Ecology of Cross River Gorillas (*Gorilla gorilla diehli*) on Afi Mountain, Cross River State, Nigeria

by

Kelley Lee McFarland

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Abstract

Ecology of Cross River Gorillas (*Gorilla gorilla diehli*) on Afi Mountain,
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Advisor: John F. Oates

This dissertation presents the first detailed descriptions of Cross River gorilla habitat, diet, ranging behavior and grouping patterns. Field work was conducted during 32 months between 1996 and 1999 on Afi Mountain in Cross River State, Nigeria. The types of data collected include: 1) habitat types and topography mapped using line transects, 2) climate, 3) temporal and spatial availability of tree and herb foods using phenological and enumeration studies and 4) gorilla diet, ranging behavior and grouping patterns assessed from indirect evidence (feeding trails, nests and feces).

The Afi gorilla diet was found to be similar to that of other western gorillas, but differed in several ways. Most notably, Afi gorillas experience a prolonged and more severe period of fruit scarcity due to the region's special climate and the absence of important fallback fruit foods that are common at other sites. This likely explains why leaves and particularly bark, were more abundant in the Afi gorilla diet compared to other western gorillas.

As predicted by their frugivorous diet, Afi gorillas had a relatively large annual home range. Ranging behavior was clearly influenced by variation in temporal and spatial availability of tree and herb food resources and predation risk (human hunting) across their home range. The study group traveled longer distances daily when consuming widely scattered and/or patchy fruit or herb food resources. The study group utilized different sectors within their range in a non-random efficient manner corresponding to variation in availability of preferred foods across sectors and avoidance of sectors with high hunting pressure.

The study group most often contained 18 nesting individuals including at least two adult males. Nest group size was highly variable between consecutive nest sites and seems to be best explained by flexible grouping behavior; alternative explanations were investigated and eliminated. The pattern of nest group size variability suggests that at times individuals of a smaller-sized group may have joined the study group, while on other occasions the study group may have divided into subgroups. Group flexibility occurred relatively frequently when gorillas consumed large amounts of fruit or preferred herbs during the period of fruit scarcity.

This dissertation is dedicated to:

My family, especially my parents and sister,
for their endless loving encouragement and belief in me.
I could not have done it without you.

AND

The Cross River gorillas for persisting
despite what would appear to be insurmountable obstacles thereby
affording me the extreme pleasure of studying them.

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Table of Contents

List of Tables

List of Figures

CHAPTER ONE – INTRODUCTION

Cross River gorillas were neglected after their first description in 1904 (Matschie 1904) and were thought to be extinct (Dixson 1981), until their "rediscovery" in 1983 when an orphaned infant, a victim of poaching, was discovered in a village in Nigeria (Oates 1999a). Prior to the late 1980s, little was written about the Cross River gorilla other than in morphological studies using museum specimens (Coolidge 1929; Groves 1967, 1970; Rothschild 1904, 1908; Rzasnicki 1936; Schwarz 1928). Early written accounts of Cross River gorillas are sparse and based on personal observations (i.e., sightings, nests and feeding remains) during short visits to the forest, hunter interviews (Allen 1931; Anonymous 1934) and informal surveys (Critchley 1968; March 1957).

From the late 1980s to present, the Cross River gorilla has received much greater attention. Surveys covering greater proportions of their range have provided information concerning the Cross River gorillas' current geographical range, distribution and population size. In addition, several morphological and genetic studies have led to the re-examination of their taxonomic status (Clifford et al. 2003; Oates 1999b; Oates et al. 2003; Sarmiento & Oates 2000; Stumpf et al. 1998; Stumpf et al. 2003; Wickings et al. 2004). Results of these studies have allowed us to better understand their distinctive taxonomic status, threats to their survival, and ultimately, their critically endangered status.

The present study, conducted at Afi Mountain between 1996 and 1999, is the first to provide a detailed description of the Cross River gorilla's, habitat, diet, ranging behavior and social organization. Preliminary information indicated that several aspects of the Afi gorillas' habitat, such as climate, altitude, and the spatial and temporal distribution of important foods (e.g., herbs, fruit), differ from other gorilla habitats (McFarland 1994). Consequently, the overall goals of this dissertation are to document these habitat differences and how they may influence the Afi gorillas' diet, ranging behavior, and grouping patterns. The ultimate aim of this dissertation is to compare the ecology of Cross River gorillas to other gorilla populations to improve our understanding of intra-specific variation in the ecology of gorillas.

In this chapter, I first provide background information on classification and geographical range of gorillas and a brief description of the current size, distribution and structure of Cross River gorillas (for a more detailed review see Oates et al. 2003 and Bergl, 2006). Secondly, I provide a review of ecological factors, particularly food availability, that influence primate diets, ranging behavior and social organization. Thirdly, I review variation in gorilla socioecology, specifically the relationship between habitat differences in the availability of food resources across gorilla habitats and variation in gorilla diet, ranging behavior, and patterns of sociality. Finally, I describe the aims of the present study and an overview of the dissertation chapters.

BACKGROUND INFORMATION

Gorilla Classification and Geographical Range

Traditionally, gorillas have been classified as one species (*Gorilla gorilla*) with three subspecies, the mountain gorilla (*Gorilla g. beringei*), eastern lowland (*Gorilla g. graueri*) and western lowland (*Gorilla g. gorilla*) (Groves 1967, 1970; Groves 1986).

Based on more recent genetic and morphological studies, the classification of gorillas has been re-evaluated (Clifford et al. 2004; Garner & Ryder 1996; Groves 2001; Lukas et al. 2004; Ruvolo et al. 1994; Stumpf et al. 2003; Vigilant & Bradley 2004). Two gorilla species, eastern (*Gorilla beringei*) and western (*Gorilla gorilla*), and four subspecies are now recognized. In this dissertation I will use the following terminology: 1) mountain gorilla (*Gorilla beringei beringei*), 2) Grauer's gorilla (*Gorilla beringei graueri*), 3) western lowland gorilla (*Gorilla gorilla gorilla*), and 4) Cross River gorilla (*Gorilla gorilla diehli*) (Groves 2001; Grubb et al. 2003; Tuttle 2003).

Figure 1.1 illustrates the geographical distribution of *Gorilla*. Mountain gorillas inhabit the Virunga Volcano region spanning the borders of Rwanda, Uganda, and the Democratic Republic of Congo (DRC) at altitudes ranging between 2,000 and 3,500 m. Mountain gorillas also occur approximately 30 km north of the Virunga mountain gorilla population in the Bwindi Impenetrable National Park, Uganda, at altitudes between 1,400 and 2,300 m. Approximately 100 km west of the mountain gorilla range in DRC, Grauer's gorillas occur within the Kahuzi-Biega National Park in montane forests at 1,800 – 2,500 m and in lowland forests in the Itebero region at intermediate altitudes of 600 – 1,300 m; however, the majority of Grauer's gorillas occur at lower elevations in the forest region further west. Western lowland gorillas have the greatest range of the gorilla subspecies and inhabit lowland tropical forests below 600 m elevations in southwestern Central African Republic (CAR), Republic of Congo, Gabon, Equatorial Guinea, and southeastern Cameroon.

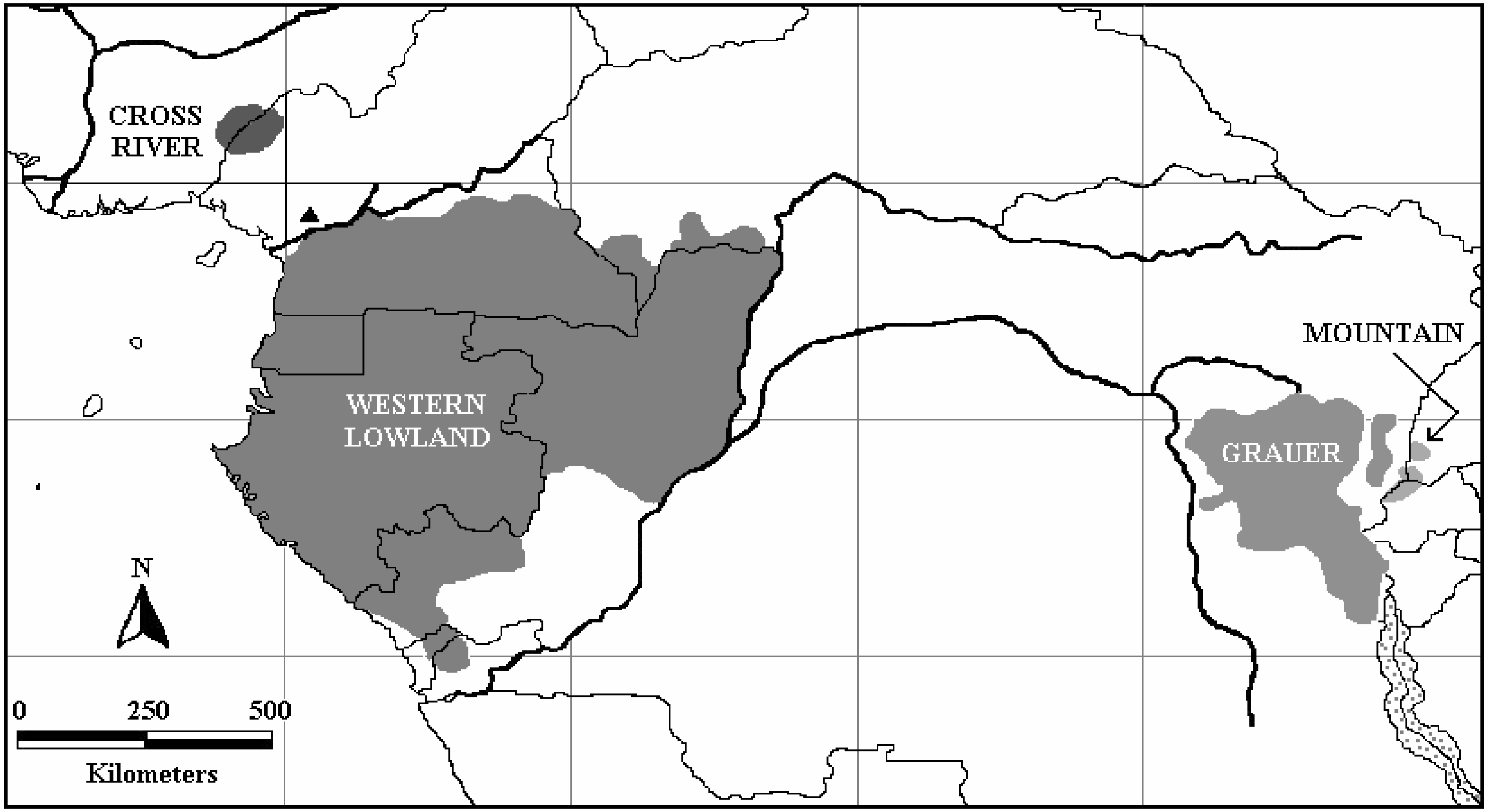


Figure 1.1 Distribution of *Gorilla gorilla*, adapted from Butynski (2001) and Oates et al. (2003), including mountain (*G. g. beringei*), grauer (*G. g. graueri*), western (*G. g. gorilla*) and Cross River (*G. g. diehli*) gorillas. The triangle (▲) indicates the location of the gorilla population in the Ebo Forest, Cameroon (Morgan 2004; Morgan et al. 2003).

Cross River gorillas inhabit forests of the eastern Nigeria and western Cameroon border region at altitudes between 200 and 1,500 m. They represent the most northwestern population within all gorillas' range and are geographically isolated from the main population of western lowland gorillas. The closest confirmed gorilla population north of the Sanaga River, existing 200 km east of the currently known Cross River range, occurs in the Ebo Forest, Cameroon (Morgan 2004; Morgan et al. 2003) (Figure 1.1).

Cross River Gorilla Current Population Size, Distribution and Structure

Since 1990, extensive surveys of Cross River gorillas have been conducted in Cameroon, including areas not previously surveyed (Groves 2002; Groves & Maisels 1999; Sunderland-Groves et al. 2003), and multiple re-censusing has occurred in Nigeria (Nwufoh 2001; Nwufoh 1999; Obot et al. 1997). Current estimates indicate that only approximately 250 - 300 Cross River gorillas remain at eleven fragmented localities that occur predominantly in rugged highland areas with altitudes of ≥ 500 m. Approximately 10 to 35 gorillas exist at each locality covering areas between 15 and 40 km^2 and only one gorilla group likely occupies most of these localities (Bergl 2006; Oates et al. 2003).

Figure 1.2 shows the eleven localities where definite evidence (nest, dung and direct sightings) of Cross River gorillas has been found (Bergl 2006; Bergl & Vigilant 2007). In Nigeria, Cross River gorillas occur in the Afi Mountain Wildlife Sanctuary within the Afi River Forest Reserve (1), Mbe Mountains (2), and Boshi Extension of the Cross River National Park, Okwangwo Division (3). They inhabit the Obonyi-Okwa hills along the Nigeria-Cameroon border within the Cross River National Park in Nigeria and the Takamanda Forest Reserve in Cameroon (4). In Cameroon, the presence of Cross River gorillas has been confirmed south of the Takamanda Forest Reserve (5), in the hills of eastern and northern Takamanda Forest Reserve (6 and 7), the northern highland area of the Mone River Forest Reserve (8), the Upper Mbulu Forest (9), Kagwene Mountains (10) and in the Bechati-Lebialem forest (11) (Bergl 2006; Groves 2002; Groves & Maisels 1999; Oates et al. 1990; Pouakouyou & Beamont 2004; Sunderland-Groves et al. 2003).

The Cross River gorilla population has become fragmented due to the activities of the dense human population within their range (Bergl 2006). Compared to most western lowland gorilla populations, the Cross River gorilla habitat experiences greater pressure from human activities. Based on the Landscan Global Population database for 1998, human population densities along the Nigeria-Cameroon border region range between 51 and 500 people per km^2. In forested areas of Gabon, Central African Republic and Congo where western lowland gorillas occur, human densities are much lower, ranging between 1 and 25 people per km^2. Hunting for bushmeat is one of the greatest threats to the Cross River gorillas' survival currently as well in the past. Habitat erosion due to other human activities, such as agriculture and fire, also threaten the survival of Cross River gorillas. Cross River gorillas have likely persisted in highland areas due to the steep rugged nature of this habitat limiting hunter access as well as other human activities such as logging and farming.

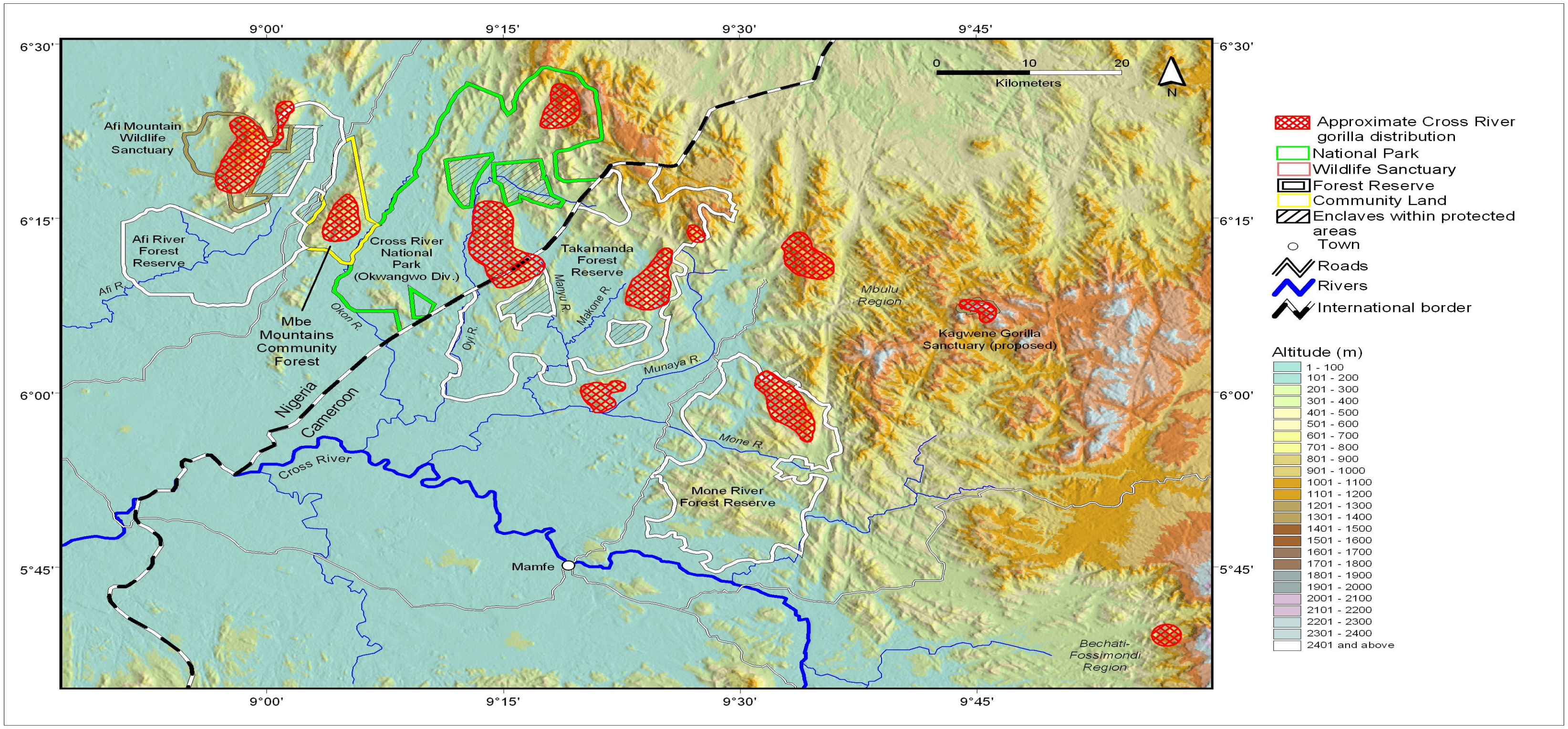


Figure 1.2 Approximate distribution of the Cross River gorilla in Nigeria and Cameroon (from Bergl, 2006; topographic data from the Shuttle Radar-Topography Mission – United States Geological Survey).

The fragmented nature of the Cross River gorilla population suggests that gene flow between localities is now limited. A recent genetic study, however, found that fragmentation has likely only occurred recently and that localities are not yet completely isolated from each other. The population structure of Cross River gorillas was investigated through the examination of nuclear DNA from 74 individuals collected at 7 localities (Bergl 2006; Bergl & Vigilant 2007). This study found that the Cross River gorilla population consists of three subpopulations including a large Central subpopulation (Mbe Mountain, Boshi Extension, Takamanda South, Upper Mbulu and Mone North) and two peripheral subpopulations, Afi Mountain in the west and Kagwene Mountains in the east. The two latter subpopulations each likely consist of one large gorilla group and are the most isolated of the localities. At four localities recent migrants from neighboring localities were identified, including migrants from the Afi and Kagwene subpopulations. This suggests that gene flow between localities is on-going; however, due to the particularly dense human population and associated activities surrounding most hill areas, male transfer between localities is likely difficult.

FACTORS INFLUENCING PRIMATE DIET, RANGING BEHAVIOR, AND SOCIAL ORGANIZATION

Primate Diets

Primate dietary niches are often described using broad categories including frugivores, folivores, herbivores, and insectivores. These categories generally correlate with body size and morphology (Clutton-Brock & Harvey 1977), which can place phylogenetic constraints on diet. Metabolic rate, which determines an individual's energy requirements, and gut size, which determines an individual's capacity to process food, both increase with body size; metabolic rate increases nonlinearly and gut size increases linearly with body size (Demment & Van Soest 1985). In general, large-bodied animals have relatively lower energy requirements per unit body weight and larger gut size allowing them, but not restricting them, to rely on large amounts of low-quality foods (e.g., leaves, stem pith, bark) with low concentrations of energy, protein and nutrients, and high concentrations of fiber, digestion deterrents and toxins. Large-bodied primates, such as gorillas, have larger digestive capacities, longer gut retention times and some have gut specializations, such as microbiotic fermentation, that are particularly suited to processing the large amounts of low-quality foods required to meet energy and nutritional needs (Chivers & Hladik 1984; Martin et al. 1985; Milton 1998; Remis 2000; Remis & Dierenfeld 2004). On the other hand, small-bodied animals require greater amounts of high-quality foods (e.g., fruit, insects, flowers, gums) that contain high concentrations of readily digested energy, protein and nutrients, and low concentrations of fiber, digestion deterrents and toxins in order to meet their higher energy requirements.

Dietary categories have been related to gross ecological factors, and specifically to food distribution (Clutton-Brock & Harvey 1977). Folivorous/herbivorous foods are generally regarded to be abundant, evenly distributed, and available throughout the year. By contrast, frugivores rely on foods that have spatially and temporally variable distributions in patches that are often widely scattered. Hence, frugivores are hypothesized to face greater foraging challenges, such as increased feeding competition and travel costs, than folivores/herbivores.

Primate diets, however, are more complex than broad dietary categories suggest. Whereas primates tend to focus on one type of food, many incorporate a wide variety of different foods but can also be highly selective. Foraging models predict that animals should choose foods high in nutrients, and low in fiber, digestive inhibitors and toxins (Garber 1987). Specifically, animals should consume high-quality foods (e.g., fruit) when available (Pyke et al. 1977). For example, folivorous primates often incorporate fruit and other high quality foods when they are available (Milton 1979, 1984, 1998). Folivore food choice can be influenced by nutrient and fiber content, and the presence of digestion inhibitors and toxins, which vary across plant species and parts, developmental stage and possibly season (Oates et al. 1980; Waterman 1984). Some folivores consume leaves of only a few select species, or prefer young leaves and/or particular plant parts with high protein to fiber ratios and low levels of tannins and toxins (Oates et al. 1977). Thus, leaves are often less abundantly and evenly distributed than has been suggested, but are still generally more abundant and evenly spread than fruits.

Furthermore, most primate foods, particularly fruit, vary temporally throughout the year and inter-annually, and composition of diet varies accordingly. Thus, many primates face some period of food scarcity when the abundance of their preferred foods is reduced, though the length and severity of this period varies considerably across different habitats. The dietary flexibility of large-bodied folivores/herbivores provides them with an advantage during food scarcity since they can rely solely on low-quality foods by increasing consumption rates and/or increase food species diversity with little consequence (Remis & Dierenfeld 2004; Remis et al. 2001). Small-bodied frugivorous primates also often increase consumption of low quality foods during periods of fruit scarcity; however, due to body size constraints they cannot rely solely on these foods. Consequently, additional responses to increase foraging efficiency for sparsely distributed high-quality foods and to reduce energy costs are required to compensate for the overall reduction in net energy intake.

Primate Ranging Behavior

Foraging strategies are described as a balance between maximizing energy intake and minimizing energy costs of travel. Therefore, many aspects of food availability in space and time, including abundance, distribution, and patch size and density, are among the most important factors influencing ranging behavior (Garber 1987; Pyke et al. 1977; Schoener 1971; Stephens & Krebs 1986), though predator avoidance will certainly be a major factor as well (Boinski et al. 2000). Primates relying on foods that are distributed unevenly in patches tend to have longer day ranges and larger home ranges thereby increasing their food encounter rate. This characterizes the ranging patterns of frugivorous primates whose increased travel costs are offset by the high energy content of fruit. Folivorous primates, however, rely on foods providing low energy but have reduced travel costs since these foods are generally abundantly and evenly available (though see above).

Ecological constraint models predict that travel costs, and hence ranging behavior, are strongly influenced by food patch size, density and distribution (Chapman & Chapman 2000; Janson 2000). Assuming patches are depleting (e.g., a fruiting tree containing a finite number of fruits), the length of time spent at a given patch will be determined by the amount of food available (i.e., patch size). Costs of traveling to a subsequent patch will be determined by patch density. Distance between patches is inversely related to patch density and hence travel costs. When patch density is high, indicating short travel distances between patches, travel costs will be low and vice versa. Travel costs will also be low if patches have a clumped distribution, regardless of patch density, at least while animals are feeding in a given clump. When patches are uniformly distributed, regardless of patch size, density is expected to be the most important factor influencing intensity of travel costs.

These relationships between food availability and travel costs suggest that if areas within a primate's home range differ in food availability, a primate will prefer those areas containing food patches that are large and/or dense in order to maximize food intake and minimize travel costs. Where exceptions occur, other factors such as predator avoidance and inter-group and/or interspecific competition may be more important.

Primate Grouping Patterns

Diurnal primates tend to forage in groups; thus, ranging behavior and grouping patterns (e.g., group size and flexibility) are inextricably connected. There are inherent disadvantages of group living, such as increased conspicuousness to predators, increased feeding competition, and increased exposure to diseases and parasites (Alexander 1974). But if members of a group cooperate with each other, group living can provide many advantages that increase a member's ability to avoid predation and improve foraging efficiency. If group living is adaptive, groups will form only when members incur greater benefits from living in a group than being solitary.

The two primary ecological factors that have been proposed to explain variation in the social organizations of primates are predation and the abundance and distribution of food (Dunbar 1988; Eisenberg et al. 1972; Terborgh 1983; van Schaik & van Hooff 1983; Wrangham 1987). Whereas access to mates is a major factor limiting male reproductive success, the primary limiting factor influencing female reproductive success is access to food (Trivers 1972). Consequently, ecological explanations focus on how females are spatially distributed in relation to habitats with differing food availability, which may limit male reproductive strategies and ultimately determine social organization (Emlen & Oring 1977; Trivers 1972; Vehrencamp & Bradbury 1984).

Primate socioecological models specifically focus on the relationship between food distribution, type and intensity of feeding competition, and female social relationships. Some of these models assume that groups initially form in response to predation risk (Sterck et al. 1997; van Schaik 1989) but others argue that food availability alone can explain why groups form (Isbell 1991; Isbell & Young 2002; Wrangham 1980). Regardless of the initial impetus, once groups form feeding competition increases. Females compensate for this cost of group living by adopting various foraging and social strategies.

Food abundance and distribution strongly influence the type and intensity of feeding competition. Contest competition occurs when foods are distributed in discrete and clumped patches that individuals or groups can successfully defend. Under these ecological conditions, females are expected to form alliances and stable consistent dominance relationships, and female philopatry should be favored and maintained. Scramble competition occurs when food resources are either evenly and abundantly distributed, or sparsely distributed. Food resources are therefore non-monopolizable and aggression between individuals or groups will not provide greater access to food. Consequently, there is no advantage provided by forming alliances or dominance relationships with other females including kin and female transfer is common.

Whereas abundantly and evenly distributed food resources allows females to live in close proximity without significant costs of feeding competition, it does not fully explain why they do so. Van Schaik (1989) and Sterck et al. (1997) suggest that for some primates, such as gorillas and langurs, infanticide avoidance is the key benefit selecting group living under certain conditions: 1) the cost of female grouping is low, 2) there is variation in male quality allowing opportunity for female mate choice, and 3) female transfer is common. Females tolerate presence of other females in order to maintain close proximity to the resident male(s), which provide protection against infanticide by non-resident males as well as from predators.

Individuals and groups can reduce feeding competition, and hence, maintain group living using several strategies (Isbell 1991; Isbell & Young 2002). Group size can be restricted through voluntary or forced dispersal. On a daily basis, individuals may temporarily forage singly or in small parties, thus, increasing group spread, though compromising safety. In order to maintain cohesiveness, dietary switching by some individuals can alleviate feeding competition when patch size of preferred foods cannot accommodate nutritional needs of all members. When the costs of feeding competition are high, particularly during periods when preferred foods are scarce, solitary foraging or sub-group formation may be selected. These responses (regulation of group size, group spread, dietary switching, and/or subgrouping), as well as female dominance hierarchies, and increased day range and home range size, are often used as indicators that group members are experiencing within-group feeding competition.

GORILLA SOCIOECOLOGY

Socioecological theory predicts that intraspecific variation in gorilla diet, ranging behavior, and sociality are related to habitat differences in the availability of food resources. The staple diet of all gorilla subspecies consists of herbaceous vegetation, and gorillas have several adaptations for subsisting on a low-quality folivorous diet: large body size as well as the morphology of teeth, skull and gut (Chivers & Hladik 1984; Collet et al. 1984; Remis 2000; Remis & Dierenfeld 2004; Shea 1983; Taylor 2002; Uchida 1998). Where fruit is available, however, gorillas take advantage of this high quality food resource. Whereas abundance of herbaceous vegetation tends to vary positively with altitude, fruit abundance varies inversely with altitude, though not all gorilla habitats strictly conform to these general relationships (Goldsmith 2003; Yamagiwa et al. 2003b). Consequently, the ratio of folivory to frugivory in gorilla diets varies across populations. Differences in the distribution of herbaceous vegetation and fruit between gorilla habitats suggest that the level of feeding competition varies among these populations and influences gorilla ranging and social behavior in important ways.

Gorilla habitats, diets, ranging behavior and patterns of sociality, however, do not necessarily vary across gorilla populations according to subspecific designation. Some populations of a particular subspecies show socioecological features more similar to populations of other subspecies than to their own. Therefore, in this account I group gorilla populations in the following manner based on similarities in the above parameters:

1) Virunga mountain gorillas, 2) Bwindi mountain gorillas and Grauer's montane gorillas at Kahuzi, 3) Grauer's lowland gorillas (including the Itebero population) and western lowland gorillas (together referred to as 'lowland gorillas').

Current Status of Gorilla Research

There is a disparity between the vast amount of information gathered on the ecology and sociality of mountain gorillas compared to the relatively lesser known populations of Grauer's montane and western lowland gorillas, and the least known Grauer's lowland and Cross River gorillas. Habituated groups of Virunga mountain gorillas at the Karisoke Research Center have been studied for over 30 years producing detailed information on habitat, diet, ranging behavior, social relationships, social organization, demography, and life history variables (Robbins et al. 2001). Research has only recently provided ecological, dietary and ranging behavior information for the Bwindi mountain gorilla population, including four habituated groups (Ganas & Robbins 2004, 2005; Ganas et al. 2004; Goldsmith 2003; Nkurunungi 2004; Nkurunungi et al. 2004; Robbins & McNeilage 2003; Stanford & Nkurunungi 2003). Research and habituation of the Grauer's montane gorilla population at Kahuzi-Biega has been conducted since the 1970's and has generated long-term information on diet, ranging behavior, and demography of four habituated groups (Casimir 1975, 1979; Yamagiwa 1983; Yamagiwa & Basabose 2006; Yamagiwa et al. 2003a, 2005; Yamagiwa & Kahekwa 2001; Yamagiwa et al. 1996).

