate encounter in this study was estimated.

All censuses were made from the census routes and care was taken to avoid recounting the same groups, especially where the census route B bent at right angles (Fig. 3.1).

B. Data Analysis

I found that afternoon censuses produced significantly fewer sightings of both *C. mona* (two-tailed T test: morning, $\bar{x} = 2.25$, *s.d.* = 1.27, $n = 44$; afternoon, $\bar{x} = 1.62$, *s.d.*= 1.21, $n = 29$; $H_0 \neq 0$, $T = 2.12$; *d.f.* = 62; $p < 0.001$, $n = 73$) and *C. erythrogaster* (morning $\bar{x} = 0.68$, *s.d.* = 0.6741, $n = 44$; afternoon $\bar{x} = 0.27$, *s.d.* = 0.5275, $n = 29$; $H_0 \neq 0$, $T = -2.8757$, *d.f.* = 62, $p < 0.001$, $n = 73$). It is possible that monkeys avoided returning to the same area, since their activities were disturbed by our passage on the same route in the morning. Although Chapman *et al.* (1988) did not find any evidence that different time periods with differing activity levels of *Cebus capucinus* and *Alouatta seniculus* influenced the frequency of group sightings in their census study in Santa Rosa National Park in Costa Rica, Struhsaker (1981) had recommended that censuses should take place when arboreal monkeys are most active. Consequently, all afternoon census data were eliminated from analyses.

The proportional length of the three different habitat types and tree basal areas of fast- and slow-growing species were not significantly different between the two census routes (Chapter 3). Therefore, the number of groups sighted per survey and estimated perpendicular distance at group sightings during censuses are expected not to be significantly different between the two census routes. However, if the number of groups sighted per census or estimated perpendicular sighting distance during censuses differ due to walking direction (i.e., east or west bound), estimated population density is likely to differ among portions of the census routes; thus, density estimates should be made in segments. Wilcoxon Mann-Whitney tests were used to determine the significance of the above measures. If the number of groups sighted per census and/or estimated perpendicular distance differ among habitats and/or seasons, density estimates would have to be made separately for each habitat type and/or season. One-sample Kolmogorov-Smirnov Goodness of Fit tests were used to determine the significance of the above measures.

The numbers of groups encountered during censuses were not significantly different between census routes A and B (*C. mona*: $U = 156.5$, $n^A = 29$, $n^B = 15$, $p = 0.2688$; *C. erythrogaste*r: $U = 156.5$, $n^A = 29$, $n^B = 15$, $p = 0.2688$) and walking direction had no effect on the number of group sightings (*C. mona*: $U = 188$, $n^E = 12$, $n^W = 32$, $p = 0.9724$; *C. erythrogaste*r: $U = 180.5$, $n^E = 12$, $n^W = 32$, $p = 0.8093$). Perpendicular distance was also not significantly different between the two census routes (*C. mona*: $t = -.685$, d.f. = 101, $p = .495$; *C. erythrogaster*: $t = 1.547$, *d.f.* = 42, $p = 0.129$). Therefore, data from both census routes were pooled for population estimation.

Sighting frequencies did not vary among seasons (*C. mona*: $F = 2.372$, *d.f.* = 5, $p = 0.059$; *C. erythrogaster*: $F = 1.468$, *d.f.* = 5, $p = 0.223$). The perpendicular distance of *C. mona* group sightings varied among habitat types ($F = 3.648$; d.f. = 2, $p = 0.03$), while the perpendicular distance of *C. erythrogaster* group sightings did not vary among habitat types ($F = 2.07$; d.f. = 2, $p = 0.075$). These results indicated that *C. mona* density varies among habitats, but *C. erythrogaster* density probably does not vary among habitats. Thus, separate density estimate were made for each habitat type for *C. mona*, and for *C. erythrogaster,* a density estimate was made for dense forest in contrast with a density estimate made for disturbed forest and farmbush combined.

One of the main points of discussion among researchers has been how to determine the effective width of the area covered along transects (Struhsaker, 1975; 1981, 1997; Defler and Pintor, 1985; Whitesides *et al.*, 1988; Dunn, 1993; Glenn, 1996, 1998; Fashing and Cords, 2000). Many variations of both perpendicular distance and sighting distance have been used to calculate an effective transect width. In this study, I used the method of Whitesides *et al.* (1988), which adds a correction factor of 1/2 to the species-typical average group spread to the maximum reliable perpendicular distance (MRPD) inspected from a frequency distribution in calculating the effective width, w. Sighting data with perpendicular distance measurements ≥ 100 m were eliminated from density estimation.

Total area sampled "a" is calculated by the following equation:

$$a = 2(lw) \ldots\ldots \text{ (Equation 7.1)}$$

where "l" is the total length (km) walked during censuses; "w" is the effective transect width. Because the Whitesides method incorporates 1/2 of group spread, the equation becomes:

$$a = 2(1/2s + d)l \; \ldots \text{ (Equation 7.2)}$$

where l is the total length of all censuses conducted, while s is an estimate of species-specific mean group spread "d" is an estimate of species-specific effective distance. The group spread "s" of 80 m for *C. mona* and 75 m for *C. erythrogaster* obtained during the systematic walks were used. The effective distance, d, is obtained by the following equation:

$$d = (Nt/Ni)fd \ldots \text{ (Equation 7.3)}$$

where fd is the fall-off distance; N_t is the total number of groups observed during all censuses, N_i is the total number of groups observed at and below the fall-off distance (fd) which can be defined as the maximum distance of the previous distance interval from which the frequency of group sightings falls to 1/2 of the sighting frequency observed in the next interval in a histogram of all perpendicular distance plotted for each group sighting. The rationale behind this procedure is that the longer the perpendicular distance becomes, the less efficient detection becomes (Whitesides *et al.,* 1988). To obtain group density, the following equation is used:

$$Density\ of\ Groups = \frac{N}{a} \ldots \text{ (Equation 7.4)}$$

where N is the total number of groups sighted during censuses; "*a*" is the area sampled (Struhsaker, 1981).

A density estimate was made for each habitat type and multiplied by the proportional area of each habitat type in the *Noyau Central* to obtain total population size of each species (Table 7.1). It was assumed that both *C. mona* and *C. erythrogaster* do not occur in plantation plots, since *C. aethiops* was the only species observed in plantation during censuses. Both groups and solitary individuals were included in the population and biomass estimation of *C. mona* and *C. erythrogaster*.

To calculate primate population biomass, 3/4 of wild adult male body weight obtained from Glenn *et al.*, (1996) for *C. mona* and published body weight of Tiwai *C. petaurista*, a closely related species to *C. erythrogaster*, and Tiwai *P. verus* were used per individual in a group (Oates *et al.*, 1990). Most data analysis and statistical tests were performed using SPSS 11.5 (SPSS, 2002). Confidence levels were set at 95%.

Table 7.1 Vegetation types along two census routes

Habitat Types	Census Route (m)		Total Distance (km)	%	Distance Walked (km)	Total Area in *N.C* .** (km^2)
	A	B				
Dense Forest	2,190	2,000	4.19	52.4	82.2	6.3
Disturbed Forest	800	1,300	2.10	26.3	46.2	12.7
Farmbush	1,010	700	1.71	21.4	37.6	25.9
Total	4,000	4,000	8.00	100.0	176.0	44.9

* 292 ha (2.92km^2) of the plantation area was eliminated from the total area of the *Noyau Central* in primate density estimation. Due to a lack of precise data on the proportion of Dense Forest and Disturbed Forest, the ratios of these habitat types were assumed to be 1/3 and 2/3.

III. Results

A. Primate Encounters

During the censuses, I encountered 117 associations (single-species groups and mixed-species groups) and 16 solitary individuals (*C. mona*: $n = 12$; *C. erythrogaster*: $n = 4$) that I was able to identify species (Table 7.2). There were 103 associations that contained *C. mona* and 30 that contained *C. erythrogaster*. A group of *P. verus* was sighted twice in mixed-species associations that also contained *C. mona* and *C. erythrogaster*. A group of *C. aethiops* was seen twice, but solitary individuals of *P. verus* or *C. aethiops* were never sighted. Furthermore, *C. vellerosus* groups or solitary individuals were never sighted.

B. Population Size and Density Estimates

1. Cercopithecus mona

An inspection of the frequency distribution of perpendicular distance in dense forest, disturbed forest, and farm bush determined the fall-off distances of 29 m, 49 m, and 19 m, respectively (Fig. 7.2). Using these fall-off distances, effective distances (*d*) in dense forest, disturbed forest, and farm bush were calculated as 43.9 m, 85.8 m, and 25.3 m, respectively. These figures produces group density estimates of 3.6/km^2, 2.7/km^2, and 2.2/km^2 in dense forest, disturbed forest, and farm bush, respectively (Table 7.3).

The sightings of all-male groups during censuses comprised 10.7% of all *C. mona* group sightings. Therefore, 10.7% of all *C. mona* groups in the Lama Forest were assumed to contain all-male groups. Using the mean group sizes of 2.8 for all-male groups and 13.5 for mixed-sex groups, *C. mona* population densities in dense forest,

Table 7.2 Sightings of groups and solitary individuals during 44 censuses

Single-Species & Mixed-Species Groups	Frequency of Group Sightings	Frequency of Solitary Sightings	Total Frequency	%
C. mona	85	12	97	68.8
C. erythrogaster	12	4	16	11.3
C. mona *C. erythrogaster*	16	-	16	11.3
C. mona *C. erythrogaster* *Procolobus verus*	2	-	2	1.4
Chlorocebus aethiops	2	0	2	1.4
Colobus vellerosus	0	0	0	0.0
Subtotal	**117**	**16**	**133**	**94.3**
Uncertain Spp.	8	0	8	5.7
Grand Total	125	16	141	100.0

Fig. 7.2 Frequency distributions of Perpendicular Distance (PD) at group sightings

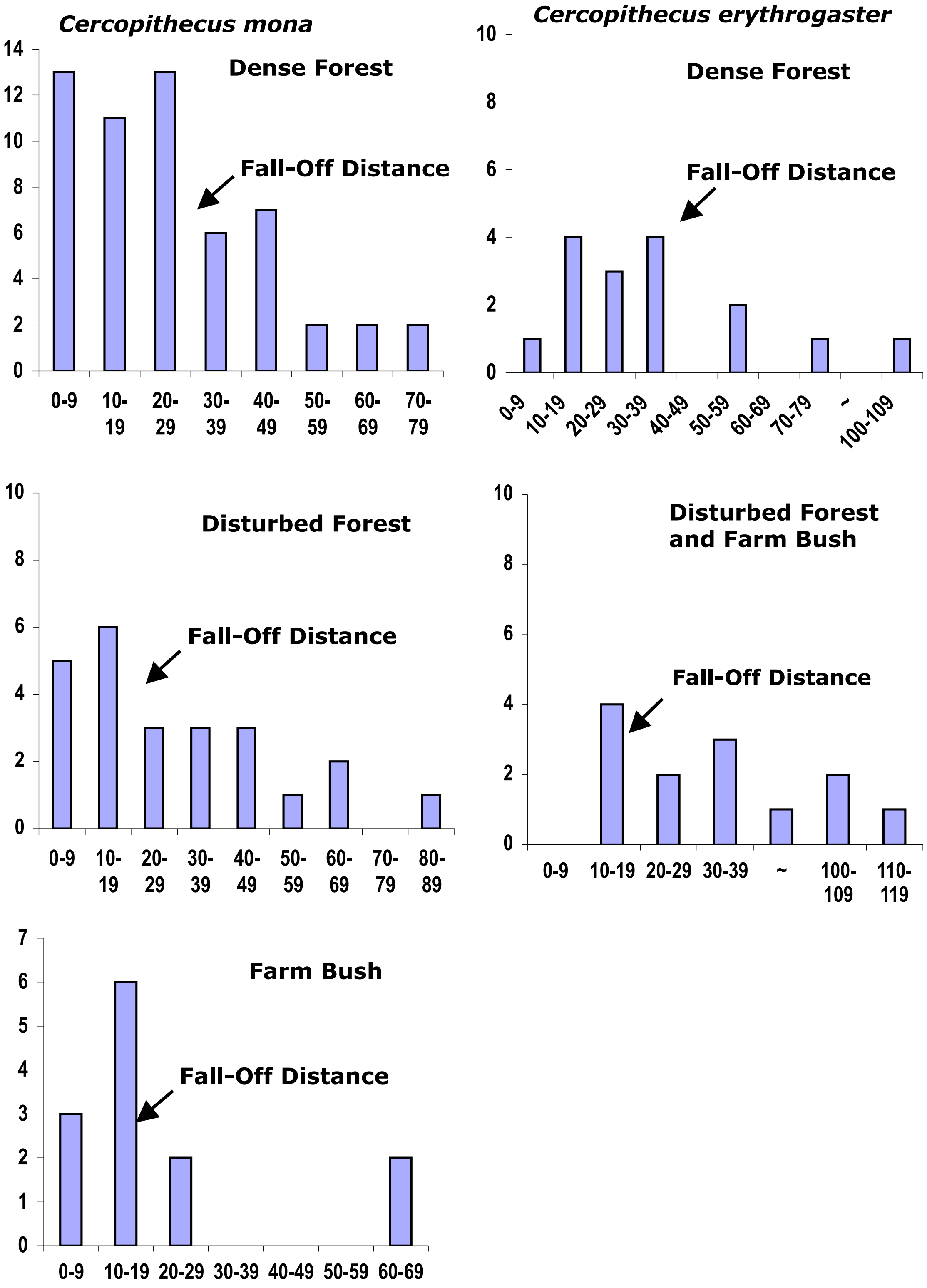


Table 7.3 Parameters used in the estimates of *C. mona* population densities

Habitat Type	Fall-off Distance	Effective Distance	Total Sample widths (m)	Number of Groups Sighted Below *fd* (*Ni*)	Total Number of Groups Sighted (*Nt*)	Area Sampled (km^2)*	Density Estimates#			Total Population	s.d.
	fd	*d=(Nt/Ni)fd*	*w=2(1/2s+d)*			*a=lw*	Groups/km^2 (N_t/a)	Ind./km^2	s.d.		
Dense Forest	29	43.9	167.8	37	56	13.8	4.1	49.4	± 5.8	311	± 36
Disturbed Forest	49	85.8	251.5	20	35	11.6	3.0	36.7	± 4.4	466	± 56
Farmbush	19	25.3	130.7	9	12	4.9	2.4	29.7	± 3.6	770	± 94
								Total		1547	± 186

Table 7.4 Parameters used in the estimates of *C. erythrogaster* population densities

Habitat Type	Fall-off Distance	Effective Distance	Total Sample Widths (m)	Number of Groups Sighted Below *fd* (*Ni*)	Total Number of Groups Sighted (*Nt*)	Area Sampled (km^2)*	Density Estimates##			Total Population	s.d.
	fd	*d=(Nt/Ni)fd*	*w=2(1/2s+d)*			*a=lw*	Groups/km^2	Ind./km^2	s.d.		
Dense Forest	39	52.0	179.0	12	16	14.7	1.1	10.4	± 3.4	66	± 21
Disturbed Forest and Farm Bush	19	61.8	198.5	4	13	16.6	0.8	7.5	± 2.9	290	± 30
								Total		355	± 51

* Due to a lack of precise area of dense and disturbed forest, the areas of dense and disturbed forests were considered 1/3 and 2/3 of the entire forested area estimated in 1990. # Group size for *C. mona* = 13.3±0.67 for mixed-sex group and 2.8 ± 0.87 for all-male groups. ## Group size for *C. erythrogaster* = 9.6± 0.87.

disturbed forest, and farm bush were estimated to be 49.4 ± 36/km^2, 36.7 ± 4.4/km^2, and 29.7± 3.6/km^2, respectively. These figures produce a population size of 1,547 ± 186 and a biomass of 153 kg/km^2 (Table 7.3).

2. Cercopithecus erythrogaster

An inspection of the frequency distribution of perpendicular distance at sightings of *C. erythrogaster* groups and solitaries indicates the fall-off distances for dense forest was 39 m. Sightings of this species in disturbed forest and farm bush were rare. Therefore, the data from these two habitat types were combined. The fall-off distance in these habitats was determined as 19 m (Fig. 7.2). These produced effective distances of 52.0 m for dense forest and 61.8 m for disturbed forest and farmbush and group density estimates of 1.1 /km^2 in disturbed forest and 0.8 /km^2 in disturbed fores and farm bush. Using a mean group size of 9.6, *C. erythrogaster* population densities were estimated to be 10.4 ± 3.4 /km^2 in dense forest and 7.5 ± 2.9 /km^2 in disturbed forest and farm bush. These densities give an estimated population size of 355 ± 51 and a biomass of 25 kg/km^2 for *C. erythrogaster*.

3. Procolobus verus

Procolobus verus was seen only twice during 176 km of censuses. Because I could not obtain accurate group size for this species in the Lama Forest, I use the group sizes of 8.4–6.0, the mean group sizes of *P. verus* on Tiwai (Whitesides *et al.,* 1988; Oates and Whitesides, 1996) and 4.5, the mean group size of *P. verus* in Taï Forest (Korstjens and Schippers, 2003). Population density of *P. verus* is estimated to be approximately 0.8–1/km^2. These figures translate to the *P. verus* population of 15–19 for the entire *Noyau Central* in the Lama Forest and a biomass of 15.2–19.0 kg/km^2.

IV. Discussion and Conclusion

A. Population Density and Biomass

1. Cercopithecus mona in the Lama Forest

In this study, *C. mona*'s densities were highest in dense forest (49.4 ± 5.8/km^2), lower in disturbed forest (36.7 ± 4.4/km^2), and lowest in farm bush (29.7 ± 3.6/km^2). The highest density in dense forest is probably related to *C. mona's* food preferences (Lwanga, 2006). Lwanga (2006) attributed a higher density of *C. ascanius* in colonizing forests than old growth forest in the Kibale Forest to an abundance of small fruits of pioneer species and arthropods. The preferred foods of *C. mona* in the Lama Forest were *Dialium guineense* seeds, *Diospyros mespiliformis* fruits, arils of *Afzelia africana seeds*, and *Ceiba pentandra* nectar and flowers. These species are more abundant in sample quadrats that contained more dense forest (S141, Q131) than disturbed forest (S140, L134) or farmbush (T140, UV140)(see Table 3.5), indicating that dense forest provides more foods for *C. mona*. Plant parts of pioneer species, that are more abundant in disturbed forest, were not abundantly available and eaten opportunistically.

In comparison with the result of this study, Kassa (2001) produced two estimates of *C. mona* population densities in the Lama Forest by using DISTANCE. Based upon the line-transect method, he estimated a group density of 10/km^2 (92 monkeys/km^2) and a total population size of 2,394, which is 50% greater than my estimate. Based upon the point count method, he estimated a group density of 4.45/km^2 (24 monkeys/km^2) and a population size of 2,814. The point count method is often used to estimate bird population densities; it is rarely used to estimate mammalian densities (Rosee and Reeve, 2003). He rejected the estimate based upon the point count method, since the probability of detection for the point count method (27%) was much lower than the line transect method (76%). DISTANCE, which requires a large sample and stringent field conditions that are not met in a forest such as the Lama Forest, tends to overestimate mammalian population densities (Fashing and Cords, 2000).

2. *Other* Cercopithecus mona *Populations*

In this study, *C. mona*'s densities were highest in dense forest (49.4 ± 5.8 /km^2), lower in disturbed forest (36.7 ± 4.4/km^2), and lowest in farm bush (29.7 ± 3.6/km^2). The density in dense forest at Lama is the highest of all the estimates made in field sites where *C. mona* has been censused or studied, but the densities in disturbed forest and farm bush were within the range of variation found in published studies (Table 7.5). In Douala-Edéa F.R. in southeastern Cameroon, *C. mona* densities averaged 0.8 groups/km^2 or 15.2 monkeys/km^2 (Whitesides, 1981). Douala-Edéa is a forest with poor sandy soil and low tree species diversity (Whitesides, 1981) and Caesalpinioidae trees are dominant (McKey *et al.*, 1981). The low densities of *C. mona*, as well as those of *C. pogonias*, are in contrast to higher densities of sympatric arboreal guenons, *C. nictitans* and *C. erythrotis*. In Douala-Edéa, *C. mona* and *C. pogonias* appear to be outcompeted by other frugivorous primates.

Using Howard's (1977) data on group and range sizes, I estimate that *C. mona* density at Mungo is 1.4 groups/km^2 or 27 monkeys/km^2. This is the second lowest estimate made for *C. mona* in West Africa (Table 7.5). The densities of *C. mona* in four different forest types in the Gashaka Gumti N.P. varied by habitat (Dunn, 1993); the densities were low in lowland gallery forests (1.1 ± 0.26 ~ 2.0 ± 0.27 groups/km^2) and highest in montane forest (3.2 ± 0.45 groups/km^2). If Dunn's (1993) average group size

Table 7.5 **Population density of *C. mona***

Country	Field Site	Habitat Type		Density		Reference
				Group	Individuals	
Cameroon	Douala-Edéa	Rain forest (not hunted)		1.0, 1.2	19.7, 23.3	Whitesides 1981
		Rain forest (hunted)		0.4, 0.2	7.3, 10.7	
	Mungo	Rain forest		1.4	27	Howard 1977
Nigeria	Gashaka Gumti	Lowland gallery forest		2.0 ± 0.27	49 (Mean)	Dunn 1993
				1.5 ± 0.31		
				1.1 ± 0.26		
		Montane forest		3.2 ± 0.26		
Grenada	Grand Etang	Evergreen rain forest		2.3	42.1	Glenn 1996
Benin	Lama	Seasonally Dry Forest	Dense forest	4.1	49.4 ± 5.8	This study
			Disturbed forest	3	36.7 ± 4.4	
			Farmbush	2.4	29.7 ± 3.6	
São Tomé		Evergreen rain forest			18.75	Glenn *et al.* unpublished a
Príncipe		Evergreen rain forest			23.67	

of 20–30 is used, the mean density would be 49 monkeys/km^2: 22 ± 5.2 ~ 60 ± 8.1 monkeys/km^2 for the gallery forest, 64 ± 9 ~ 96 ± 13.5 monkeys/km^2 in montane forest. Dunn (1993) suggested that *C. mona*'s higher density in the montane forest was due to the abundance of secondary tree species there. Still, in comparison with the sympatric *C. nictitans* and *C. guereza*, *C. mona*'s densities were lower in all habitats.

Hunting occurs in Grenada, but 2.3 groups/km^2 or 42.1 monkeys/km^2 estimated by Glenn (1998) is one of the highest estimates made for *C. mona*. A lack of sympatric primates may be a factor contributing to the high density. On São Tomé and Príncipe, Glenn *et al.* (unpublished a) estimated *C. mona* densities of 18.75 and 23.67 monkeys/km^2, respectively. *Cercopithecus mona*, the only non-human primate that exists on these islands, was introduced to these islands between 160 and 500 years ago from somewhere in mainland West Africa (Glenn *et al.*, 2002). Glenn *et al.* (unpublished a) reasoned that the difference in the densities of two island populations was due to a much smaller sample size in Príncipe that probably inflated the density. Eighty percent of their encounters with *C. mona* in São Tomé occurred in "regenerating forest" rather than in agricultural lands or primary forests. Similarly, ≥ 90 % of encounters with *C. mona* in Príncipe occurred in regenerating forests (Glenn *et al.*, unpublished a) where *C. mona* preferred feeding on many cultivars. These are essentially abandoned farm bush areas that continue to produce abundant food crops. The low densities of *C. mona* populations on São Tomé and Príncipe are probably due to a combination of hunting and competition over fruits with endemic frugivorous birds (≥ 26 bird spp. occur) and bats (Jones, 1992; Monza *et al.*, 1996).

The mean density of *C. mona* in the Lama Forest is the highest among all sites where *C. mona* has previously been surveyed or studied. What are some possible reasons for this? A number of factors can be considered. First, the Lama Forest has a high density of *Dialium guineense* trees that produce preferred food of *C. mona*. Second, although hunting takes place, hunting pressure on *C. mona* appears to be low. Third, near extinction of *C. vellerosus* may have caused *competitive releas*e: *C. mona* may have extended its fundamental niche in utilizing *Dialium guineense* seeds and other foods in the absence of its competitor and its population may have increased. Fourth, *C. erythrogaster* prefers to feed in the liana tangle and thick secondary growth (Oates, 1985). Therefore, competition over food between the two frugivorous primates is probably low, since they exploit foods in different microhabitats, but without a study focusing on *C. erythrogaster*, any conclusions that can be made about its ecology remain tentative. It is uncertain how hunting has adversely influenced the population density of *C. mona* in the Lama Forest, since there are no comparable data from previous years. Above factors, however, appear to interplay to produce a high density of *C. mona* in the Lama Forest.

In sum, the high population densities of *C. mona* in Mungo F.R., Grenada, São Tomé and Príncipe, and the Lama Forest are probably achieved due to the low number or absence of sympatric frugivorous primate species coupled with year-round access by monkeys in these forests to either cultivated foods (Mungo F.R., São Tomé and Príncipe), fleshy fruits (Grenada), or dry seeds in major dry seasons (Lama Forest).

In forests where *C. mona* coexists with several other frugivorous primates, its realized niche is presumably a consequence of exploitative and/or interference competition with sympatric guenons, mangabeys, seed-eating colobines, and apes. Interspecific competition and predation are the two most important factors that partition ecological niches among species living in the same habitat (Ganzhorn *et al.*, 1997). To infer a direct relationship between the densities of a guenon species and absence or presence of sympatric species, however, is difficult without conducting an experimental design (an impractical option) or a comparative study with a large number of study populations. Not only current ecological conditions, but also historical events (e.g., disturbance, logging, fire, human habitation) that have occurred in the forest must be taken into account to understand the reasons and causes for the variation of population densities within a guenon species (Butynski, 1990).

3. Cercopithecus erythrogaster

Kassa's (2001) group density estimates for *C. erythrogaster* in the Lama Forest were 3/km^2 (or 31 monkeys/km^2) and 1.71/km^2 (or 8 monkeys/km^2), based upon the line-transect and point count methods, respectively. Using these densities, Kassa (2001) estimated the total population size of *C. erythrogaster* as 806 and 338, respectively. Because the probability of detection was 98% for the line transect method and 45 % for the point count method, Kassa (2001) rejected the density estimate produced by the point count method. Kassa's estimate based upon the line transect method is twice as many as my estimate, but his estimate is probably an overestimate, because many assumptions DISTANCE makes are not met in a field condition like the Lama Forest. The group density of *C. e. erythrogaster* estimated in this study is close to Oates' (1985) extrapolation (1.0 group/km^2) of *C. e. pococki* in the Okomu Forest in Nigeria.

Hunting is a major threat to primates in general, but the effect of hunting on *C. erythrogaster* may have been minimal due to its cryptic behavior. Oates (1985) noted that the carcasses of *C. e. pococki* were less common than the carcasses of other monkeys in bushmeat markets in Nigeria. Some Nigerian hunters also told him that *C. e. pococki* was more difficult to shoot than other arboreal monkeys. Hunters prefer to shoot larger-bodied slow-moving primates rather than smaller-bodied fast-moving primates such as guenons (Johns and Skorupa, 1987). Larger-bodied primates provide them with more meat or income. Although in the forest interior, *C. e. erythrogaster* may be protected due to its cryptic behavior, they are particularly vulnerable when they come to feed in liana tangles at forest edges. Increasingly, such edges are becoming a large part of the Lama Forest, possibly posing a greater threat to the *C. e. erythrogaster* population than the past.

According to a hunter, who was detained due to monkey hunting, he preferred to hunt Agbe (*C. e. erythrogaster* in Yoruba Nagot, a local language) rather than Akko (*C. mona*), since it tastes better, but that Akko tastes better than Eiyaifo (*C. aethiops*). He also said that he preferred to hunt the bushpig since it tastes better than monkeys. Such taste preference is an important factor in hunters' decisions of which animals to hunt. Forest managers can relate such information with census data to determine if a direct correlation exists or not in the pattern of faunal diversity and structure in the forest.

According to Sinsin *et al.*'s (2002) survey, suitable habitats for *C. e. erythrogaster* in Bénin have been reduced from 5,965 km^2 to 1,430 km^2 in the last 50–100 years. The Lama Forest is the largest remaining suitable habitat for *C. e. erythrogaster*. Many areas where *C. e erythrogaster* now exists are small fragmented areas (Sinsin *et al.*, 2002).

Some of which are in farmed areas where the red-bellied guenon feeds on food crops and invertebrates. Other areas are fragmented swamp forests or gallery forests.

4. Procolobus verus and Colobus vellerosus

According to Booth (1956, 1957), *Procolobus verus* prefers to feed in thick vegetation in areas that have been disturbed or cultivated or near swamps or along riverbanks (Oates, 1994b). The Lama Forest seems to provide an ideal habitat for this species, although I do not know the species' level of tolerance towards seasonal habitats. My density estimate for this species (0.8–1 group/km^2) in the Lama Forest may be an underestimate, because this species' pelage blends in well with the vegetation.

During my study, *Colobus vellerosus* was never clearly observed. The loud rustling vegetation noise that Black-and-White Colobus monkeys make when they move from tree to tree and the dawn and dusk chorus of male loud calls that are prominent behavioral features of these monkeys in non-hunted forests were absent in the Lama Forest. *Colobus vellerosus*' normative behavior has been modified due to hunting pressure. In intensively hunted areas in the Taï Forest, primates infrequently give loud calls and alarm calls (Zuberbühler *et al.*, 1999). While not being able to use auditory cues was a contributing factor for a lack of clear observation of *C. vellerous* during this study, the main factor was probably the great rarity of this species. I estimate that fewer than 50 individuals of *C. vellerosus* occur in the Lama Forest.

Why is *C. vellerosus*' population density so low in the Lama Forest? Two likely causes are considered. First is the seasonality of its food. The black-and-white colobus monkeys are known to prefer young leaves (Oates, 1994b) and seeds (McKey *et al.*, 1981). It is also known to thrive in secondary vegetation that abundantly produces young leaves of pioneer species. Therefore, as long as its preferred foods are available throughout the year, *C. vellerous* should be able to maintain a high population density even in a forest such as the Lama Forest. The Lama Forest, however, goes through periods of scarcity of leaves, especially of young leaves and seeds (Fig. 4.3). Thus, *C. vellerosus*' preferred foods at Lama appear to be too seasonal to sustain a large population. Supporting evidence comes from the low *C. vellerosus* density at the Boabeng-Fiema Monkey Sanctuary in Ghana. The Boabeng-Fiema Monkey Sanctuary is a seasonal forest where no hunting takes place. Yet, *C. vellerosus* population at Boabeng-Fiema is low (Wong and Sicotte, 2006). A more likely explanation for its low population density at Lama is hunting pressure. Since *C. vellerosus* has a low tolerance to hunting, hunting pressure most likely has driven this species to near extinction in the Lama Forest. In other parts of West Africa where hunting takes place, *C. vellerosus* is now rare (Saj *et al.*, 2005).

B. Line-Transect Censuses

Line-transect sampling methods have been used to estimate population densities of many primate species (Defler and Pintor, 1985; Chapman *et al.*, 1988; Bobadilla and Ferrari, 2000; Peres, 2000; Srivastava *et al.*, 2001) as well as many other vertebrate species (e.g., ungulates, elephants, whales, birds, lizards, fish) inhabiting a variety of habitats.

This method makes the following assumptions: (1) the probability of detection decreases as detection distance increases; (2) the probability of detecting animals directly above the transect is 1.0; (3) behavior of animals does not affect the sighting distance; (4) all individuals/groups are counted only once; (5) groups are distributed at random with respect to the survey path; (6) the behavior of individuals/groups is species-typical along the transect; (7) response behavior of individuals/groups towards the observer is the same at every location along the survey path; (8) distances and angles are measured accurately to avoid measurement and rounding errors; and (9) sightings are independent events (Burnham *et al.,* 1980; Seber, 1982; Brockelman, 1988; Whitesides *et al.*, 1988; Buckland *et al.*, 1993).

Because the Lama Forest consists of a mosaic of habitat types at various successional stages with different degrees of disturbance history, visibility varies depending upon habitat types. Visibility is more limited in farm bush. Furthermore, large mammals are skittish toward humans due to hunting pressure. These circumstances make it likely that one or more of the above assumptions are being violated at Lama, potentially leading to either an underestimate or overestimate of population density. Many authors have advocated the use of an index of abundance in monitoring populations in difficult habitats; however, the use of an index of abundance is limited (Plumptre, 2000). Caro (1999), however, has argued that line-transect surveying is about the only method that can be used to estimate population density under such circumstances.

Because *C. mona* was never studied in the Lama Forest prior to this study, it is not possible to verify the accuracy of the analytical method employed by comparing with the true group density obtained by home range size and overlap (Whitesides *et al.*, 1988; Fashing and Cords, 2000). The conclusions drawn in several studies, which compared a few analytical methods, are inconsistent about the efficacy of the use of perpendicular distance, sighting distance, or modified perpendicular distance. For example, Struhsaker (1981) advocates the use of Maximum Reliable Sighting Distance (MRSD) over

Maximum Reliable Perpendicular Distance (MRPD). He pointed out that the use of perpendicular distance is a problem: if animals are observed above or near a transect, perpendicular distance would be recorded as zero or near zero. Thus, it will underestimate the area sampled. Plumptre (2000) objects to the idea of adding 1/2 of group spread, since group does not always spread out in a circle and the group spread changes as a group moves. Struhsaker (1981) found that MRPD method resulted in overestimates of *Procolobus badius* and *Cercopithecus ascanius* in the Kibale Forest, but Defler and Pintor (1985) found that MRSD method was most accurate in estimating population densities of *Alouatta seniculus* and *Callicebus torquatus* in El Tuparo National Park in eastern Columbia. According to J. Linder (pers. comm.), the MRSD method yields better estimates for species with low population densities. Chapman *et al.* (1988) tested the perpendicular distance and MRSD methods in a census study of *Cebus capucinus* and *Alouatta palliata* and found that the mean SD method was more accurate than the perpendicular distance method, which resulted in an overestimate of both species. Fashing and Cords (2000) on the other hand found that the method of Whitesides et al. (1988) was superior to the MRSD method, which underestimated the density of *C. guereza* by 8%, but overestimated the density of *C. mitis* by 36% in Kakamega Forest, Kenya. Plumptre (2006) stated that the use of sighting distance has no theoretical basis, because sighting distance only indicates how far an observer is able to see animals. Therefore, he advocates the use of perpendicular distance. The least effective method, according to Fashing and Cords (2000) was the TRANSAN program (a prototype of DISTANCE program) that overestimated the colobus and blue monkey densities by 21% and 114%, respectively. Brugière and Fleury (2000) tested four analytical methods in a census study of *C. satanas* in Makandé, Gabon and found that perpendicular distance method, which incorporated a fixed sample width of 100 m, and MRPD method produced better estimates of the true density of the black colobus monkey. In their study, the use of MRSD resulted in an underestimate of *C. satanas* by 17%. Since the condition of the forest and the degree of habituation of the animals influence the efficacy and accuracy of censuses, simultaneous use of several methods to examinine the reasons for differences that occur in the results may be able to provide some new insights.