In contrast to montane habitats, the dense vegetation characteristic of lowland tropical forests, inhabited by Grauer's lowland and western lowland gorillas, makes habituation and hence direct observation extremely difficult. Consequently, the majority of what we know about lowland gorilla ecology is based on indirect evidence such as feeding remains, feces, and nests. The diet, ranging behavior and group characteristics of Grauer's lowland gorillas are currently known only from short-term studies conducted at Itebero between 1987 and 1991 (Mwanza et al. 1992; Yamagiwa et al. 2003b; Yamagiwa et al. 1991, 1992, 1994; Yamagiwa et al. 1993b).

Relatively complete descriptions of diet and ranging behavior now exist for unhabituated or semi-habituated western lowland gorilla groups studied at research sites across their range, especially, Lopé in Gabon (Tutin 1996; Tutin & Fernandez 1983, 1992, 1993a, b; Tutin et al. 1992; Tutin et al. 1991; Tutin et al. 1995), Bai Hokou in Central African Republic (Carroll 1996; Cipolletta 2003, 2004; Goldsmith 1996, 1999, 2003; Remis 1993, 1995, 1997a; Remis 1997b; Remis 1999; Remis et al. 2001), Mondika in CAR/Congo (Doran & McNeilage 2001; Doran et al. 2002; Doran-Sheehy et al. 2004; Mehlman & Doran 2002) and Ndoki in the Congo Republic (Kuroda 1992; Mitani 1992; Mitani et al. 1993; Nishihara 1992; Nishihara 1995). Information based on direct observation of western lowland gorillas comes primarily from studies at large swampy forest clearings (or 'bais'). These studies have produced data on population size and structure, group size and composition, inter-group encounters, dispersal, and social relationships (Gatti et al. 2004a, b; Gatti et al. 2003; Levréro et al. 2002; Magliocca & Gautier-Hion 2002, 2004; Magliocca et al. 1999; Olejniczak 1996; Parnell 2002; Robbins et al. 2004; Stokes 2004; Stokes et al. 2003). Results of these studies, however, are preliminary and should be interpreted with caution since they represent behavior in a limited ecological context. Consequently, many aspects of lowland gorilla sociality are relatively unknown compared to knowledge of Virunga mountain gorillas.

Virunga Mountain Gorillas

In the high altitude habitat of mountain gorillas in the Virungas, where edible fruit is virtually absent, gorillas consume mostly herbs and vines that are relatively abundant, evenly distributed and perennially available (herb stem density: 8.8 per m^2) (Fossey & Harcourt 1977; McNeilage 1995; Plumptre 1995; Watts 1984, 1991b). Diet and ranging behavior varies little seasonally, except for those groups with access to seasonally available young bamboo shoots; consequently, mountain gorillas do not experience a period of food shortage (Fossey & Harcourt 1977; Schaller 1963; Vedder 1989; Vedder 1984; Watts 1984, 1991b, 1998b). Small-scale spatial variation in food quality has been found to influence habitat use patterns (Vedder 1984; Watts 1991b, 1998a, 2000b). This suggests that habitat use by Virunga gorillas maximizes their foraging efficiency (Watts 1996, 2000b). Compared to other gorilla populations, Virunga gorilla groups have short day ranges (570 m) and small annual home range size (3 – 15 km^2) (McNeilage 1995; Vedder 1984; Watts 1991b).

Virunga mountain gorillas likely experience little if any within-group scramble competition and fit socioecological theory well (McNeilage 2001; Watts 1985, 2003). Travel costs are minimal and likely do not constrain group size. No consistent or weak relationships between group size and day ranges or home range size have been recorded (Watts 1991b, 1996, 1998a). Females may experience higher levels of feeding competition when groups are particularly large, but increased group spread can easily compensate for any loss in foraging efficiency (Robbins 2001; Sterck et al. 1997).

Virunga gorilla social relationships, female-female and male-female, also indicate low levels of feeding competition. Resident females are usually unrelated and tend to avoid social interaction, though exceptions have been observed (Harcourt 1979a; Stewart & Harcourt 1987; Watts 1991a, 1994a, b, 1995a, b). Aggressive contests between females involving food are infrequent and dominance hierarchies are weak or undetectable (Robbins et al. 2005; Watts 1994b, 1996, 2003). Natal and secondary transfers are common and are not related to group size (Harcourt 1978; Stewart & Harcourt 1987; Watts 1990, 1996, 2000a). Additionally, ecological and social costs of dispersal are minimal since females gain little from remaining with kin (Harcourt & Stewart 1989; Watts 1985, 1994a; Wrangham 1979) and there is little variation in large-scale habitat quality (McNeilage 1995). In addition, immigrant females usually do not encounter resistance from resident females, except in large groups (Harcourt 1978; Watts 1991a, 1996).

Virunga gorillas live in relatively stable one-male or multi-male groups with an average size of 9 individuals and a range between 2 and 25 individuals, though one group of 41 has been observed; all-male and lone males have also been observed (Steklis & Gerald-Steklis 2001). The permanent male-female association of Virunga gorilla groups is likely explained by females' need for male protection against infanticide (Harcourt 2001; Harcourt & Greenberg 2001; Sterck et al. 1997; van Schaik 1989; Watts 1996, 2003). Females transfer into multimale groups more often than expected; multimale groups retain greater numbers of females and have lower risks of infanticide compared to one-male groups (Robbins 1995; Watts 2000a). Most female affiliative social interactions are directed toward adult males (Harcourt 1979b). When female-female aggression does occur, it usually involves gaining proximity and social access to adult males, which may indicate competition for safety and/or protection from aggressive females (Watts 1994a, 2003). Males commonly mediate conflicts between females through controlled interventions that do not support any particular female participant (Watts 1991a, 1997).

To summarize, low levels of feeding competition, related to abundantly and evenly distributed food resources, provides the opportunity for several or more female Virunga gorillas to gain from permanent association with at least one adult male. Males minimize costs imposed on females by male-male mating competition (infanticide) and reduce female-female competition (Watts 1996, 2003).

Bwindi Mountain Gorillas and Grauer's Montane Gorillas at Kahuzi

Herbaceous vegetation is abundant and evenly distributed at Kahuzi and Bwindi (stem density: 4.3 – 10.6 per m^2), similar to the Virungas; however, fruit is also available, though less abundantly than in lowland forests (Nkurunungi et al. 2004; Yamagiwa et al. 2003a). Consequently, degree of frugivory for these two populations is intermediate between that found in the Virunga and lowland gorillas. Compared to lowland gorillas, the diets of Kahuzi and Bwindi gorilla groups are characterized by lower fruit-species diversity (44 and 11 – 36 fruit species, respectively) and lower levels of fruit consumption (53% and 27 – 47% of fecal samples contained fruit, respectively) (Goldsmith 2003; Robbins & McNeilage 2003; Stanford & Nkurunungi 2003; Yamagiwa et al. 2005). Higher levels of fruit consumption have been reported for some Bwindi groups (66 – 82% of fecal samples) (Ganas et al. 2004), but may be related to differences in methodology between studies.

The availability of gorilla fruit resources and the consumption of fruit at both sites vary monthly, and are positively correlated (Goldsmith 2003; Robbins & McNeilage 2003; Stanford & Nkurunungi 2003; Yamagiwa & Basabose 2006; Yamagiwa et al. 2003a, 2005). Unlike what has been found in the habitats of lowland populations, phenological studies at Kahuzi and Bwindi found that fruit availability and consumption do not strictly correspond with rainfall seasonality, and both are relatively high during some dry season months (Nkurunungi et al. 2004; Stanford & Nkurunungi 2003; Yamagiwa & Basabose 2006). On study, however, found that fruit consumption at Bwindi was significantly greater during the wet compared to dry season months (Goldsmith 2003).

As in lowland gorillas, the ranging behavior of Kahuzi and Bwindi groups is influenced by the spatial and temporal availability of fruit. Groups at Kahuzi and Bwindi have relatively large annual and total home range sizes (mean annual home range: 14.1 and 28 km^2 and total range size: 42.2 and 40 km^2, respectively), which are similar to those of lowland gorillas (Robbins & McNeilage 2003; Yamagiwa et al. 2003b). Day ranges for groups at Kahuzi (mean = 716 m, range = 242 – 2,055 m) and Bwindi (mean = 547 – 1,034 m, range = 222 – 1,720 m) are most similar to, though longer than, Virunga gorilla groups (Ganas & Robbins 2005; Yamagiwa et al. 2003b). Fruit consumption does, however, positively correlate with daily path length and/or monthly home range size for all groups at both sites (Ganas & Robbins 2005; Goldsmith 2003; Robbins &

McNeilage 2003; Yamagiwa & Basabose 2006; Yamagiwa et al. 2003b). These data suggest that the ranging behavior of these two populations differs from Virunga mountain gorillas due to increased fruit consumption.

Whereas foraging behavior of Bwindi Mountain gorillas is similar to the Virunga mountain gorilla population, Grauer's montane gorillas at Kahuzi exhibit foraging strategies similar to some lowland populations. Bwindi gorilla groups forage in relatively cohesive groups and subgrouping or supergrouping has not been observed (Goldsmith 2003). By contrast, increased group spread, subgrouping and supergrouping have been observed at Kahuzi, though subgrouping may also occur during the process of group fission as well (Yamagiwa et al. 2003a; Yamagiwa et al. 2003b).

The social organization of Kahuzi gorillas is similar to that of Virunga and Bwindi mountain gorillas, but differs in several important ways (Yamagiwa & Kahekwa 2001; Yamagiwa et al. 2003b). First, multi-male groups are rare (7 – 8% of groups) (Murnyak 1981; Yamagiwa et al. 1993a) compared to populations at Virunga and Bwindi, where the proportion of multi-male groups ranges between 25% and 46% (McNeilage 2001; Sholley 1991; Weber & Vedder 1983; Yamagiwa 1999). Second, infanticide has not been observed at Kahuzi and females with dependent infants successfully immigrate between groups without subsequent injury or killing of infants. Third, groups do not disintegrate after the death of the resident adult male, and females and immatures remained cohesive and ranged without an adult male for up to 29 months. Yamagiwa and Kahekwa (2001) provide evidence suggesting that predation, rather than infanticide, is the major factor promoting associations between females and adult males at Kahuzi.

Lowland Gorilla Diet and Ranging Behavior

In lowland forest habitats of western and Grauer's gorillas, herbaceous vegetation is less abundant and evenly distributed (herb stem density: 0.78 - 2.25 per m^2) (Doran et al. 2002; Goldsmith 1996; Malenky et al. 1993; Rogers et al. 2004; White et al. 1995) and fruit abundance is higher than other gorilla habitats. On a daily basis throughout the year, lowland gorillas consume herbaceous vegetation and leaves, but also consume large amounts and a great diversity of fruit (89% - 99.9% of fecal samples contain fruit remains, 70 – 115 fruit species) (Cipolletta 2004; Doran et al. 2002; Goldsmith 1996; Nishihara 1995; Remis 1997b; Tutin & Fernandez 1993b; Yamagiwa et al. 1994). Fruit availability varies temporally within and between years and is positively correlated with rainfall (Carroll 1996; Cipolletta 2004; Doran et al. 2002; Doran-Sheehy et al. 2004; Goldsmith 1996; Kuroda et al. 1996; Remis 1994, 1997b; Tutin & Fernandez 1993c; Tutin et al. 1991; White 1994; Williamson 1989). Consequently, fruit consumption is highest during the wet season and lowest in the dry season. During periods of fruit scarcity, lowland gorillas increase consumption of herbaceous vegetation and fallback foods such as leaves and bark.

The spatial and temporal variation of fruit availability clearly influences the ranging behavior of lowland gorillas. In general, they tend to have larger annual and total home range sizes (7 – 20 km^2 and 11 – 30 km^2, respectively) and longer daily path lengths (range of means = 1,105 – 2,590 m) than other gorilla populations, and habitat use varies monthly and annually in relation to fruiting patterns and distribution of particular important fruit resources (Bermejo 1997; Cipolletta 2004; Doran & McNeilage 2001; Doran-Sheehy et al. 2004; Goldsmith 1996, 1999; Remis 1994; Remis 1997a;

Tutin 1996). Day ranges vary seasonally in relation to fruit abundance; gorillas travel further in the wet season, when fruit consumption is high, than during the dry season, when concentrating on non-fruit foods. Habitats of some western lowland gorilla populations include bais, containing mineral rich herbs (Kuroda et al. 1996; Magliocca & Gautier-Hion 2002), and swamp use has been found to influence ranging behavior for groups in at least one study site, Mondika (Doran & McNeilage 2001; Doran-Sheehy et al. 2004).

When foraging, lowland gorilla groups are less cohesive and exhibit more flexible foraging strategies than other gorilla populations. Group spread is often large, with individuals or small parties temporarily foraging up to 500 m from each other, particularly when feeding on fruit (Bermejo 2004; Doran & McNeilage 1998; Doran & McNeilage 2001; Goldsmith 1996, 2003; Kuroda et al. 1996; Remis 1994; Remis 1997a; Tutin 1996). Different individuals of the same group are frequently observed consuming different food types (e.g., herbs, fruits) simultaneously (Doran & McNeilage 1998; Doran & McNeilage 2001; Kuroda et al. 1996; Remis 1994; Remis 1997a). Formation of temporary subgroups that forage and nest separately for one or more days has been recorded at Bai Hokou and Ndoki, and occurs most frequently during the period of high fruit availability (Goldsmith 1996, 2003; Kuroda et al. 1996; Mitani 1992; Remis 1994; Remis 1997a). On the other hand, groups are also known to peacefully forage in close proximity to others at rare but abundant food resources such as bais and large fruiting trees (Bermejo 1999, 2004; Doran-Sheehy et al. 2004; Olejniczak 1996; Parnell 2002; Stokes et al. 2003; Tutin 1996). At Lossi, some groups also on occasion maintain close proximity (within 30 – 50 m) overnight resulting in supergroup formation (Bermejo 2004).

Based on the greater level of frugivory of lowland gorillas and the lower abundance of herbaceous vegetation in lowland gorilla habitats, socioecological models predict that they should experience higher levels of feeding competition than mountain gorillas. Several lines of evidence suggest that lowland gorillas do experience some level of within-group feeding competition, including increased day range, home range size and group spread, dietary switching by individuals at feeding sites, and occurrence of temporary subgrouping. Though aggressive inter-group encounters are not common at sites for which published data are available (Lopé and Lossi), encounters involving close proximity displays and/or physical contact occur most frequently in relation to access or defense of fruit resources (Bermejo 2004; Tutin 1996); similar results were found for Kahuzi gorillas (Yamagiwa et al. 2003a). This suggests that between-group contest competition may also occur.

Lowland Gorilla Sociality

Despite differences in food availability, diets, ranging behavior, and levels of feeding competition, preliminary evidence suggests that aspects of lowland gorilla sociality (group size, social organization and social relationships) are remarkably similar to those of montane gorilla populations (although some differences are apparent and are discussed below). Group sizes vary across different lowland gorilla populations (2 – 32 individuals), but still tend to fall within the range of mountain gorilla group sizes; mean group sizes are similar as well (4 – 11 individuals) (Bermejo 1997, 1999; Gatti et al.

2004b; Goldsmith 1996; Hall et al. 1998; Magliocca et al. 1999; Mehlman & Doran 2002; Mitani et al. 1993; Parnell 2002; Remis 1993; Tutin & Fernandez 1984; Tutin et al. 1992; Yamagiwa et al. 2003b). Maximum group sizes of lowland groups tend, however, to be lower (< 20 individuals) than montane groups and this suggests that maximum group size may be constrained for most lowland populations (Yamagiwa et al. 2003b). Large groups at Lossi (26 – 32 individuals) likely occur due to superabundant herbaceous vegetation at this site (Bermejo 1999, 2004).

Some aspects of lowland gorilla social organization are similar to that of Virunga gorillas, yet other aspects differ and are more similar to Kahuzi gorillas. Both males and females emigrate from their natal groups and secondary female transfers have been observed (Stokes et al. 2003). Generally, lowland gorillas form stable groups that most often contain only one adult silverback male. Lone males have been observed at all western lowland study sites, but all-male groups have been observed at only one site (Gatti et al. 2004a, b; Gatti et al. 2003). Studies of western lowland gorilla groups at forest clearings report the presence of one-male groups exclusively (Gatti et al. 2004a; Magliocca et al. 1999; Parnell 2002). Multi-male groups have been observed, though rarely, at four western lowland gorilla study sites (Lopé, Mondika, Ndoki, and Bai Hokou) (Doran et al. 2002; Goldsmith 1996, 2003; Mitani et al. 1993; Remis 1994; Remis 1997a; Tutin 1996; Tutin et al. 1992). The subgrouping behavior reported for western lowland gorillas occurred only when groups were multi-male so that each subgroup contains at least one male (Goldsmith 1996; Kuroda et al. 1996; Remis 1994; Remis 1997a).

The above evidence suggest that lowland gorilla females likely benefit from permanent association with at least one adult male that provides protection against infanticide and/or predators. Stokes et al. (2003) describe three cases of putative infanticide at Mbeli Bai, Congo. In addition, females tended to disband and immigrate into existing groups after the death of the resident adult male in a similar manner to Virunga mountain gorillas. Several lines of evidence suggest, however, that rates of infanticide may be intermediate between Virunga and Kahuzi populations.

Stokes et al. (2003) also report four instances of females with dependent infants successfully joining other groups without subsequent injury or death of their infants. Whereas encounters between Virunga gorilla groups are relatively rare and the majority involve aggression (Sicotte 1993), inter-group encounters occur more frequently at western lowland sites but most often involve avoidance, tolerance or peaceful co-mingling (Bermejo 2004; Doran-Sheehy et al. 2004; Levréro et al. 2002; Magliocca & Gautier-Hion 2004). More tolerant relationships between western lowland males may be expected if males ranging in close proximity (in a group or solitarily) are related, as suggested by a genetic study of males at Mondika (Bradley et al. 2004). This high degree of relatedness among neighboring males may produce reduced risks of infanticide in lowland gorilla populations.

In conclusion, lowland and montane gorilla habitats, diets and ranging behavior differ greatly, yet the social organization of the gorillas is remarkably similar. Consequently, lowland gorilla flexible foraging strategies likely sufficiently compensate for any loss of foraging efficiency related to increased frugivory, which allows the formation of relatively stable groups and permanent associations between females and males.

PILOT STUDY RESULTS

I conducted a pilot study between October 1993 and January 1994 to collect preliminary data for the design of my main study (McFarland 1994). I focused on the gorilla population at Afi Mountain gorilla in Nigeria for two reasons: 1) previous surveys had indicated that gorillas existed at a high density at this location (Harcourt et al., 1988; Oates et al., 1990; 1.4-1.8 gorillas/km^2 and 1.3 gorillas/km^2, respectively) and 2) Harcourt et al. (1988) had concluded that this population had the greatest potential for long term research and conservation. During my 3-week survey of Afi Mountain, I found a total of 18 nest sites, including a few fresh sites ($\leq$ 2 days old); number of nests per site ranged between 1 and 16 nests. Brief surveys of the Mbe Mountains and Okwangwo Division of the Cross River National Park yielded no gorilla evidence and confirmed Harcourt et al.'s conclusion.

The Afi Mountain survey covered three different areas or sectors that corresponded to areas with which the three hunters who served as my guides were most familiar. Despite this essentially random delineation of sectors, the frequency of different habitat types, number of large dense gorilla herb food patches and overall herb stem density of each sector appeared to differ quite dramatically. Herbs were most often found in large patches, which were often separated from one another by large distances. Based on evidence available at the time, this pattern of herb availability at Afi contrasted with that of western lowland gorilla habitats at Lopé, Gabon, where gorilla herb foods was reported to be relatively evenly dispersed and occur at densities similar to Mountain gorilla habitats (Rogers & Williamson 1987; Vedder 1984; Watts 1991b).

The frequency of gorilla evidence (i.e., nests, feeding remains, and feces) found in each sector also varied. The majority of nest sites (83%) and feeding evidence was found in one sector (referred to as the Central sector in subsequent chapters) where herb patches and overall density appeared to be the greatest. Little evidence of fruit consumption in feces was recorded but little fruit was available at the time of the survey. Hunters/guides, however, reported that gorillas frequently consumed fruit during other times of the year. These preliminary results suggested that the Afi gorillas' diet varied seasonally as at other western gorilla study sites, and additionally that variation in food availability between sectors might be an important factor influencing Afi gorillas' range use.

Evidence suggesting that hunting might influence ranging behavior was also observed. Hunting of animals for meat by humans was still prevalent on Afi Mountain at this time. I frequently heard gunshots while I was on the mountain and these shots appeared to influence gorilla ranging behavior even when shots were not aimed directly at the gorillas. After shots were heard in one sector, gorilla trails were observed moving toward another sector and no fresh nests were subsequently found in the sector where the shots originated.

SPECIFIC AIMS OF THE STUDY

Since little was known about the Cross River gorilla population before the present study, the main objective was to collect as much data possible to describe the habitat, food availability, diet, ranging behavior and grouping patterns of the Cross River gorillas.

Based on previous primate studies, particularly those of western lowland gorillas, and observations from my pilot study, the following predictions were made. The Afi gorillas' diet was expected to vary seasonally in relation to fruit availability. Specifically, they were expected to consume a wide variety and large amount fruit when it was available and rely on non-fruit vegetation foods (i.e., herb pith, leaves, and bark) when fruit was scarce. In western lowland gorilla habitats, periods of fruit scarcity coincide with the three-month dry season. Dry seasons last up to five months at Afi suggesting that Afi gorillas may experience a prolonged period of fruit scarcity compared to western lowland gorillas and may influence the Afi gorillas' diet.

The predicted highly frugivorous Afi diet was expected to influence their ranging behavior in a manner similar to other frugivorous primates. Afi gorillas were expected to have a large annual home range and were expected to travel longer distances daily when consuming fruit. Based on preliminary observations of Afi gorilla food distribution, food availability and predator pressure was expected to vary spatially across different areas within the Afi gorillas' range and influence their pattern of range use. The Afi gorillas were expected to utilize their range in a non-random fashion reflecting efficient use of their range in relation to food availability and predator pressure. Specifically, Afi gorillas were expected to prefer areas with high food availability in order to increase foraging efficiency, and avoid areas with high hunting pressure.

Since western lowland gorillas consume large amounts of fruit, a patchy widely scattered resource, some have suggested that they should exhibit flexible grouping patterns and this behavior has been observed for study groups, which subgrouping behavior was possible (i.e., multi-male group) (Doran & McNeilage 1998; Doran &

McNeilage 2001; Goldsmith 1996, 2003; Kuroda et al. 1996; Mitani 1992; Remis 1994; Remis 1997a). Preliminary observations suggest that both fruit and herb foods at Afi occur in widely scattered patches. Consequently, there was a high likelihood of observing flexible grouping patterns at Afi, if the study group contained multiple adult males (composition of Afi gorilla groups was not known prior to the present study).

OVERVIEW OF CHAPTERS

Following this introduction, Chapter Two describes the Afi gorilla habitat including altitude, habitat structure, climate, and temporal and spatial availability of tree food resources, and spatial availability of herbaceous vegetation. The following relationships between these aspects are investigated: 1) altitude, habitat structure, and abundance of herbaceous vegetation and 2) climate variables and temporal availability of fruit. Whether food availability differs across sectors observed during the pilot study is also addressed. Finally, aspects of the Afi gorilla habitat, particularly climate and food availability, are compared to other western gorilla habitats. This information allowed me to make more specific predictions about relationships between food availability, diet, and ranging behavior.

Chapter Three describes the Afi gorilla diet using indirect evidence from feces and feeding remains. Species composition and relative contribution of different food categories are described. The relationship between monthly variation in fruit availability and fruit consumption is then investigated to identify periods of high fruit abundance and fruit scarcity in the gorillas' diet. Seasonal variation in the diversity, frequency and abundance of different food categories are then investigated. Finally, important food species are identified on a monthly basis to determine important staple, seasonal, and fallback food species.

Chapter Four describes the ranging behavior of Afi gorillas using information from feeding trails followed during the study. First, home range size and overall habitat use patterns were determined using frequency of quadrat use. Secondly, overall and monthly frequency with which the gorillas utilized different sectors within their home range are employed to identify the gorillas' core area and investigate whether Afi gorillas used their home range randomly or exhibited preference for certain sectors during different months and seasons. To explore why Afi gorillas might have preferences for particular sectors, these results are then related to variation in the spatial availability of herbs and tree food species, as well as the temporal variation in fruit abundance, across sectors. Lastly, day ranges are described and possible factors producing variation in daily path length are investigated including fruit availability and consumption, non-fruit food consumption, climate, predation and spatial variation in food availability across sectors.

Chapter Five provides estimates of the group size and composition of the Afi study group based on night nest counts. In addition, possible factors explaining the observed variation in nest group size are explored and the likelihood that the Afi group exhibits flexible grouping patterns is evaluated.

Chapter Six summarizes the results of the previous chapters on the Afi gorillas' diet, ranging behavior and social organization and compares them to other gorilla populations. Where Cross River gorillas 'fit' within the range of gorilla variation is discussed as well as ecological factors that might explain why they differ from other populations in certain respects.

CHAPTER TWO – ECOLOGY OF THE AFI MOUNTAIN STUDY SITE

INTRODUCTION

As no previous long-term studies had been conducted on Cross River gorillas or at Afi Mountain, this study was the first to provide basic habitat descriptions including: mapping, climate, and vegetation studies. The chapter aims to establish the uniqueness of the Cross River gorilla habitat relative to other gorilla study sites. Thus, whenever possible, comparisons are made to other gorilla studies, particularly those of western lowland gorilla populations. Another goal of this chapter is to provide background for the following chapters.

Food availability has been found to vary both spatially and temporally in gorilla habitats and influences gorilla diet, ranging behavior and grouping patterns (Carroll 1996; Doran & McNeilage 1998; Doran & McNeilage 2001; Doran et al. 2002; Goldsmith 1996, 1999; Kuroda et al. 1996; Nishihara 1995; Remis 1994; Remis 1997a; Remis 1997b; Robbins & McNeilage 2003; Tutin 1996, 2003; Williamson 1989; Yamagiwa et al. 2003). For example, fruit availability at other western sites varies seasonally and has been suggested to be related to rainfall and temperature fluctuations. Abundance of fruit in the gorilla diets varies seasonally as well and has been found to influence gorilla ranging and grouping patterns. Subspecific variation in gorilla diet, ranging behavior and grouping patterns are often attributed to differences in habitat structure among the sites.

Preliminary information indicated that several aspects of the Afi gorillas' habitat, such as climate, altitude, and spatial distribution of important foods (e.g., herbs), differ from other western gorilla habitats. Thus, it is important to document these possible habitat differences in order to understand how they might influence the Afi gorillas' diet, ranging behavior and grouping patterns. The specific aims of this chapter are to: 1) describe the habitat of the study site (e.g., topography, climate), 2) document temporal availability of tree foods and its relationship to climate, 3) determine spatial availability of tree and herb foods and their relationship with altitude and habitat type.

STUDY PERIOD

In March 1996 a Base Camp, at 700m altitude, was established within the Afi Mountain study site (see Figures 2.1 and 2.2). The Base Camp is located 4 km from Buanchor village. Research was conducted during a total of 32 months. From March – December 1996, mapping and the herb enumeration were conducted. From December 1997 – June 1999 gorilla diet, ranging behavior and grouping patterns were investigated. Tree enumeration was the focus of the study during October – December 1999. Between July 1999 and December 2000, collection of climate and phenological data continued under the supervision of James Coleman (employed by conservation organizations to manage the Afi site) and was combined with data from the original study to provide a longer-term dataset.

STUDY SITE LOCATION

The Afi Mountain study site (50 km^2) is located in northern Cross River State, Nigeria, between 6° 15.5' – 6° 24.5' north and 8° 54' – 9° 00' east. The site encompasses the mountainous area (40 km^2) of the Afi Mountain Wildlife Sanctuary (85 km^2), established in May 2000 (Suter & Oates 2000), and is situated within the Afi River Forest Reserve (see Figure 1.2). The Afi Mountain is the most western of the Cross River gorilla localities. It is separated from the other localities by villages, farms and a highway, which lie between Afi Mountain and the nearest Cross River gorilla locality, the Mbe Mountains, which lies 14 km to the southeast (see Figure 1.2). Sixteen villages, with estimated human populations ranging from 500 – 3,000 people per village, surround the Afi Mountain Wildlife Sanctuary (Figure 2.1). Farms abut and in some cases encroach upon the Sanctuary boundary, except along approximately 4.5 km on the western and northeastern boundary. Whereas selective logging occurs in the lowland areas of the forest reserve, no logging has occurred within the study site area because of its rugged terrain.

Previous surveys in 1988 and 1990 estimated that 40 – 50 gorillas inhabited Afi Mountain (Harcourt et al. 1988, 1989; Oates et al. 1990). Those estimates were not, however, based on intensive field research. The present study estimates that there are 25 – 30 gorillas living on Afi Mountain (Oates et al. 2003). Among the Nigerian Cross River gorilla localities, gorilla numbers and density appear to be greatest at Afi Mountain; some Cameroonian localities may contain similar or larger numbers of gorillas (J. Sunderland-Groves, personal communication). Other primates and some of the larger mammals inhabiting Afi Mountain are listed in Table 2.1.