In addition to determining whether to use perpendicular or sighting distance, when monitoring primate populations over many years we must take into account that different census takers can differentially influence the outcome of the census results (Ringvall *et al.*, 2000). Ringvall *et al.* (2000) conducted an experimental census study in two types of forests in northern Sweden. They placed 115 colored grouse-shaped boards on the ground within a 50 m zone (25 m each side of transect) along four 1,000 m transect. Eleven surveyors, who were given a 1/2 day training to become familiar with the line-transect survey method, walked on four transects and recorded the detection of the objects. Ringvall *et al.* (2000) found that density estimates calculated from the surveyors observations varied between 8.9 and 28.2 objects/ha. Actual density of the objects was 23 objects/ha. About 15% of the objects that were placed within 1 m of the transect line were not detected. These results indicated that different observation ability is a significant problem in estimating animal populations. They stated that, "If surveyors violate the assumption to differing degrees, the differences in their estimates can give an illusion of trends that do not exist or disguise real trends." Perhaps one way to find out whether subjectivity is a concern in estimating a primate population or not is by conducting a test similar to that conducted by Ringvall *et al.* (2000) by using inanimate objects placed in trees.

There is a wide conceptual and practical gap between the theory and the practice of estimating primate population densities in disturbed and hunted forests. Most endangered primate species currently live in areas where human population density and hunting pressure are high, and where their habitats are disturbed or fragmented. Estimating primate densities in such habitats is crucial, since only when we have good estimates, can we begin to formulate conservation projects that are appropriate for the species in particular situations. There is an urgent need to develop better census methods and analytical tools that take into account the fact that some of the assumptions in population estimation protocols may be violated.

CHAPTER 8: DISCUSSION AND SUMMARY

I. Guenon Guild Structure

A. Different Propensity to Digest Leaves

In Chapter 5, I examined the feeding ecology of the mona monkey in the Lama Forest and found that although most guenons incorporate many types of alternative foods when ripe fruits are not available, within the tribe Cercopithecini different species groups have different propensities for incorporating alternative foods. Members of the *mona* species group, especially *Cercopithecus mona* and *Cercopithecus pogonias*, include a significant amount of seeds in their diets. In contrast, the mitis, nictitans, and diana species groups incorporate more leaves, but when leaves are not available, they can turn to other food items such as seeds; the cephus group, turns to insects, while semi-terrestrial *Cercopithecus neglectus* and *Chlorocebus lhoesti* incorporate terrestrial herbaceous vegetation (THV) (Cords, 1987a; Gautier-Hion *et al.*, 1999; Kaplin and Moermond, 2000; Chapman *et al.*, 2002; Kaplin, 2002). Allthough *Cercopithecus preussi* and *Cercopithecus solatus* are also semi-terrestrial species, they mainly feed on fruits, insects, and leaves at low height and on the ground (Gonzales-Krichner, 1997, 2004; Kaplin, 2002). The variation found in their preferred tree strata also indicates the differences in the ecological niches of different guenon groups (McGraw, 2002).

Although patterns of geographical distribution of the guenons (Oates, 1988a; Kaplin, 2002), vegetation history (Hamilton, 1988), habitat heterogeneity (Oates *et al.*, 1990; Chapman *et al.,* 1999), and seasonality largely determine which guenon species may coexist with one another at any locality, the differences in preferred ecological niches among guenon species groups indicate the presence of a guenon guild structure within a forest (Chapman *et al.*, 1999; van Schaik *et al.*, 2005). In a relatively undisturbed forest, there are usually three or four guenon guilds: a large-bodied frugivorous-folivorous guild that is occupied by the nictitans, mitis, or diana groups; the medium-sized frugivorous-semivorous guild, which is occupied by the mona species group; and the small-bodied frugivorous-insectivorous guild, which is occupied by the cephus group (Chapman *et al.*, 2002). In addition to these guilds, there may exist the frugivorous-THV guild occupied by the neglectus group in inundated forests and *C. lhoesti* in montane forests (Kaplin and Moermond, 2000). Furthermore, *Cercopithecus hamlyni*[*], *Allenopithecus* and *Miopithecus* occupy unique ecological niches that complicate the picture of the guenon guild structure in many forests (Oates, 1988a). In most undisturbed forests, only one species occupies each guild. There are certainly deviations to this guild structure. For example, in some West and Central African forests, both *C. mona* and *C. pogonias* are sympatric (e.g. Douala-Edéa in Cameroon). In some West African forests, *C. nictitans* and *C. diana* co-occur, but in these forests, *C. nictitans* appears to be out-competed by *C. diana* (Oates, 1988a). In the Lama Forest, there are only two guenon guilds, lacking the frugivorous-folivorous guild.

Members of the mitis, nictitans, and diana groups are more flexible in incorporating alternative foods than the members of the mona and cephus species groups. When leaves, their preferred alternative foods, are not available, the mitis, nictitans, and diana groups can turn to seeds and insects. *Cercopithecus mitis* is exceptionally catholic. Even in areas where other arboreal guenons cannot subsist, *C. mitis* can coexist with baboons and savanna-living guenons. When leaves are not available, it can also feed on

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[*] Although dietary data on the semi-terrestrial *Cercopithecus hamlyni* are not available, THV is not the main food of *C. hamlyni*. It appears to occupy a unique ecological niche not occupied by other guenon species.

insects and seeds. For example, *C. mitis* in Nyungwe F.R. included a lot of insects and seeds when its five most preferred foods were scarce, but did not include many leaves during this period. It is possible that the availability of palatable leaves is very limited in Nyungwe (Kaplin *et al.*, 1998). In the Bia N.P., seeds comprised 25.2 % of *C. diana*'s annual diet, but only 6 % consisted of legume seeds (Curtin, 2002). Fig. 5.2 shows that on an annual basis, members of the nictitans, mitis, and diana groups are able to reduce their fruit consumption to lower than 20 % of their annual diets. In comparison, the mona and cephus groups seem to maintain their fruit consumption to above 20 % and 30 % of their annual diets, respectively (see Fig. 5.2). The mona species group has not been observed to feed on a significant amount of leaves.

B. Form and Biorole

The propensities for different guenons to more or less specialize on particular alternative foods appear to have their basis in certain morphological differences. For example, the incisors of *C. cephus* (frugivorous-insectivore) and *C. pogonias* (frugivorous-semivore) are large in relation to their body size, while the incisors of *C. mitis*, *C. nictitans*, *C. diana*, *C. hamlyni*, THV specialists (*i.e., Chlorocebus lhoesti*, *C. neglectus*), and *Allenopithecus* are small in relation to their body size, indicating that the foods they consume (e.g., leaves and berries) require little incisal preparation (Hylander, 1975). This indicates that the foods they consume differ among the frugivorous–insectivore and frugivorous-semivore on one hand and the latter species on the other.

Singleton (2005) conducted a landmark-based morphometric analysis of facial scaling in papionins that included *Cercocebus galeritus*, *Cercocebus torquatus*, and

Lophocebus albigena to examine the adptie significance of facial allometries. Small-bodied and relatively arboreal mangabeys have a short face that is contrasted with a long prognathic face of large-bodied terrestrial *Papio* species and the diet is related to the facial scaling (Singleton, 2005). *Papio* species feed on grass and mangabeys incorporate a significant amount of seeds in their diets (Poulsen *et al.*, 2001b). Singleton (2005) used several cercopithecin species, including *C. mona, C. ascaniu*s, *Chlorocebus nigroviridis, Chlorocebus patas,* and *Miopithecus talapoin* as an outgroup. She found that the mangabeys share almost identical masticatory apparatus scaling with *Miopithecus* and *C. mona*, but not with *C. ascanius*. She concluded that the face of *Miopithecus* is shortened because of biomechanical scaling due to dwarfism, while the morphology of *C. mona* suggests that there may be a latent morphological diversity in the guenon clade. It has been widely stated that mangabeys (genera *Lophocebus* and *Cercocebus*), having their molar teeth capped with the thickest enamel of all extant primate species, have an advantage over the guenons in masticating hard seeds (Waser, 1977; Lambert *et al.*, 2004). The similarity in masticatory apparatus scaling found between the mangabeys and *C. mona*, two distantly related taxa, suggests convergent evolution: an adaptation to hard-to-process foods such as seeds. Only five guenon species were included in Singleton's outgroup and within-species sample size for *C. nigroviridis* and *Chlorocebus patas* was small. Therefore, further studies using larger samples from more guenon species are needed to examine whether the similarities found in the facial complex of *C. mona* and mangabeys are unique to this pair of taxa or also apply to other guenons.

Molar enamel thickness is an attribute often described as an adaptation to hard-to-digest foods (Martin, 1990). Although data on the M3 molar enamel is not available, according to D.J. Reid's data on the M2 distal molar enamel thickness, *C. mona* (18.58) has thicker relative molar enamel* than *C. mitis* (14.96) or *C. aethiops* (13.90) (D.J. Reid, pers. comm.). Whether these differences indicate statistically significant differences or not among these taxa is not clear.

The differences in the diets found among sympatric or allopatric guenons may partly be explained by different metabolic requirements due to body size and other physiological constraints, but there may also be significant differences in their dental morphology, digestive morphology, digestive modularity, and gut microbes (Happel, 1988; Lambert, 1994, 1998). Bruorton *et al.*'s (1991) study provides insight into differences in the population of gut microbes, accounting for differences in the ability to process hard-to-digest foods between *C. mitis* and *C. aethiops*. Their study warns us that generalizing digestive capabilities of closely related frugivorous cercopithecins is overly simplistic. Bruorton *et al.* (1991) found that the gastrointestinal tracts of *C. aethiops* and *C. mitis*, inhabiting South Africa, are morphologically similar. *Cercopithecus mitis*, however, possesses a larger cecum and colon than *C. aethiops*. Furthermore, more than four times as many bacteria were found in the cecum and colon of *C. mitis* than *C. aethiops*. Many of these were cellulose-digesting bacteria, confirming that bacterial fermentation is active not only in *C. aethiops*, but even more so in *C. mitis*. The bacteria's primary role is probably degradation of cellulose and carbohydrates, but most likely detoxication of allelochemicals also occurs (Janzen, 1979; Foley and McArthur, 1994). The study of Bruorton *et al.* (1991) lends support to the idea that although guenons have been lumped together as a monogastric primate genus, a species level

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* Average enamel thickness is defined as the area of the enamel cap divided by the length of the enamel-dentine junction. Relative enamel thickness is defined as the quotient of average enamel thickness over the square root of the dentine area, multiplied by 100 (D. Reid, pers. comm.)

examination of their gastrointestinal tracts and symbiotic gut microbes may reveal intriguing differences in their capability to digest cellulose and other hard to digest foods such as seeds, or to detoxify secondary compounds.

Differences in the proportions of the gastrointestinal tract may also represent adaptations to different types of supplementary foods. Although his sample size was small and intraspecific variation was great, Jones (1970) found that on the average, wild *C. pogonias* has a longer small intestine than other wild guenons (*C. cephus*, *C. nictitans*, *C. neglectus*), but the caecum of *C. nictitans* was longer than that of *C. cephus*, *C. pogonias*, and *C. neglectus*.

The observable differences that are found among guenons may indicate adaptations to different kinds of foods they each consume especially during critical times. It would be interesting to study further how these observable differences in guenon morphology (form) relate to the differences that occur in their preferences for different alternative foods or foods that are important during critical times (biorole).

II. Biomass of the Mona Species Group

The fact that significant amounts of leaves are not eaten, or cannot be eaten, by *C. mona*, *C. campbelli*, and *C. pogonias* has consequences for their biomass at particular sites in relation to other frugivorous guenons. I compared the biomass of frugivorous guenons in West and Central Africa to examine whether seasonality, rainfall, and percentages of Caesalpinioideae in each forest influence, if not determine, the biomass of the members of the mona species group. An inherent problem with this kind of cross-site comparison is that studies conducted at different sites often use different methods at different points in time, and that study durations differ. There may also be confounding variables such as different levels of hunting pressure and habitat disturbances that cannot be easily quantified (Struhsaker, 1999). Despite these caveats, I gathered cross-site comparative data of the biomass of frugivorous guenons in forests where the members of the mona species group occur.*

Table 8.1 shows the result of this comparison. In seasonal forests where a member of the mona species group is the only guenon species or occurs with a few other primate species, its biomass is high (Lomako: McGraw, 1994; Boabeng-Fiema, Ghana: Fargey, 1992; Grenada: Glenn *et al.*, unpublished a; this study). In contrast, in most high forests where colobines, mangabeys, and other guenons coexist and fleshy fruit producing trees are dominant, the biomass of each member of the *mona* species group is lowest or second lowest in comparison with other sympatric arboreal guenons (Dunn, 1993; Chapman *et al.*, 1999; Chapman *et al.*, 2002). For example, in the Lopé Reserve (North Lopé) and Makokou in Gabon, where fleshy fruit producing trees are abundant (Chapman *et al.*, 1999), the biomass of *C. pogonias* is lowest of all arboreal guenons (Lopé, 10.1 kg/km^2; Makokou, 60 kg/km^2). These observations support the idea that in mature forests where fleshy fruits producing trees are abundant, members of frugivorous-folivorous species that are well equipped to digest leaves have an advantage over members of the *mona* species group. This could explain the fact that the biomass of each member of the *mona* species group is lowest or second lowest in the above forests.

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* Data on the biomass of frugivorous guenons from the Kibale Forest and Kakamega Forest, where no members of the mona species group occur, were also included.

Table 8.1 Biomass (kg/km^2) of diurnal frugivorous and folivorous anthropoid primates in African forests in relation with some ecological features of the forests (Sites are ordered from West to East. Shaded cells indicate members of the mona species group.)

Research Site Species	Sierra Leone	Côte d'Ivoire	Ghana	Bénin	Cameroon			Gabon	
	Tiwai	Taï	Boabeng-Fiema	Lama	Dja	Douala-Edéa	Mungo	N Lopé	Makokou
Rainfall	2708	1800	1050	1100	1600	3900	2614	1548	1755
Number of dry months	4	3	6	6	4	3	3	6	3
Dryness Index (T/P Ratio)	1	1.4	2.4	2.4	–	0.6	0.8	1.9	1.3
% Caesalpinioideae	11.7	15.3	4.7	44.6	–	9.8	8.9	9.2	20.3
% Leguminosae	41	22	–	45.8	–	18	13.9	28	22.5
Soil PH	4.3	–	–	6.5	–	3.9	–	4.5	3.8
Seasonal Flooding^{+}	U	N	N	Y	N	Y	U	N	N
# of diurnal frugivorous spp.*	5	5	1	2	8	6	3(6)**	7	10
Cercopithecus nictitans					80.9	67.0	12.0	80.6	100.0
Cercopithecus mitis									
Cercopithecus diana	165.0	75.3							
Cercopithecus cephus					37.1			12.4	80.0
Cercopithecus ascanius									
Cercopithecus petaurista	120.0	52.7							
Cercopithecus erythrotis						55.0	24.0		
Cercopithecus erythrogaster				25.0					
Cercopithecus campbelli	88.0	61.5	114$^{\#}$						
Cercopithecus mona				153.0		14.0	114.0		
Cercopithecus p. pogonias					88.6	15.0		10.6	60.0
Cercopithecus p. wolfi									
Cercopithecus neglectus					–				110.0
Chlorocebus lhoesti									
Cercopithecus hamlyni									
Chlorocebus solatus									
Miopithecus talapoin					–				60.0
Allenopithecus nigroviridis									
Total Guenon Biomass	373.0	189.5	114.0	178.0	206.6	151.0	150.0	103.6	410.0
Cercocebus agilis					–				
Cercocebus atys	196.0	58.0							
Cercocebus galeritus									–
Lophocebus atterimus									
Lophocebus albigena					134.0	88.0		35.3	–
Mandrillus sphinx								15.3	5.0
Pan troglodytes	25.0	58.5			42.2	25.0		22.5	–
Pan paniscus									
Gorilla gorilla					206.6	–		45.3	–
Total Frugivore Biomass	594.0	306.0	114.0	178.0	589.4	264.0	150.0	222.0	415.0
Colobine Biomass	786	704	7.5	19	55.9	198		91	–
Total Primate Biomass	1,380.0	1,010.0	121.5	197.0	645.3	462.0	150.0	313.0	415.0
Reference	15, 19	16, 17, 19	14. 20, 21	13, 25	22, 24	1, 19	2	3, 19	4, 19

[*] *Chlorocebus aethiops* and *Papio* spp. were excluded. * Outside Howard's (1977) study area, three other frugivorous species occur. # Inferred from population size reported in Porter (2005); – : no data. —: not considered. +U: Unknown, Y = Yes, N = No. Reference: 1. Mckey 1978; 2. Howard 1977; 3. White 1994; 4. Gautier-Hion *et al.* 1985; 5. Brugière *et al* .2002; 6. Brugière 2005; 7. Struhsaker 1975; 8. Plumptre & Reynolds 1994; 9. Fashing& Cords 2000; 10. Thomas 1991; 11. McGraw 1994; 12. Lahm 1993; 13. This study; 14. Fargey 1992; 15. Oates *et al.* 1990; 16. Bourliére 1985; 17. McGraw 1996; 18. Glenn 1996; 19. Chapman *et al* 1999; 20. Porter 2005; 21. Wong & Sicotte 2005; 22. Poulsen et al. 2001a, ; 23. Poulsen *et al.* 2001b; 24. Zapfack *et al.* 2002; 25. Gaiser *et al.* 2002

(Table 8.1 cont'd from previous page)