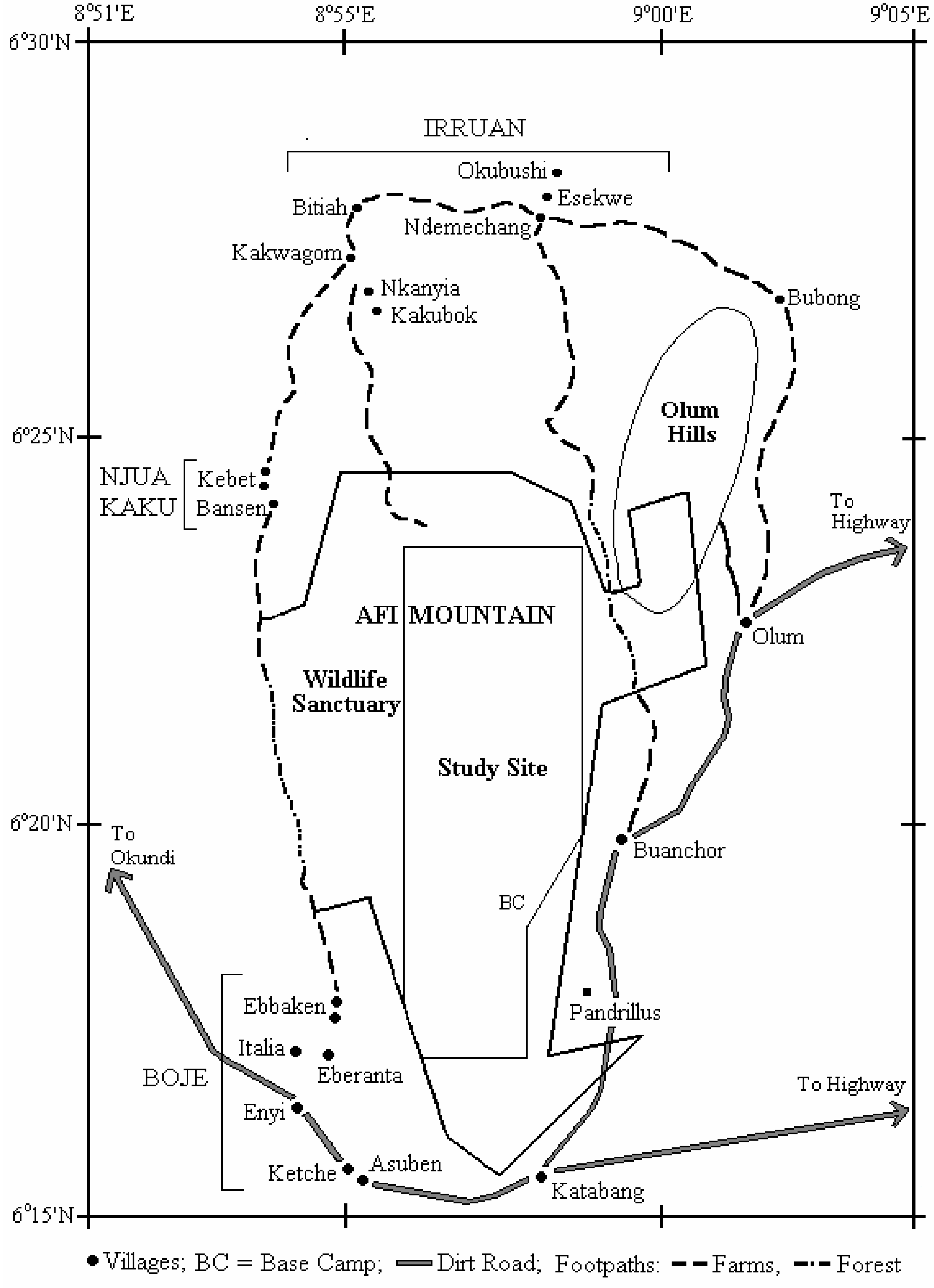


Figure 2.1 The Afi Mountain Wildlife Sanctuary and study site

Table 2.1 List of primates and some other larger mammals present at the Afi Mountain Wildlife Sanctuary (Grubb et al. 2003; Kingdon 1997).

FAMILY	**SPECIES**	**COMMON NAME**
Pongidae	*Pan troglodytes vellerosus*	Nigeria Chimpanzee
	Gorilla gorilla diehli	Cross River Gorilla
Cercopithecidae	*Mandrillus leucophaeus*	Drill Monkey
	Cercopithecus nictitans	Putty-nose Monkey
	Cercopithecus mona	Mona Monkey
	Cercopithecus ascanius	Red-tailed Monkey
Galagidae	*Sciurocheirus alleni*	Allen's Galago
	Galagoides demidovii	Demidoff's Dwarf Galago
Lorisidae	*Perodicticus potto*	Potto
Bovidae	*Cephalophus monticola*	Blue Duiker
	Cephalophus sylvicultor	Yellow-backed Duiker
	Cephalophus dorsalis	Bay Duiker
	Cephalophus ogilbyi	Ogilby's Duiker
Procavidae	*Procavia* sp.	Rock Hyrax
Sciuridae	*Protoxerus stangeri*	Giant Forest Squirrel
Hystricidae	*Atherurus africanus*	Brush-tailed Porcupine
Thryonomyidae	*Thryonomys* sp.	Cane Rat
Manidae	*Uromanis tricuspis*	Tree Pangolin
Viverridae	*Nandinia binotata*	Palm Civet
Suidae	*Potamochoerus porcus*	Red River Hog

HABITAT DESCRIPTION

Afi Mountain is a rocky massif containing several distinct rocky peaks (the highest of which is 1,300 m) separated by deep valleys (reaching down to 200 m). The steep slopes and large rocks make movement difficult for gorillas as well as human observers. Trekking 1 kilometer on the mountain often involves climbing 250 m in altitude and then immediately descending another 250 m. Because no other study had been previously conducted on Afi, a map of the study site was created.

Mapping Methods

To map the study site, describe the habitat, and provide ground reference points to aid recording distances traveled by the gorillas and location of nest sites, an attempt to cut straight-line transects that would delineate 30 1 km x 1 km grid cells was made during March – December 1996. A point in the southwest corner of the study site was randomly selected and transects were cut along north-south and east-west axes corresponding to X and Y coordinates (Figure 2.2). When obstacles were encountered such as large rocks, diversions were made at 90° angles until the diversion intersected the point where the original transect could be continued on the opposite side of the obstacle. Along some of the north lines, obstacles (rocks) were very large and diversions were not possible (i.e., 08, 16, and 20 north lines). In these cases, transects were continued from a different X coordinate (i.e., 09, 18 and 22, respectively).

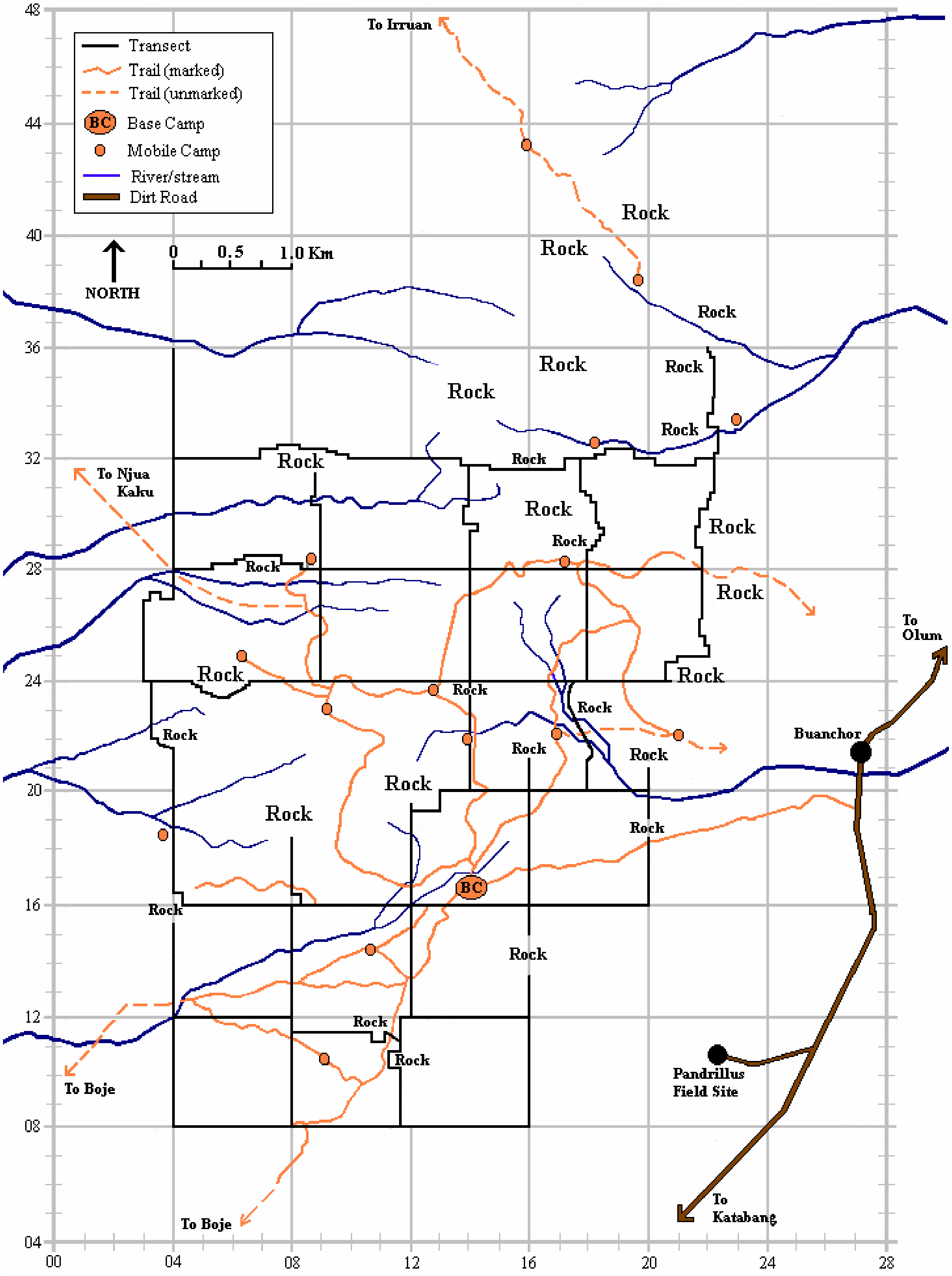
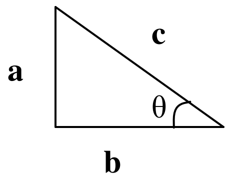


Figure 2.2 Map of Afi Mountain Study Site
(including location of north and east transects)

Due to the rugged terrain, transect cutting proved to be extremely difficult and time consuming and in the end approximately 20 of the 1 km x 1 km grid cells were completed, involving cutting 53 one km transects (Figure 2.2). This proved to be sufficient as it included the majority of the gorillas' range. Transects were marked with flagging every 25m and aluminum tags every 50m (e.g., 08,12 N150 and 12,16 E100). Several previously existing hunter trails were also marked with flagging every 25 m. These markings did not appear to influence the gorillas' behavior. Gorillas used or crossed marked trails and transects regularly, and nest sites often occurred directly on or near them.

After completing the first grid cell, it became clear that because the steepness of the slope along each 1 km transect varied greatly, transect lengths were unequal relative to each other and consequently, the different sides of the cell did not intersect. To account for slope angle variation, a 'corrective distance' (length to correct for slope angle) was added at each 25 m point so that the length of each transect would be equal to 1 km if the slope was flat (0°). Consequently, the ground distance of each transect was actually greater than 1 km. The 'corrective distance' added was calculated using the following formulas based on a right triangle.



Where: c = distance measured on ground
b = actual distance (if slope is flat)
θ = angle of slope

Formula: Actual distance (b) = cosine θ x c
'Corrective distance' = c – b

Angle of slope (using a clinometer) was recorded at least every 25 m and altitude, direction of downward slope, and habitat type were recorded every 50 m. Habitat type was characterized using seven categories that are defined below (see Habitat Type section). At each 50 m point, one of these habitat categories was recorded based on a 360° scan of the habitat. Each scan encompassed a circular area with a radius of approximately 25 m so that they did not overlap and represent independent data points. If during a scan the presence of more than one habitat type was detected, only the dominant habitat type was recorded. Wherever possible latitude and longitude were recorded using a Global Positioning System (GPS) receiver. The presence of rivers and streams, fallen trees and major tree branches, and any evidence that the area had been previously burned were also noted when encountered.

During the pilot study, I observed potential habitat differences (i.e., altitude, frequency of different habitat types, and herb density) distinguishing certain ‘sectors’ within the study site (see Chapter 1). To examine whether these general impressions were accurate, the study site was divided into four relatively equal sectors covering the gorillas’ entire range on Afi (South, Central, West, and North, see Figure 2.7).

The following statistical analyses were conducted on data collected during the mapping exercise. Kruskal-Wallis tests, including individual pair-wise comparisons, were performed (Siegel & Castellan Jr. 1988) to determine whether habitat characteristics (i.e., frequency of habitat types, fallen trees, and fire) differed in relation to altitude and whether altitude and frequency of habitat types vary across study sectors. Regressions were conducted to test if results of the above statistical tests were influenced by variation in sample size of the different measures (e.g., number of plots in each habitat type). None of these regressions produced a significant result for any measures, indicating that the frequency with which each measure was recorded (habitat types, fallen trees, and fire) was not significantly correlated with sample size.

Topography

This small mountain range has five main ridges, running approximately east-west. The topography along the tops of each main ridge undulates between three to four rocky peaks of altitudes between 900 and 1300 m. Secondary ridges, along north-south directions through the center of Afi, form valleys (500 – 900 m altitude) between the tallest peaks of each main ridge. Rivers form on either side of these valleys and flow east or west down to the lowlands through valleys that separate each main ridge. These rivers provide the main water source for the surrounding villages.

Altitude was recorded along 43.7 km of the map transects and averaged 656 m (SD = 244.6, range = 200 – 1185 m, N = 864 records). Figure 2.3 shows variation in altitude recorded every 50 m along each of the ‘north transects’ from the southernmost to the northernmost point. Distance between most ‘north transects’ was 500 m (between 04 and 08/09 transects = 1 km). Figure 2.4 shows variation in altitude recorded every 50 m along each of the ‘east transects’ from the westernmost to the easternmost point. Distance between ‘east transects’ was 1 km. Frequency of rocky peaks on Afi increases from south to north (see Figure 2.7). Variation in the frequency of habitat types, fallen trees, and occurrence of fire with altitude are described in subsequent sections.

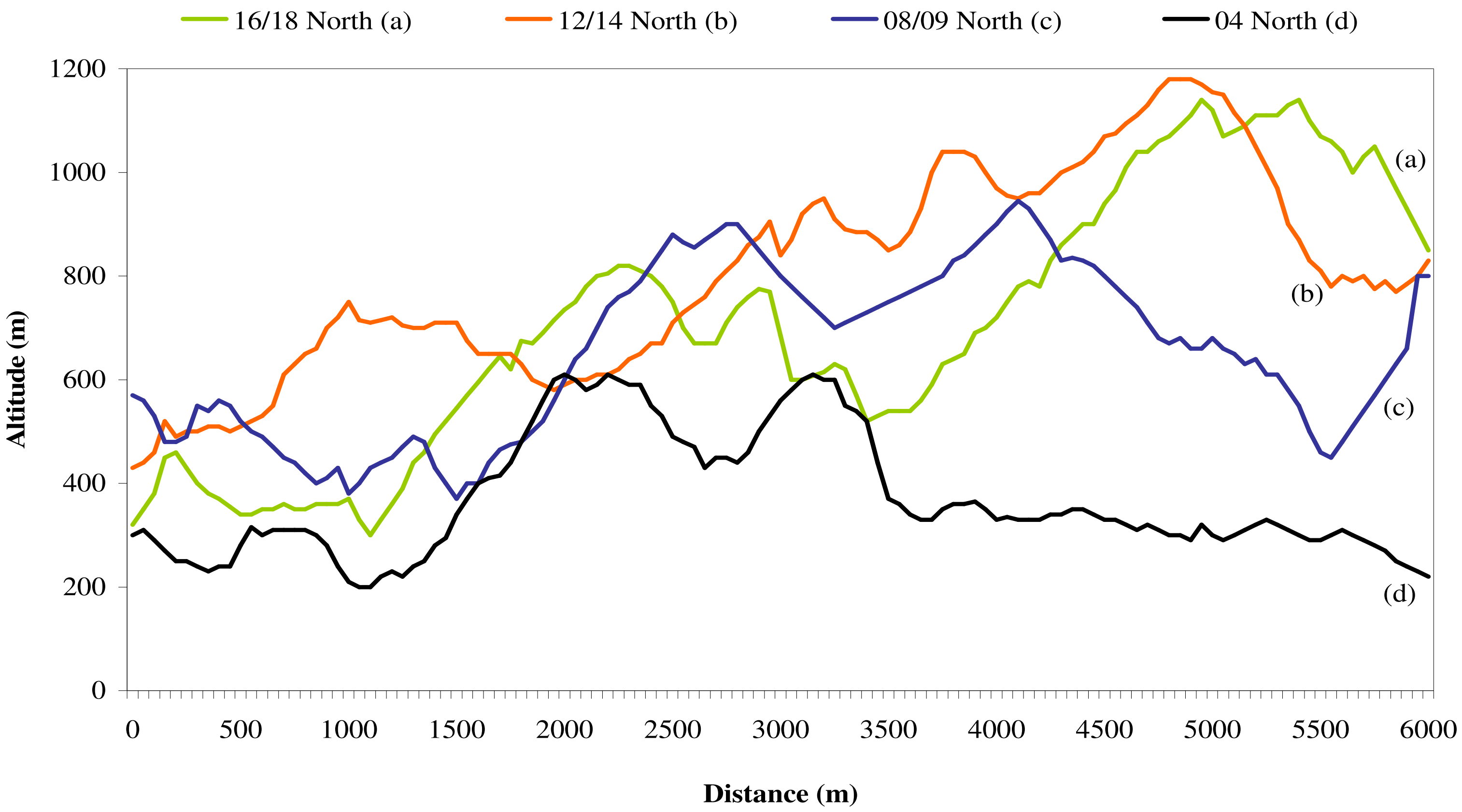


Figure 2.3 Variation in altitude along 'north transects' within the Afi Mountain study site (altitude recorded every 50 m; distance between most transects = 500 m; see text for details)

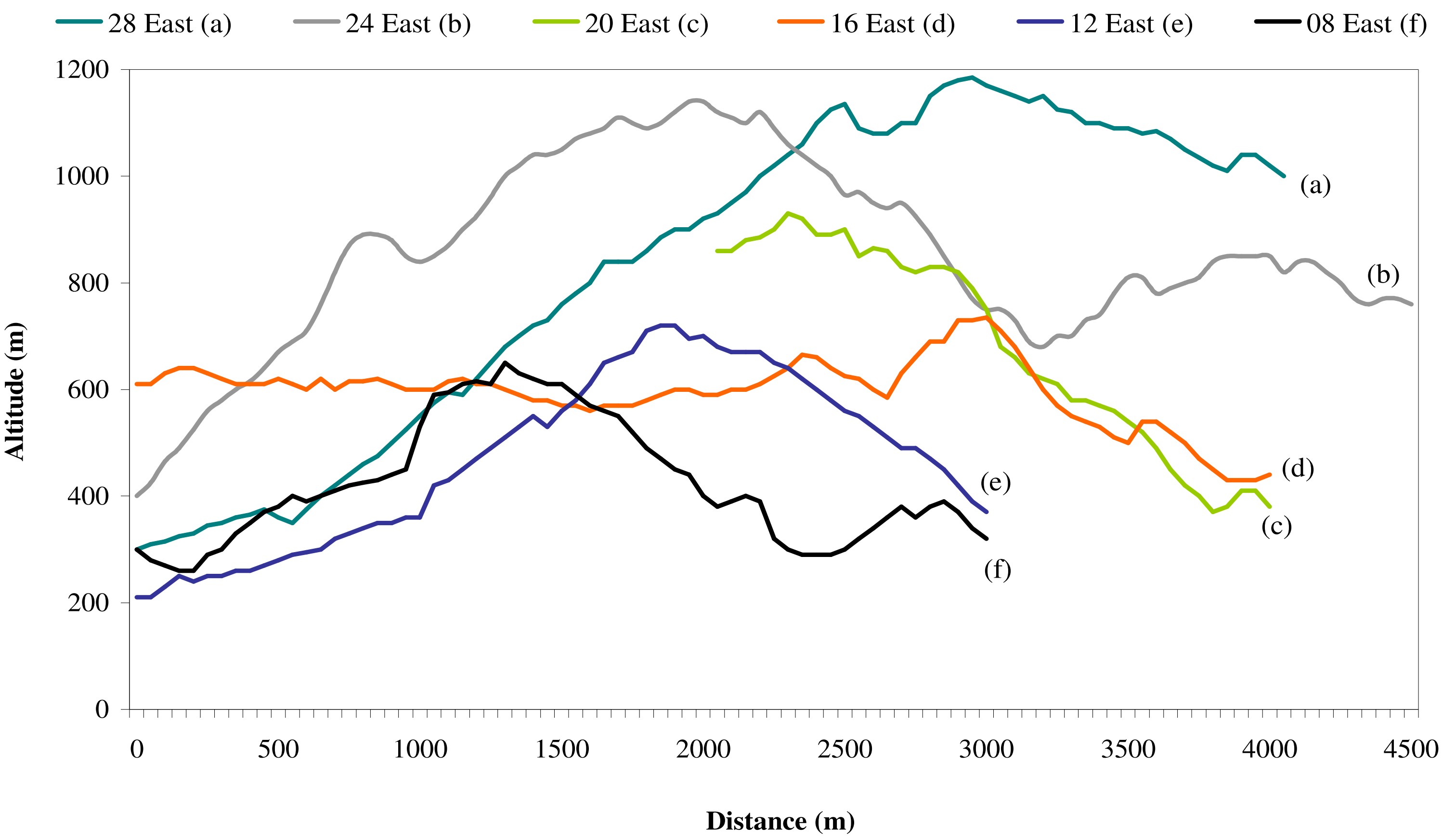


Figure 2.4 Variation in altitude along 'east transects' within the Afi Mountain study site (altitude recorded every 50 m; distance between transects = 1 km; see text for details)

Habitat Types: Overall Frequencies and Variation Across Altitudes

To describe the different habitats present within the Afi Mountain study site, one of the following seven habitat types was recorded every 50 m along 43.5 km of transects. Where noted, these categories are similar to those described for Lopé, Gabon (Tutin & Fernandez 1984; White et al. 1995) and Bai Hokou, Central African Republic (Goldsmith 1996; Remis 1993).

1. Closed Mature Forest: Dominated by large (DBH: ≥ 60 cm) tall mature trees with a continuous canopy and little undergrowth (i.e., saplings and herbs) (similar to open primary forest of Tutin & Fernandez, mature closed canopy forest of White, and primary forest of Remis and Goldsmith).
2. Open Mature Forest: Dominated by medium sized (DBH: 30 – 60 cm) trees with few large trees, a relatively continuous canopy, though slightly less so than in closed mature forest, and some undergrowth (similar to dense primary forest of Tutin & Fernandez, mixed forest of White and Goldsmith, and primary forest of Remis).
3. Secondary Forest: Dominated by small trees (DBH: ≤ 30 cm), with few medium and even fewer large trees, and a relatively discontinuous canopy and abundant undergrowth, compared to closed and open mature forests (similar to gallery forest of Tutin & Fernandez, Marantaceae forest of White, light gap forest of Goldsmith and secondary forest of Remis).
4. Vine Tangle: Secondary forest with abundant lianas and vines, making movement difficult (as in Remis).

5. Forest Gap: Gaps in forest canopy due to presence of large rocks, tree falls, and rockslides, with no tree cover and dominated by grasses, vines, and/or shrubs as described in Nielsen (1965) (similar to thicket of Tutin & Fernandez, disturbed areas of White, and light gaps of Remis).
6. Herb Patch: A forest gap dominated by herbs from the Families Marantaceae and/or Zingiberaceae (similar to thicket of Tutin & Fernandez and road edges of Remis).
7. Rock: Rock with no plant growth. Rocks with a thin soil and vegetation cover were assigned to other habitat types.

For some analyses, habitat types were grouped into larger categories as follows: mature forests (including closed and open mature forest habitat types), secondary forest/vine tangle (including secondary forest and vine tangle habitat types), and light gaps (including forest gap and herb patch habitat types).

Figure 2.5 shows the frequency with which the different habitat types occurred along transects. The most frequently recorded habitat type was secondary forest (44.3%) followed by open mature forest (24.8%), and forest gaps (15.0%) and herb patches (8.8%). The least frequently recorded habitat types were vine tangle (4.4%), rock (1.6%) and closed mature forest (1.0%). Because 6,454 m along transects were diverted around large rocks, frequency of the rock habitat type was greatly underestimated. In addition, 35% of forest gaps and 14% of herb patches occurred on large rocks. Estimated rock sizes range between approximately 50 m^2 and 0.25 km^2.

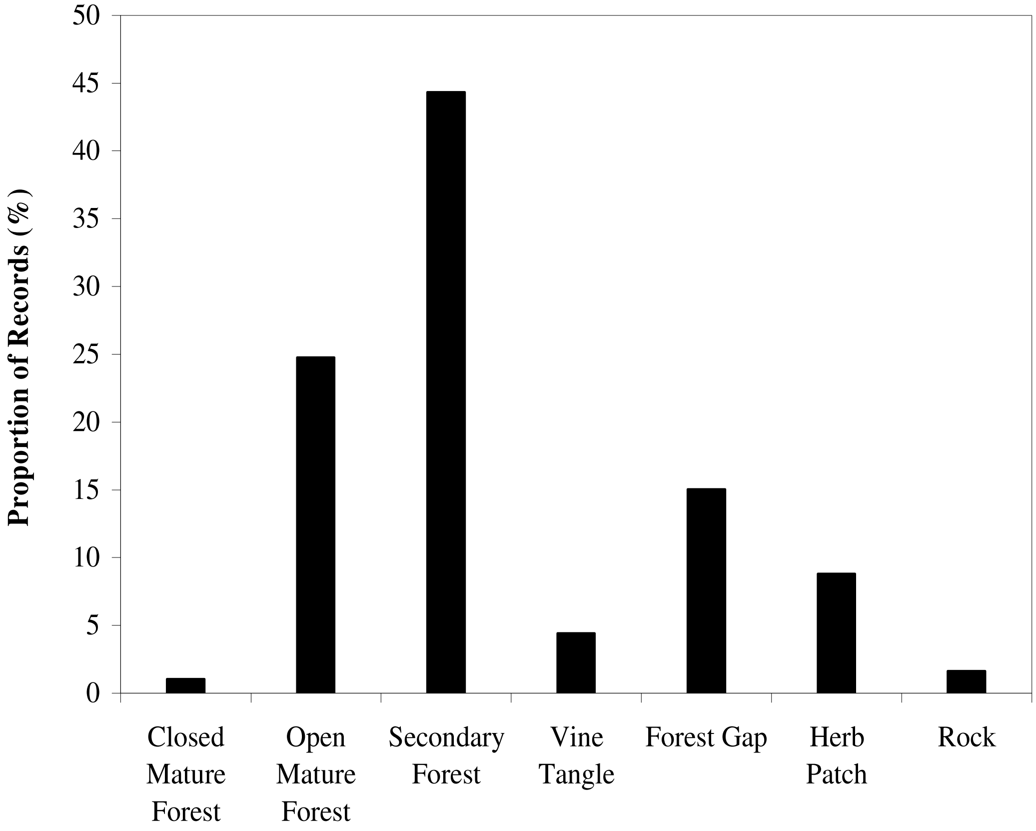


Figure 2.5 Proportion of habitat types along transects
(recorded every 50m; N = 864 records along 43.5 km)

Table 2.2 presents mean altitudes (including standard deviation and range) of the six different habitat types. All habitat types, except one, were present at most altitudes sampled (200 – 1,185 m), but were more frequent at particular altitudinal ranges; closed mature forest was only recorded at altitudes below 610 m. Altitudes differ significantly across habitat types (Kruskal-Wallis: $X^2 = 37.1$, df = 5, $p < 0.001$). Pair-wise comparisons, however, show the following three groupings for which altitude did not differ significantly (p > 0.05) but were significantly different from all other habitat types: 1) closed and open mature forest, 2) secondary forest and vine tangle, and 3) forest gap and herb patch, referred to as light gaps.

Table 2.2 Mean, standard deviation (SD) and range of altitudes for different habitat types within the Afi Mountain study site.

HABITAT TYPE *	**ALTITUDE (m)**		
	Mean	**SD**	**Range**
Closed Mature Forest	422	127	280 – 610
Open Mature Forest	606	207	250 – 1180
Secondary Forest	660	251	220 – 1180
Vine Tangle	649	263	210 – 1180
Forest Gap	714	241	200 – 1160
Herb Patch	750	244	210 – 1150

* Based on Kruskal-Wallis pair-wise comparisons, altitudes of habitat types presented in the same row do not differ significantly (p > 0.05) from each other but are significantly lower or higher than all other habitat types (p < 0.05).

To illustrate the relationship between frequencies of different habitat types and altitude, proportion of the three habitat type groupings listed above were calculated for 200 m increments in altitude (mature forest, secondary/vine forest and light gaps; Figure 2.6). Proportion of secondary forest/vine tangle occurs relatively consistently at most altitudes sampled. There is a negative relationship between altitude and frequency of mature forest habitats, which occur most frequently at or below 600 m. Conversely, light gaps occur more frequently at altitudes between 600 and 1100 m resulting in a positive relationship between frequency of light gaps and altitude. The above results suggest that there is an overall negative relationship between proportion of tree cover and altitude.

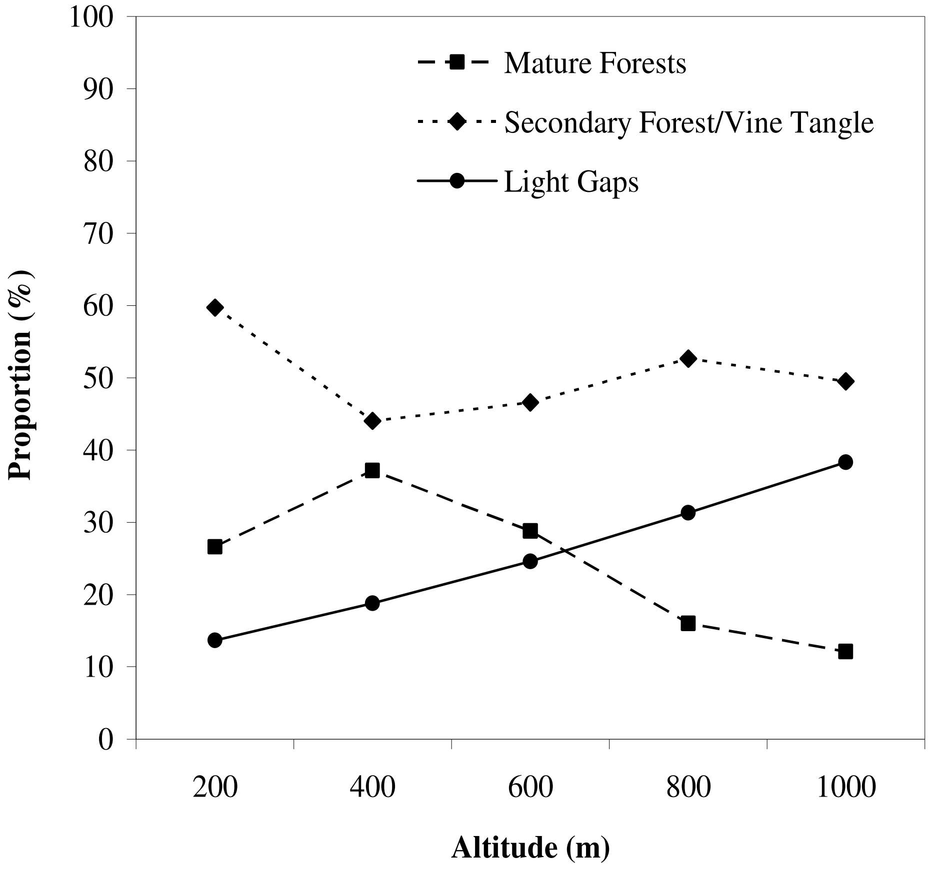


Figure 2.6 Proportion of different habitat types at altitudes in 200 m increments.