Research Site / Species	Gabon		DRC		Uganda		Kenya	Grenada
	Makandé	Salonga (S Lopé)	Ituri	Lomako	Kibale	Budongo	Kakamega	Grand Etang
Rainfall	1753	1756	1802	1800	1475	1500	2275	2613
Number of dry months	5	1	2	–	1	–	1	– –
Dryness Index (T/P Ratio)	1.3	1.4	1.7	1.4	1.3	–	1.1	– –
% Caesalpinioideae	23.9	38.9	63.1	4.7	2.4	–	0	– –
% Leguminosae	28.8	45.6	66.3	–	3	–	4.6	– –
Soil PH	4.2	4.2	4	–	5.6	–	–	– –
Seasonal Flooding	Y	Y	Y	N	N	N	N	N
# of diurnal frugivorous spp.*	8	8	9	6	5	3	4	1
Cercopithecus nictitans	41.3	41.6						
Cercopithecus mitis			145.2		133.0	93.6	645.0	
Cercopithecus diana								
Cercopithecus cephus	5.9	9.2						
Cercopithecus ascanius			68.0	154.0	328.0	29.5	220.0	
Cercopithecus petaurista								
Cercopithecus erythrotis								
Cercopithecus erythrogaster								
Cercopithecus campbelli								
Cercopithecus mona								160.0
Cercopithecus p. pogonias	9.0	10.1						
Cercopithecus p. wolfi			87.8	168.0				
Cercopithecus neglectus			2.1	–				
Chlorocebus lhoesti			2.5		13.0			
Cercopithecus hamlyni			0.8					
Chlorocebus solatus	73.1	5.9						
Miopithecus talapoin								
Allenopithecus nigroviridis		–		–				
Total Guenon Biomass	129.3	66.8	306.4	322.0	474.0	123.1	865.0	160.0
Cercocebus agilis								
Cercocebus atys								
Cercocebus galeritus								
Lophocebus atterimus		–	15.4	585.0				
Lophocebus albigena	13.0	30.7	53.1		60.0			
Mandrillus sphinx	5.3	21.8						
Pan troglodytes	–		27.7		85.0	89.2		
Pan paniscus		–		70.0				
Gorilla gorilla	–							
Total Frugivore Biomass	147.6	119.3	402.6	977.0	619.0	212.3	865.0	160.0
Colobine Biomass	–	–	308	57	2,386	275	1,035	
Total Primate Biomass	147.6	119.3	710.6	1,034.0	3,005.0	487.3	1,900.0	160.0
Reference	5	6	10, 19	11, 12	7, 19	8, 19	9	18

In some forests where caesalpinioid legumes are dominant and seasonality is moderate, the biomass of each member of the mona species group is often higher than that of sympatric species belonging to the cephus group and, to a lesser extent, than that of the nictitans and diana groups. For example, at Mungo, Cameroon, where Caesalpinioideae is one of the most dominant families, the biomass of *C. mona* (114 kg/km^2) is much greater than that of *C. nictitans* (12 kg/km^2) or *C. erythrotis* (24 kg/km^2).

In Makandé, Salonga, and Ituri, although trees belonging to the Caesalpinioideae subfamily are dominant and rainfall seasonality is moderate, the biomass of *C. pogonias* is lower than that of *C. nictitans*, but higher than the biomass of members of the cephus species group. In Makandé, the biomass of *C. pogonias* (9.0 kg/km^2) is about 1/6 of *C. nictitans'* (41.3 kg/km^2), but higher than that of *C. cephus* (5.9 kg/km^2). In Salonga, (DRC), the biomass of *C. pogonias* (10.1 kg/km^2) is about 1/4 of *C. nictitans'* (41.6 kg/km^2), but higher than that of *C. cephus*. In the Ituri Forest, where Caesalpinioideae trees are dominant (90–40% of the canopy level trees depending on habitat type), the biomass of *C. pogonias* is higher (87.8 kg/km^2) than that of *C. ascanius* (68 kg/km^2), but much lower than that of *C. mitis* (145.2 kg/km^2) (Thomas, 1991). It appears that *C. pogonias* has an advantage over a member of the cephus group but not over *C. nictitans* in Makandé and Salonga or *C. mitis* in Ituri. The dominance of caesalpinioid trees coupled with a moderate level of seasonality may limit the availability of digestible insects that are more important for the cephus group than other sympatric guenons.

The relationship between the biomass of the mona species group and the abundance of caesalpinioid legumes suggested above is probably simplistic and needs to be improved in future studies, since it cannot explain the biomass proportions of the guenons in some other forests where caesalpinioid legumes are dominant (Stevenson, 2001). For example, the biomass of *C. mona* and *C. pogonias* at Douala-Edéa is lower than that of *C. nictitans* or *C. ascanius* even though Caesalpinioideae is dominant. Similarly, at Tiwai, Sierra Leone, caesalpinioid legumes are abundant, but the biomass of *C. campbelli* (88 kg/km^2) is much lower than the two other guenons (*C. petaurista*: 120 kg/km^2, *C. diana*: 165 kg/km^2) (Oates *et al.*, 1990). The high biomass of colobines appears to have an influence.

The biomass of a member of the mona species group is also high in forests that include regenerating forests and forests that are bordered by cultivated lands in which fast-growing pioneer species that produce fleshy fruits, albeit seasonally, are abundant (young secondary forest in Tiwai: Fimbel, 1992; São Tomé and Príncipe; Glenn *et al.*, unpublished b).

At Tiwai, *C. campbelli* was more dependent on the fruits of a pioneer species than two other sympatric guenons in the young secondary forest. I observed the rates and quantity of the consumption of *Musanga* fruits[*] by birds and mammals at a cluster of five trees from a vintage point for 208.5 hr (2–5 hrs each day) in 1989 in the young secondary forest in Tiwai. *Cercopithecus campbelli*, *C. petaurista*, and *C. diana* removed approximately 377 fruits in 32 visited hrs, 99 fruits in 6.1/4 visited hrs, and 14 fruits in 1.1/2 visited hrs, respectively (Table 8.2). The rank of reliance on *Musanga* fruits in the young secondary forest by the guenons was the reverse of their biomass in old secondary forest in Tiwai. Fimbel (1992) found that the biomass of *C. campbelli* was the greatest,

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[*] *Musanga cecropioides,* a pioneer species with a short life expectancy of 15–20 yrs is common in West Africa. *Musanga* fruits, abundantly produced in regenerating forests, are high in sugar, protein, and fiber (Gartlan and Struhsaker, 1972; Hladik, 1977; Howard, 1986 cited in Johns and Skorupa, 1987; Fimbel, 1992).

Table 8.2 Consumption of *Musanga cecropioides* fruits by frugivorous anthropoid primates in Young Secondary Forest on the Tiwai Island, Sierra Leone

Species	Time spent on trees*	Time spent feeding*	Estimated # of fruits eaten**	%	Biomass[#] (kg/km^2)
Cercopithecus campbelli	32:00:22	6:16:48	377	57.6%	88
Pan troglodytes	8:36:52	2:20:29	140	21.4%	25
Cercopithecus petaurista	6:17:17	1:39:07	99	15.1%	120
Cercocebus atys	2:11:24	25:19	25	3.8%	196
Cercopithecus diana	1:38:32	14:12	14	2.1%	165
Total			655	100.0%	594

*hh:mm:ss ** The number of fruits eaten was calculated based upon assumed feeding rate of 1 fruit per 1 minute.

[#] = estimated from Fimbel's (1992) population density that of *C. petaurista* was second greatest, and that the biomass of *C. diana* was least in young secondary forest, but the rank of the three guenons' biomass in old secondary forest was exactly the reverse. At Tiwai, *C. diana* and *C. petaurista* are able to find enough foods in old secondary forest, but *C. campbelli* need to rely on foods in young secondary forest.

Competitive ability in interspecific interactions can influence primates' population density, and thus biomass (Davies, 1994). There is evidence that the competitive ability of the mona species group in feeding and other contexts is low. For example, in the Mungo F.R., 39 out of 45 interactions between individuals of different species that occurred on fruiting trees, sleeping sites, or territory were agonistic (Howard, 1977). Among 39 agonistic interactions, *C. mona* was a victim in a majority of displacements (n = 13/39, 33.3%) and chases (n = 5/39, 12.8%) involving *C. nictitans*. *Cercopithecus mona*'s aggressive acts towards *C. nictitans* or *C. erythrotis* were limited to head bobbing. In the Taï Forest, *C. campbelli* was a victim of 36 out of 59 (61%) aggressive acts committed by *C. diana* (Buzzard, 2004, 2006).

In most forests, the biomass of a member that belongs to the mitis, nictitans, and diana groups is usually greater than the biomass of its sympatric counterpart belonging to the cephus species group. In the Kibale Forest, however, the biomass of *C. ascanius* (147-332 kg/km^2) is much higher than that of *C. mitis* (14.3-111.3 kg/km^2) in the old growth forest (Struhsaker, 1997). Struhsaker (1978) suggested that the reason for the low density of *C. mitis* is due to interspecific competition with colobus monkeys and mangabeys. Interspecific competition among guenon species and with other primates undoubtedly has an influence on the guenon biomass (Tutin *et al.*, 1997a; Chapman *et al.*, 1999). However, how much influence does it exert? We need to obtain and analyze comparative data on competitive interactions that occur among sympatric primate species from different forests to thoroughly understand this issue.

III. Summary

(1) I examined the ecology and behavior of the mona monkey and how seasonality may influence the mona monkey's behavior. Prior to examining the ecology and behavior of the mona monkey, I documented the climate, vegetation composition and structure, and tree basal areas in the Lama Forest. Two dry seasons (one long and one short) and two wet seasons characterize the Lama Forest climate. The dominant trees in the Lama Forest were *Dialium guineense* and *Diospyros mespiliformis*. The most dominant family of trees was Leguminosae, especially the subfamily Caesalpinioideae represented by *Dialium guineense* and *Afzelia africana*.

(2) I found that *Cercopithecus mona* forms two types of mixed-sex groups: one-male and multi-male groups. Outside mixed-sex groups, males are either solitary or found in small all-male groups. Males that belong to different social groups were agonistic to each other. In contrast, males within social groups were friendly to each other. Male intra-sexual competition appears to be intense in *C. mona*. In *C. mona,* males play an important role in territorial defense. In contrast, friendly interactions among males and grooming by males is infrequent in *C. mitis*, *C. nictitans*, and *C. diana*. Furthermore, male role in territorial defense seems insignificant in *C. mitis*, *C. nictitans*, and *C. diana*. These observations suggest that male relationships in *C. mona* is similar to the male relationships reported in Taï *C. campbelli*, but is different from male relationships reported in the above frugivorous-folivorous guenons.

(3) Intrasite and intersite variations that exist in the number of adult males per mixed-sex group suggest that the social system of *C. mona* is facultatively multi-male. Four possible causal factors, predation, limited dispersal, widely dispersed females, and

the number of females per group were discussed, but with the available data, which factor or other factor primarily influences the number of males in mixed-sex groups remains obscure.

(4) *Cercopithecus mona* fed on large amounts of fruit in wet seasons. Overall, *Dialium guineense* (dry fruit) and *Diospyros mespiliformis* (fleshy fruit) provided nearly 40% of *Cercopithecus mona*'s annual foods. Although interannual variation in phenophases influenced *C. mona*'s resource availability and diet, *C. mona* incorporated in its diet a significant amount of *Dialium* seeds, which were abundantly available in long dry seasons when fleshy fruits were scarce. During the first major dry season, nectar and floral parts of *Ceiba pentandra*, seed arils of *Afzelia africana*, and immature seeds of *Dialium guineense* were the most important foods for *C. mona*. During the second major dry season, seed arils of *Afzelia africana*, immature seeds of *Dialium guineense* and nectar and floral parts of *Ceiba pentandra* were most important. *Cercopithecus mona* relied on the abundant foods that they can rely on during the periods of low ripe fleshy fruits. It remains to be seen whether *C. mona*'s food choice is based upon some particular nutritional contents (e.g., lipids) of its foods.

(5) The biomass of *C. mona* in the Lama Forest is much higher than the biomass of *C. erythrogaster*. Three factors can be considered as potentially producing *C. mona*'s high biomass. First, there is no frugivorous-folivorous guenon in the Lama Forest. Second, the legume seeds of *Dialium*, *C. mona*'s preferred food item are abundant when fleshy fruits are scarce. Third, *C. mona*'s high biomass may have been partially achieved due to competitive release. *Cercopithecus mona* may have extended its fundamental niche incorporating significant amounts of *Dialium guineense* seeds in its diet in the

absence of a competitor. In most West African forests where primates are not hunted and Caesalpinioideae or other leguminous trees are abundant, the population biomass of black-and-white colobus monkeys is high. *Colobus vellerosus* in the Lama Forest, however, is on the verge of extinction despite the fact that Caesalpinioideae trees are abundant. A likely explanation for the low population density of *C. vellerosus* in the Lama Forest is that *C. vellerosus* has been driven to near extinction due to hunting pressure.

(6) The biomass of *C. mona* is also high in the Mungo Forest, Cameroon and Grand Etang in Grenada. Its high biomass in these forests is achieved due to a lack of frugivorous-folivorous guenons coupled with its perennial access to a combination of fleshy fruits and cultivated foods.

(7) Each member of the mona species group has a low biomass in most forests where it coexists with other guenons. Its digestive system may lack an ability to digest significant amounts of leaves in comparison with more folivorous guenons that may also have a competitive advantage in interspecific competitions.

IV. Suggestions for Future Studies

A. Understanding the Monodominance of Caesalpinioideae in the Lama Forest

The factors contributing to Caesalpinioideae dominance, in particular of *Dialium guineense* in the Lama Forest need to be investigated. The associations of the ecotomycorrhizae and vesicular-arbucular mycorrhizae with *Dialium* and *Afzelia* should also be examined. Furthermore, a comparative study of the sapling growth, leaf growth, and leaf chemistry during and post flooding between Caesalpinioideae trees and trees of other families could help us understand how these trees survive (or do not survive) the extreme seasonality of the Lama Forest.

B. Understanding the Determining Factors for Multi-Male Sociality

To find the determining factors for multi-male sociality in *C. mona*, I suggest that researchers examine how seasonality influences not only the temporal availability of food, but also the spatial availability of foods and how these factors influence the spatial distribution of females and males.

C. Understanding the Availability of Foods and Food Choice

We need to begin to obtain data regarding the chemistry of foods consumed by *C. mona*. What is *C. mona*'s food choice based upon? Is a high lipid content in seeds a primary factor? Furthermore, we need to obtain data regarding the diversity and availability of arthropods that occur at the strata level in which *C. mona* is active to examine the relationship between seasonality of arthropod abundance and food preference.

D. Understanding the Digestion and Diet in the Guenons

I suggest it would be worthwhile to consider research that examines the relationship between guenon's diets and their morphological adaptation at the species level. An examination of digestive retention time, gut microbes in particular of cellulose-digesting microbes, enamel structure of the molar teeth, and the masticatory apparatus could help us understand the reasons for some of the differences that occur in the ability to digest leaves among guenons.

E. Hope for the Future

As a prerequisite for many of the future research topics I have suggested above, we need to find *C. mona* groups somewhere in West Africa that can be readily habituated. Finding tame guenon groups that can be habituated in West and Central African forests is extremely difficult in light of the fact that many primate populations are hunted and some are becoming locally extinct (e.g., C. *diana*, *C. erythrotis*, *C. solatus*) (Butynski, 2002; McGraw, 2005). Still, we should not hesitate to study guenons living in hunted forests, because the presence of researchers can dramatically decrease the rate of hunting. Over the course of a few years, guenons would become a little tamer, if not habituated, providing for better observation (as seen in this study). It is my hope that this document stimulates further studies on and interest in the mona species group and other *Cercopithecus* spp. yet to be studied. I still hope that somewhere in West Africa, a small patch of forest may still contain some guenons that are readily observable, quietly waiting for the arrival of researchers like us.

APPENDIX A. CONSERVATION OF THE LAMA FOREST

I. History of Deforestation

In 1946, when the Lama Forest was classified as a "*forêt classée*" (i.e., forest reserve) by a government decree, the entire area was estimated to contain 16,250 ha of natural forest. Although the protection of the Lama Forest is written into law, enforcement of the law has not been effective. Many forms of disturbance (e.g., clear-cutting, shifting-cultivation of maize, selective tree-cutting, natural and artificial fire) have affected almost all, if not all, parts of the Lama Forest. According to an analysis of aerial photography of the forest taken in 1957, there were 10,787 ha (64.6%) dense forest, 3,936 ha (23.5%) disturbed forest, 1,457 ha (8.7%) farm bush, and 570 ha (3.4%) plantation (Marsch, 1976). An extensive forest survey conducted twenty years later shows a drastic reduction in the size of the forest; dense forest was reduced to 6,696 ha, disturbed forest was reduced to 1,017 ha, and farm bush increased to 1,873 ha (total 9,586 ha)(Marsch, 1976). In the meantime, the area of tree plantations (mostly of teak) increased to about 7,000 ha. More than 3,500 ha of the dense forest were destroyed in 18 years. A study undertaken in 1984 estimated that the natural forest was reduced even further, to 3,784 ha. The rate of forest destruction was about 435 ha per year between 1976 and 1984. Another estimate made in 1987 indicated that the entire natural forest was reduced to 2,500 ha. Extensive exploitation by humans continued. In 1988, the forestry police force that was established by the *Direction des Eaux, Fôrets, et Chasse* in conjunction with *Office National du Bois* (ONAB) relocated the local inhabitants outside the forest. At the same time, 4,777 ha of *Noyau Central*, which consists of 1,900 ha forest, 2,585 ha farm bush, and 292 ha plantation, was set aside in the center of the Lama

Forest as a protected area. The future of the Lama flora and fauna, however, is still threatened by continuous occurrences of illegal activities such as poaching, trapping, tree and liana cutting (for honey collection, charcoal making, and construction purposes), and fire setting. When this study began, none of the remaining area appeared to be pristine (Marsch, 1976; Baglo and Guedegbe, 1995; Kassa, 2001). Table A.1 summarizes the historical development of deforestation and degradation of the Lama Forest.

II. Illegal Activities in Recent Years

Between April 1996 and June 1997, I heard 53 gunshots in the *Noyau Central* (Fig. A.1). Gunshots were mostly heard in early morning (63%) and in the evening (35.3%). Only one gunshot was heard in late afternoon. The peak of gunshots heard occurred in July (22.5%) in the first study year and May (20%) in the second study year. These months appear to correspond with the seasons of maize scarcity for the villagers. Maize, which is planted March–May, will not be ready for harvest until August or September. Cassava is available between September and February and groundnuts (i.e., peanuts) become ready for harvest in October, but the staple food of the Holi people is maize. For this reason, it appears that the frequency of hunting is highest during the season of food scarcity for humans, during the rainiest months of the year.

According to Kassa (2001), ONAB apprehended 63 offenders between 1993 and 2000. Among the 63 arrests made, 53 cases were due to hunting, six cases were due to tree cutting, three cases were due to liana gathering, and one case was due to illegal fishing. Kassa’s (2001) data show that 11 and 8 hunters were apprehended in 1994 and 1995, respectively. Between 1996 and 1998, only 1–2 hunters per year were

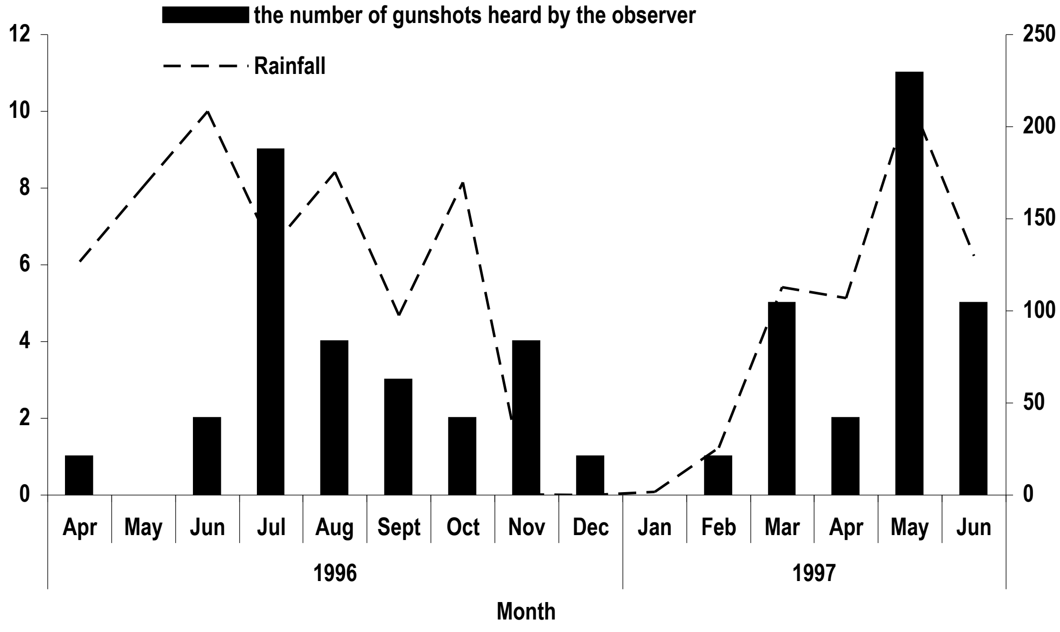
Table A.1 The historical loss of forested areas in the Lama Forest

Only about 10 % of the original size of the forest remains in the Lama Forest.

Year	A	OF	YF	FB	Plantation	B	C	D	Total
1946	16250	16250	(Data are not available)						16250
1957	14723	10787	3936	1457	570	1527	139	9.4%	16750*
1975	7703	6686	1017	1873	7000	7020	390	43.2%	16576**
1984	3784	3784		8883		3919	435	24.1%	16586**
1988	1900	1900		2585	12101	1884	471	12.8%	16586

A = Size of Forest (ha)
B = Size of Lossed Forest
C = Rate of Deforestation per year
D = % loss of original forest
* An increase is due to an inclusion of neighboring forests.
** It is not clear why the total area is changed from the previous year.

Fig. A.1 The number of gunshots heard in Apr. 96–Jun. 97



* No data were collected in May 1996

apprehended. In 1999 and 2000, however, 13 and 15 hunters were apprehended, respectively. His data also show that there was a dramatic decrease in the number of game animals confiscated between 1996 and 1998 and a dramatic increase between 1999 and 2000. It is likely that my presence as a researcher in the forest acted as a deterrence against hunting, since more hunters entered the forest before this research began and after the termination of this research. Six hunters interviewed by Kassa (2001) all preferred to hunt antelopes and red river-hogs to other smaller games, because of their higher prices. The wholesale price of an antelope is 12,000–14,000 CFA (500 CFA = $1), and a pig can bring 20,000 CFA. Hunters, however, frequently end up killing monkeys, which sell for 1,000 CFA per head, or duikers, which sell for 3,000 CFA per head. Hunters usually enter into the forest after sunset. During the day, they set steel traps. In June 2001 alone, ONAB found eight steel traps. Monkeys and young antelopes are usually eaten by hunters and their families themselves, but other larger game is sold in nearby markets (Kassa, 2001). All arrested hunters are inhabitants of nearby villages. Of the 63 arrested, 30% came from Agadjaligbo village, the closest village to the Lama Forest.

During my study, although there were eight ONAB patrol guards in the forest during my study, they were not very effective in eradicating hunting. One of the reasons for the inefficacy is that they are equipped only with a machete, flashlight, and a pair of rain boots. How could unarmed guards effectively capture armed hunters? Another reason is that they are not in the forest when the hunters are in the forest. The guards commute on their bicycles from the nearby villages that are 10–16 km away from the Lama Forest and start patrolling at 08:00 GMT. They go home promptly at 18:00 GMT. At night, only two guards are on duty. Only occasionally do all of them stay until 21:00

GMT, but hunters seem to know the guards' schedule. The guards are not in the forest during early morning hours and at dusk when most mammalian diurnal species actively feed. Monkeys are more easily located by hunters when they are most active. Furthermore, the primary goal of the guards' service to the ONAB is not to capture hunters. The guards patrol to apprehend thieves and fire setters. The ONAB is mostly concerned about the protection of the teak plantation from theft and fire. The protection of the fauna appears to be secondary. I was told by a high-ranking ONAB official that if I was concerned about the protection of the monkeys, I must personally pay for night guards.

The ONAB allows the locals to hunt monkeys and other animals that come to raid cash and food crops such as the maize and bananas, but the bush pigs that come out of the forest to drink water (without raiding crops) during the long dry seasons when standing water in the forest becomes scarce also become targets of bushmeat hunting.

The rare red-bellied monkey is harassed by the local people when the monkeys appear at forest edges near the maize farms. Although there is no direct evidence that *C. erythrogaster* raids the crops, the *C. erythrogaster* population at Lama is too small to pose a threat to the crops. *Cercopithecus aethiops* seems to be mostly responsible for crop raiding, but this issue needs to be studied and confirmed. The problem is that farmers indiscriminately suspect and harass all diurnal primates.

Cercopithecus mona is still common in the Lama Forest, other small forest reserves, riparian forests, and woodland in Bénin, but in Cameroon, Nigeria, and Ghana, *C. mona* populations have been locally reduced or eliminated due to hunting (Glenn and Bensen, unpubl. data cited in Glenn *et al.*, 2002; J. Mason pers. comm. in Glenn *et al.*, unpublished a). For example, Chapman *et al*. (2004) conducted a survey at four areas in the southeastern part of Gashaka Gumti N.P. in Nigeria and found that at three out of five sites where *C. mona* was found in 1970s, *C. mona* was not found in 2002. Ukizintambara and Thebaud (2002) have examined the intrinsic causes of vulnerability to extinction in *Cercopithecus* monkeys and found that guenons that occur in West African countries, Sierra Leone, Ghana, Guinea, Angola, Benin, Nigeria, and Democratic Republic of Congo (DRC) are particularly threatened. They recommended that strong conservation measures must be installed to protect *C. erythrogaster*, *C. diana*, *C. petaurista*, *C. campbelli, and C. mona* in West Africa. *Cercopithecus mona* and *C. campbelli* have been traditionally rated as having low vulnerability to extinction by the IUCN Red List (Baillie *et al.,* 2004). It is thus possible that even species that are at low risk of extinction are also rapidly decreasing their numbers in the face of a lack of their habitat protection and enforcement of hunting bans.

There were other signs of disturbance. On three occasions (January 18, 1996, January 3, 1997, February 15, 1997), I found felled large *Dialium guineense* trees (≥ 20 cm DBH). All of them were felled for honey collection. On March 18, 1996, I also found two cut *Landolphia* liana (> 20 cm DBH). These lianas were probably cut for charcoal making.

In addition to the above local level problems, there were larger problems: corruptions by officials involved in many forestry projects. According to Siebert and Elwert (2002), the GTZ financed Teak plantation project in Bohicon closed in 2000 after many incidents of project design failures, management problems, and corruption of ONAB officials, local staff, and German staff. This was a great setback for the Lama

Forest, since GTZ has been financing the entire forestry and projects to ONAB since 1970s.

III. Future of the Lama Forest

Despite the closure of the Bohicon sawmill, between 1998 and 2003 the IUCN has funded some coordinated biodiversity research projects between Swiss scientists (University of Basel) and the faculty and graduate students in the Biology Dept. of the *Université Nationale du Bénin* in Bénin that included the Lama Forest. It would be valuable to continue developing coordinated programs in cooperation with faculty and graduate students in the Biology Dept. of the *Université Nationale du Bénin* in Abomey-Calavi, researchers from *International Institute of Tropical Agriculture* (IITA), governmental ministries and agencies (Ministry of Environment, ONAB, etc.), and international conservation organizations to train and educate Bénin field biologists. Close cooperation between biologists based in habitat countries with local counterparts has proven successful in some forests such as the Kibale Forest in Uganda (Struhsaker, 1997), Taï Forest in Côte d'Ivoire (until a military coup broke out in 1999), and Tiwai Island, Sierra Leone (until civil war broke out in 1991).

One of the management directions that could be taken in the Lama Forest is the establishment of a protected area for ecotourism. Development of ecotourism should be encouraged. The Lama Forest has considerable potential to attract tourists. It is easily accessible by vehicles on a well-maintained paved road from major cities such as Cotonou, Parakou, and Porto Novo, and would be a nice stopover site for tourists interested in observing forest fauna. A national park could employ former hunters in

Koto and Massi villages, where the Holis now live, as protection staff members. Former hunters are often knowledgeable about where animals and small bush paths can be found and how poachers use the forest. The villagers could also be employed as visitors' guides for the park. If hunting can be eliminated or at least diminished, Lama Forest fauna would gradually lose their fear of humans. Such trust is important for ecotourism to succeed, since only when the animals feel secure in the presence of humans will their skittish behavior diminish and viewing of the animals would become possible. If run without diversion of conservation funds to corrupt officials or staff members, the cost of running a national park can be kept as low as \$ 50–200/km^2 per year (Struhsaker, 2001).

Bénin offers many tourist attractions. Many tourists from abroad visit the Pendjari National Park and "W" Niger National Park, located in the far north of Bénin to safari savanna animals (e.g., lions, elephants, roan antelopes, topis) (Poché, 1974; Alpers *et al.*, 2004). The roan antelope (*Hippotragus equinus*) is a threatened species (IUCN, 1996). On the way to these parks is Abomey, 35 km north of Lama. The Abomey Museum (*Musée Abomey*), located in the old Royal Palace in Abomey that displays cultural artifacts from the former Dahomey Kingdom is an excellent museum for learning the history of the country. Not far from Cotonou is Ouidah, which once served as a slave port, is known as the center of the Voodoo religion. A museum in Ouidah, established in the former Portuguese fort, exhibits various cultural items related to slave trade that show links with Brazil and the Caribbean. Also near Cotonou is Ganvié, a fishing village built on stilts in a lagoon.

Although there were some political upheavals in the 2001 presidential election, in contrast to neighboring countries in West Africa, there have been few disruptions or violence in Bénin in the last five years. In recent years, Bénin has been relatively more politically stable than neighboring countries. The last National Assembly elections that took place in March 2003 were largely free and fair and the citizens have been enjoying peace. Such a political background is extremely important in securing a safe environment for conservation programs to succeed within habitat countries (Oates, 1999; Dudley *et al.*, 2001).

Funds should also be raised for the development of an educational program that teaches the importance of the forest fauna and flora to the forest ecosystem to all levels of students (from primary to college). It is extremely important to educate the local people that the benefits of protecting the forest and its biodiversity far outweigh the costs in lost opportunities to hunt, cultivate, or gather. Disseminating current information regarding the risk of disease transmission from bushmeat to the local people is also an important aspect of salvaging both biodiversity and humanity.

Concurrent to installing a conservation program, further research on primates, other fauna, and flora should be encouraged. Although this research focused on *C. mona*, studies on the more secretive *C. erythrogaster*, *P. verus*, *C. aethiops* and the nocturnal prosimians should also be conducted. Although the habituation of *C. mona* was not successful during this study, it became apparent by the conclusion of this study that the longer I stayed in the forest, the longer the average contact duration with groups became. Habituation of the primates may also become possible once a long-term conservation project is installed. The presence of researchers in the forest often effectively discourages many, if not all, hunters and trespassers from entering into the forest (Oates, 1999).

APPENDIX B. THE DAHOMEY GAP

The Dahomey Gap[*] is the area along the Guinea Coast, which interrupts the continuous belt of closed tropical rain forest along the West African coast (Booth, 1955, 1958a, b; Robbins, 1978; White, 1983; Oates, 1988a). It is an area of low rainfall with pronounced dry seasons (Sayer *et al.*, 1992). The term “Gap” gives a false impression of the vegetation of this area as if it is entirely dominated by the savanna. In fact, the climate and the phytogeography of this region are more complex than the term implies (White, 1981; Jenik, 1994; Juhe-Beaulaton, 1995). White’s (1983) vegetation map of Africa shows that eastern Ghana, Togo, and Bénin contain at least four different vegetation types, however, the majority of the area is a mixture of semi-deciduous forest and grassland. Jenik (1994), who examined the vegetation of the coastal Gulf of Guinea in the 1960’s, concluded that southern Bénin was able to support semi-deciduous closed-canopy forests and the western limit of the Lower Guinea Forest Region is about the middle of the coastal Bénin and the eastern limit of the Upper Guinea Forest Region is the Accra Plains.

According to some authors’ (Aubréville, 1949; Booth, 1954; Moreau, 1969) descriptions of the Dahomey Gap’s boundaries, the Lama Forest would be defined as dominated by savanna. In contrast, according to Dekeyser (1955), Ern (1988), and Jenik’s (1994) descriptions and White’s (1983) vegetation map, the Lama Forest appears to be included in the Lower Guinea Forest Region. Keay (1959) categorized much of the Bénin vegetation as a “forest-savanna mosaic.” He wrote (1959: 7), “If the fires are

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[*] It is also known as Dahomey Interval (White, 2001), Togo Gap (Heyward and Oguntoyinbo, 1987), Gap of Bénin (Polanyi, 1966), “*le savane du Bénin*” (Gayibor, 1986), or “*la coupure du Dahomey*” (Maley, 1996).

excluded for several years this kind of savanna may be invaded by moist-forest species. In much of the country mapped as forest-savanna mosaic the climate is not more arid than parts of the moist forest regions, and it is generally agreed that the savanna in the mosaic has been derived by degradation from moist forest."

The coastal western Gulf of Guinea is an area of low rainfall (700–1,200 mm per year), but it is more variable along the coast than the interior. Along the coast, the lowest rainfall (700– 900 mm) is found between Accra (Ghana) and Lomé (Togo). Cotonou (Bénin) receives more rain (about 1,300 mm) than Lomé. At 40–240 km inland, the rainfall is uniform (about 1,100 mm) between Dimbokro (Ghana) and Bohicon (southern Bénin) (near the Lama Forest)(Heyward and Oguntoyinbo, 1987).

At least three interacting factors produce low rainfall in this region. The first factor is the friction between predominantly southwesterly wind and easterly wind. The convergence and uplift of humid air that occurs between the southwesterly wind and easterly jet is weakened due to the parallel alignment of the coast and the southwesterly air, leaving much reduced rain between Lomé in Togo and Takoradi in Ghana. The second factor is the coastal upwelling of cold water between July and October, which reduces the tendency for uplift and rain. Another factor is the location of the ITCZ (Inter-Tropical Convergence Zone), a narrow zone of discontinuity between a dry air mass to the north and a tropical humid air mass to the south. In January, when moist air is beginning to find its way to the west and east, the ITCZ is found near the Guinea coast around coastal Togo, bringing the dry air mass to this area (Heyward and Oguntoyinbo, 1987; Jenik, 1994). Lower rainfall may also have been reinforced due to a drastic reduction of the original forest cover which took place in the recent past in this region particular and in West Africa as a whole (Heyward and Oguntoyinbo, 1987; Jenik, 1994). The precipitation along the coast of Gulf of Guinea illustrates that at least the eastern half of southern Bénin would be climatically able to support semi-deciduous forest, but the current vegetation and biogeographic reality is different from what one might expect from examining the climate alone in this region. Jenik (1994) illustrated the complex interactions among various terrestrial, atmospheric, and oceanographic factors for the savannization of the Dahomey Gap and its influence on the fauna and flora (Figure B).