Variation in Altitude and Habitat Types Across Sectors

Figure 2.7 shows the location of four different sectors of the mountain and location of major rocky peaks with altitudes ranging between 650 and 1300 m. Frequency of rocky peaks increases from south to north and altitude decreases to the east and west. Map transects did not enter the North sector of the study site, thus statistical analyses were only possible for South, Central, and West sectors. Altitude differs significantly among these sectors (Kruskal-Wallis $X^2 = 350.5$, df = 2, $p < 0.001$; all pair-wise comparisons are significant, $p < 0.05$) and is lowest on average in the South, highest in the Central sector and intermediate in the West (Table 2.3).

Frequencies of habitat types also differed across sectors in relation to altitude (Table 2.3). To test whether frequency of habitat types differed among sectors numeric values were assigned to habitat types reflecting magnitude of tree cover (1 = light gaps, 2 = secondary forest/vine tangle, 3 = closed/open mature forest). Habitat type frequencies differ significantly across sectors ($X^2 = 24.3$, df = 2, $p < 0.001$); however, pair-wise comparisons show that only the South was significantly different than Central and West sectors, which did not differ from each other.

Frequencies of habitat types vary across sectors as expected based on the relationship between altitude and habitat type frequencies for the entire study site described in the previous section. Proportion of secondary forest/vine tangle habitats is relatively consistent across all sectors. Mature forest habitats occur most frequently in the South where altitudes were on average relatively low (below 600 m). Frequency of light gaps is higher in the Central and West sectors, where altitudes are relatively high (above 600 m).

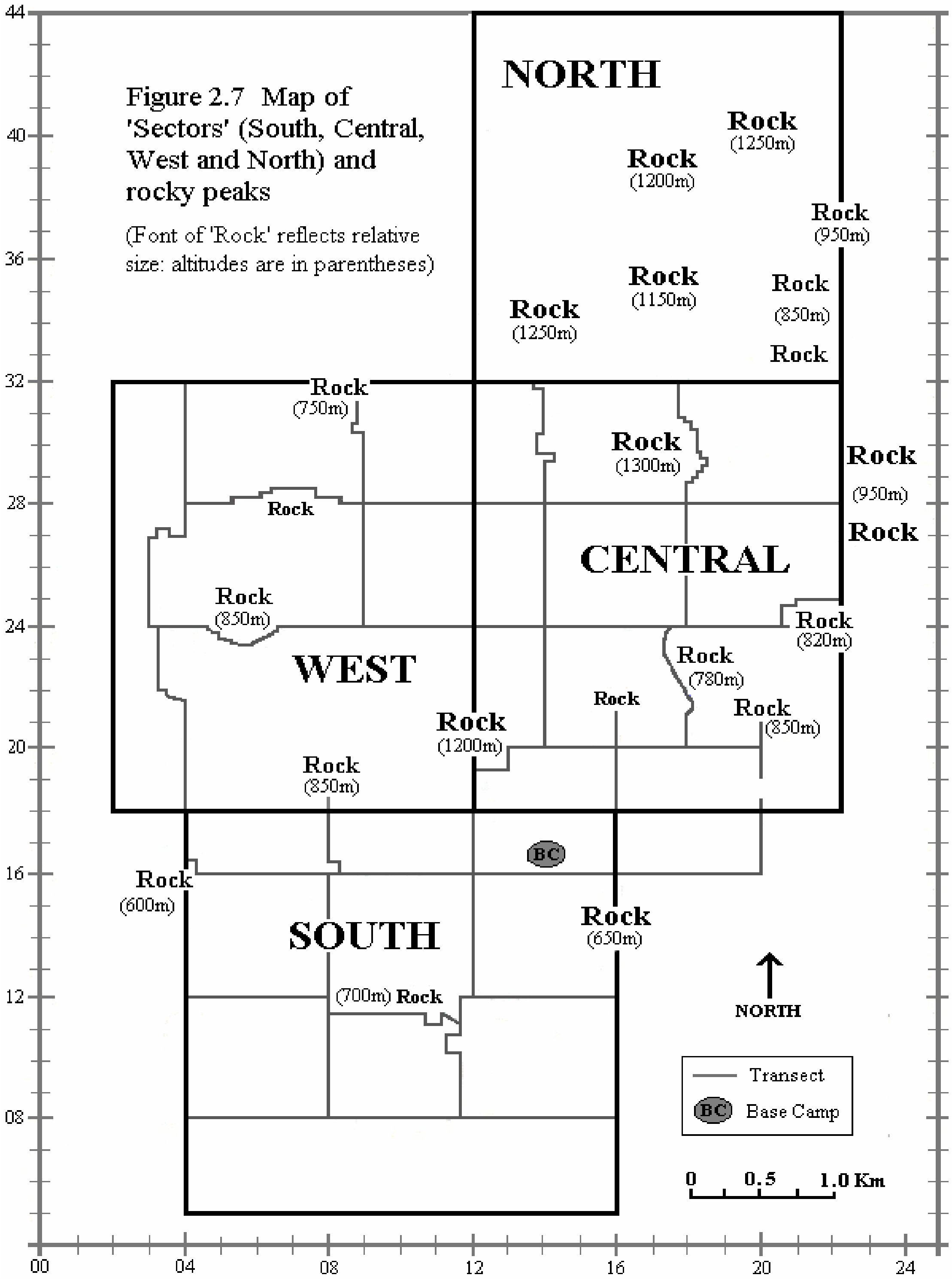


Figure 2.7 Map of 'sectors' (South, Central, West and North) and rocky peaks within the Afi Mountain study site

Table 2.3 Altitude and habitat type frequency across three different sectors (South, Central and West; sample sizes and numeric values for habitat types are in parentheses).

		SOUTH (417)	**CENTRAL** (314)	**WEST** (133)
Altitude (m):	Mean	509	850	670
	Standard Deviation	148	206	230
	Range	200 - 850	340 - 1180	330 - 1140
Habitat Type Frequency:				
	Closed & Open Mature Forest (= 3)	33 %	21 %	18 %
	Secondary Forest/Vine Tangle (= 2)	48 %	49 %	55 %
	Light Gaps (= 1)	19 %	30 %	27 %

Habitat Type Frequency: Proportion of records noted every 50 m along transects.

Though the North sector was not systematically sampled, frequency and altitudes of rocky peaks are known (Figure 2.7). The North sector contains four large rocky peaks of altitudes between 1150 and 1200 m, compared to only two within the Central sector. Thus, mean altitude for the North is most likely higher than all three of the other sectors. Consequently, the frequency of mature forest habitats are likely to be relatively lower and frequency of light gaps to be relatively higher in the North than in the other three sectors.

Fallen Trees

The presence of fallen trees and major tree branches (≥ 30cm diameter) was noted along 38.4 km of map transects. A total of 190 fallen trees and 43 fallen major branches were recorded along transects resulting in a density of 6.0 fallen trees or branches per kilometer. Fallen trees and branches occurred most frequently in secondary forest (50%) followed by forest gap (19%), herb patch (13%), open mature forest (14%), and vine tangle (4%). The majority of fallen trees and branches (73.1%) occurred on relatively steep slopes with angles between 15° and 40°. They occurred most frequently between altitudes of 600 and 1100 m.

Fire

The close proximity of human settlements to the mountain and its long and intense dry season (see Climate section) make Afi particularly vulnerable to fires that are originally set in the lowlands for farm clearing and, due to lack of monitoring, spread onto the mountain. Evidence of fire (i.e., darkened earth, charcoal, damaged trees) was noted when encountered along 44.6 km of transects. Previous to 1996, at least 14% of the study area had been burned. Evidence of fire was recorded most frequently in secondary forest (33.3%), forest gaps (32.2%), and herb patches (19.0%). Burned areas were observed most frequently at altitudes of 300 to 700 m, but were also recorded up to 1100 m (mean = 677.5, SD = 236.8, range = 240 – 1100m). The damaging effects of fire on the forest may occur long after the fire has died out. For example, 34% of fallen trees recorded occurred in previously burned areas.

During 1997 – 2000, at least some portion of Afi Mountain was burned almost every year. In January through March 1997, one of the most devastating fires in many years occurred. Lowland fires spread onto the mountain from all sides burning at least 50% of the vegetation and reaching as far inward as the 14-north line (see Figure 2.2). In February and March 1998, fire burned portions of the southwest reaching to within 750 m of Base Camp. No fires occurred in 1999, most likely due to the unusually high amount of rain during the dry season. However, in January through March 2000, three fires burned the northeast, northwest, and southwest areas on Afi (Coleman 2000).

CLIMATE

Methods

To document seasonal variation in climate, rainfall and temperature were measured at the Afi Base Camp (altitude 700m). Rainfall was collected in a rain gauge placed under the open sky. Rainfall data were recorded in millimeters (mm) once daily at 6:30 AM during April – December 1996, and twice daily at 6:30 AM and 6:30 PM during December 1997 – 2000. Temperatures were recorded daily in Celsius (˚C) using a minimum/maximum thermometer placed in a shaded area within the camp situated within the forest. Rainfall and temperature were also measured once daily (between 6:30 and 7:00 AM) in the lowlands (altitude 150 m) at the Pandrillus Field Station located at the foot of Afi Mountain, 2 km from Afi Base Camp. The thermometer at the Pandrillus field station was placed under a roofed structure in a formerly open area on the edge of the forest.

To better understand how rainfall and/or temperature may influence temporal food availability, it is important to document monthly variation in rainfall and temperature, and the relationship between monthly rainfall and mean temperatures, which was explored using Pearson correlations. Student t-tests were used to compare monthly rainfall and mean temperatures (minimum and maximum) on Afi Mountain and in the lowlands as well as temperatures between seasons.

Rainfall

At the Afi Base Camp, rainfall was collected on 1,401 days during April – December 1996 and December 1997 – December 2000 (46 months total). Mean annual rainfall on Afi Mountain, during 1998 – 2000, was 3528 mm (1998: 3652 mm, 1999: 3422 mm, 2000: 3511 mm). Mean daily rainfall on Afi was 9.7 mm (SD = 18.5, range = 0 – 127 mm/day) and mean monthly rainfall was 296.7 mm (SD = 269.0, range = 0 – 922 mm/month). Figure 2.8 shows the total amount of rainfall on Afi Mountain for each month in which rainfall was collected (see Figure 2.11 for monthly mean rainfall).

Intensity and length of dry and wet seasons varied annually during the present study. Long-term rainfall records collected in neighboring areas, Obudu Town and Obudu Plateau (Hall 1981; Oates et al. 1990) indicate that the more extreme pattern of rainfall observed at Afi in 1998 and 2000 best characterize typical pattern of rainfall seasonality. The dry season (months with < 50 mm of rain) typically lasts for 4 – 5 months (November – March), with up to four months of no or less than 15 mm of rain.

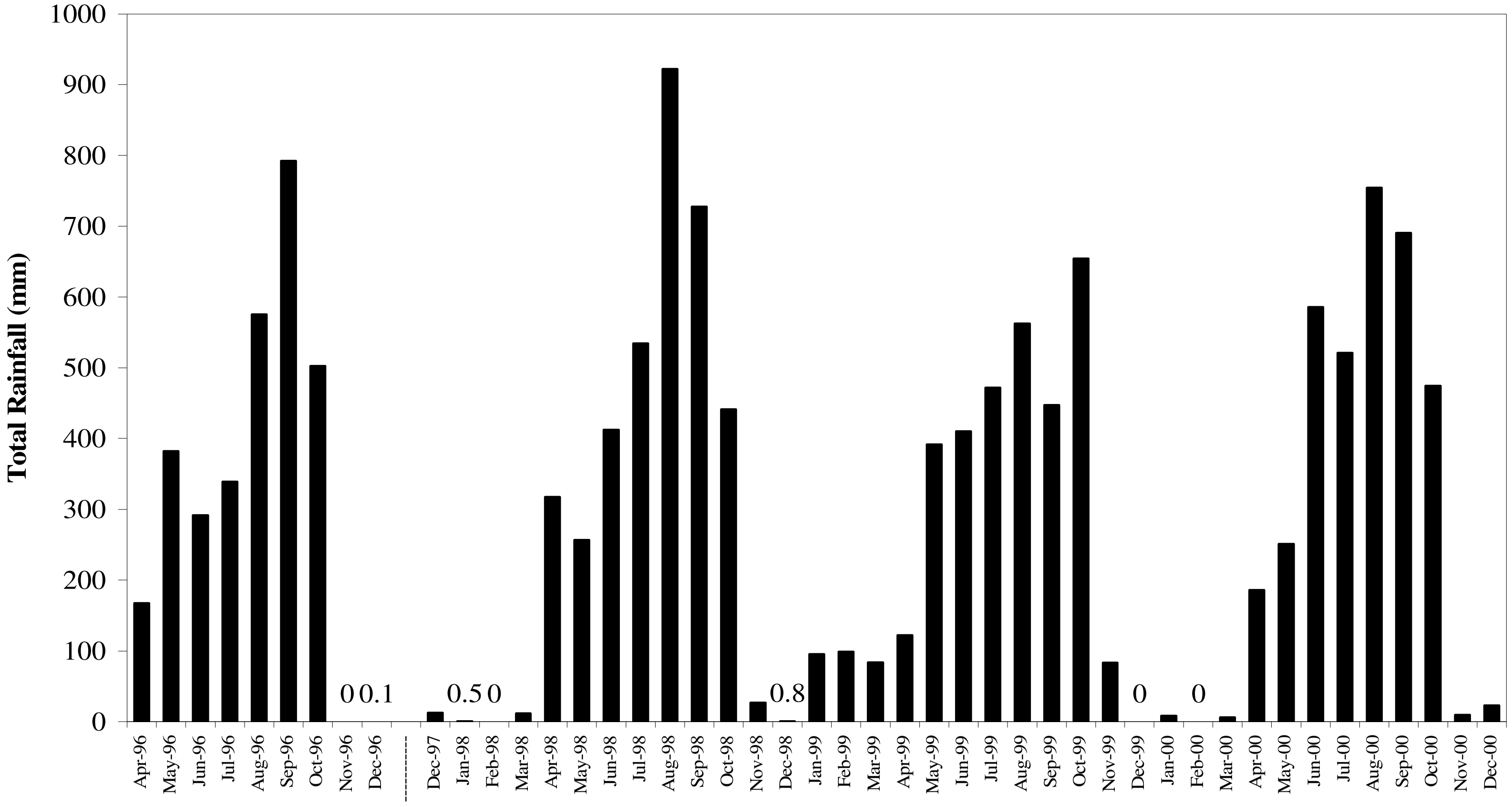


Figure 2.8 Total monthly rainfall on Afi Mountain from April – December 1996 and December 1997 – December 2000

The wet season occurs between April and October, when on Afi between 89% and 99% of the annual rainfall fell during 1998 through 2000. June through October tend to be the wettest months when total monthly rainfall is usually above 400 mm and rain falls on all but a few days during these months. In 1999, an unusual amount of rain fell (but still < 100 mm/month) during the typically dry month of January – March and rainfall was distributed more evenly throughout the year.

Night and Daytime Rainfall

Night and daytime rainfall were collected on 1,127 days between December 1997 and December 2000 (37 months total). Figure 2.9 shows the total night and daytime rainfall for each month sampled. The majority (67%) of rain fell during nighttime hours (6:30 PM – 6:30 AM) and significantly more rain fell during the night than during daytime hours (6:30 AM – 6:30 PM) ($t = 4.88$, $df = 36$, $p = < 0.001$). Mean nightly rainfall averaged 6.3 mm/night (SD = 15.6, range = 0 – 125 mm/night) and mean monthly nighttime rainfall averaged 190.6 mm/month (SD = 186.9, range = 0 – 610 mm/month). By comparison, on average 3.2 mm of rain fell during the daytime (SD = 8.0, range = 0 – 83 mm/day) and mean monthly daytime rainfall averaged 95.8 mm/month (SD = 96.5, range = 0 – 312 mm/month).

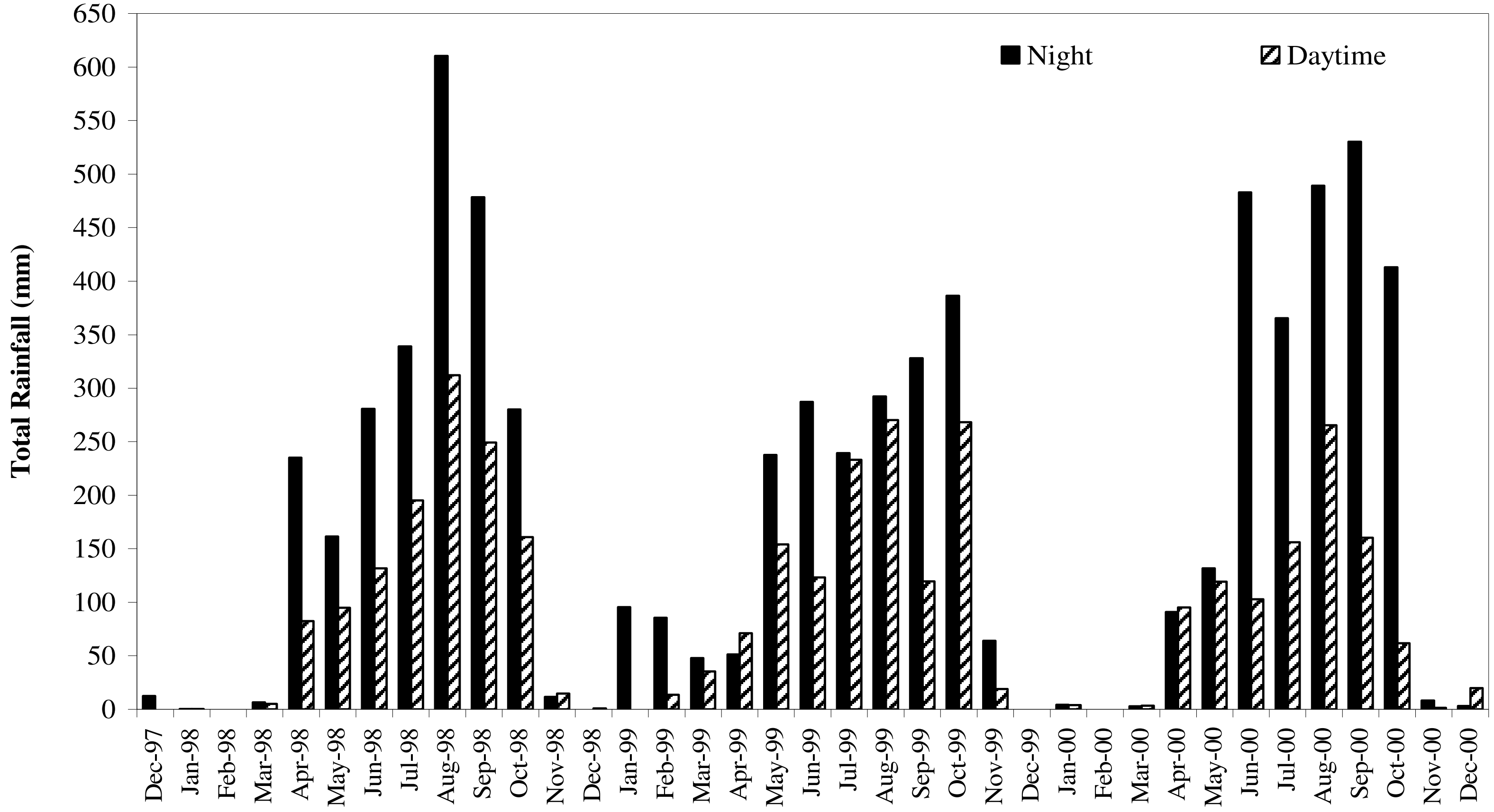


Figure 2.9 Total monthly night and daytime rainfall on Afi Mountain for December 1997 – 2000

Temperature

At the Afi Base Camp, temperature (minimum/maximum) was collected on 1,386 days between April to December 1996 and December 1997 to December 2000 (46 months total). Mean temperature during the study period was 22.2 °C (SD = 1.36, range = 19 – 27 °C). Daily minimum temperatures averaged 18.7 °C (SD = 1.42, range = 14–24°C) and daily maximum temperatures averaged 25.7 °C (SD = 2.0, range = 21 – 33 °C). Figure 2.10 shows mean monthly minimum and maximum temperatures on Afi Mountain (also see Figure 2.12). Mean monthly minimum temperatures ranged from 16.3 – 20.6 °C and mean monthly maximum temperatures ranged from 23.3 – 28.7 °C.

Nights are coolest during December – February (middle of dry season), with mean monthly minimum temperatures of 17.2 – 18.5 °C. In contrast, days are coolest during July – October (the wettest months), with mean maximum temperatures of 23.7 – 24.6 °C. Days are warmest during February – May (end of the dry and beginning of wet season), with mean maximum temperatures of 27.1 – 27.6 °C. Consequently, months with coolest and warmest temperatures overlap seasons. However, during dry season months, minimum temperatures were on average (18.2 °C) significantly lower than wet months (19°C; $t = 9.44$, $df = 784$, $p < 0.001$), and maximum temperatures were on average (26.2°C) significantly higher than wet season months (25.5°C; $t = 8.89$, $df = 1375$, $p < 0.001$).

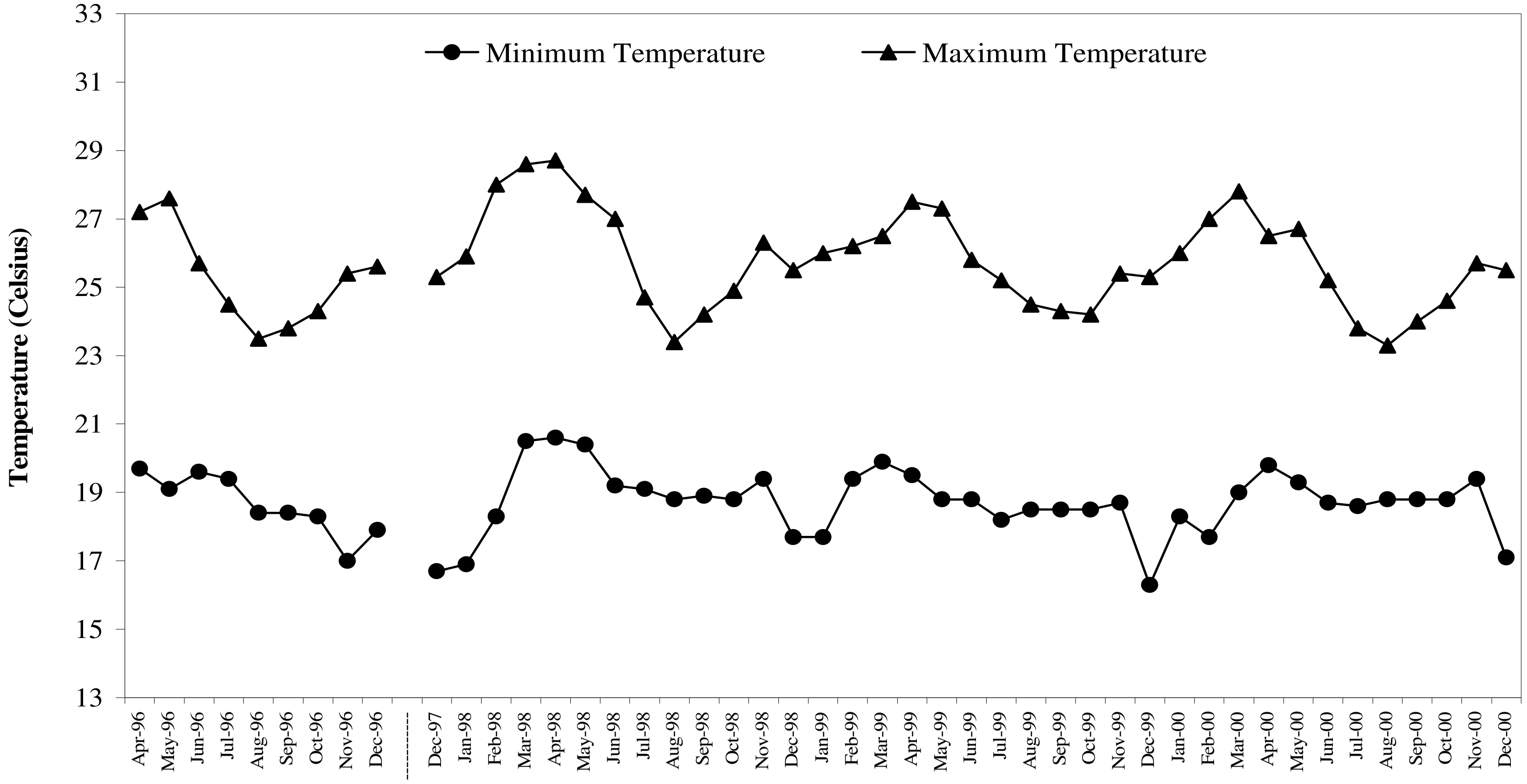


Figure 2.10 Mean monthly minimum and maximum temperatures on Afi Mountain from April – December 1996 and December 1997 – December 2000

Comparison Between Afi Mountain and the Lowlands

Figures 2.11 and 2.12 compare mean monthly total rainfall and temperatures between the Pandrillus Field Station in the lowlands and on Afi Mountain during 1996 and from December 1997 through December 2000 when rainfall was recorded at both sites. Monthly rainfall was significantly greater on the mountain than in the lowlands ($t = 3.86$, $df = 45$, $p < 0.001$), but the greatest differences occurred during the height of the wet season (July – September).

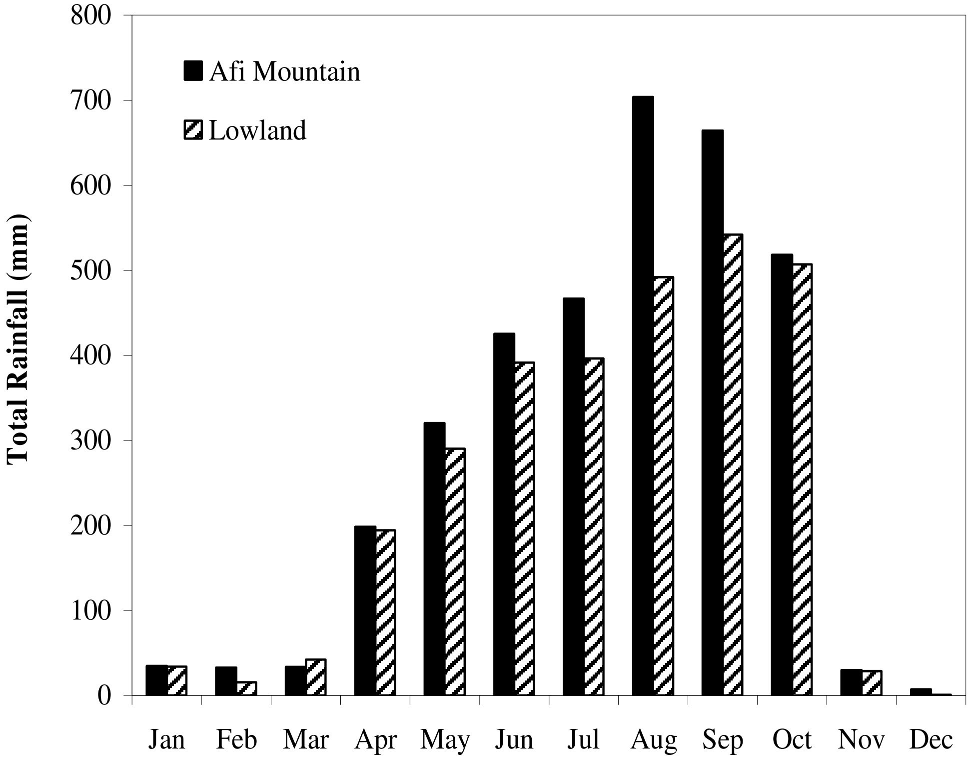


Figure 2.11 Average monthly total rainfall at Afi Mountain and in the lowlands (at Pandrillus Field Station)

Whereas patterns of monthly variation in temperature are similar at both sites (Figure 2.12), minimum and maximum temperatures on Afi were significantly lower than in the lowlands (Minimum: t = -69.5, df = 1319, p < 0.001; Maximum: t = -89.9, df = 1353, p < 0.001). This difference may be partially explained by the fact that the Pandrillus Field Station is located in an open area and consequently, the thermometer was less shaded than at the Afi Base Camp, which is situated within the forest. Lower temperatures on Afi Mountain, however, are more likely related to its higher altitude.

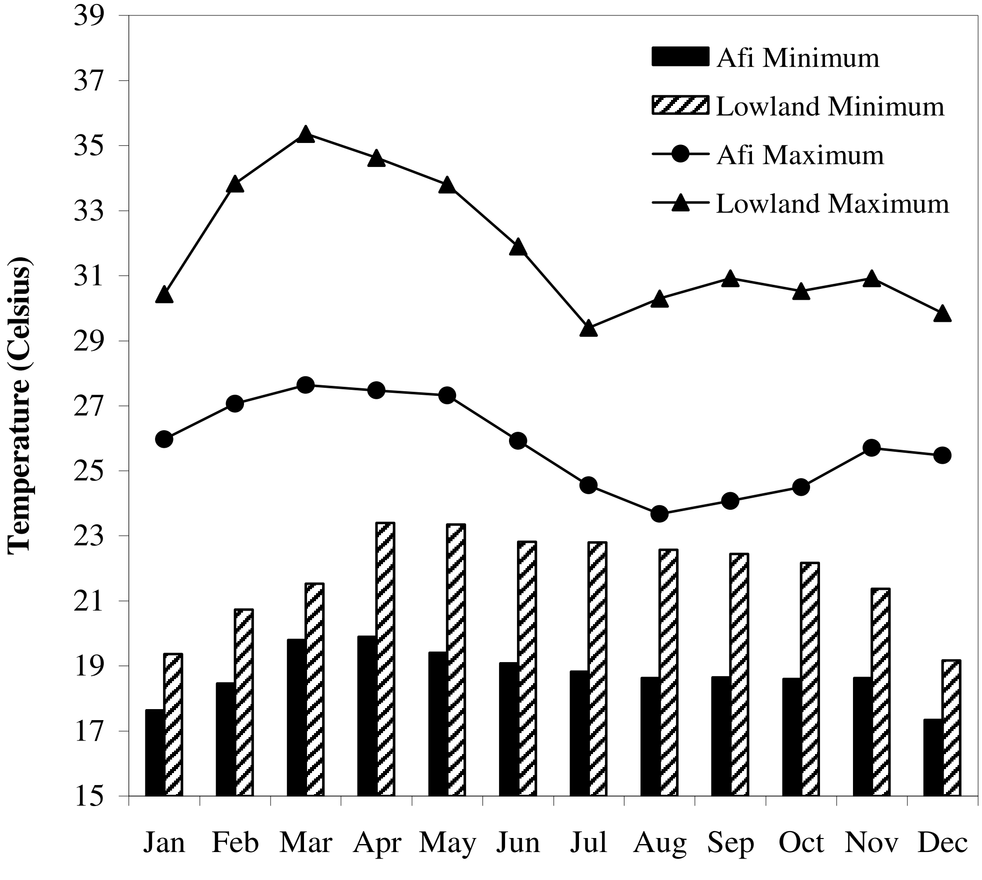


Figure 2.12 Average mean monthly minimum and maximum temperature on Afi Mountain and in the lowlands (at Pandrillus Field Station)

Relationship between Rainfall and Temperatures

Relationships between rainfall and temperatures on the mountain and in the lowlands differed. Table 2.4 summarizes the results of correlations between rainfall and temperature at Afi and in the lowlands. There was a moderate, but significant, positive correlation ($r = 0.569$, $p < 0.001$) between lowland minimum temperature and rainfall. In contrast, significant correlations at Afi were between maximum temperature and total, nighttime, and daytime rainfall ($r = -0.630$, -0.642, and -0.578, respectively, $p < 0.001$) and between mean temperature and total and nighttime rainfall ($r = -0.362$ and -0.367, $p < 0.03$). The difference between Afi and the lowlands is most likely related to the more dramatic increase in rainfall during August and September on Afi Mountain when maximum temperatures are the lowest.

Table 2.4 Correlation (r) matrix between rainfall and temperature on Afi Mountain and in the lowlands (at Pandrillus Field Station).

	AFI MOUNTAIN				**LOWLAND**
	Total rainfall (n = 46)	**Nighttime rainfall** (n = 37)	**Daytime rainfall** (n = 37)		**Total rainfall** (n = 57)
Mean minimum temperature	0.183	0.176	0.175		0.569**
Mean maximum temperature	-0.630**	-0.642**	-0.578**		-0.219
Mean temperature	-0.362*	-0.367*	-0.322		0.098

* $p < 0.03$, ** $p < 0.001$

See Discussion for comparisons of climate between Afi Mountain and other gorilla study sites.

TEMPORAL AVAILABILITY OF TREE FOODS

Phenology Methods

The temporal availability of young leaves, flowers, and fruits was determined by monitoring trees on a monthly basis along 6.5 km of trails (4.5 km on trails emanating from Base Camp and 2.0 km on randomly selected transects) between May 1998 and December 2000 (32 months). Tree species suspected to be consumed by gorillas, including those species from which gorillas eat fruit and leaves, were selected based on published studies of western lowland gorillas and hunter interviews. As additional gorilla food species were identified from fecal analysis and feeding evidence, trees of these species were added to phenology trails. In 2000, trees along eight 250 m randomly selected tree enumeration transects were also monitored (see Figure 2.21). Many of these additional species are not known gorilla foods; thus, data from 2000 are more representative of availability of phenophases in the forest as a whole than data collected in 1998 and 1999. Only mature trees, which produce fruit, were selected based on tree height category and diameter at breast height (DBH): 1) Upper Canopy trees: ≥ 30 cm dbh, 2) Mid-story trees: ≥ 20 cm dbh, and 3) Understory trees: ≥ 3 cm dbh. The DBH of phenology trees averaged 34.3 cm (SD = 31.8, range = 3.1 – 251.0 cm).

Species were identified using *Trees of Nigeria* (Keay 1989)and *Nigerian Trees* (Keay 1989; Keay et al. 1964) and *Field Guide to the Forest Trees of Ghana* (Hawthorne

1990), and with the assistance of a retired Chief Ranger of the Cross River State Forestry Department. Plant samples were collected and preserved.

From May 1998 to October 1999, 397 trees of 63 species and from November – December 1999, 453 trees of 75 species with 1 – 21 individual trees/species were monitored. In 2000, 880 trees of 156 species with 1 – 34 individual trees/species were monitored including trees along eight 250 m tree enumeration transects. Appendix I for list of species and number of individual trees per species monitored during 1998 – 1999 and 2000. The number of trees monitored each month also varied because a total of 16 trees died, fell, or were severely damaged by other fallen trees during the study. In addition, only 283 trees were monitored in October 2000.

Phenology trails were monitored during 4 – 6 days of each month. For the first six months Peter Eshin, a local field assistant, and I conducted monitoring together. Thereafter, monitoring was conducted by Peter Eshin and in 2000, by Peter Eshin and Donatus Nyiamson. For each tree, the presence of young leaves, flowers, and fruit (both unripe and ripe) was noted and abundance was estimated based on percentage of potential production present. This estimate was recorded by rounding to the nearest percentage represented as one of the following six abundance scores: 0 = none present, 0.5 = ≤ 15% of potential production, 1 = 25% of potential production, 2 = 50% of potential production, 3 = 75% of potential production, and 4 = 100% of potential production (Williamson 1989).

Young leaves were identified based on size and color, and included newly produced leaves as well as fully opened leaves which remained a brighter green, yellow, or red color. The presence of ripe fruit was also noted and abundance estimated using the same 0 to 4 point scale described above but based on proportion of fruit present at time of monitoring rather than potential crop. Ripe fruit was identified by color and/or fact that it had fallen to the ground; however, it was difficult to distinguish unripe and ripe fruit for many species (see below for details).

To demonstrate monthly variation in availability of young leaves, flowers, and fruit, three measures were determined: 1) proportion of individual trees with that phenophase, 2) proportion of species with that phenophase, and 3) an abundance index, which is based on abundance scores for each phenophase and calculated as (sum of abundance scores/number of trees sampled) x 100 (van Schaik 1986). Fruit availability was investigated using four different categories including:

1. Fruit (unripe and ripe) in the entire phenology sample ('all fruit'),
2. Ripe fruit = ripe fruit from the entire sample (ripe 'all fruit'),
3. 'Gorilla fruit' = both unripe and ripe fruit eaten by gorillas,
4. Ripe 'gorilla fruit' = ripe fruit eaten by gorillas.

Fruit eaten by gorillas includes tree species that Afi gorillas consumed during the present study identified based on presence in fecal samples and/or along feeding trails, or that gorillas were suspected to eat based on previous western lowland gorilla studies and hunter interviews (see Appendix I for list). Proportion of individual trees, proportion of species, and the abundance index were positively and significantly correlated for each phenophase separately (young leaves, $r_s = 0.85 – 0.93$; flowers, $r_s = 0.90 – 0.98$; 'all fruit', $r_s = 0.91 – 0.99$; ripe 'all fruit', $r_s = 0.83 – 0.90$; 'gorilla fruit', $r_s = 0.91 – 0.98$; ripe 'gorilla fruit', $r_s = 0.90 – 0.93$; $p < 0.01$; $n = 32$ months).

To investigate how climate may be influencing the temporal availability of tree foods, two-tailed Spearman rank correlations were performed between different climate measures (total rainfall and mean minimum and maximum temperature) and proportion of individual trees and species of each phenophase. Seasonal variation (dry versus wet season months) was examined for each phenophase and two-tailed independent t-tests were used to determine significant differences. Since different phenology measures were significantly correlated for each phenophase (see above) and results of seasonal comparisons were similar for each of the different phenology measures, results using mean proportion of individual trees only are reported for each phenophase.

Results should be interpreted cautiously for the following reasons. During 1998 and 1999, my assistant and I had difficulty distinguishing ripe from unripe fruit; however, in 2000, our ability to distinguish ripe fruit was much improved due to experience gained in previous years and additional training provided at end of 1999. During 1999, several important fruit species for the gorillas during February and March were not included in the sample (they were monitored in 2000). In 1999, the monthly rainfall pattern was atypical while in 2000 a more typical pattern occurred. Short-term fluctuations in rainfall and temperature have been suggested to produce deviations from typical cycles of phenophases (Anderson 2001). Therefore, phenology data collected in 2000 likely represent the more typical pattern of temporal food availability variation, particularly ripe ‘gorilla fruit’ availability.

Temporal Availability of Young Leaves

Figure 2.13 shows monthly variation in the proportion of individual trees and species with young leaves and in abundance index (mean abundance scores x 100). The proportion of individual trees with young leaves averaged 34.9% per month (SD = 12.0%, range = 15.4 – 56.6%), the proportion of species averaged 60.6% per month (SD = 14.7%, range = 28.7 – 83.3% species) and the abundance index averaged 34.7 per month (SD = 15.8, range = 12.3 – 86.3). Though peaks in young leaf availability occurred during some months (November – January and May – July), leaf renewal generally occurred continuously at a relatively low rate throughout the study period. The proportion of individual trees with abundance scores of 0.5 – 1 (≤ 25% of potential crop) ranged from 12.1% to 43.5% with an average of 28.4% per month. In addition, the majority of individual trees and species produced young leaves during the study. In 1998 (May – December), 1999 and 2000 between 78% and 97% of the individual trees and between 87% and 100% of the species produced young leaves.

Table 2.5 presents Spearman rank correlations between young leaf availability (proportion of individual trees and species, and abundance index) and climate (total monthly rainfall, and mean monthly minimum and maximum temperatures), and seasonal variation (dry versus wet months) in availability of young leaves. Most measures of young leaf availability did not significantly correlate with rainfall or minimum and maximum temperatures; abundance index was significantly related to rainfall ($r_s = -0.45$) and maximum temperature ($r_s = 0.43$). No measures of leaf availability differed significantly between dry and wet season months ($t = 0.60 – 1.37$, $p = 0.183 – 0.552$, df = 30 months).

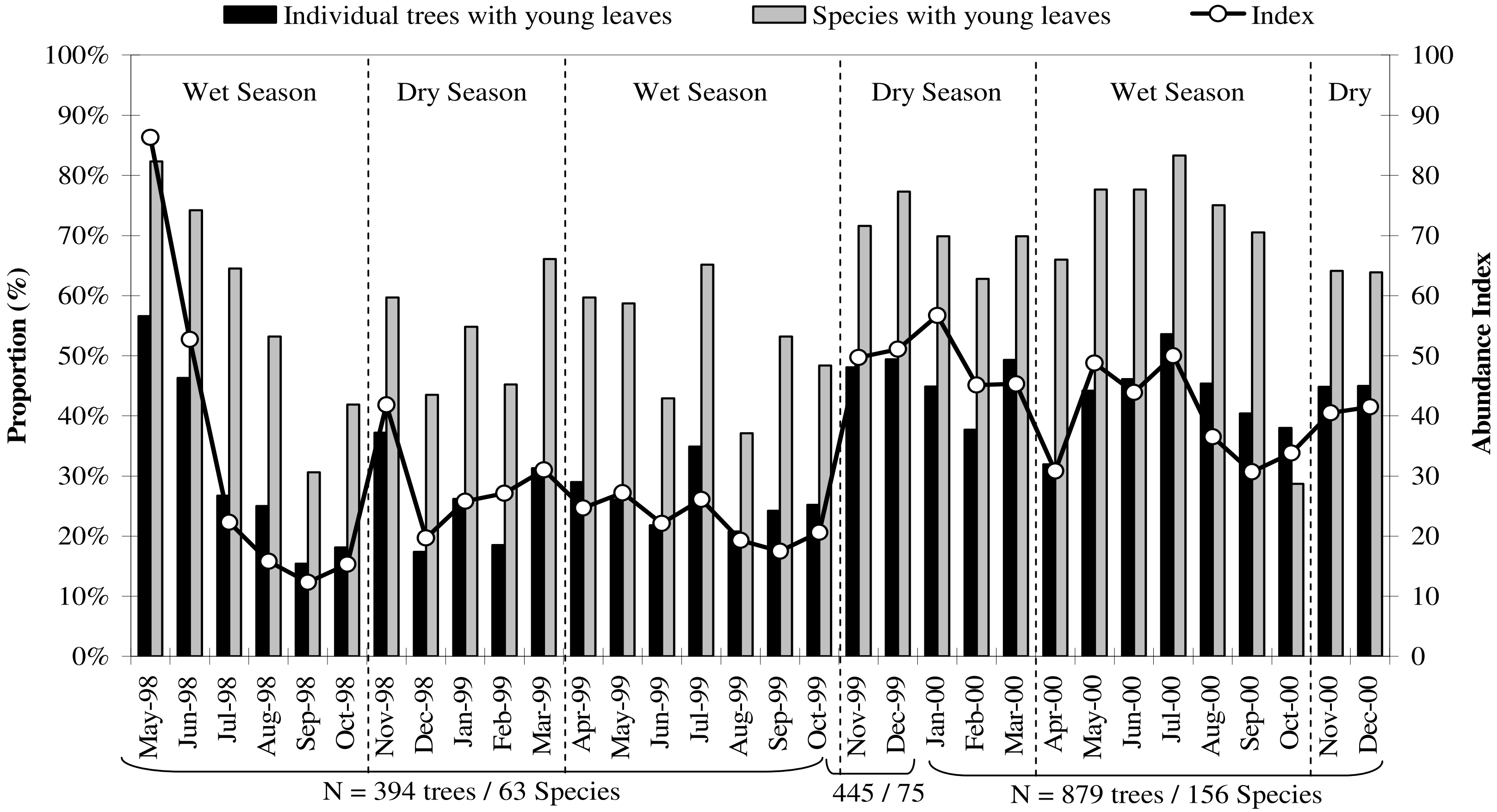


Figure 2.13 Proportion of individual trees and species with young leaves and abundance index

Table 2.5 Relationship between young leaf and flower availability and climate, and seasonal variation for all phenological measures (proportion of individual trees, proportion of species in parentheses and abundance index in brackets).

	YOUNG LEAVES	**FLOWERS**
CLIMATE (Spearman rank correlations, r_s)		
TOTAL RAINFALL	-0.24 (-0.18) [-0.45*]	-0.83** (-0.81**) [-0.83**]
MINIMUM TEMPERATURE	0.02 (0.13) [0.07]	-0.05 (-0.05) [-0.12]
MAXIMUM TEMPERATURE	0.20 (0.24) [0.43*]	0.66** (0.70**) [0.59**]
SEASON (Mean)		
DRY	37.5% (62.4%) [39.6]	13.0%*** (20.8%***) [26.1***]
WET	33.4% (59.2%) [31.8]	4.5% (11.2%) [8.2]

* Significant at the 0.05 level (2-tailed)
** Significant at the 0.01 level (2-tailed)
*** Significantly greater than wet season months, $p < 0.001$

Temporal Availability of Flowers

Figure 2.14 shows monthly variation in the proportion of individual trees and species with flowers and in abundance index (mean abundance scores x 100). The proportion of individual trees with flowers averaged 7.7% per month (SD = 6.0%, range = 0.5 – 21.4%), the proportion of species averaged 14.8% per month (SD = 7.1%, range = 3.0 – 27.6% species) and the abundance index averaged 14.9 per month (SD = 12.2, range = 0.5 – 42.9). In general, flower availability was relatively high during dry months (November – March), peaked in January or February, was intermediate at the beginning of the wet season (April – May), and was lowest during the wettest months (July – October).

Table 2.5 (column 3) presents Spearman rank correlations between different measures of flower availability and climate, and seasonal variation (dry vs. wet months). All measures of flower availability were highly, significantly, and negatively related with rainfall (r_s = -0.81 and -0.083) and were significantly greater during dry compared to wet season months ($t = 4.86 – 5.71$, $p < 0.001$, df = 30). All measures of flower availability were positively and significantly correlated with maximum temperature, which was highest during February – May and negatively correlated with rainfall (see climate section).

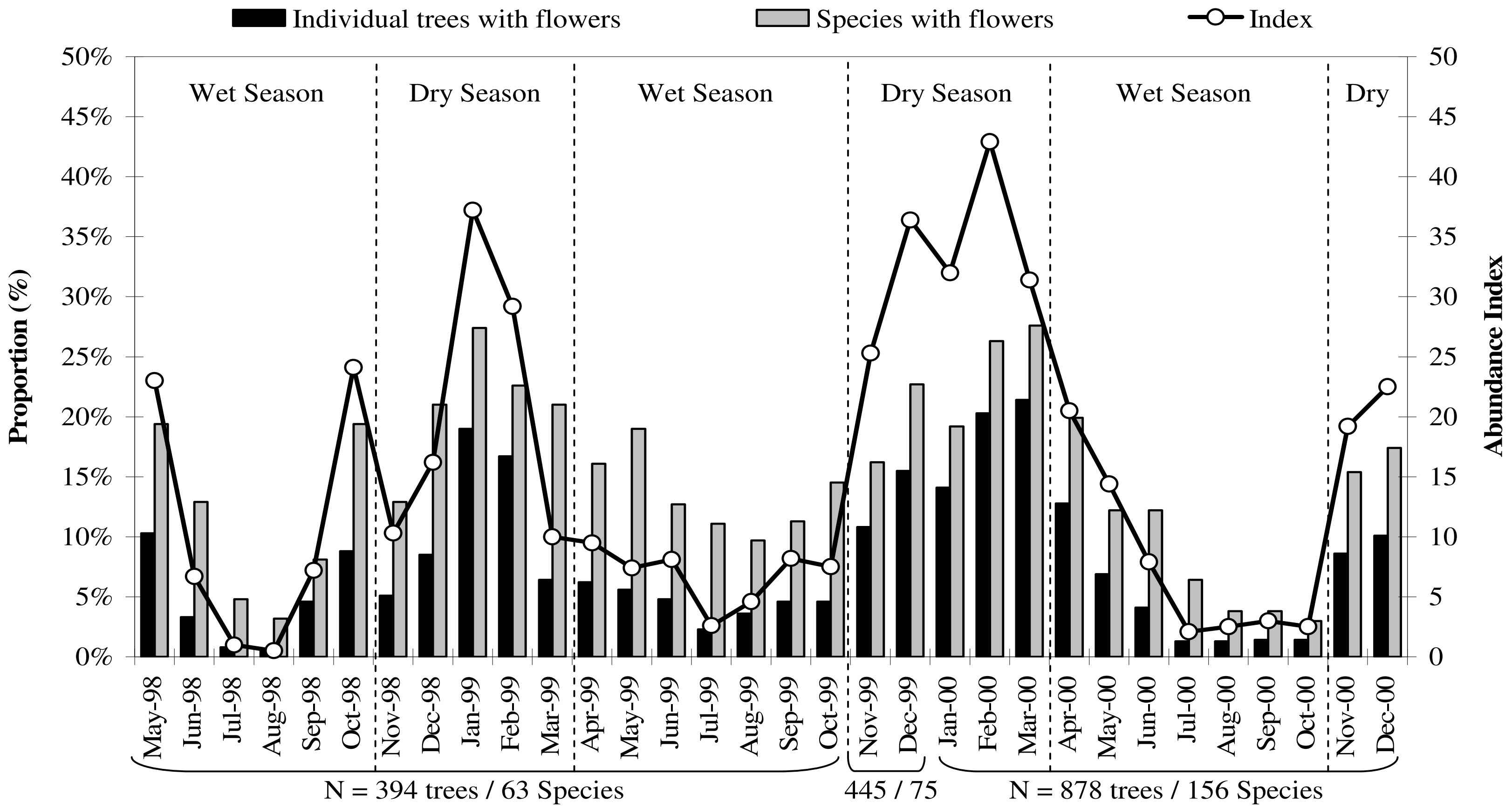


Figure 2.14 Proportion of individual trees and species with flowers and abundance index

Temporal Availability of Fruit

Figure 2.15 shows monthly variation in the proportion of individual trees and species with fruit (unripe and ripe, ‘all fruit’) and in abundance index. The proportion of individual trees with fruit averaged 14.6% per month (SD = 9.1%, range = 2.4 – 40.1%), the proportion of species averaged 31.7% per month (SD = 15.9%, range = 5.9 – 69.4%) and the abundance index averaged 29.8 per month (SD = 18.8, range = 4.7 – 85.2). Figure 2.16 shows monthly variation in proportion of individual trees and species with fruit eaten by gorillas (unripe and ripe, ‘gorilla fruit’) and abundance index. Proportion of individual trees with ‘gorilla fruit’ averaged 14.7% per month (SD = 10.1%, range = 1.3 – 39.0%), proportion of species averaged 36.7% per month (SD = 18.4%, range = 5.4 – 72.7%) and the abundance index averaged 29.3 per month (SD = 20.5, range = 1.4 – 79.1). Availability of ‘all fruit’ and ‘gorilla fruit’ was highly and significantly correlated for all three phenology measures (r_s ranged between 0.922 and 0.976).

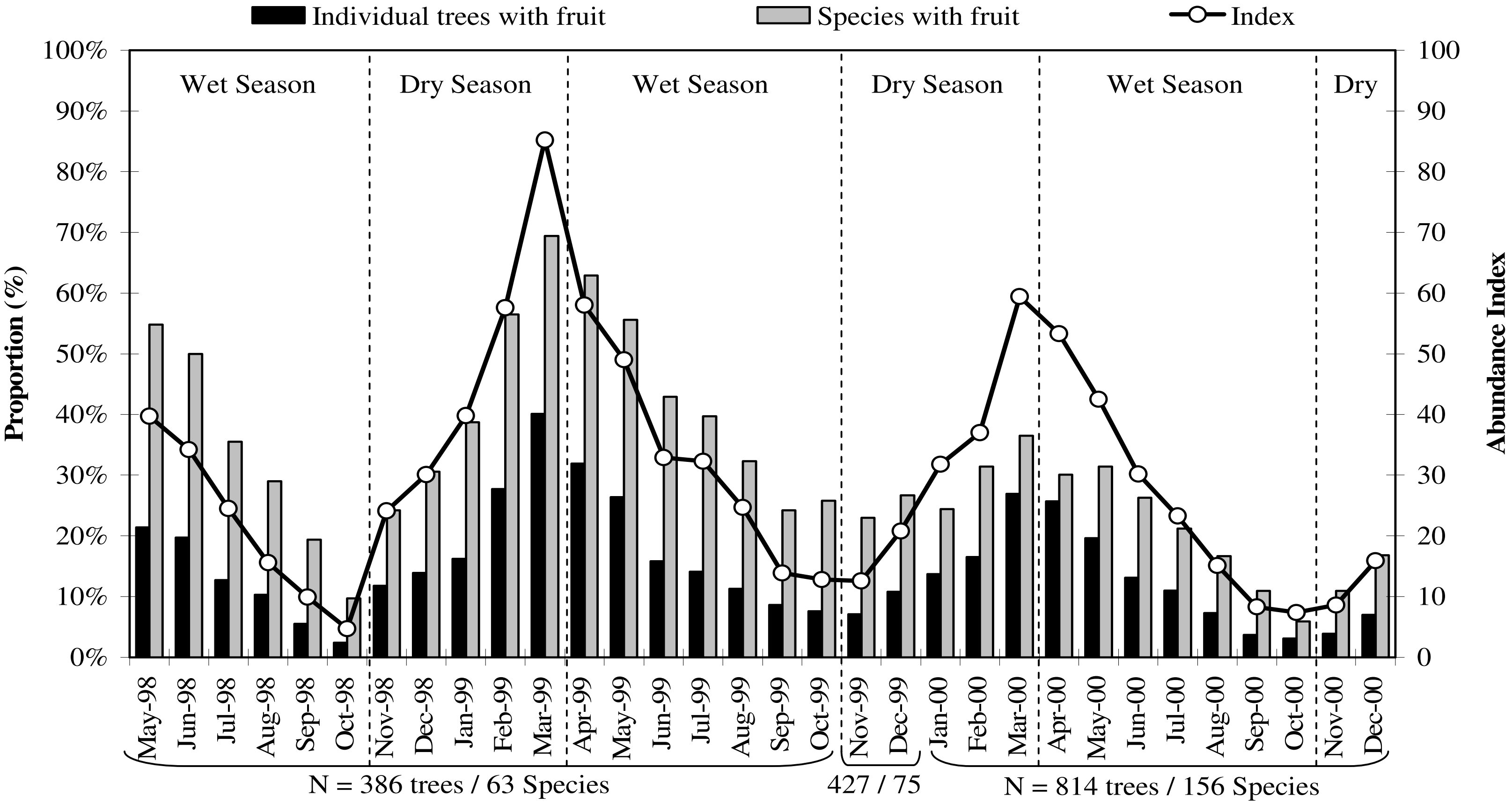


Figure 2.15 Proportion of individual trees and species with fruit (unripe and ripe) and abundance index

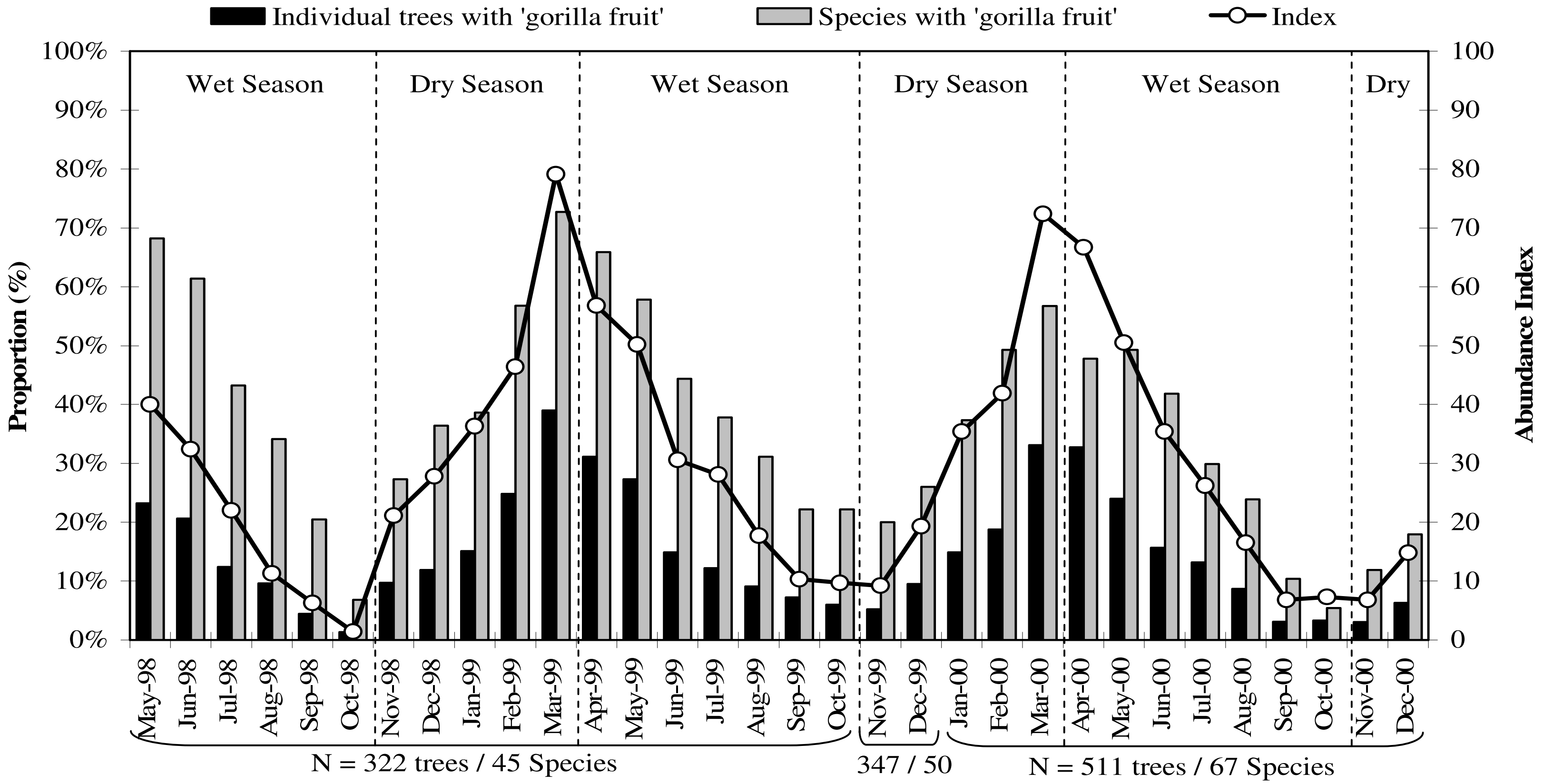


Figure 2.16 Proportion of individual trees and species with fruit eaten by gorillas (unripe & ripe 'gorilla fruit') and abundance index

Figure 2.17 shows monthly variation in the proportion of individual trees and species with ripe fruit (ripe 'all fruit') and in abundance index. The proportion of individual trees with ripe fruit averaged 4.7% per month (SD = 2.9%, range = 0.4 – 12.8%), the proportion of species averaged 13.3% per month (SD = 6.7%, range = 1.0 – 24.2%) and the abundance index averaged 10.2 per month (SD = 7.0, range = 0.8 – 29.0). Figure 2.18 shows monthly variation in proportion of individual trees and species with ripe fruit eaten by gorillas (ripe 'gorilla fruit') and abundance index. Proportion of individual trees with ripe 'gorilla fruit' averaged 4.8% per month (SD = 3.3%, range = 0 – 13.8%), proportion of species averaged 16.1% per month (SD = 9.0%, range = 0 – 34.3%) and the abundance index averaged 10.2 per month (SD = 8.7, range = 0 – 35.0). Availability of ripe 'all fruit' and ripe 'gorilla fruit' was highly and significantly correlated for all three phenology measures (r_s ranged between 0.860 and 0.940).