Most authors who have examined the distribution of primates (Booth 1955, 1958b; Oates 1988a), other mammals (Booth 1955, 1958a), and tree frogs (Shiøtz, 1967) in West Africa concluded that the Dahomey Gap acted as a faunal barrier at some time in the past and still does so at present day. These authors, however, differ in their opinions in regard to the significance of the barrier. Authors who have investigated the distribution of plants (Leonard, 1965; Brenan, 1978; White, 1983), birds (Moreau, 1966; Diamond and Hamilton, 1980; Crowe and Crowe, 1982), insects (Carcasson, 1964), and other vertebrates (Grubb, 1978), however, have concluded that the Dahomey Gap had a minor influence in the past (Maley, 1996, 2001). It appears that the distribution of large mammals such as primates that require a continuous belt of forest or gallery forest for long-distance dispersal and are most susceptible to human modification of the habitats has been particularly influenced by the spread of the derived savanna in the Dahomey Gap.

Although there are differences in scientific opinions on the importance of the Dahomey Gap as a distributional barrier, most authors agree that the oscillations of Quaternary climatic cycles have had a profound influence on the vegetation of the region

(Lézine and Vergnau-Grazzini, 1993; Elenga *et al.*, 2000). Deep lake core pollen data or nitrogen data from the marine deposits are available from several sites in West Africa, but direct evidence from Togo and Bénin is rare. Reconstructed vegetation prehistory using deep core palynological and marine sediments from more humid areas of West Africa (Cameroon, Nigeria, Ghana, Côte d'Ivoire) indicate that 28,000–20,000 B.P was a warm period, which sustained extensive humid forest in throughout West Africa. During the last major global and regional cold period between 20,000 B.P. and 10,000 B.P., much of the forest was replaced by the savanna. Between 9,500 B.P. and 2,800 B.P., forest was most dominant. Between 2,800 B.P. and 2,000 B.P., forest retreat and savanna expansion continued. After 2,000 B.P., however, forest expansion again occurred in this region (Maley, 1991, 1999, 2001; Dupont *et al.*, 2000; Elenga *et al.*, 2000; White, 2001).

A recent analysis of the fossil pollen obtained from Lac Selé (7°I'N, 2°26'E) in southern Bénin indicates that the Dahomey Gap was closed during the mid-Holocene (about 6,000 B.P.). It shows that pollen of *Celtis* and Sapotaceae trees were abundant in southern Bénin until 4,000 B.P, indicating that semi-evergreen forest existed in this region (Saltzman and Hoelzmann, 2005). After the period of Dahomey Gap closure, around 3,800–3,600 yrs B.P. dry conditions ensued, resulting in the reduction of the forests. This conclusion is roughly in agreement with Maley's (1991) conclusion that the Dahomey Gap existed around 3,800–3,700 yrs. B.P. Wetter climatic conditions were again recorded after 3,000 B.P. with an expansion of the pollen of *E. guineensis* at about the same time, renewing the spread of semi-evergreen forest.

In the past, there were many larger forested areas in Bénin, especially in the south, which now supports about 63% of the total Bénin population of about 5.6 million

(Baglo and Guedegbe, 1995). The fact that much of the southern Bénin currently is covered with “derived savanna,” lacking large forested areas except a few forests such as the Lama Forest is the ecological reality, but a belt of semi-deciduous forests continuous with the lower Guinea Forest region in Nigeria once existed. Authors, however, disagree when deforestation started: only in the last century or much earlier (Gayibor, 1986; Blanc-Pamard and Peltre, 1987; Martin, 1987; Ern, 1988; Sayer *et al.*, 1992; Jenik, 1994; Fairhead and Leach, 1998). Aubréville (1949) thought that the Dahomey Gap is a recent phenomenon. He (1949: 204) wrote, “*La forêt nigérienne est séparée de la précédente par une large clairière de savanes boisées, de palmeraies d’*Elaeis guineensi*s et de brousses secondaires, qui commence immédiatement à l’Est du Cap des Trois Pointes en Gold Coast, et se termine vers la frontière de Dahomey et de la Nigeria. Cette disolution de continuité est relativement récente*. [i.e., The Nigerian forest is separated from the above-mentioned forest (in Côte d’Ivoire) by a largely cleared tree savanna, palm trees, and secondary forest, which immediately begins east of Cape of Three Points in Gold Coast and ends at the border of Dahomey and Nigeria. This interruption of continuity occurred quite recently.]” The modification of the forests in southern Bénin may have started long before the arrival of Europeans at the slave-coast.

The rapid and significant increase of the pollen of *E. guineensis* about 2,800 B.P. in a deep core taken from the Niger Delta suggested that a farming technique involving deliberate clearing of forests led to the spread of the oil palm there (Sowunmi, 1981, 1985). The evidence of human use of the oil palm dates back to 3,000 B.P. in Cameroon, Gabon, and Congo (Maley, 1999). The evidence of human modification of forests in Africa dates back to 2,400–900 B.P. in Ndoki Forest in Congo (Fay, 1997 cited in White, 2001). Expansion of agriculture is related to technological change that took place in Africa. The first evidence of unequivocal food crop cultivation in West Africa comes from southern Cameroon where bananas and other plant taxa found in unearthed pit fills were dated to about 2,400 B.P. (Mbida, 2000). The earliest record of metallurgy in Africa is available from Nubia in 6,000 B.P. Elsewhere in West Africa, the first evidence of metallurgy is iron smelting in Nigeria and Niger from 2,500 - 3,000 B.P. (Childs and Killick, 1993). These dates are close to the beginning of agriculture in Africa. It is unfortunate that few excavations have been conducted in Bénin, which could potentially provide valuable data on the beginning of metallurgy, agriculture, and human modification of the forest in this country (Davies, 1968; Harlan, 1971; McIntosh and McIntosh, 1983; Childs and Killick, 1993; Kelly, 2001). Nevertheless, at least a rudimentary form of slash-and-burn agriculture was perhaps taking place by this time in southern Bénin, since there is evidence that there was an expansion of the oil palm pollen around 2,800 B.P in both Central and West Africa. Expansion of agricultural lands may have contributed to the savanization in this region as early as these dates.

Accelerated rates of deforestation probably occurred in the early 17th century when powerful kingdoms of Allada and Hueda and subsequently Dahomey flourished and human populations dramatically increased in Bénin (Aubréville, 1937; Law, 1991). The only reason that the Lama Forest was saved from a complete destruction during the last many centuries may have been due to the swampy nature of the area (Law, 1991).

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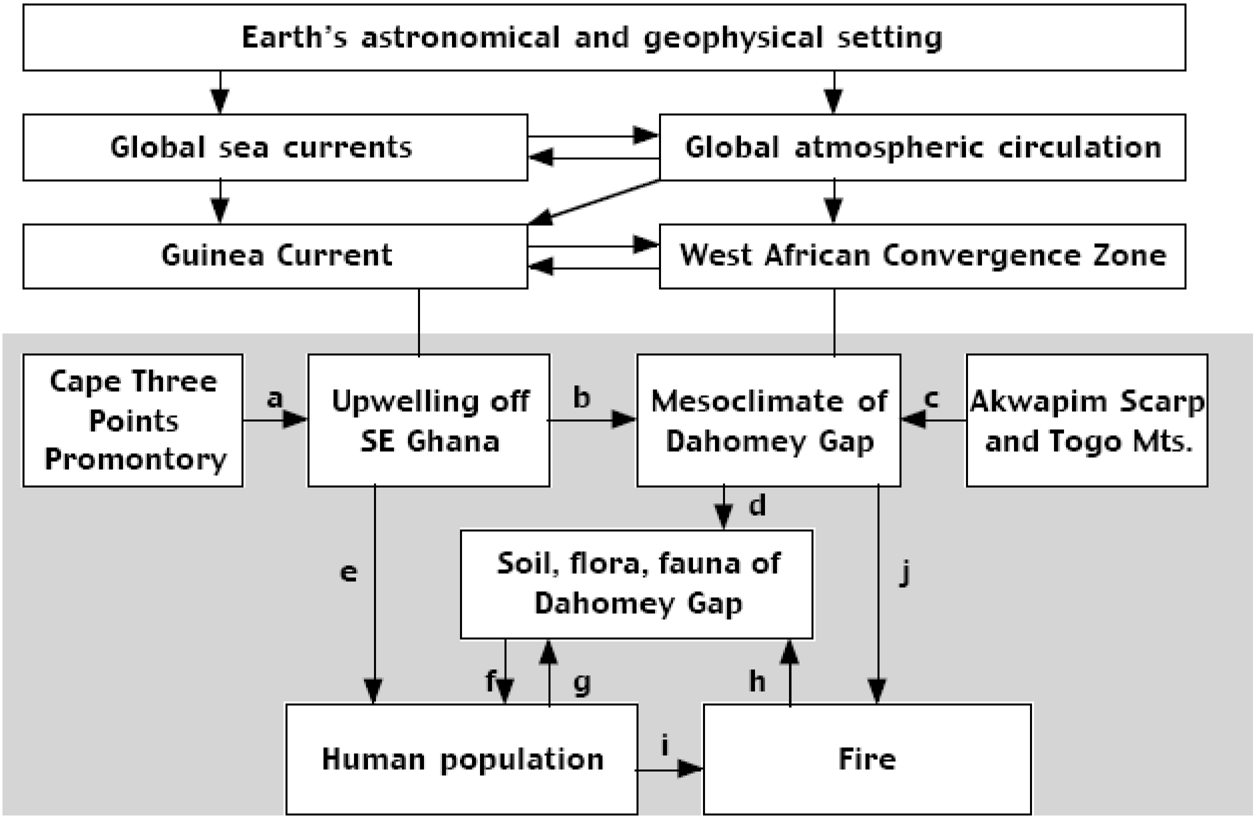


Fig. B. Compartment model of the cause-and-effect system leading to the existence of the Dahomey Gap. Dominant factors at the regional scale (shaded area): **a**. mechanically induced sea eddies; **b**. cool air entering the warm coastland and losing precipitation power; **c**. channeling of the daily sea breeze by scarps and hills; **d**. impact of moisture and temperature, **e**. abundance of fish offshore and prodigious fish harvest; **f**. fertile and healthy environment for crops, livestock and humans; **g**. cultivation of soil and introduction of crops; **h**. disturbance of ecosystems by fire; **i**. intentionally lit fires; **j**. enhancing effect of two dry seasons and onshore sea breeze. Redrawn from Jenik (1994) with the permission of the author.

APPENDIX C. List of Lama Forest vascular plants

1

Family*	Scientific Name	Local Name	Abbrev.	Growth Form
		Monocot		
Arecaceae	*Elaeis guineensis*		ELGU	palm
		Dicot		
Anacardiaceae	*Lannea nigritana*	Arekan	LANI	tree
	Sorindeia werneckeii	Babaokun	SOWE	shrub
	Spondias mombin	Ekan	SPMO	tree
Annonaceae	*Artabothrys velutinus*	Okouigbo	ARVE	shrub
	Dennettia tripetala	Eweigbo	DETR	climber
Apocynaceae	*Carissa edulis*	Agobai	CAED	shrub
	Holarrhena floribunda	Irè	HOFL	tree
	Landolphia spp.	Assan-Igbo-dudu	LASP	liana
	Rauvolfia vomitoria		RAVO	shrub
	Saba senegalensis	Assan-Igbo-Koupa	SASE	liana
Araceae	*Culcasia saxatilis*	Iman	CUSA	herb
Asclepiadaceae	*Parquetina nigrescens*	Orobi-Ogbon	PANI	climber
Asteraceae	*Vernonia colorata*	Anokoro	VECO	shrub
	Chromolaena odorana		CHOD	herb
Bignoniaceae	*Nenbauldia laevis*	Iye	NELA	tree
	Spathodea campanulata	Oshiri	SPCA	tree
Bombacaceae	*Ceiba pentandra*	Angou	CEPE	tree
Cappariaceae	*Capparis thonningii*	Achoumchoun (Ojouagouton)	CATH	climber
Combretaceae	*Anogeissus leiocarpus*	Ayin	ANLE	tree
	Combretum hispidum	Ogan	COHI	climber
	Combretum paniculatum	Ogan	CPPA	climber
	Combretum obarense		COOB	climber
	Terminalia glaucescens		TEGL	tree
Conaraceae	*Agelaea obliqua*	Abpavadja doudou	AGOB	climber
Cucurbitaceae	*Pararistolochia triactina*	Iton-Ogbin	PATR	climber
Dioscoreaceae	*Dioscorea cayennensis*	Oho	DICA	climber
Ebenaceae	*Diospyros mespiliformis*	Adou	DIME	tree
	Diospyros ferrea	Akolemadu	DIFE	shrub
	Diospyros monbutensis	Okocho	DIMO	tree
Euphorbiaceae	*Drypetes floribunda*	Tagbesso	DRFL	tree
	Mallotus oppositifolius	Eidja	MAOP	shrub
	Margaritaria discodeus	Awewe	MADI	shrub
	Bridelia ferruginea	Erra	BRFE	shrub
Flacourtiaceae	*Flacourtia flavescens*	Elegégé	FLFL	shrub
Hippocrateaceae	*Salacia lomensis*	Egba	SALO	liana
	Salacia standtii	N/A	SAST	climber
Icacinaceae	*Neostachyanthus occidenta*	Aromishai	NEOC	climber

* For family Leguminosae, subfamilies are listed

(cont'd) APPENDIX C. 2

Family*	Scientific Name	Local Name	Abbrev.	Growth Form
Leguminosae				
Caesalpinioideae	*Afzelia africana*	Akpa	AFAF	tree
	Cynometra megalophylla		CYME	tree
	Dialium guineense	Aïran	DIGU	tree
	Mezoneuron benthamianum	Ikakun	MEBE	liana
Mimosoideae	*Acacia caphra*	Eden	ACCA	tree
	Albizia ferruginea	Ayorè Ogo	ALFE	tree
	Albizia zygia	Ayorè	ALZY	tree
	Dalbergia afzeliana	Aragba	DAAF	liana
	Tetrapleura tetraptera	Oridan	TETE	tree
Papilionoideae	*Lonchocarpus cyanescens*		LOCY	tree
	Lonchocarpus periceus	Akpó	LOPE	tree
	Lonchocarpus sericeus	Akpó	LOSE	tree
Loganiaceae	*Anthocleista djalonesis*	Okpo	ANDJ	tree
	Strychnos africanus	Gbelé	STAF	liana
	Strychnos congolana		STCO	liana
	Strychnos nigritana	Comme Gbélé	STNI	liana
Malpighiaceae	*Flabellaria paniculata*	Iferin	FLPA	climber
Melastomataceae	*Spathandra dinklagei*	Eweikpa	SPDI	shrub
Menispermaceae	*Chasmanthera dependens*		CHDE	shrub
Moraceae	*Antiaris toxicaria*	Oro	ANTO	tree
	Ficus excelsa	Ikpin	FIEX	tree
	Ficus natalensis	Aba (type B)	FINA	epiphyte
	Ficus obovata	Aba (type XL)	FIOB	liana
	Ficus sagittifolia	ABA (type L)	FISA	liana
	Ficus sur	Okpoto	FISU	tree
	Ficus thonningii	Aba (Type A)	FITH	shrub
	Milicia excelsa	Iroko	MIEX	tree
Myrtaceae	*Psidium guinienses*	Yagarou	PSGU	tree
Ochnaceae	*Ochna kibbiensis*	comme Gbadu 1	OCKI	shrub
	Ochna membranacea	Gbadu	OCME	shrub
	Ouratea flara	comme Gbadu 2	OUFL	shrub
Passifloraceae	*Adenia lobata*	Elemin	ADLO	climber
Rhizophoraceae	*Cassipourea congoensis*	Issilo	CACO	tree
Rubiaceae	*Canthium multiflorum*		CAMU	shrub
	Canthium schimperianum	Ajajigbo?	CASC	climber
	Canthium spp.	Budjé	CASP	shrub
	Canthium vulgare	comme Elégégé	CAVU	shrub
	Cremaspora triflora	Ajajigbo	CRTR	shrub
	Morinda lucida	Howo-Igbo	MOLU	tree
	Mussaenda elegans	Kpochè	MUEL	shrub
	Nauclea latifolia	Agbossi	NALA	shrub
	Pouchetia africana	Oweida	POAF	shrub
	Psychotria calva	Okpaoro	PSCA	shrub
	Psychotria vogeliana	Ichiko	PSVO	shrub
	Rytigynia senegalensis	comme Elègègè	RYSE	shrub