Generally, availability of fruit and 'gorilla fruit' separately was relatively high during the late dry season months (February – March) and early wet season months (April – July). Fruit (unripe and ripe) availability peaked in the dry month of March and ripe fruit peaked sometime during early wet season months, April – June. Fruit availability started to decline in July or August and the period of lowest gorilla fruit availability occurred during at least two wet season months (September and October) and three dry season months (November – January).

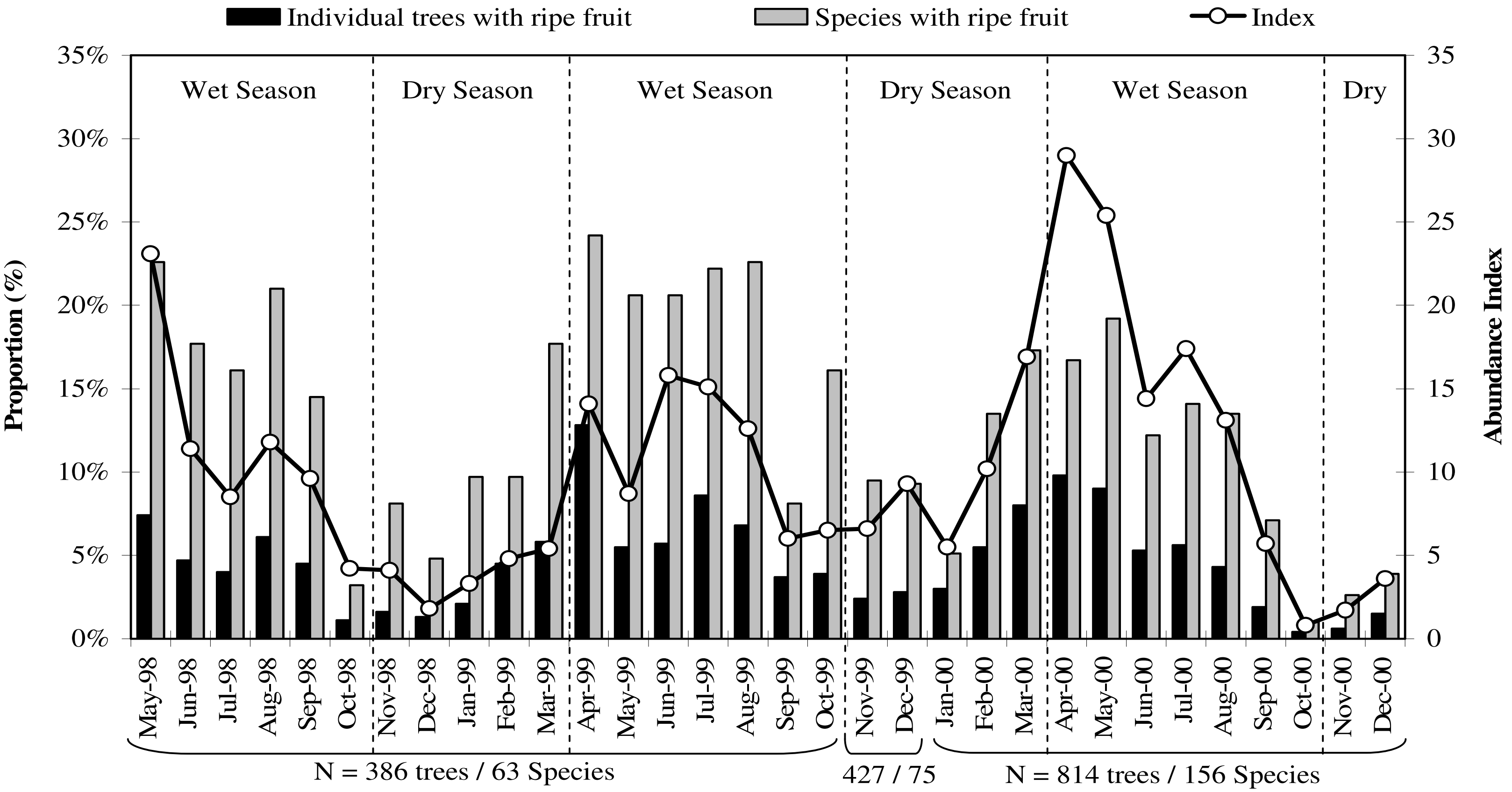


Figure 2.17 Proportion of individual trees and species with ripe fruit and abundance index

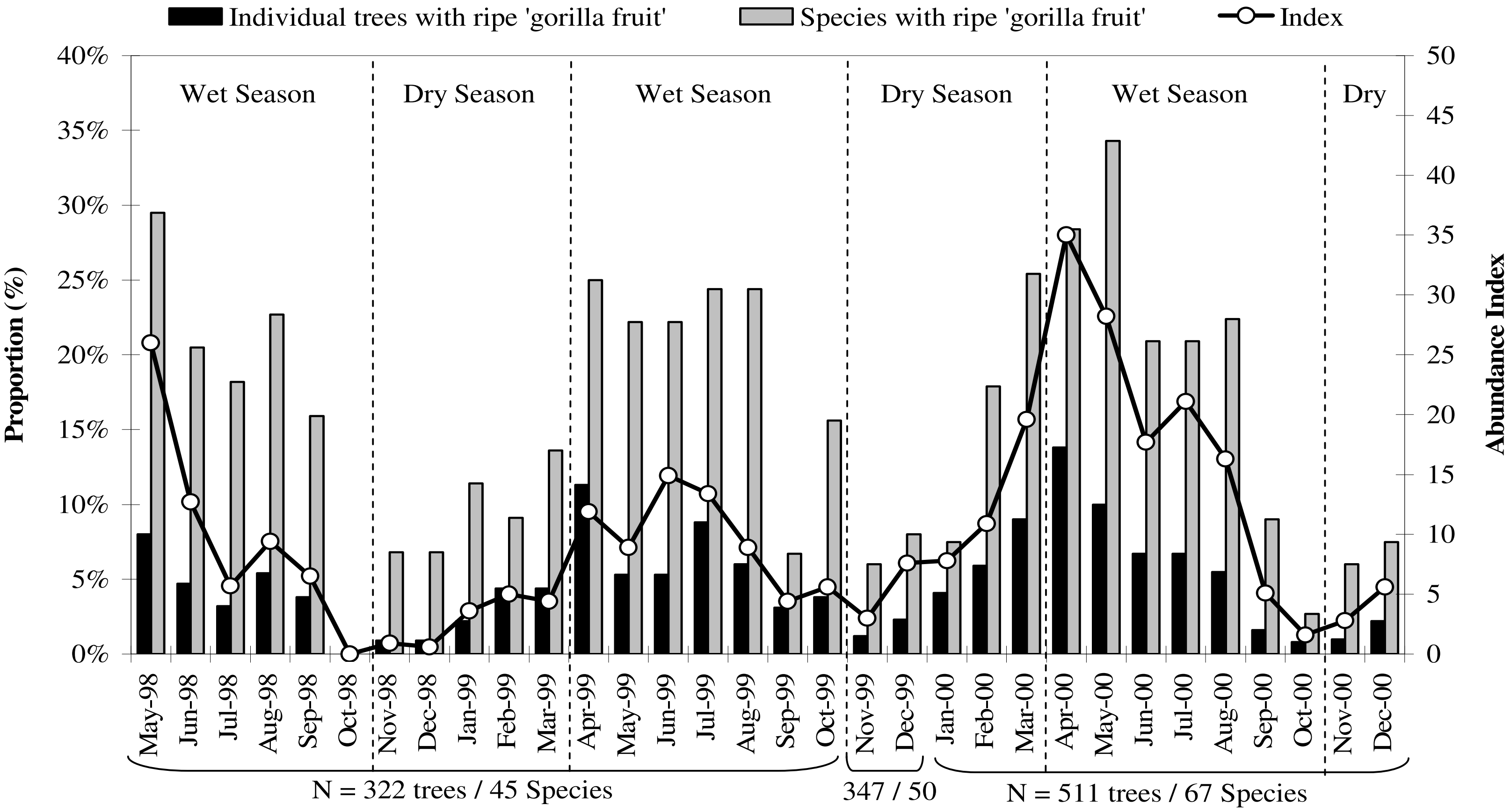


Figure 2.18 Proportion of individual trees and species with ripe fruit eaten by gorillas and abundance index

Table 2.6 (column 2) presents Spearman rank correlations between different measures of fruit availability and rainfall and Figure 2.19 shows seasonal variation in proportion of individual trees with fruit. Availability of ‘all fruit’, and ‘gorilla fruit’ separately, was negatively related to rainfall but correlations did not reach significance for all measures; significant results were found for proportion of individual trees and/or abundance index. Availability of fruit and ‘gorilla fruit’ did not differ significantly between dry and wet season months ($t = 0.82$ and 0.52, $p = 0.418$ and 0.605, respectively, $df = 30$). Availability of ripe ‘all fruit’ and ripe ‘gorilla fruit’ were not significantly related to rainfall, but were significantly greater during wet season months compared to dry months ($t = 2.33$ and 2.30, $p = 0.027$ and 0.035, respectively, $df = 30$). However, phenology data collected during 2000 likely represent the more typical pattern of ripe ‘gorilla fruit’ (see Phenology Methods section). When examining ripe ‘gorilla fruit’ in 2000 separately, ripe ‘gorilla fruit’ availability did not differ significantly between wet and dry season months. These results indicate that periods of high and low fruit availability at Afi Mountain do not strictly coincide with rainfall seasonality and differs from other western gorilla sites where periods of high and low fruit availability coincide with wet and dry seasons, respectively (see Discussion for further details).

Table 2.6 Spearman Rank correlations between climate factors and fruit availability (proportion of individual trees, proportion of species in parentheses and abundance index in brackets).

	TOTAL RAINFALL		**TEMPERATURE**	
			Minimum	**Maximum**
'All Fruit' (unripe/ripe)	-0.37* (-0.21) [-0.39*]		0.36* (0.28) [0.31]	0.78** (0.64**) [0.78**]
'Gorilla Fruit' (unripe/ripe)	-0.32 (-0.24) [-0.41*]		0.37* (0.41*) [0.29]	0.74** (0.73**) [0.78**]
Ripe 'All Fruit'	0.16 (0.28) [0.26]		0.34 (0.33) [0.22]	0.33 (0.28) [0.15]
Ripe 'Gorilla Fruit'	0.15 (0.27) [0.20]		0.26 (0.29) [0.18]	0.31 (0.24) [0.22]

* Significant at the 0.05 level (2-tailed)
** Significant at 0.01 level (2-tailed)

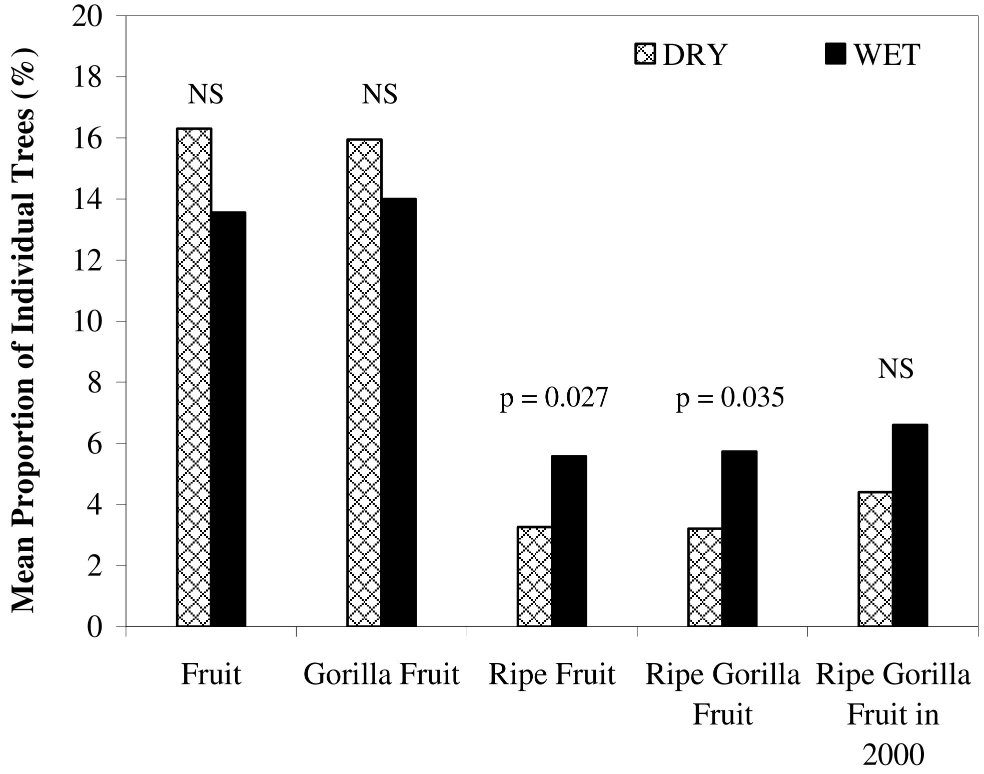


Figure 2.19 Seasonal variation in proportion of individual trees with fruit (unripe and ripe) and ripe fruit

Results of Spearman rank correlations between fruit availability and temperature are presented in Table 2.6 (columns 3 and 4). All measures of fruit (unripe and ripe 'all fruit' and 'gorilla fruit') were highly, positively and significantly correlated with maximum temperature (r_s ranged between 0.64 and 0.78, $p \leq 0.01$). Fruit (unripe and ripe) availability was also positively related to minimum temperature but correlations were relatively low and only some were statistical significant, indicating that maximum temperatures were a more important factor influencing fruit availability. Ripe fruit availability for ‘all fruit’ and ‘gorilla fruit’ was not related to minimum or maximum temperatures.

See Discussion for comparisons of fruit availability between Afi Mountain and other western gorilla study sites.

TREE FOOD DIVERSITY AND DENSITY

Tree Enumeration Methods

A tree enumeration was conducted to describe the array of tree foods available to the Afi gorillas and investigate whether availability of tree foods consumed by gorillas varied across their range. The diversity and density of trees at Afi were estimated using a random stratified line transect plot method. Samples were restricted to the core area of the gorillas’ range, which encompassed the Central and South sectors of the study area (Figure 2.20). The gorillas did utilize the North and West sectors of the mountain but these sectors were less frequently visited by gorillas and were difficult to sample because of logistic and time constraints. In each 1 km x 1 km grid cell within the core area, one to two plots, depending on the frequency of gorilla activity, were established by randomly choosing points and direction (north, south, east, west) from along marked trails and mapping transects. In total, eleven 250 x 5 m and one 265 x 10 m plots, totaling 16,400 m^2 (or 1.64 ha), were sampled (Figure 2.20). All trees with diameters at breast height (1.3 m above ground) $\geq$ 10 cm were tagged with an identification number, their locations noted and identification to genus or species was attempted. Whenever possible, plant

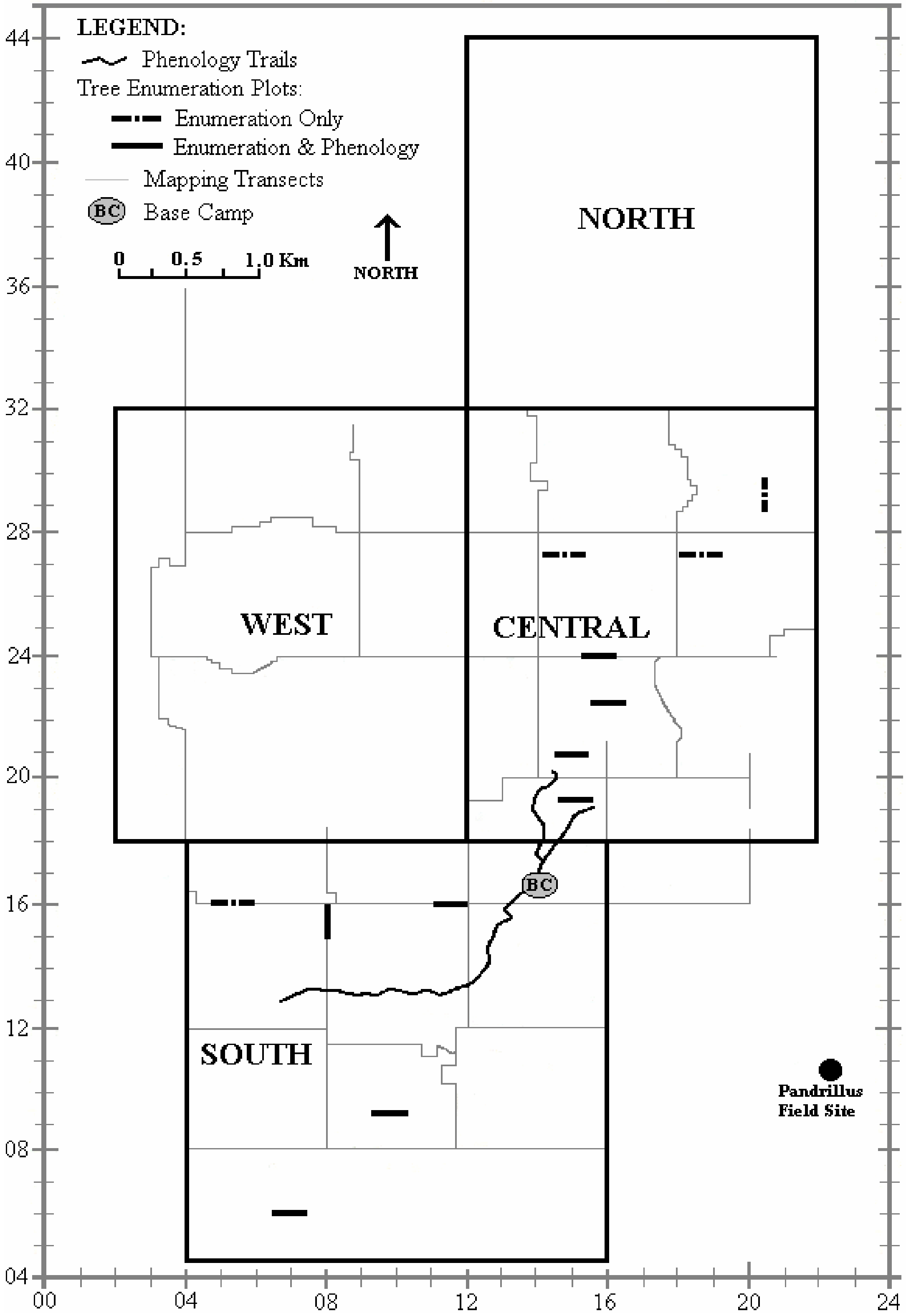


Figure 2.20 Location of Phenology Trails and Tree Enumeration Plots

samples were collected and preserved for future identification. Tree plots encompassed all habitat types, which occurred at frequencies similar to those found along mapping transects described above. Tree plots also encompassed the full range of altitudes present within the study site; altitude in plots ranged from 380 m to 1130 m.

For analysis, plots were divided into 5 x 50 m (250 m^2) quadrats (n = 63 quadrats). Mean number of species and trees per quadrat were calculated to describe diversity and density. Diameter at breast height (DBH) can be used to calculate basal area per tree. Basal area has been shown to correlate with tree height and crown volume (Oates et al. 1980) and can be used to produce a measure of relative biomass (m^2/ha) when combined with tree density. In addition, relative frequency, density, and dominance were calculated to produce an Importance Value (IV) for each species, following Carroll (1996) as described below:

Relative Frequency = Number of individual trees per species (F) / Total number of trees of all species (F Total) x 100

Relative Density = F / Total number of species x 100

Relative Dominance = Basal area of species / Total basal area for all species x 100

Importance Value (IV) = Sum of Relative Frequency, Density & Dominance

Because the area sampled was relatively small in proportion to the gorillas' range, I increased sample size by combining data from phenology trails with that of the tree enumeration plots to determine mean density of trees per 250m^2 quadrat for each species. Mean densities were calculated only for those species found on both phenology trails and enumeration plots or on phenology trails exclusively. Trees along phenology trails were included in the larger enumeration sample only if they were located within 5 m of either side of phenology trails (n = 999 trees and 178 species).

To investigate whether Afi gorillas exhibit food selectivity, Pearson correlations were performed between importance of tree species in the gorillas' diet and their availability in the habitat (IV). Afi gorillas consumed different foods to varying degrees; hence, foods could be ranked based on their relative importance in the gorillas' diet ('food rank', see Chapter 3 for details). Ranks of important gorilla foods ranged between 1 and 54 (1 = most important and 54 = least important). Tree foods that were consumed rarely by gorillas (i.e., non-important gorilla foods) were given a rank of 55. Suspected gorilla tree foods were given a rank of 56 and tree foods that gorillas did not consume during the present study were given a rank of 57. Consequently, a negative relationship between tree species 'food rank' and importance in the habitat (IV) would indicate that Afi gorillas consume tree foods as predicted by tree species availability in the environment.

To determine whether tree food availability varied across the study site, the presence of species within the four sectors described earlier (North, West, Central, and South; Figure 2.20) was determined. Densities of trees within the South and Central sectors were determined using tree enumeration plots and phenology trails. The presence and relative frequency of species within the West and North sectors were estimated based on presence along gorilla feeding trails and field notes taken when searching for gorilla activity in these sectors. Because the West and North sectors were not systematically sampled, the presence of other species in these sectors cannot be ruled out. Therefore, my results focus on distribution within the central and south sectors, which correspond to the area where the majority of gorilla activity was recorded during this study.

Diversity and Density of Trees on Afi Mountain

A total of 700 trees of 159 species (113 identified to at least genus, 46 unidentified) were enumerated and are listed in Appendix I. Number of individual trees per species ranged from 1 to 33, with 63 species recorded only once and 14 species recorded ≥ 10 times. Mean diversity per 5 x 50 m quadrat is 7.9 species (SD = 3.8, range = 0 – 16 species, n = 63 quadrats) and mean density per 5 x 50 m quadrat is 10.8 trees (SD = 6.3, range = 0 – 30 trees) or 432 trees/ha. No trees were recorded in two of the quadrats. Using trees found in enumeration and phenology trails plots, mean density of trees per 250 m^2 quadrat for each species ranged from 0.01 – 0.31 trees/ha (Appendix I).

Diversity and Density of Afi Gorilla Tree Foods

Not all species found in enumeration plots were food resources for gorillas nor were all gorilla tree food species identified in this study found in these plots. A total of 44 known gorilla tree food species (68% of the total known species) were recorded in plots (Table 2.7); consequently, the overall mean diversity and density for Afi gorilla tree foods are underestimated. When only known gorilla food tree species were considered, mean diversity was 3.5 species per quadrat (SD = 2.0, range, = 0 – 10 species) and mean density was 4.9 trees per quadrat (SD = 3.5, range = 0 – 20 trees). Mean density per quadrat for known and suspected food species ranged between 0.01 and 0.31 trees/quadrat. In four quadrats, no known gorilla tree foods were recorded.

Table 2.7 Characteristics of the 44 known Afi gorilla tree foods recorded along tree enumeration and phenology transects (see legend for definitions and units).

SPECIES (Number of species)	**PART EATEN**	**IMP. FOOD RANK**	**IV**	**MEAN DENSITY** (Number per 250 m^2 quadrat)				
				Total *	**South**	**Central**	**West**	**North**
Ficus spp. (3)	FR, L, B	4	---	0.06	0.07	0.04	X	X
Milicia excelsa	FR, L, B	6	1.0	0.05	0.05	0.04	X	
Treculia africana	FR	9	3.5	0.04	0.03	0.04		X
Myrianthus arboreus	FR	10	5.2	0.09	0.06	**0.12**		
Pterocarpus osun / P. mildbraedii	B	11	10.4	0.05	0.03	**0.07**	X	X
Morus mesozygia	FR, L, B	12	---	0.03	**0.03**	0.0	X	
Turreanthus africanus	FR, L	17	5.4	0.08	**0.09**	0.04		
Pseudospondias microcarpa	FR	18	5.9	0.05	0.01	**0.04**	X	X
Musanga cecropioides	L	19	6.7	0.06	0.05	0.07	X	X
Sorindeia grandifolia	FR	20	23.7	0.20	0.06	**0.40**		
Parkia bicolor	FR	21	2.3	0.08	0.09	0.07		X
Dialium guineensis	FR	22	0.8	0.02	0.0	**0.02**	X	X
Tabernaemontana pachysiphon	FR	23	27.5	0.31	0.17	**0.49**	X	X
Vitex sp. 1	FR	29	---	0.05	0.04	0.05	**X**	
Maesopsis eminii	FR	30	1.7	0.02	0.02	0.02		
Grewia mollis	B	31	1.6	0.03	**0.02**	0.0	X	
UK-A (SD-01)	FR	33	4.0	0.15	0.16	0.12	X	X
Chrysophyllum spp. (2)	FR	34	13.0	0.15	0.01	**0.16**		X
Garcinia kola	FR	37	0.8	0.02	0.0	0.02	X	**X**
Pycnanthus angolensis	L	38	2.0	0.06	**0.09**	0.02		
Antiaris toxicaria africana	FR	41	5.7	0.09	**0.11**	0.05		
Dracaena arborea	L	43	1.7	0.03	**0.04**	0.02		

Table 2.7 Continued on next page.

Table 2.7 Continued.

SPECIES	PART EATEN	IMP. FOOD RANK	IV	**MEAN DENSITY** (Number per 250 m^2 quadrat)				
				Total *	**South**	**Central**	**West**	**North**
Cola millenia	FR	46	---	0.02	0.01	**0.02**		
Uvariodendron calophyllum	FR	48	8.7	0.09	0.09	0.09		
Monodora myristica	FR	49	5.9	0.07	0.07	0.05		
Albizia zygia	L	50	7.4	0.10	0.03	**0.21**	X	X
Bosqueia angolensis	FR	52	3.5	0.07	0.06	0.09		
Santiria trimera	FR	*	3.3	0.07	0.09	0.07		**X**
Trichoscypha sp.	FR	*	7.6	0.07	0.0	**0.18**		X
Antrocaryon micraster	FR	---	---	0.03	0.02	0.02		
Blighia sp.	FR	---	6.4	0.05	0.06	0.04		
Caloncoba glauca	FR	---	2.8	0.03	0.0	**0.09**		
Canarium schweinfurthii	FR	---	0.9	0.03	0.03	0.02		
Cola latiritia	FR	---	5.1	0.05	0.07	0.02		
Elaeis guineense	FR	---	1.9	0.03	0.03	0.02		
Newbouldia laevis	B	---	0.8	0.01	X		X	
Placodiscus glandulosus	FR	---	16.1	0.18	**0.21**	0.12		
Ricinodendron heudelottii	FR	---	4.1	0.03	0.04	X		
Trema guineense	B	---	1.6	0.02	0.0	0.02		
Xylopia sp.	FR	---	6.6	0.08	0.03	**0.16**		

Part eaten: B = bark, FR = fruit, L = leaves; Important Food Rank: numbers indicates the species' importance rank in the Afi gorillas' diet, --- species rarely consumed by the gorillas, * species that were important Afi gorilla foods but food rank not available; IV = Importance values calculated using tree enumeration data only (see text for details); Mean density: mean number of trees per 250 m^2 quadrats on tree enumeration and phenology transects in South and Central sectors (total) and in South and Central sectors separately, X = species present but not enumerated, blank = no data available, **bold** indicates sector(s) in which density was ≥ 2 times greater.

Known gorilla tree foods made up only 28% of the total number of species found in quadrats. Whereas four known gorilla tree foods (11%) were among the most abundantly available tree foods on Afi Mountain (IV $\geq$ 10), the majority of known gorilla tree foods (58%) were among the least abundantly available tree species (IV $\leq$ 4.5; Table 2.7). For all tree species enumerated, relative importance in the gorillas' diet (represented by 'food rank', see methods for definition) was negatively and significantly correlated with availability in the environment (represented by importance values), though this relationship is weak ($r = -0.172$, $p = 0.031$); 'food rank' and importance value measures are also negatively related [1]. Consequently, tree species availability explains little of the Afi gorillas' tree food choice. These results suggest that the Afi gorillas are selective in the tree foods they choose to consume.

Variation in Density of Gorilla Tree Foods Across Sectors

All but a few gorilla tree food species were present in at least two sectors within the study site, indicating that they are widely distributed across the Afi gorillas' range (Table 2.7). However, comparisons of gorilla tree food densities in Central and South sectors indicate that many are concentrated within particular areas. Central and South sectors were systematically sampled and include the core area utilized by the gorillas. Density of tree food species consumed by Afi gorillas was significantly greater in the Central sector (mean = 2.9 trees per 250 m^2 quadrat, SD = 2.2, range = 0 – 10 trees, n = 57 quadrats) compared to the South sector (mean = 1.7 trees per 250 m^2 quadrat, SD = 2.0, range = 0 – 10 trees, n = 94 quadrats; $z = 4.0$, $p \leq 0.001$). Of the 40 known Afi

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[1] A food rank of 1 indicates greatest importance in the diet and an importance value of 1 indicates low availability (see Tree Enumeration Methods for details).

gorilla tree food species sampled along tree enumeration and phenology transects, 19 were more densely available (i.e., mean density ≥ two times greater) in the Central or South sector (Table 2.7), including 16 important tree foods in the gorillas' diet. Based on gorilla feeding records and notations made while searching for gorilla signs, three additional tree foods were likely concentrated in the North or West sector.

AVAILABILITY OF GORILLA HERB FOODS

Herb Enumeration Methods

An herb enumeration was conducted to estimate diversity, density, biomass and spatial distribution of Afi gorilla herb foods throughout the study site, and describe variation across habitat types, altitudes and sectors. The diversity and density of gorilla herb foods at Afi were estimated using a line transect method. While establishing the 1 km x 1 km grid cell transects during the original mapping exercise, potential gorilla herb food species of the families Zingiberaceae, Marantaceae, Araceae, and Commelinaceae were enumerated. Herbs rooted within 0.5 m on either side of transects were identified, counted, and stage of development and presence of flowers or fruit were noted. In total, 40.9 km (40,900 1 m^2 plots) were enumerated over a 23 km^2 area. In addition, three herb patches along gorilla feeding trails were enumerated. Proportion of habitat types and altitudes represented along transects are discussed in the Habitat Description section above. Because distinguishing species of some genera was difficult without the presence of flowers or fruit, species within the same genera were pooled. Species of the genera *Megaphrynium* and *Thaumatococcus* were pooled for the same reason.

To estimate herb food biomass, ten or more representative stems for each species were selected and their wet weight measured (Rogers & Williamson 1987). The part of the plant eaten (mean length of stems or portion of leaves eaten) was then weighed to produce a mean percentage of food (in grams) per stem and biomass (g/m^2) calculated using stem density estimates. The average part of the plant eaten was calculated using lengths of stems from which gorillas had removed the pith measured along feeding trails.

To describe the spatial distribution of herbs, I calculated the coefficient of dispersion (CD), the ratio of the variance to the mean number of individual trees per species and per unit area, for all herbs pooled, and for each genus and habitat type separately. A number of primate studies have used variance to mean ratios to demonstrate spatial patterns (Goldsmith 1996; Milton 1980; Struhsaker 1975; Watts 1984).

$$\mathrm{CD} = \mathrm{S}^2 / x$$

This value will be 1.0 for Poisson distributions (i.e., randomly dispersed), greater than 1.0 for clumped samples, and less than 1.0 for uniform distributions (Sokal & Rohlf 1981). The normal approximation of chi-square (z) was calculated to determine whether coefficients were significantly different from 1.0, two chi-square tests were calculated (Krebs 1999).

z = square root of 2 X^2 – square root of ($2v - 1$)

where: z = Standard normal deviate ($\mu = 0, \sigma = 1$)

X^2 = Observed value of chi-square [CD ($n - 1$)]

v = Number of degrees of freedom = ($n - 1$)

The null hypothesis, that the spatial pattern is random, was accepted if *z* was between 1.96 and -1.96 (for a two-tailed test with an alpha level of 0.05).

Number of consecutive 1 m^2 plots containing herbs along transects were used to investigate whether herbs were clumped on a scale greater than 1 m^2 and to estimate herb patch size, diversity and density, and distribution of herb patches within the Afi study site. Henceforth, herb patches will be referred to as herb 'clumps' so as to not confuse them with the herb patch habitat type. The mean distance between plots containing herbs along transects was 15.1 m (SD = 54.8, range = 1 – 1148 m). This is a relatively short distance for a gorilla to travel; thus, herb clumps were defined using the following criteria: 1) herb clumps must begin and end with plots containing herbs that are ≤ 2 m apart, 2) when a distance of ≤ 15 m separated two series of consecutive plots with herbs, they were considered to be one herb clump. Using these criteria, herb clumps were identified and mean diversity and stem density per 1 m^2 plot were calculated for each clump separately.

The distance along transects within herb clumps (i.e., 'clump length' measured in meters) was used to estimate herb clump size. Distances along transects between herb clumps were used to estimate herb clump distribution. Distances between clumps were calculated separately for North and East mapping transects moving from south to north and west to east, respectively (e.g., 04 North or 08 East, see Figure 2.2). Consequently, this measure estimates the distance Afi gorillas would have travel in order to consume herbs in the next nearest clump, if they were traveling along these transects.

Since transects were only 1 m wide, the likelihood that transects traversed an herb clump was dependent on clump size (i.e., probability of crossing a small clump is less than that of a large clump) and clump length depended on where, within a clump, transects happened to intersect it (e.g., at the widest or most narrow point). Furthermore, gorillas certainly do not travel in straight lines and especially not in the manner transects were arranged. Therefore, estimates made here are not intended to approximate actual herb clump size or distance between clumps but rather are used only as relative measures to facilitate comparisons across habitat types and sectors within the Afi study site.

Kruskal-Wallis tests were performed, including individual pair-wise comparisons (Siegel & Castellan Jr. 1988), to determine whether measures (e.g., species diversity, stem density, clump size) differed across habitat types, altitudes and sectors. To test if measures were affected by differences in sample size (e.g., number of plots in each habitat type) regressions were conducted and no significant relationship was evident for any measures.

Diversity, Density and Biomass of Herb Foods Pooled and Different Genera

Herbs of four families (Zingiberaceae, Marantaceae, Araceae, and Commelinaceae), 8 genera (*Aframomum, Costus, Thaumatococcus, Megaphrynium, Hypselodelphys, Marantochloa, Stylochiton,* and *Palisota*) and 15 species were enumerated along transects. Mean species diversity per 1 m^2 plot was 0.21 species (SD = 0.49, range = 0 – 4 species/m^2). When considering only plots containing herbs, mean species diversity was 1.2 species/m^2 (SD = 0.46, range = 1 – 4 species).

A total of 47,369 herb stems were counted within 6,920 (16.9%) of the 40,900 plots (1 m^2) sampled. Table 2.8 shows mean density and maximum number of stems per plot for all herb species pooled and different genera separately. Mean density of all herb foods at Afi was 1.16 stems/m^2 (SD = 3.6, range = 0 – 69). When considering only those plots containing herbs, mean density was much higher (6.9 stems/m^2, SD = 6.2, range = 1 – 69). The most common genera were *Aframomum* and *Thaumatococcus/ Megaphrynium*, representing 37.0% and 25.6% of all herb stems, respectively and occurred at the highest densities (0.43 and 0.30 stems/ m^2, respectively). Whereas Afi gorillas eat the pith of mature *Aframomum* stems, they only eat the young leaves of *Thaumatococcus/ Megaphrynium*, which occurred at a much lower density (0.01 young leaves/m^2) than mature stems and their abundance varies seasonally.

The least common genus was *Palisota*, representing 5.7% of all herb stems, and it occurred at the lowest density (0.02 stems/m^2). Gorillas eat the pith of *Palisota* sp. 2 stems and leaf bases, but consume the pith of *Palisota* sp. 1 leaf bases only. The two *Palisota* species found at Afi are each shown in Table 2.8 and discussed separately because they differ in their growth form and distribution within the study site. *Palisota* sp. 2 has a single above ground stem, similar to other herb species, and its leaves (each with bases approximately 0.05 cm wide and 0.02 cm thick) are whorled at the apex of the stem. By contrast, *Palisota* sp. 1 has no main stem above ground and its leaves (each with bases up to approximately 3 cm wide and 1.5 cm thick) appear just above ground level. On average there were 7.1 leaves per *Palisota* sp. 1 plant. Density of *Palisota* sp. 1 leaves (0.05 leaves/m^2) was higher than *Palisota* sp. 2 stems, though still lower than all other herb genera.

Table 2.8 Characteristics of Afi gorilla herb foods pooled and different genera, including stem density, maximum number of stems per 1 m^2 plot, proportion and amount of stems eaten, biomass, spatial pattern and altitude (see legend for definitions and units).

Family	**Herb Genera** (No. Species)	**Mean Density**	**Maximum Number Stems/m^2**	**Mean Percent Eaten**	**Mean Amount Eaten**	**Mean Biomass**	**Spatial Pattern**	**Mean Altitude (m)**
	All Herb Foods (15)	1.16	69	-------	-------	22.2	11.2 *	762.8
Zingiberaceae	*Aframomum* (4)	0.43	33	4.6	7.4	3.2	8.2 *	839.0
	Costus (2)	0.08	32	3.9	17.4	1.4	8.4 *	715.1
Marantaceae	*Thaumatococcus/ Megaphrynium* (2) [1]	0.30 (0.01)	69 (27)	(34.0)	(4.6)	(0.04)	7.5 *	597.6
	Hypselodelphys (1)	0.14	20	2.4	59.3	8.0	4.7 *	930.0
	Marantochloa (3)	0.07	48	9.0	38.4	2.8	11.6 *	564.9
Araceae	*Stylochiton* sp. (1)	0.08	28	29.2	30.3	2.4	9.1 *	442.2
Commelinaceae	*Palisota* sp. 1 (1) [2]	0.01 (0.05)	4 (40)	(19.6)	261.8 (37.4)	2.0	1.6 *	963.7
	Palisota sp. 2 (1)	0.01	10	9.8	195.0	2.3	4.7 *	512.0

[1] Young leaves shown in parentheses (see text for details).

[2] Leaves shown in parentheses (see text for details). Mean amount eaten per stem based on an average of 7.1 leaves per plant.

Mean density: Mean number of stems per 1 m^2 plot; Mean percent eaten: Mean proportion of total stem weight eaten per stem (in grams); Mean amount eaten: Mean number of grams eaten per stem; Mean biomass: Mean number of grams per 1 m^2 plot; Spatial pattern: Coefficient of dispersion (variance/mean) per 1 m^2 plot; Mean altitude: Mean altitude of 1 m^2 plot containing herbs, altitude among genera differed significantly (see text for details); * Coefficient of dispersion is significantly greater than 1 ($p < 0\ .05$).

Mean biomass of all herb foods at Afi was 22.2 g/m^2 (or 2.2 kg/ha) and for each genus separately ranged between 0.04 for *Thaumatococcus*/*Megaphrynium* young leaves and 8.3 g/m^2 for *Hypselodelphys* stem pith and young leaves (Table 2.8). Though gorillas on average consumed a relatively small proportion of *Hypselodelphys* stems (2.4% grams of total stem weight), *Hypselodelphys* had the highest biomass (8.0 g/m^2, stem pith and young leaves). This is due to the fact that *Hypselodelphys* stems are on average 8.4 m long and the gorillas eat only pith from the younger portions of the stem. Gorillas ate the greatest proportion of *Stylochiton* stems (29.2%, stem pith and leaves) but due to its relatively small size (average height = 68.0 cm) and low density, its mean biomass is among the lowest (2.4 g/m^2) of the herb genera.

One important gorilla herb food, *Anchomanes difformis* (Araceae), was not enumerated because it was not known to be a gorilla food when enumeration was conducted. Its temporal and spatial distribution differs from the other Afi gorilla herb foods. *Anchomanes* is the only seasonally available herb at Afi; it is most abundantly available during wet season months (April – October). During the dry season, *Anchomanes* stems dry out and disappear, and develop anew after the onset of the wet season. *Anchomanes* stems tend to occur singly within open mature and secondary forests, and along forest gap edges. *Anchomanes* stems were found to provide the third largest amount of food per stem on average (157.8 g/stem, pith and leaves).

Variation Across Habitat Types: Diversity, Density and Biomass

Table 2.9 shows total number of herb species, mean species diversity, density, and biomass, and spatial pattern of all herb foods pooled within different habitat types. The greatest species diversity, stem density, and biomass were found in herb patch and forest gap habitat types, followed by secondary forest and vine tangle, and closed and open mature forests. Herb densities significantly differed across habitat types ($X^2 = 9643.3$, df = 5, $p < 0.001$); however, pair-wise comparisons show that the only densities in herb patch and forest gap habitat types consistently differed significantly from densities in all other habitat types. Since habitat type definitions were based partly on presence of herbs, the above results are not that surprising. They do, however, confirm that herb foods at Afi are concentrated in light gaps where tree cover is absent. Mean density within light gaps (herb patch and forest gap: 2.76 stems/m^2, SD = 5.5, range = 0 – 69 stems/m^2) was significantly greater than mean density within forest habitat types (mature forests, secondary forest and vine tangle: 0.56 stems/m^2, SD = 2.3, range = 0 – 40 stems/m^2; $z = 65.6$, $p < 0.001$).

Figure 2.21 shows variation in herb density across different habitat types for each herb genus separately. Species of most herb genera occurred within all of the different habitat types sampled, except closed mature forest where only three species were recorded. All but one genus was most prevalent within the herb patch habitat type, or was similarly prevalent in herb patch and forest gap (i.e., *Costus* and *Palisota* sp. 1), and occurred at much lower densities within forest habitat types. By contrast, *Stylochiton* was most prevalent in closed mature and secondary forests, and was almost completely absent from herb patch and forest gap habitat types. Stem densities for all genera pooled and each herb genus separately differed significantly between light gap and forest habitat types ($z = 4.1 – 65.6$, $p < 0.001$).

Table 2.9 Variation in Afi gorilla herb food availability across different habitat types, including species diversity, stem density, biomass and spatial distribution (see legend for definitions and units).

Habitat Type (Total No. of 1 m^2 plots sampled)	**Total Number of Species**	**Mean Species Diversity** (Range)	**Mean Density** (Range)	**Mean Biomass**	**Spatial Pattern (CD)**	**Mean Number of Consecutive Plots** (Range)
Closed Mature Forest (481)	3	0.05 (0 - 1)	0.26 (0 – 17)	7.6	8.5 **	3.8 (2 - 9)
Open Mature Forest (10,239)	15	0.06 (0 - 2)	0.31 (0 - 33)	5.9	8.8 **	3.8 (2 - 17)
Secondary Forest (17,537)	15	0.14 (0 - 3)	0.71 (0 - 40)	16.1	9.3 **	4.3 (2 - 33)
Vine Tangle (1,491)	12	0.13 (0 - 3)	0.59 (0 - 25)	14.3	7.5 **	5.0 (2 - 21)
Forest Gap (7,397)	15	0.28 * (0 - 4)	1.37 * (0 - 42)	33.2 *	9.0 **	4.6 (2 - 25)
Herb Patch (3,103)	15	1.02 * (0 - 4)	6.65 * (0 - 69)	94.7 *	8.9 **	9.0 * (2 - 50)

Total number of herb species (within each habitat type); Mean species diversity: Mean number of species per 1 m^2 plot; Mean density: Mean number of stems per 1 m^2 plot; Mean biomass: Mean number of grams per 1 m^2 plot; Spatial pattern: Coefficient of dispersion (variance/mean) per 1 m^2 plot; Mean number of consecutive plots: Mean number of consecutive 1m^2 plots containing herbs.

* Means are significantly greater than all other habitat types ($p < 0.05$).

** Coefficient of dispersion is significantly greater than 1 ($p < 0 .05$).

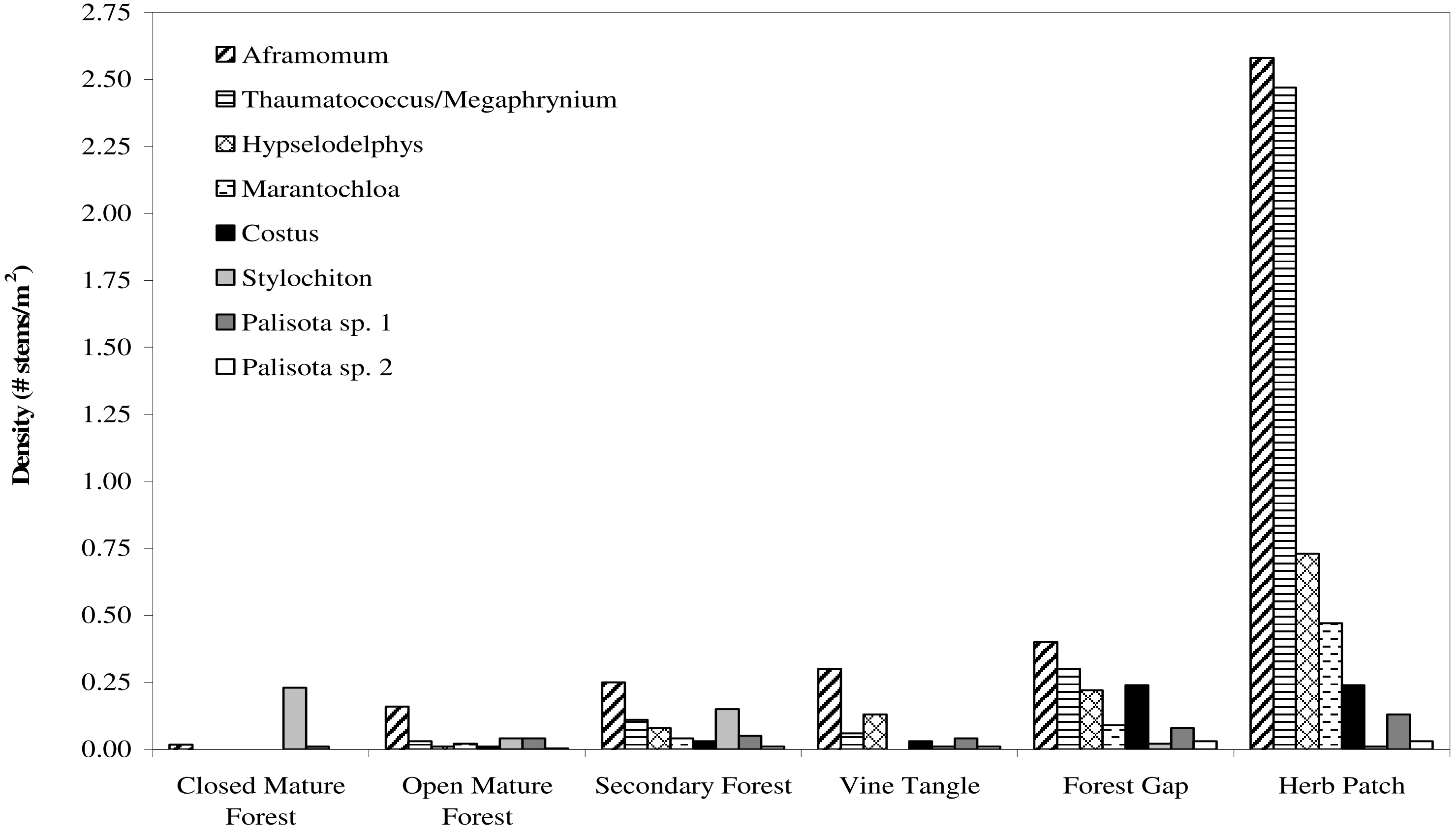

Figure 2.21 Variation in stem density of herb genera across different habitat types

Relationship between Herb Availability and Altitude

The mean altitude of plots containing herbs of all genera pooled was 763 m (SD = 254.4, range = 200 – 1180 m). Figure 2.22 shows mean herb species diversity and density of all herb foods when pooled within 200 m increments in altitude (upper graph). There was a positive relationship with altitude for both mean species diversity and mean density, which were highest at altitudes above 800 m. Differences in species diversity and stem densities across altitudes of 200 m increments were significant ($X^2 = 2054.8$ and 1966.0, respectively, $p < 0.001$, df = 4); however, pair-wise comparisons show that both diversity and density did not differ across altitudes below 600 m.

Whereas each herb genus sampled was present throughout the entire altitudinal range sampled, some occurred more frequently at low, intermediate, or high altitudes. Table 2.8 (last column) shows mean altitude of plots containing herbs for each genus separately. A comparison of stem density of plots at different altitudes across herb genera revealed that the patterns of altitudinal variation differed significantly between genera ($X^2 = 3038.7$, $p < 0.001$, df = 7); however, pair-wise comparisons show that some genera could be grouped together (i.e., did not differ significantly from each other, $p \geq 0.05$). *Palisota* sp. 1 and *Hypselodelphys*, whose mean altitudes were the highest (964 and 930 m, respectively), grouped together and differed significantly from all other genera. *Thaumatococcus/Megaphrynium*, *Marantochloa*, and *Palisota* sp. 2, whose mean altitudes are in the mid-range (598, 565, and 512 m, respectively), grouped together and differed significantly from all other genera. Altitudes of the remaining genera (*Aframomum*, *Stylochiton* and *Costus*) differed significantly from each other and all other genera.

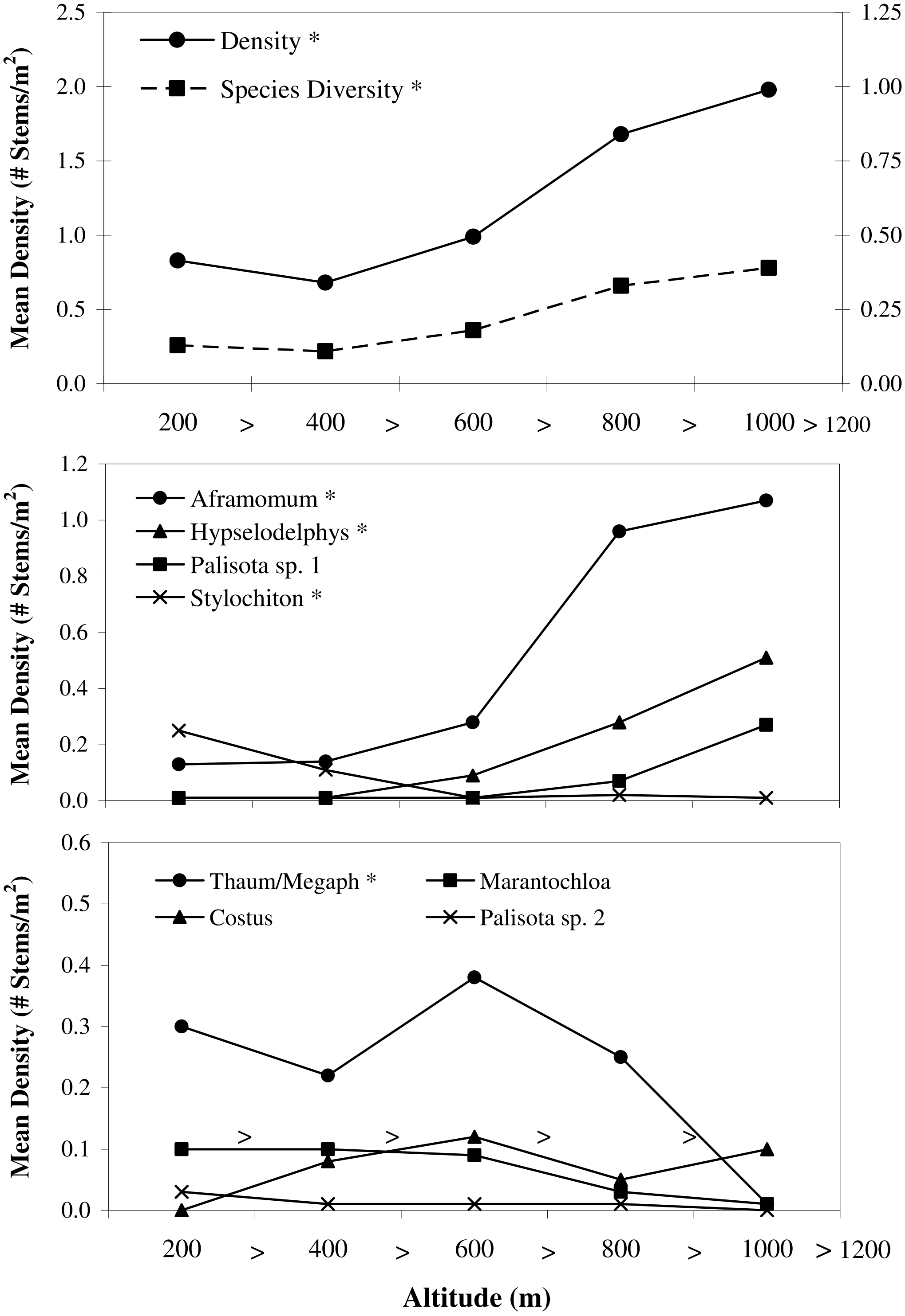

Figure 2.22 Mean species diversity and density of all herbs and some genera at altitudes in 200 m increments

(* Differences across altitudes are significant, see text for details)

To illustrate differences in the pattern of altitudinal variation across genera, mean stem densities per 1 m^2 plot within 200 m increments in altitude were calculated for each genus separately (Figure 2.22, two lower graphs). *Aframomum, Hypselodelphys*, and *Palisota* sp. 1 mean densities were highest at altitudes above 800 m. By contrast, *Stylochiton* mean density was highest at altitudes below 600 m and *Palisota* sp. 2 was highest below 400 m. Densities of the remaining genera are generally higher at altitudes below 800 m. Comparisons of stem density across 200 m increments in altitude for each genus separately shows that *Aframomum, Hypselodelphys, Thaumatococcus/ Megaphrynium*, and *Stylochiton* herb densities differed significantly across altitudes (X^2 = 2400.3, 2594.0, 239.8, and 570.6, respectively, df = 4, $p < 0.001$).

Examining the relationships between mean density and altitude illustrated in Figure 2.22, a pattern emerges where between 600 and 800 m altitudes densities either begin to increase (*Aframomum, Hypselodelphys, Palisota* sp. 1), decrease (*Marantochloa, Costus*), peak (*Thaumatococcus/Megaphrynium*) or attain the lowest density (*Stylochiton*). This pattern is most likely related to variation in altitude across habitat types (see Study Site Description - Habitat Types) and variation in stem densities across different habitat types (see above). *Aframomum, Hypselodelphys* and *Palisota* sp. 1 had greater densities above 800 m and occurred most frequently in herb patch and forest gap habitat types, which occurred more frequently at altitudes above 600 m. On the other hand, *Stylochiton* had greater densities below 600 m and occurred most frequently in closed mature forest, which also occurred most frequently below 600 m.

Spatial Distribution: Coefficients of Dispersion and Herb Clump Characteristics

The spatial pattern of all herb stems pooled showed a highly clumped distribution [coefficient of dispersion (CD) = 11.2, $z = 671.08$, $p < 0.05$, Table 2.8]. Coefficients of dispersion calculated separately for each genus were also significantly greater than one, indicating clumped distributions (Table 2.8). *Thaumatococcus/Megaphrynium* and *Marantochloa* exhibited the most clumped (CD = 17.5 and 11.6, $z = 910.4$ and 686.9, respectively, $p < 0.05$) and *Palisota* sp. 1 the least clumped distributions (CD = 1.6, $z = 79.8$, $p < 0.05$). Herbs were highly clumped in their distribution within each of the six different habitat types (all coefficients of dispersion are significantly greater than 1, $p < 0.05$, Table 2.9). Coefficients of dispersion vary little between habitat types suggesting that the degree to which herbs are clumped is similar within all habitat types.

The mean number of consecutive 1 m^2 plots containing herbs along transects was 5.5 (SD = 5.8, range = 2 – 53 consecutive plots). When considering variation across different habitat types, mean numbers of consecutive plots were lowest in mature forest types (closed and open, mean = 3.8, range = 2 – 17) and greatest in the herb patch habitat type (mean = 9.0, range = 2 – 50) than in any of the other habitat types (Table 2.9; $X^2 = 140.0$, $p < 0.001$, df = 5; only pair-wise comparisons for herb patch habitat type were significant). This suggests that herbs are clumped on a scale greater than 1 m^2 and that herb ‘clump’ (patch) size may vary across the different habitat types. Herb patches are referred to as herb ‘clumps’ so as to not confuse them with the herb patch habitat type.

Herb clump measures (i.e., herb clump length, diversity and density, and distance between clumps) did not differ significantly across closed and open mature forests, secondary forests and vine tangle habitat types (Kruskal-Wallace pair-wise comparisons,

$p > 0.05$). As a result, measures were recalculated for these four habitat types pooled into a ‘forest’ habitat category. Distances between herb clumps within forest, forest gap and herb patch habitat types were calculated for each habitat type separately as follows. For the first and last clump along a North or East transect, the nearest clump within the same habitat type on the nearest transect of the opposite direction was identified and the distance between the two calculated (e.g., for North transects the nearest clump on the nearest East transect and vice versa). In other words, if the gorillas were feeding in an herb clump within a forest gap how far would it have to travel, along the transects, to reach the closest herb clump within a forest gap.

Table 2.10 shows estimates of clump size (represented by clump length), species diversity and stem density, and mean distance between herb clumps within forest, forest gap and herb patch habitat types. Mean herb clump diversity and density in herb patch habitats were significantly greater than clumps in forest and forest gap habitats, which did not differ from each other ($X^2 = 14.1$ and 62.4, respectively, df = 2, $p < 0.001$). Mean clump length and distance between clumps differed significantly across the three habitat types ($X^2 = 102.6$ and 35.3, respectively, df = 2, $p < 0.001$; all pair-wise comparison, $p \leq 0.05$).

Compared to herb clumps in forest and forest gap habitats, clumps occurring in herb patch habitats were larger, and provided a greater variety and number of herb stems, but these herb rich clumps were more widely dispersed. Herb clump species diversity and stem density within forest and forest gap habitat types were similar but clump size and level of dispersion differed. Within forest habitats, herb clumps were on average

Table 2.10 Characteristics of all herb clumps sampled and clumps within three different habitat types, including estimated herb clump size, diversity and stem density, and distance between herb clumps (ranges in parentheses, see legend for definitions and units).

HABITAT TYPE	**Mean Clump Size** (length, m)	**Mean Clump Species Diversity**	**Mean Clump Stem Density**	**Mean Distance Between Clumps (m)**
FOREST	11.5 * (1 - 253)	0.88 (0.2 - 2.0)	4.2 (0.6 - 40.0)	224.7 * (15 - 2,394)
FOREST GAP	19.3 * (1 - 206)	0.86 (0.1 - 3.0)	4.2 (0.1 - 20.0)	400.5 * (17 - 2,556)
HERB PATCH	69.6 * (13 - 396)	1.07 * (0.6 - 1.9)	8.2 * (3.7 - 37.9)	692.9 * (21 - 2,762)
ALL	20.4 (1 - 625)	0.91 (0.1 - 3.0)	4.6 (0.1 - 40.0)	143.8 (9 - 1,949)

Forest: Closed and open mature forests, secondary forest, and vine tangle pooled (see text for details).
Mean clump size: Mean number of 1 m^2 plots along transect intersecting an herb clump
Mean clump species diversity: Mean number of species per 1 m^2 plot within an herb clump
Mean clump density: Mean number of stems per 1 m^2 plot within an herb clump

* Significantly different from all other habitat types ($p < 0.001$)

relatively small, though distance between clumps tended to be shorter. Herb clump sizes and distances between clumps were intermediate in forest gaps.

Variation in Herb Availability Across Different Sectors

Since herb availability varies with altitude and habitat type, which differ among sectors (see Habitat Description), herb density was expected to differ across sectors as well. Table 2.11 shows mean species diversity, density and biomass, mean herb clump length and density, and mean distance between herb clumps within the three sectors sampled (South, Central and West). Herb species diversity, stem density and biomass differed significantly across the different sectors; all pair-wise comparisons being significant (X^2 = 1511.2, 1587.3, and 1444.1, respectively, df = 2, $p < 0.001$). Whereas mean clump length was greater in the Central sectors, this differences did not reach statistical significance; the high degree of variance within each sector that may have masked differences (X^2 = 5.9, df = 2, p = 0.051).