* For family Leguminosae, subfamilies are listed

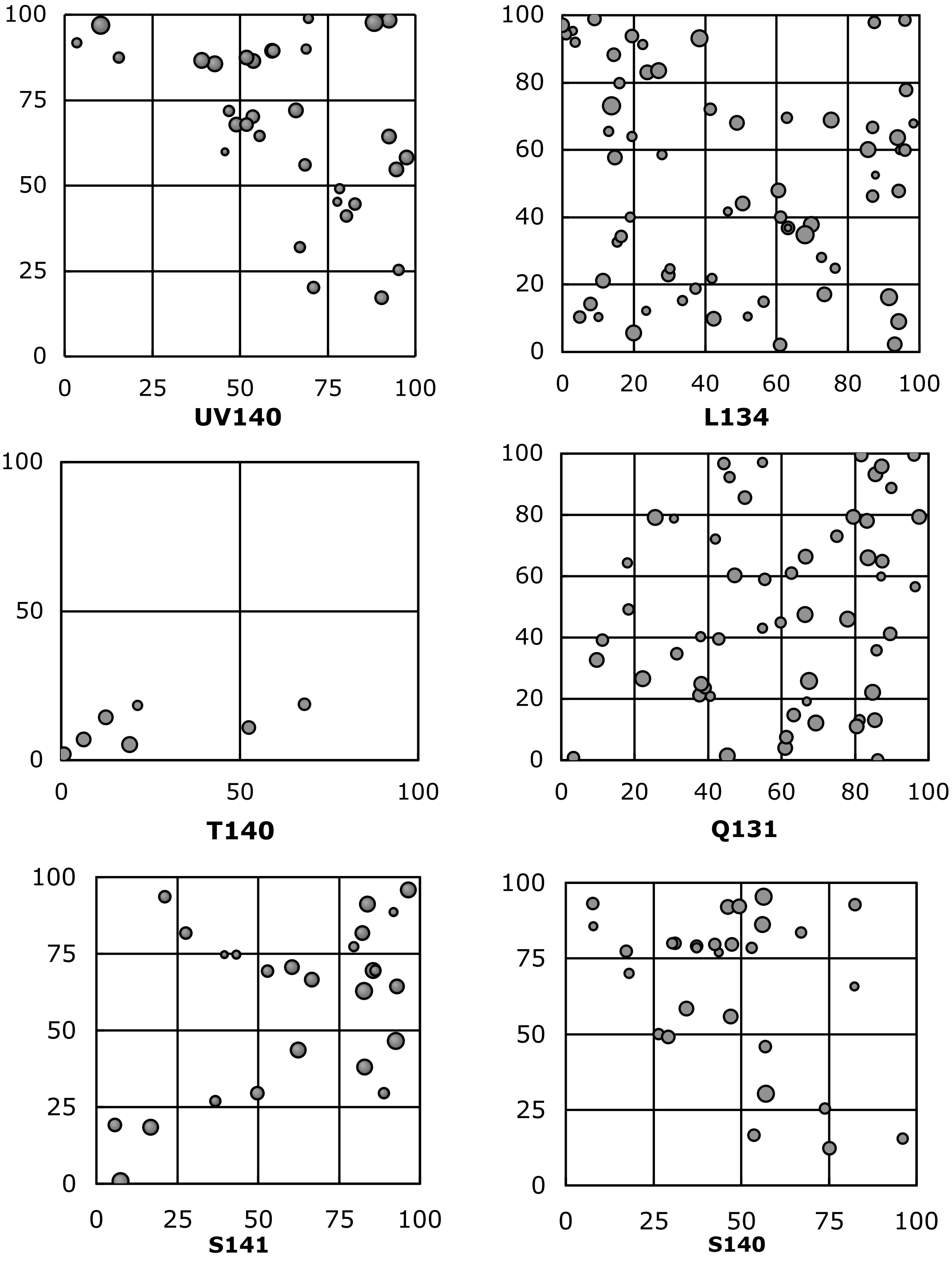
(cont'd) APPENDIX C. 3

Family*	Scientific Name	Local Name	Abbrev.	Growth Form
Rutaceae	*Clausena anisata*	Itoauko	CLAN	climber
	Zanthozylum xanthoxyoides	Itannan	ZAZA	tree
Sapindaceae	*Allophyllus africanus*	Idjeye	ALAF	shrub
	Blighia sapida	Ishi	BLSA	shrub
	Deinbollia pinnata	Kpecolo-Kpecolo	DEPI	shrub
	Gardenia triacantha	Awobalé	GATR	shrub
	Lecaniodiscus cupanioides	Ayikka	LECU	tree
	Pancovia bijuga	Eheï	PABI	shrub
	Paulinia pinnata	Owoiya	PAPI	climber
Sapotaceae	*Malcantha alnifolia*	Akkala	MAAL	tree
	Mimusopus andogensis	Ochedo	MIAN	tree
Sterculiaceae	*Sterculia tragacantha*	Oshunshun	STTR	tree
Tiliaceae	*Grewia carpinifolia*	Afoshé	GRCA	liana
	Grewia pubescens	Afé	GRPU	shrub
Ulmaceae	*Celtis brownii*	Amako	CEBR	tree
Vitaceae	*Cissus spp.*	Affala	CISP	climber

* For family Leguminosae, subfamilies are listed

APPENDIX D: TREE DISPERSION MAPS

Fig. D.1 Dispersion patterns of *Diospyros mespiliforme* trees in six quadrats (x = Distance from southwest corner of each quadrat, y = distance from south, Diameter of circles shows DBH). It is evident that dispersion pattern of this species is not the same in each quadrat. Some quadrats show areas that are completely void of any individuals of this species.



UV140 **L134**

T140 **Q131**

S141 **S140**

Fig. D.2 Dispersion patterns of *Drypetes floribunda* in six quadrats

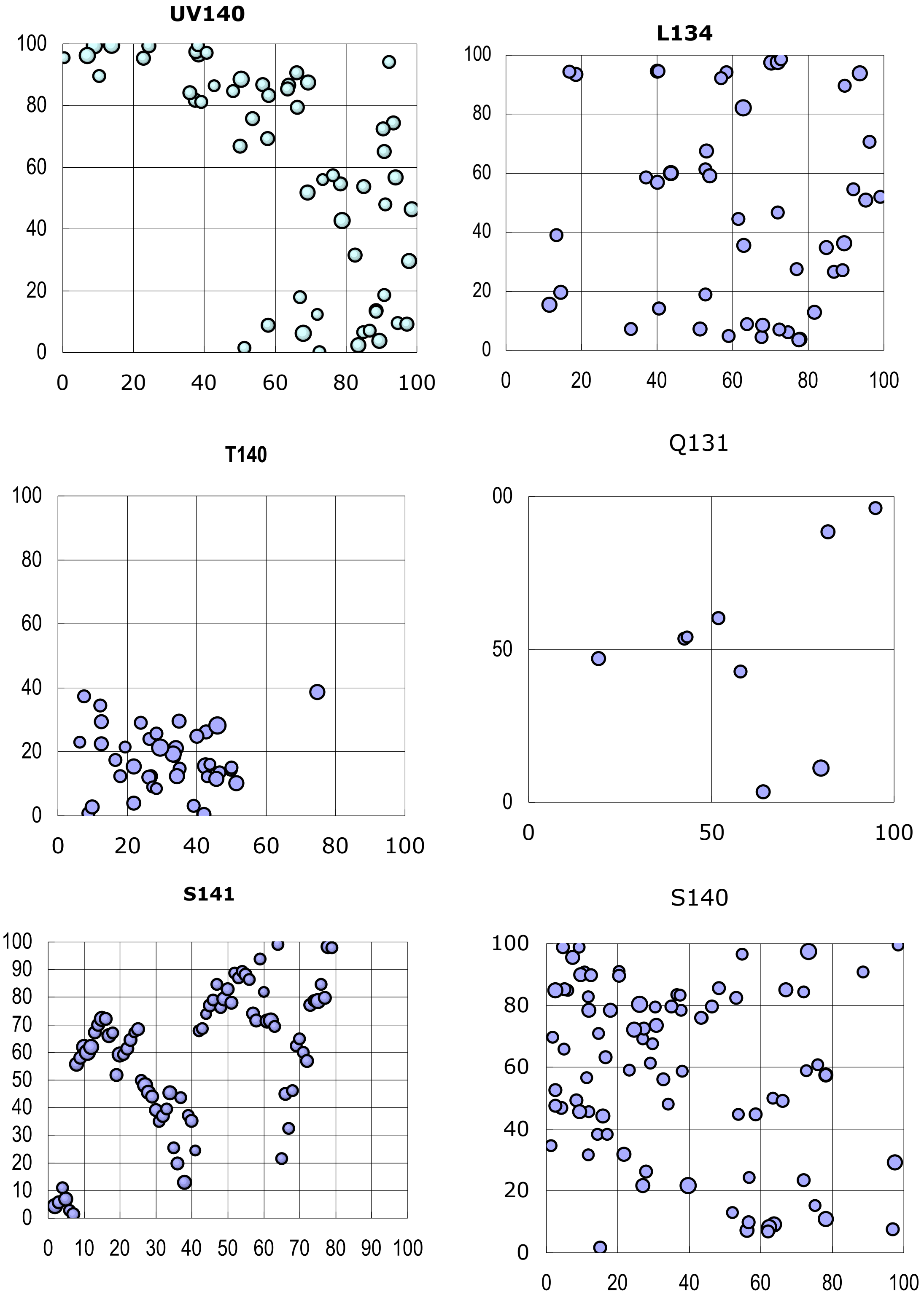


Fig. D.3 Dispersion patterns of *Celtis brownii* in six quadrats

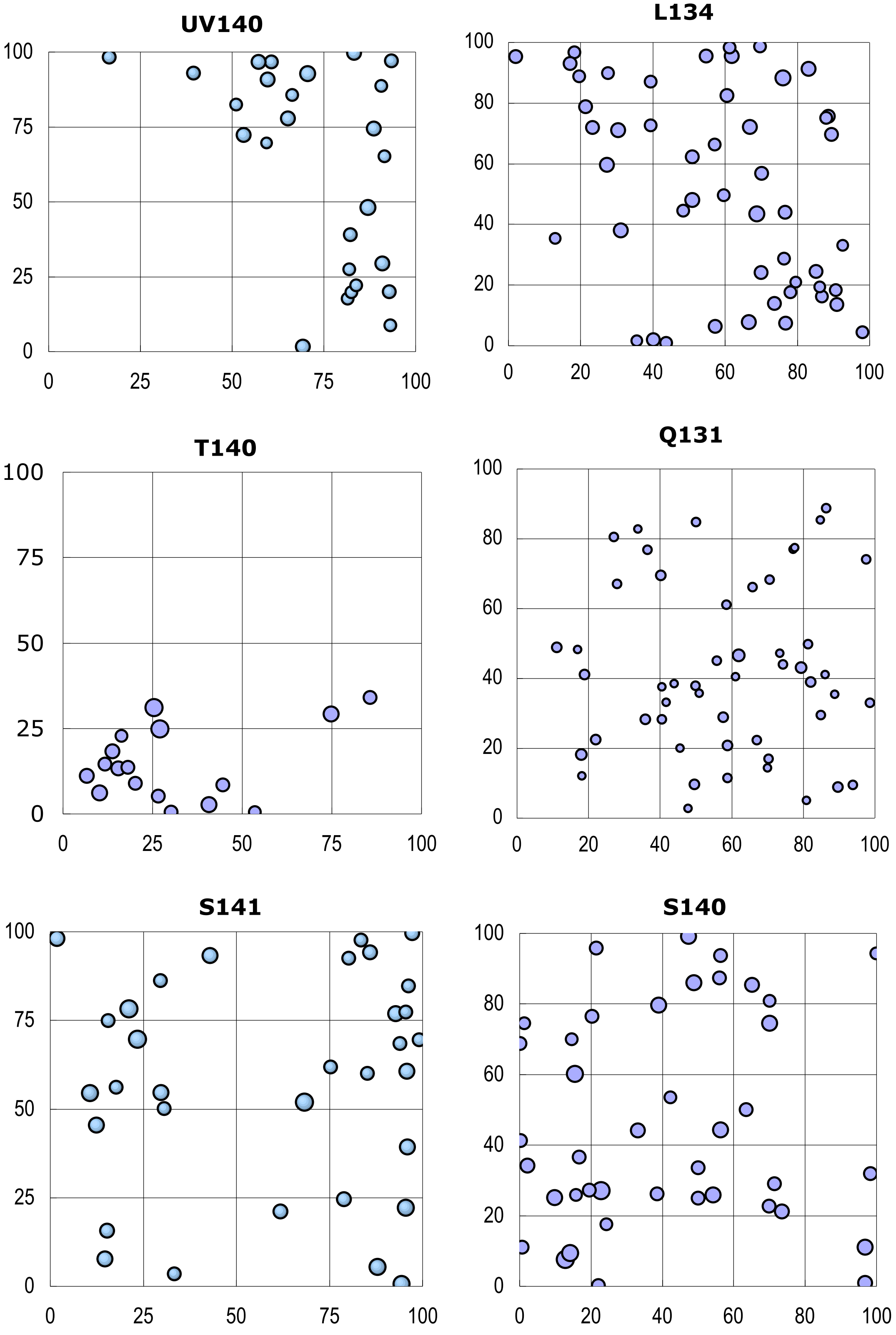


Fig. D.4 Dispersion patterns of *Dialium guineense* in six quadrats

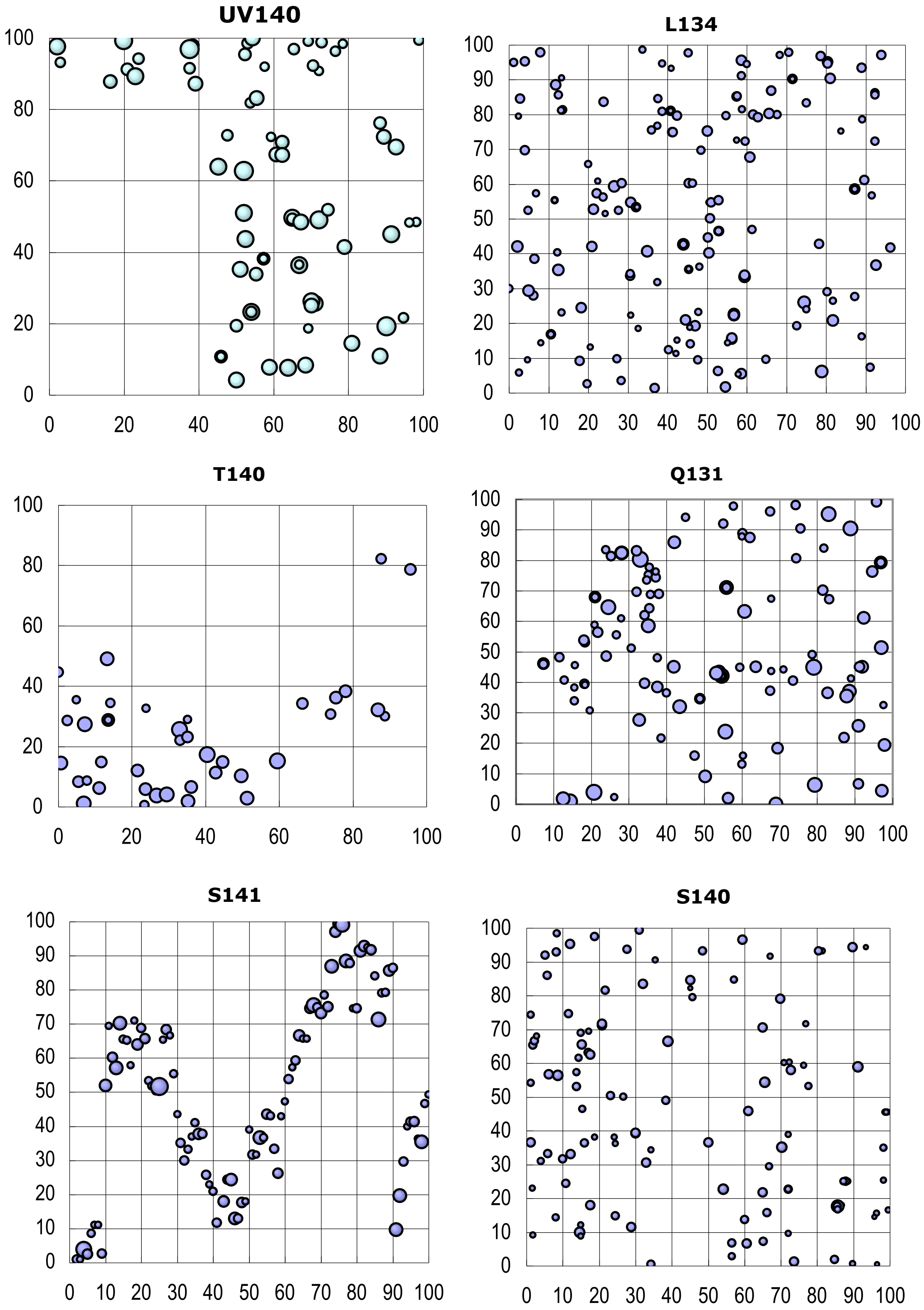
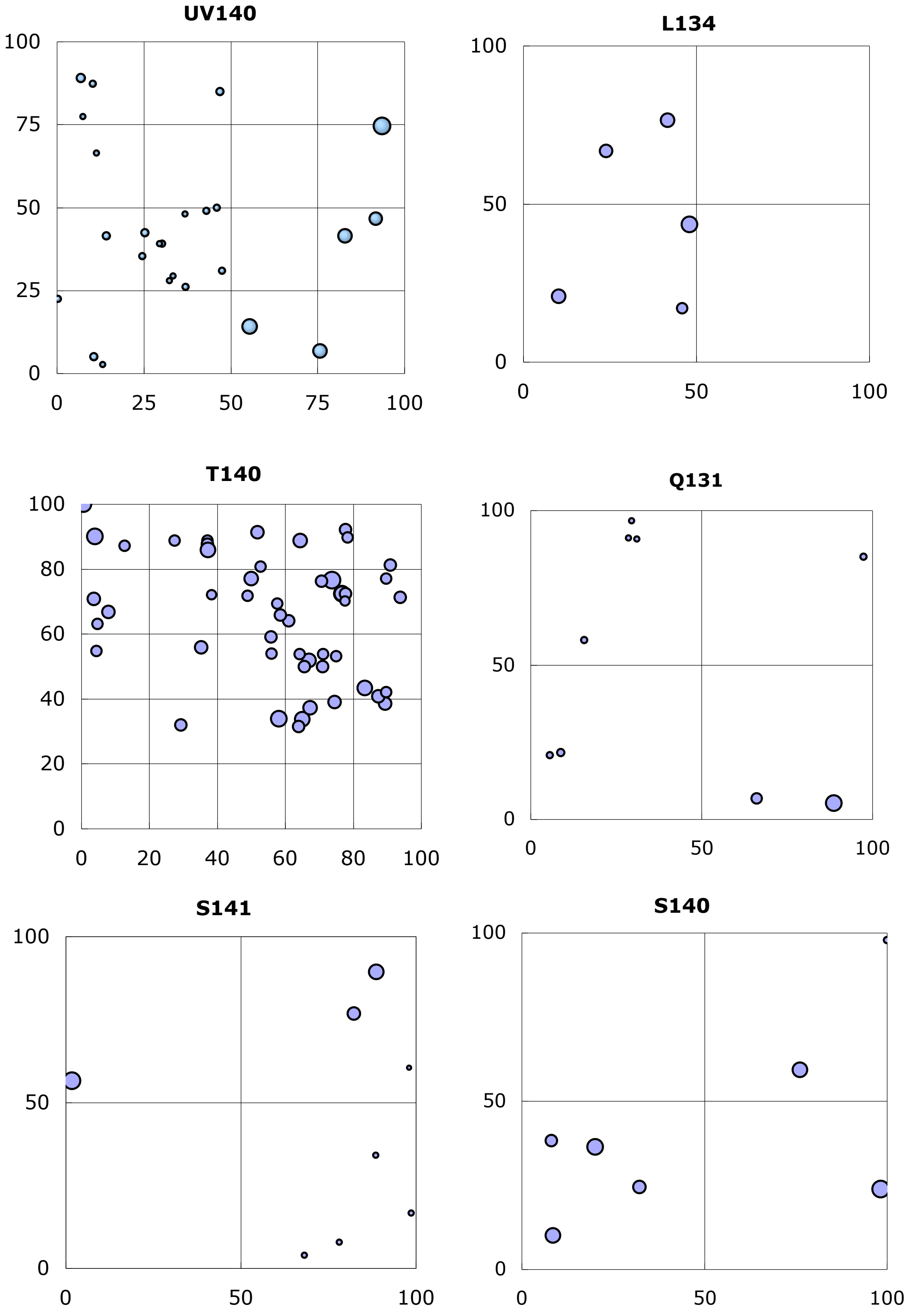


Fig. D.5 Dispersion patterns of *Ceiba pentandra* in six quadrats



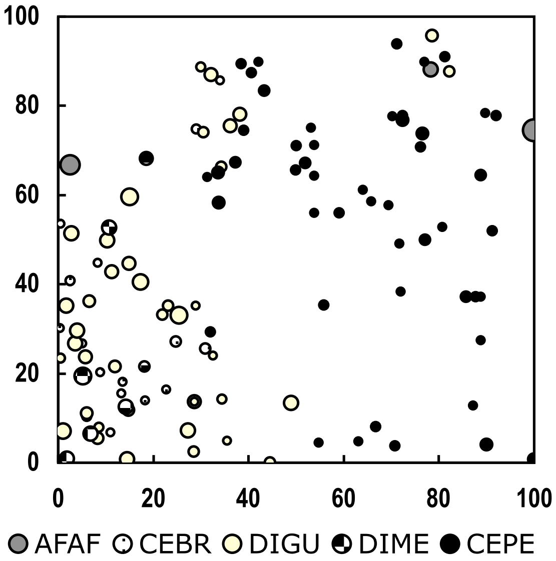


Fig. D.6 Dispersion patterns of *Afzelia* , *Celtis, Dialium, Diospyros* trees in contrast with *Ceibapentandra* in quadrat T140

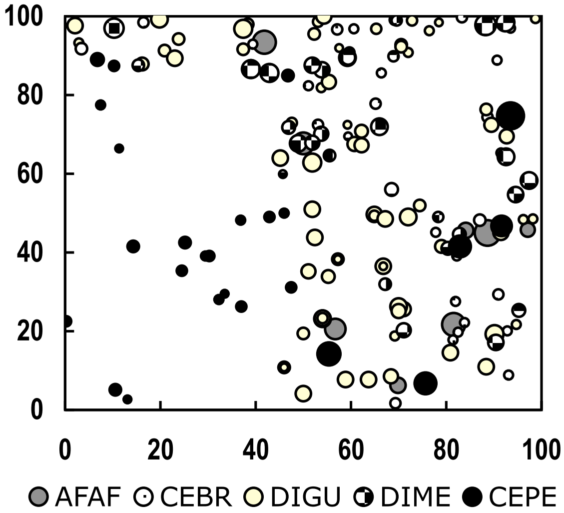
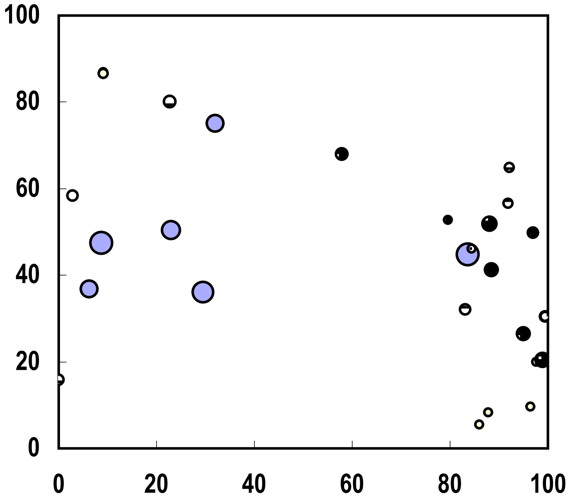


Fig. D.7 Dispersion patterns of *Afzelia, Celtis, Dialium, Diospyros* trees in contrast with *Ceiba pentandra* in quadrat UV140

Fig. D.8 Disperson patterns of *Afzelia* in contrast with some pioneer species in S141



AFAF
ALZY
Ficus Spp.
ELGU
LANI

APPENDIX E. FLOWERING DURATIONS

Fig. E.1 Flowering duration in dense forest
(Keys to the species abbreviations are found in Appendix C.)

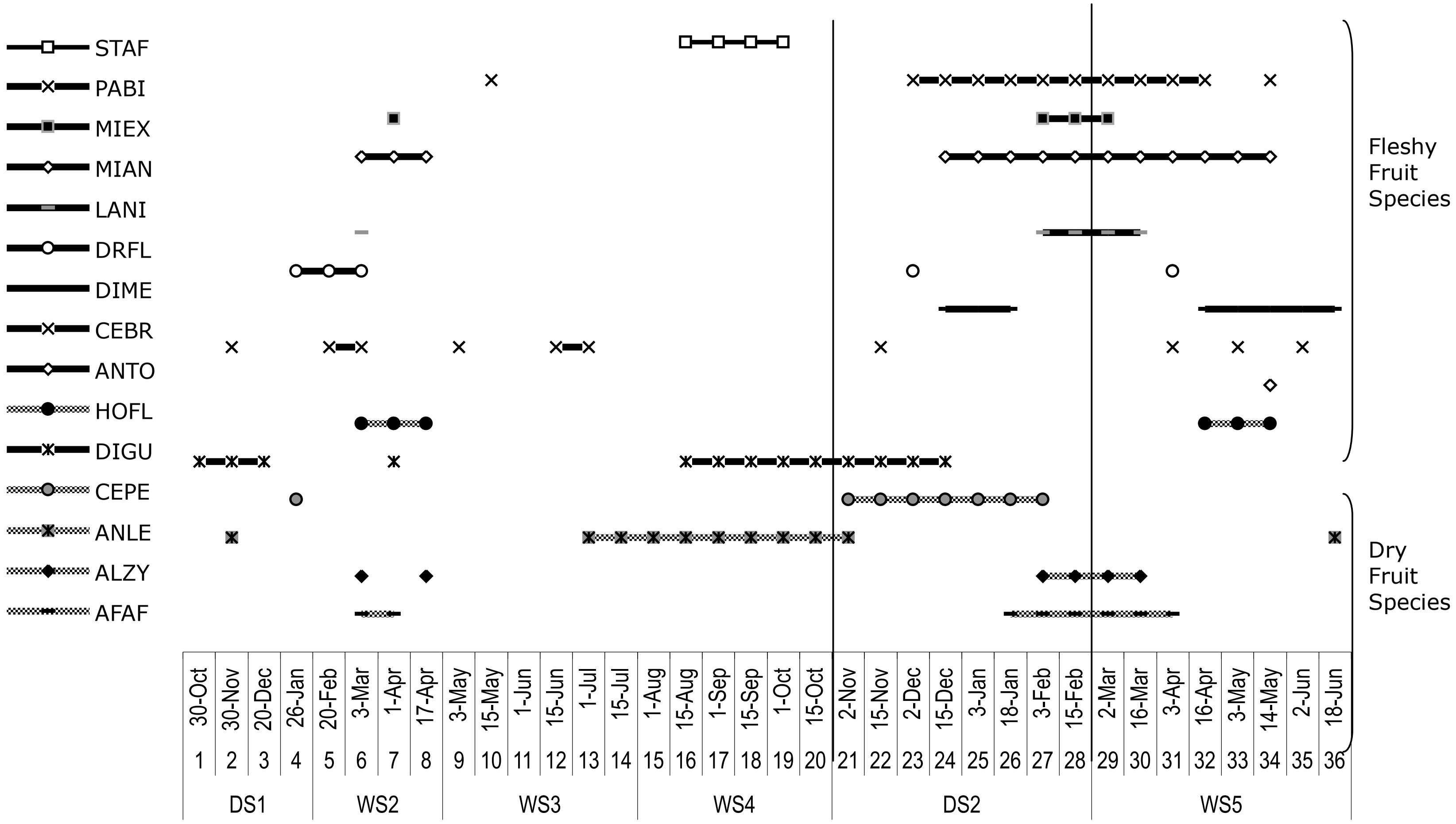


**Fig. E.2 Flowering duration in disturbed forest
(Keys to the species abbreviations are found in Appendix C.)**

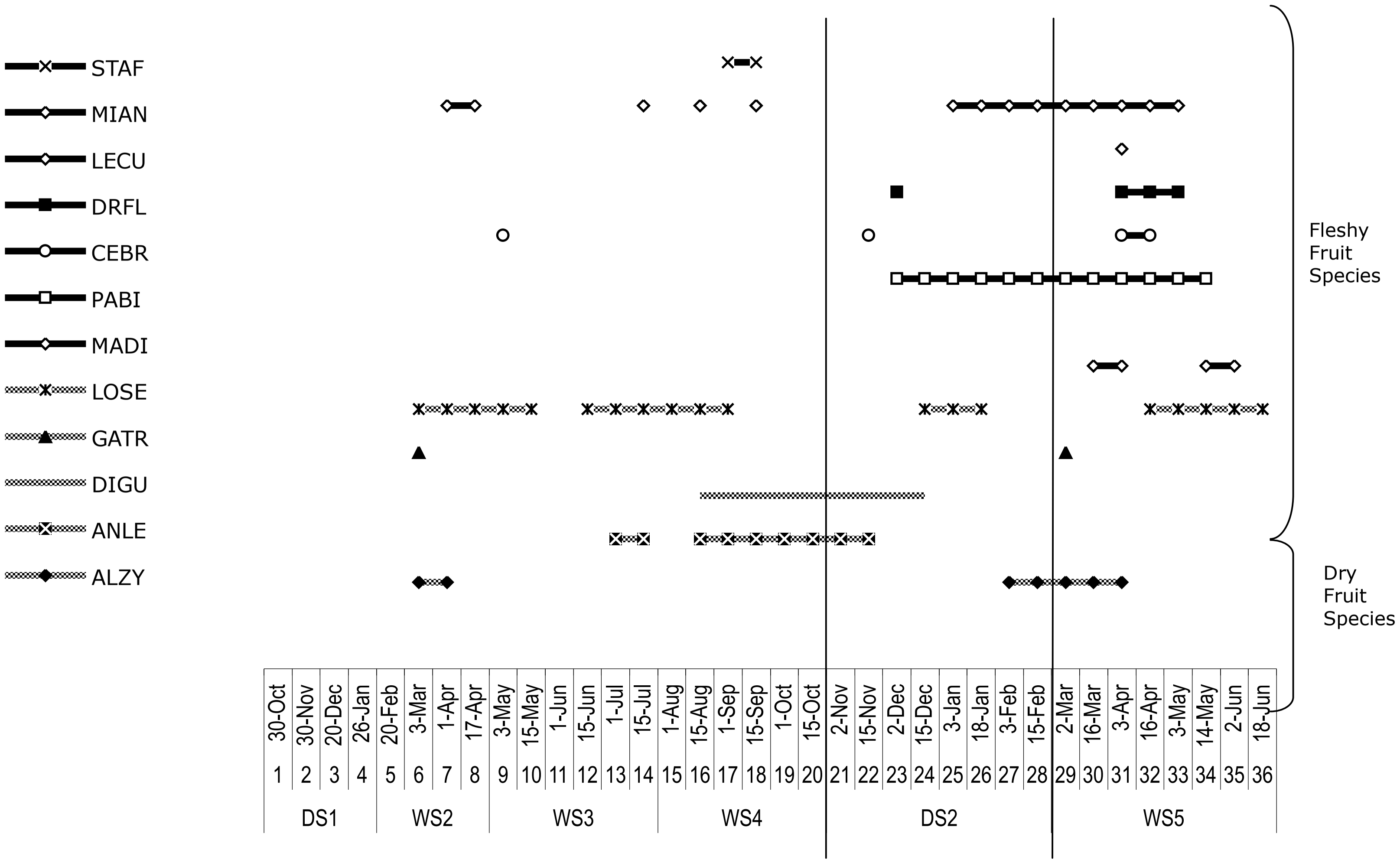
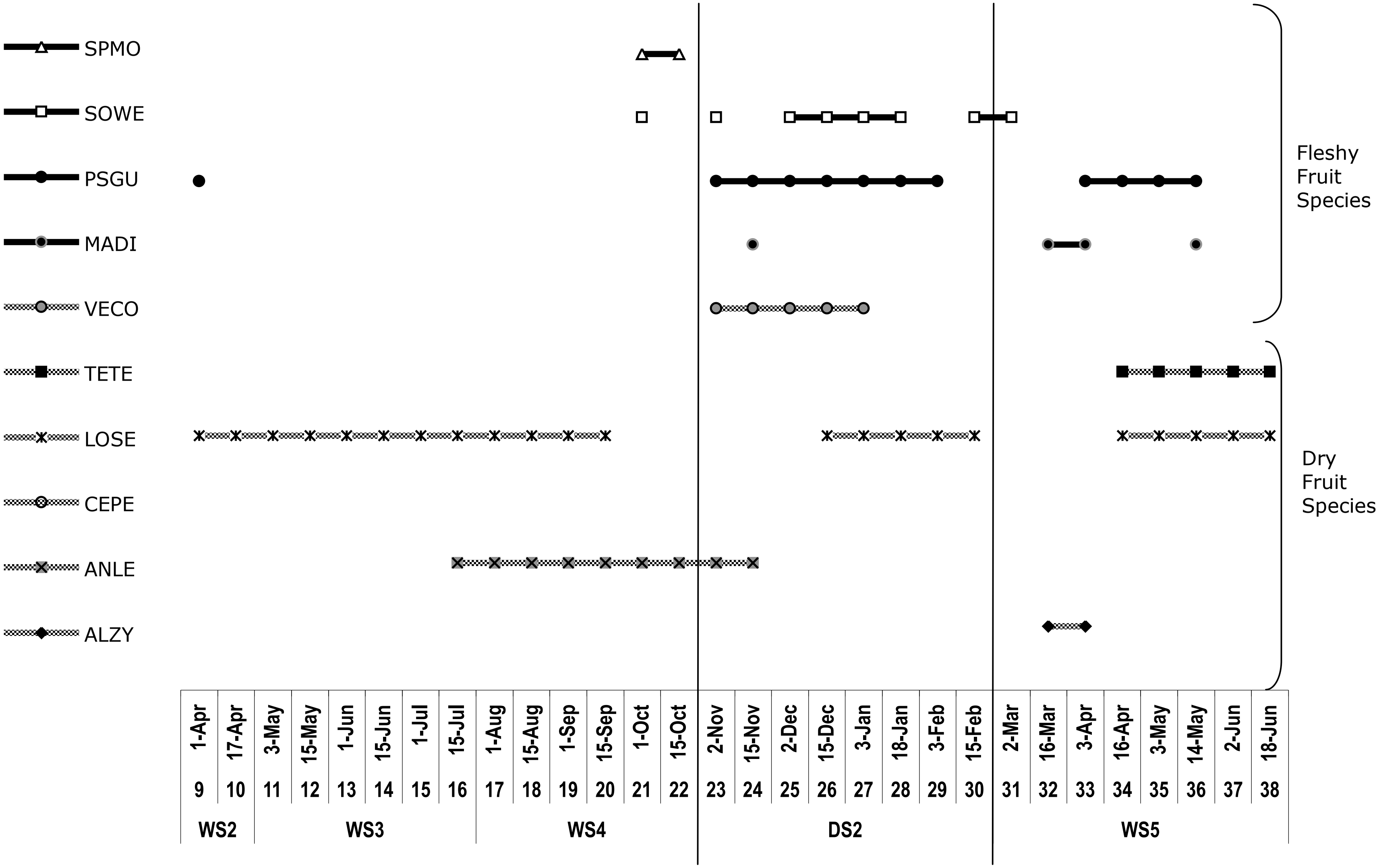


Fig. E.3 Flowering duration in farmbush
(Keys to the species' abbreviations are found in Appendix C.)



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