The Central sector has the greatest herb species diversity, stem density, biomass and average herb clump size, with relatively short distances between clumps. Herb availability in the West sector is most similar to the Central sector, though the West has lower herb biomass and smaller average clump size. The South has the lowest herb species diversity, stem density and biomass, relatively small average herb clump size, and the greatest distances between herb clumps (Kruskal-Wallis test: X^2 = 13.3, df = 2, p <0.001; pair-wise comparison significant for South sector only).

Table 2.11 Variation in Afi gorilla herb availability across different sectors within their range, including species diversity, stem density, biomass, herb clump length and density, and distance between herb clumps (ranges in parentheses, see legend for definitions and units).

SECTOR	**Mean Species Diversity**	**Mean Density**	**Mean Biomass**	**Mean Herb Clump Size** (Length, m)	**Mean Herb Clump Density**	**Mean Distance Between Herb Clumps (m)**	**Mean Density of Herb Patch Clumps**
SOUTH	0.12 *	0.71 *	13.9 *	15.5 (1 - 309)	4.6 (1.0 - 25)	132.1* (10 - 1,148)	0.8
CENTRAL	0.31 *	1.65 *	32.9 *	26.2 (1 - 625)	4.5 (0.1 - 38)	65.1 (4 - 430)	1.3
WEST	0.24 *	1.52 *	25.3 *	18.1 (1 - 247)	4.5 (0.8 – 40)	51.3 (7 - 258)	1.4

Mean species diversity: Mean number of species per 1 m^2 plot
Mean density: Mean number of stems per 1 m^2 plot
Mean biomass: Mean number of grams per 1 m^2 plot
Mean clump size: Mean number of 1 m^2 plots along transect intersecting an herb clump
Mean clump species diversity: Mean number of species per 1 m^2 plot within an herb clump
Mean clump density: Mean number of stems per 1 m^2 plot within an herb clump
Mean density of herb patch clumps: mean number of herb clumps within herb patch habitat types per km

* Differs significantly from all other sectors.
** Significantly greater than other sectors .

The distinctiveness of herb availability in the South is clearly illustrated in Figure 2.23, which shows mean herb density within 50 m^2 quadrats (50 x 1 m) along transects and three gorilla feeding trails.

Though all herb genera were present within each of the three sectors sampled, most genera occurred more frequently within at least one sector. Figure 2.24 shows variation in mean stem density of each genus across South, Central and West sectors. *Aframomum* density was almost three times as high in the Central and West sectors as in the South. *Hypselodelphys* and *Palisota* sp. 1 were most common in the Central sector and virtually absent from the South. While *Thaumatococcus/ Megaphrynium* density is highest in the Central sector, it and *Palisota* sp. 2 were relatively evenly distributed across the three sectors. *Stylochiton* was the only genus that occurred more frequently in the South than in any other sector.

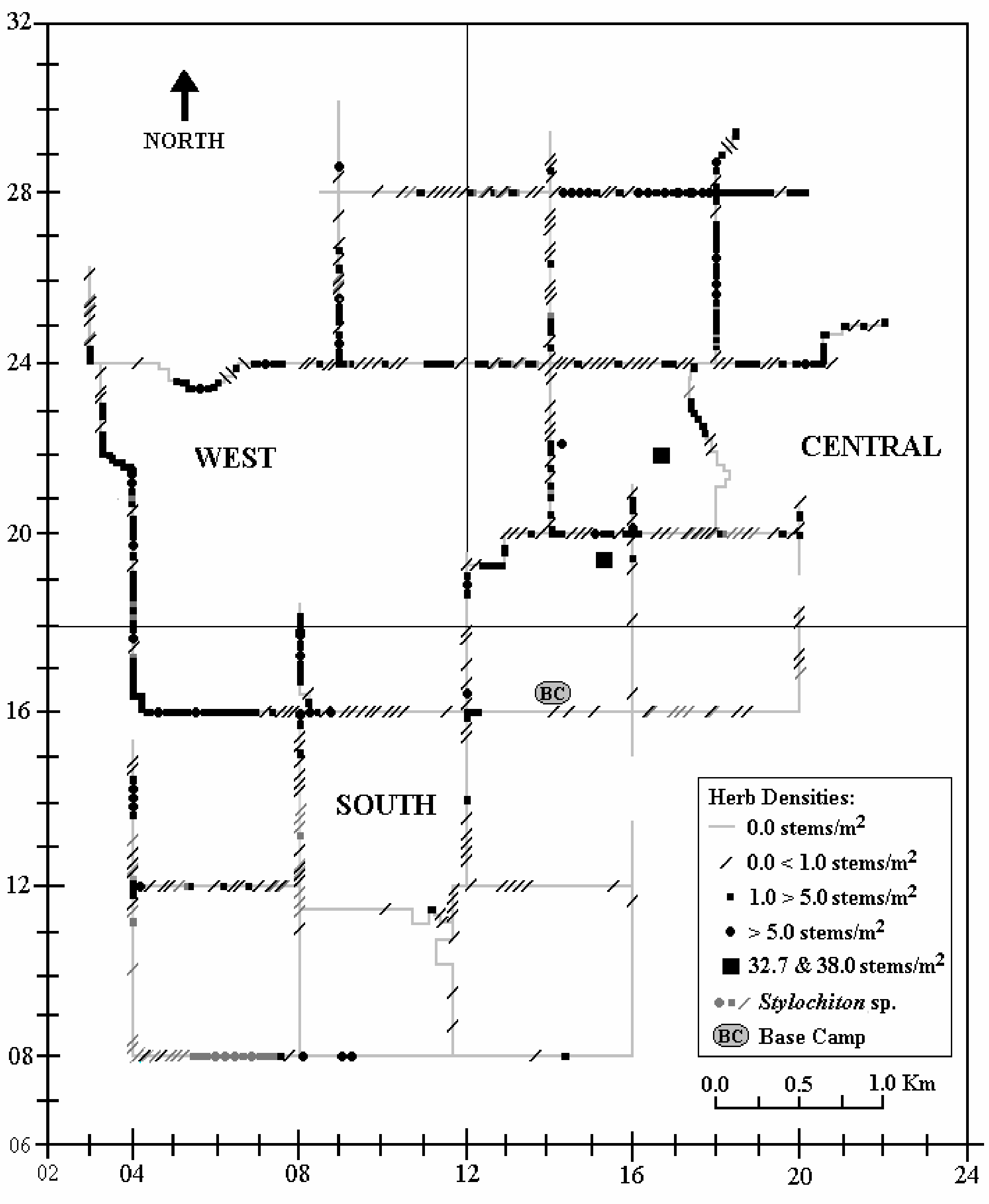

Figure 2.23 Herb density within 50 m2 quadrats (50 x 1 m) along transects and three gorilla feeding trails

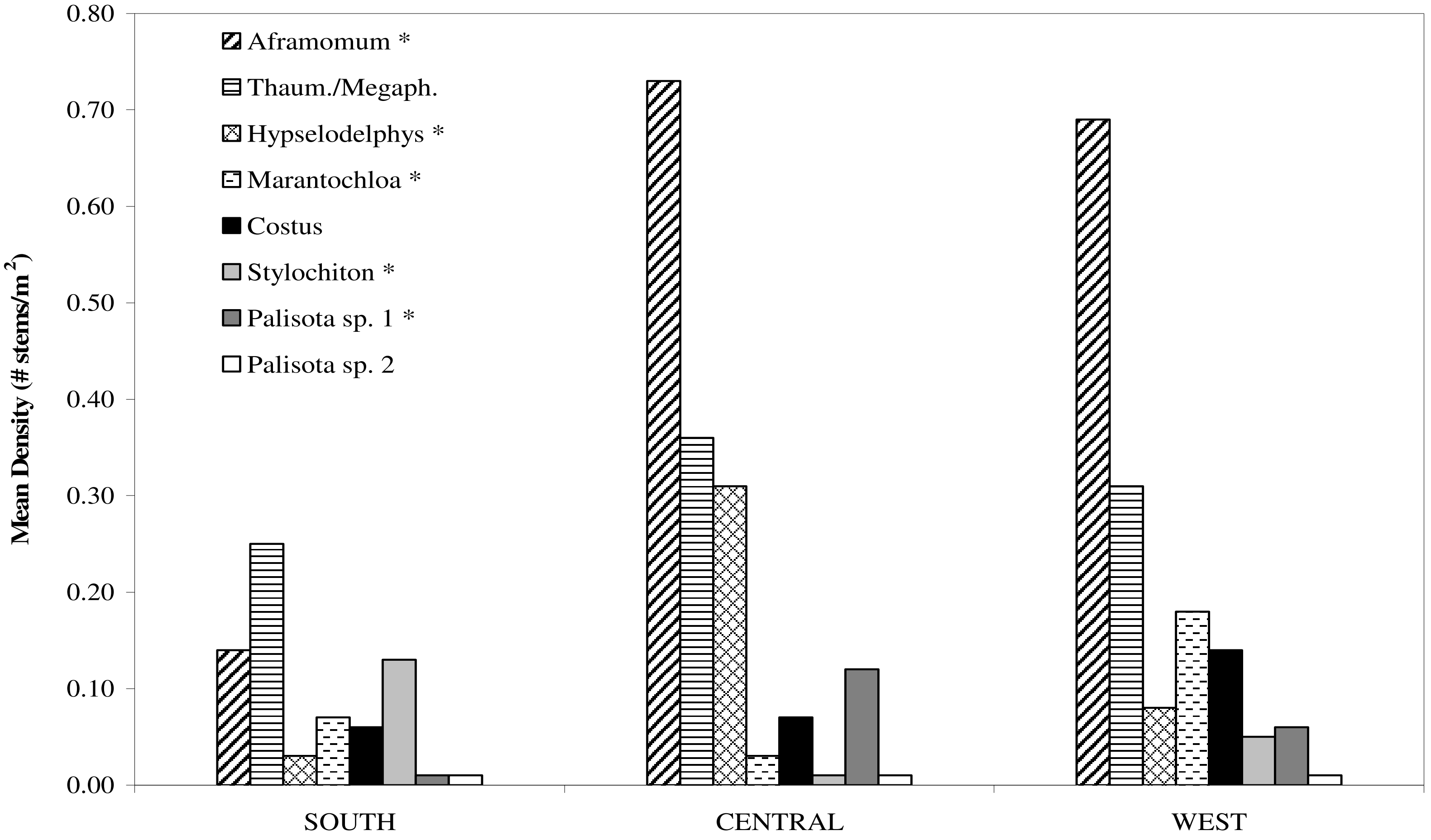

Figure 2.24 Variation in stem density of herb genera across different sectors
(* Differences between sectors are significant, see text for details)

COMPARISONS WITH OTHER GORILLA STUDY SITES

The following discussion will compare several aspects of the Afi gorilla and other gorilla habitats, including altitude, climate, temporal availability of tree fruits and availability of gorilla herb foods. The major differences between habitats of Afi and other western gorilla habits elucidated by these comparisons are highlighted in the summary along with important findings of the present study.

Altitude

One major difference between Cross River gorilla habitats and those of other western gorillas is their relatively high altitudes. Most Cross River gorillas inhabit areas with complex topographies including altitudes ranging between 200 and 1500 m (Oates et al. 2003). The Afi gorilla habitat includes altitudes between 200 and 1300 m. Altitudes at western lowland gorilla sites usually range between 200 and 500 m, and altitudes above 700 m are rare (see Table 2.12). Most Grauer's gorilla study sites have higher altitudes (e.g., Kahuzi: 1800 – 3300 m and Masisi: 1500 – 2000 m) than western gorilla sites, including Afi Mountain; however, altitudes at Itebero (600 – 1300 m) are similar to Afi (Yamagiwa et al. 1992). Results of the present study suggest that many aspects of the Afi gorillas' habitat (e.g., climate and herb availability) are related to variation in altitude and may explain some of the differences found between Afi and other western gorilla sites.

Climate

Table 2.12 compares the climate of seven gorilla study sites including 1) Afi Mountain in Nigeria, 2) Bai Hokou in Central African Republic, 3) Mondika in CAR/Republic of Congo, 4) Ndoki in the Republic of Congo, 5) Lopé in Gabon, 6) Kahuzi in Democratic Republic of Congo and 7) Karisoke in Rwanda. Figure 2.25 compares variation in monthly rainfall at Afi Mountain, Bai Hokou, Mondika, Lopé, and Kahuzi. For this comparison, monthly means for each site were calculated from estimates from graphs of several individual years. In order to depict typical rainfall patterns for each site, means from long-term data of nearby areas, where available, were also incorporated [i.e., Bayanga village, CAR (Carroll 1996; Fay 1997).

Figure 2.25 shows that length and timing of dry and wet seasons varies between the sites with three different patterns emerging that are most likely related to differences in latitude (van Schaik et al. 1993). The first seasonal pattern in rainfall occurs at Lopé, Kahuzi, and Karisoke. At Lopé, there are 4 seasons: a minor dry season (January – February), a minor wet season (March – May), a major dry season (mid-June – mid-September), and a major wet season (October – December). Kahuzi and Karisoke exhibit a similar pattern, though with shorter dry seasons (Minor: January, which is often less severe or does not occur at all; Major: June – August). The second seasonal pattern, which occurs at Bai Hokou and most likely Ndoki, is characterized by only two seasons: one dry season (mid-December – mid-March) and one wet season. The third seasonal pattern occurs at the most northwestern site within the gorillas' range, Afi Mountain, where there are also two seasons: one relatively long dry season (November – March) and one wet season.

Table 2.12 Comparison of climate across different gorilla study sites.

Study Site	Location	Altitude (m)	Mean Annual Rainfall (mm)	Mean Minimum Temp* (°C)	Mean Maximum Temp* (°C)
Cross River					
Afi Mountain [1] (1996, 1998 – 1999)	6° 18’ N 8° 58’ E	200-1300	3528	18.7 (16.3 – 20.6)	25.7 (23.3 – 28.7)
Pandrillus Field Station [1] (1996 – 1999)	6° 18’ N 9° 00’ E	150	3142	21.9 (16.0 – 24.5)	31.9 (27.2 – 37.2)
Western lowland					
Bai Hokou, CAR [2] (1990 – 1995)	2° 51’ N 16° 28’ E	300	1573	19.7 (17.5 – 22.9)	27.9 (24.0 – 31.0)
Bayanga village [3] (1973 – 1985)			1365	21.5 (20.6 – 22.9)	31.5 (28.4 – 35.7)
Mondika, CAR [4] (1995 – 2000)	2° 22’ N 16° 16’ E		1415	21.0 (± 0.8)	28.2 (± 1.7)
Ndoki, Congo [5] (1991 – 1992)	2° 20’ N 16° 19’ E	200-400	1540	(19.4 – 22.8)	(23.8 – 32.5)
Lopé, Gabon [6] (1984 – 1989)	0° 10’ S 11° 35’ E	200-500	1532	21.7 (20.1 – 23.2)	29.1 (27.0 – 32.8)
Grauer’s montane					
Kahuzi, DRC [7] (1994 – 2002)	2° 15’ S 28° 45’ E (approx.)	2000-3000	1658	13.8	26.5
Mountain					
Karisoke, Rwanda [8] (1978 – 1979)	1° 27’ S 29° 29’ E	2600-3700	1839	3.8 (± 1)	14.8 (± 1.5)

* Means and ranges were estimated from graphs for several sites. Ranges (in parentheses) are for mean monthly temperatures.

[1] Present study, [2] (Goldsmith 1996; Remis 1994), [3] (Carroll 1996; Fay 1997), [4] (Doran et al. 2002; Mehlman & Doran 2002), [5] (Kuroda et al. 1996; Mitani 1992; Nishihara 1995), [6] (Tutin & Fernandez 1993; Williamson 1989; Williamson et al. 1990), [7] (Yamagiwa & Basabose 2006; Yamagiwa et al. 2005), [8] (Watts 1988).

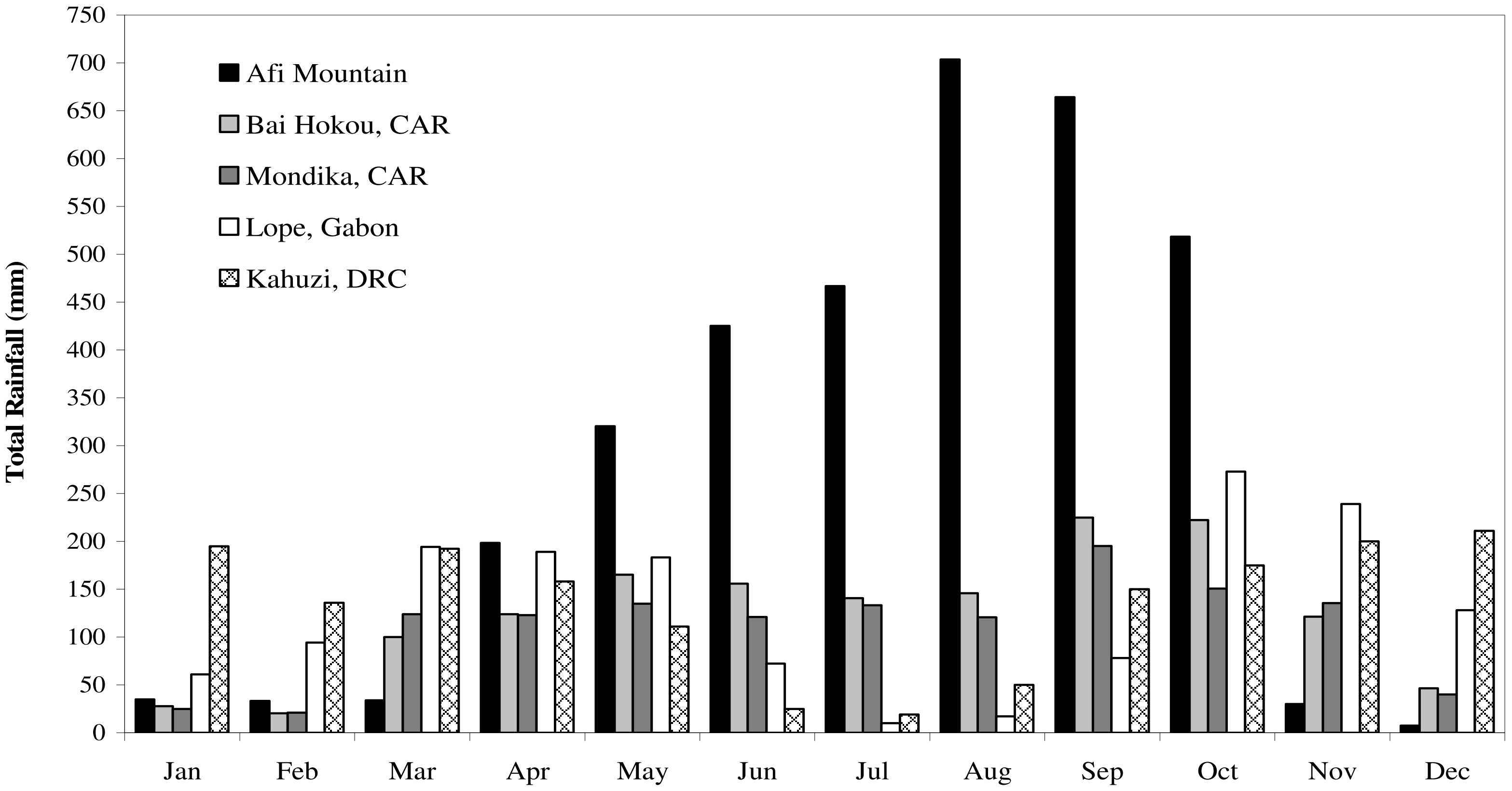

Figure 2.25 Mean monthly rainfall at five gorilla study sites

(Present study; Goldsmith 1996; Remis 1994; Doran 2002; Tutin & Fernandez 1993; Yamagiwa & Basabose 2006; see text for details)

The third seasonal pattern at Afi differs from the others in length and intensity of seasons. Similar to Bai Hokou and Ndoki, there is one dry and one wet season at Afi; however, the wet season at Afi is more intense. Whereas rainfall during June through August decreases slightly at Bai Hokou, rainfall at Afi increases during these months peaking dramatically in August and September, and then tapers during October; rainfall at Bai Hokou peaks in September and October. During the most intense part of Afi's wet season, June – October, cloud cover is persistent and sunlight is rare. During this time, charging batteries from the solar panel at base camp is virtually impossible; it takes at least three days to get a full charge.

Although mean annual rainfall on Afi is approximately two times greater than all other sites (Table 2.12), Afi's dry season, lasting five months (with up to four months of no rain) is prolonged and more intense compared to the other study sites. Dry seasons at other sites typically last no longer than 3 months and these months rarely have no rain. While little rain falls during the major dry season at Lopé, cloud cover is persistent and humidity remains high (80%) (Williamson 1989). In contrast, cloud cover is rare or more commonly non-existent during the Afi dry season, which is referred to as the 'Harmattan' period when dry winds bring dust from the Sahara desert producing a relatively constant haze. Although humidity was not recorded at Afi, immediately after these winds arrive everything (i.e., soil, leaf litter, researcher's skin and clothes, etc.) becomes dry and remains dry until the wet season begins, suggesting humidity levels on Afi are relatively low during the dry season compared to Lopé. The dry season at Bai Hokou is also characterized by hot dry winds (M. Remis, personal communication).

Differences in temperatures (minimum and maximum) are likely due to differences in altitude. Karisoke and Kahuzi have the lowest temperatures and least monthly variation. Patterns of monthly variation are similar among western sites with lowest temperatures occurring at Afi and highest at Lopé. The much higher temperatures at the Pandrillus Field Station and Bayanga village highlight the difference between recording temperature in open areas and in the forest, though at Afi this difference is confounded by altitude.

To summarize, the Cross River gorillas' habitat has a unique climate that is characterized by greater annual rainfall, an extreme seasonal rainfall pattern, a prolonged and more intense dry season, and lower temperatures than other western gorilla sites. Afi's unique pattern of rainfall is most likely related to their most northwestern location within the gorilla's range. Afi's high altitude explains its lower temperatures.

Temporal Availability of Tree Foods

Figure 2.26 summarizes monthly variation in availability of young leaves, flowers and fruits consumed by Afi gorillas ('gorilla fruit') and their relationship with rainfall seasonality on Afi Mountain. Flowers were the only tree food at Afi that clearly varied with rainfall seasonality; flowers were most abundant during dry season months. At Afi, young leaves (based on proportion of individual trees with abundance scores of ≥ 1) were available relatively consistently throughout the year, though young leaf availability peaked during the early wet season month of May and was lowest during three wet months (August – October) when rainfall was greatest.

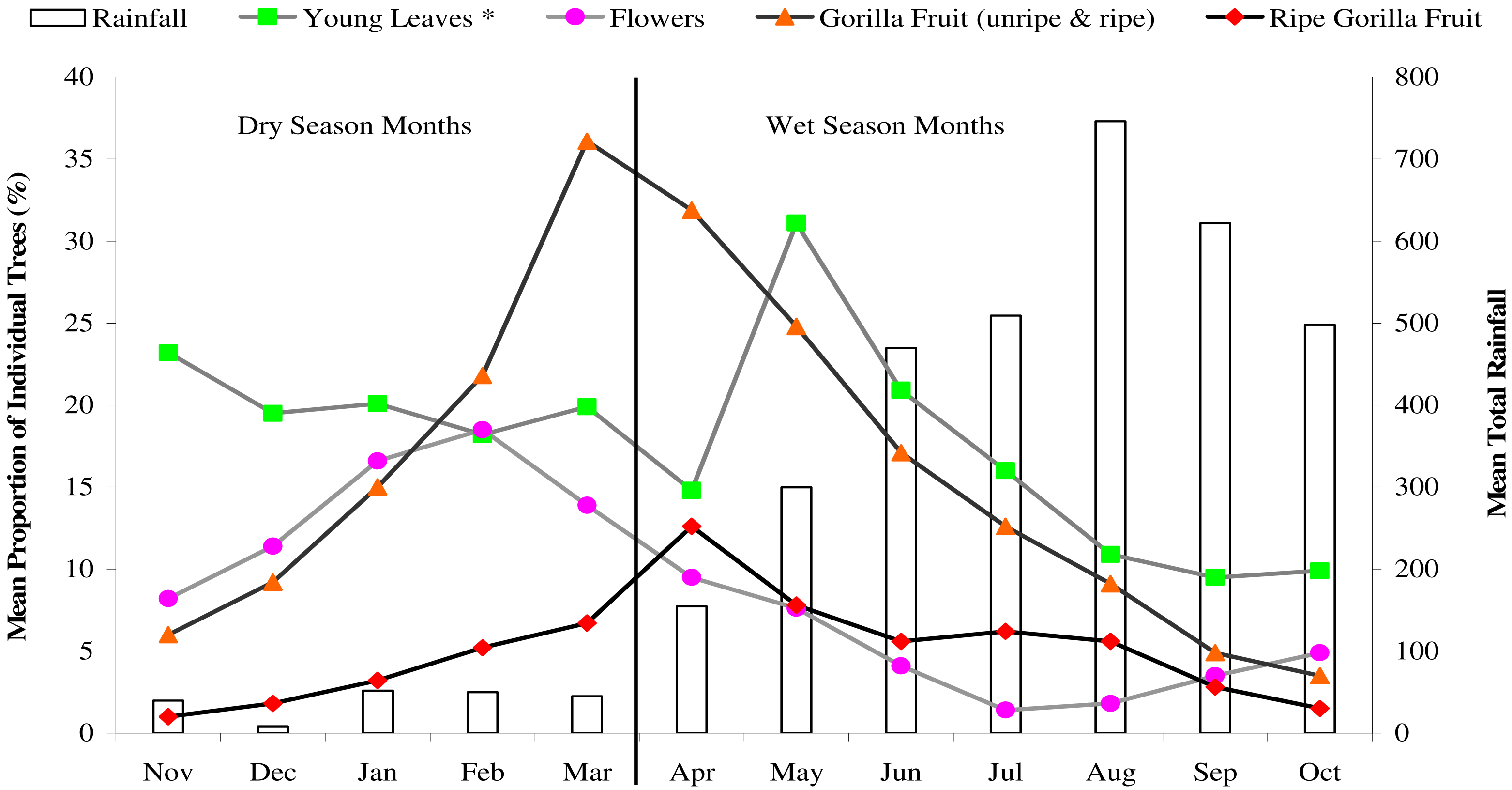

Figure 2.26 Summary of temporal variation in young leaf, flower and fruit availability and relationship with rainfall at Afi Mountain

(* includes only trees with abundance scores of ≥ 1)

Several studies have suggested that water (i.e., rainfall) is one important factor influencing fruit production and ripening (Anderson 2001; Chapman et al. 1999; van Schaik 1986; van Schaik et al. 1993; White 1994; Wright & van Schaik 1994). At western lowland gorilla sites periods of fruit scarcity tend to correspond with the dry season lasting three months, and periods of relatively high fruit availability tend to coincide with wet season months (see Figure 2.27). Therefore, one might expect that the period of fruit scarcity at Afi should be prolonged compared to other western gorilla sites due to Afi's prolonged dry season, lasting five months. The present study at Afi shows that fruit scarcity is prolonged; however, this is due to scarcity during three months of the dry season (November – January, beginning of dry season) and two to three months of the wet seasons (August – October, the wettest months at the end of the wet season). Hence, fruit availability at Afi does not strictly coincide with rainfall seasonality (Figure 2.26).

Afi's different fruiting pattern compared to other western gorilla sites, likely occurs due to Afi's extreme seasonal climate. The prolonged dry season and intense wet season at Afi may influence plant reproduction resulting in a shift in annual flowering and fruiting cycles compared to western lowland gorilla sites. To facilitate intersite comparison of flowering and fruiting patterns, I estimated the typical annual cycles in relation to rainfall seasonality for five western lowland gorilla habitats. Monthly variation in flower, fruit (unripe and ripe) and ripe fruit were examined for Afi Mountain (present study), Bai Hokou (Carroll 1996; Goldsmith 1996; Remis 1994, 1997b), Mondika (Doran et al. 2002), Ndoki in the Congo Republic (Kuroda et al. 1996), and Lopé (Tutin & Fernandez 1993; Tutin et al. 1991; White 1994; Williamson 1989).

Whenever possible both abundance (number/proportion of individual trees) and diversity (number/proportion of species) were considered when characterizing cycles.

Typical annual cycles at these sites were estimate in a manner that incorporates the following factors: 1) dry and wet seasons occur during different months of the year for some sites, 2) food availability, particularly for fruit, was not necessarily uniform across all dry or wet season months and 3) interannual fluctuations in rainfall and food availability occurs at all sites. Months sampled at each site were grouped into five periods (i.e., beginning of dry season, end of dry season, beginning of wet season, mid-wet season and end of wet season). These periods were identified using monthly rainfall records. Relative availability of flowers and fruit during each of the five periods were estimated separately using a scores ranging between 0.5 and 1.5 representing lowest and highest availability, respectively (increments of 0.25 were used). Average scores for each period were then used to estimate typical annual flowering and fruiting cycles at each site. These cycles were roughly similar across western lowland gorilla sites, so a typical cycle for western lowland gorilla sites was estimated and compared to Afi Mountain.

The pattern of overall and ripe fruit production at other sites can be characterized in relation to rainfall seasonality as follows (Figure 2.27). At other western sites, fruit (unripe and ripe) production peaks in the beginning of the wet season and ripe fruit availability peaks by the end of the mid-wet season period, followed by a peak in monthly rainfall (250 – 400 mm), at which time fruit availability rapidly declines. A similar pattern occurs at Afi, though peaks in flower and fruit availability occur earlier in the year (Figure 2.27). At Afi, peak fruit production occurs at the end of the dry season and ripe fruit availability peaks in early wet season months when rainfall is < 400 mm. Ripe fruit availability then slowly declines over several months as rainfall increases and as rainfall reaches its maximum (600 – 900 mm) ripe fruit availability drops to its lowest level (see Figures 2.8 and 2.25).

These comparisons suggest that environmental factors important for fruit production and ripening may coincide with periods when rainfall is relatively low (< 400 mm/month). Whereas monthly rainfall at other sites rarely exceeds 400 mm, such rainfall occurs during five months of the year (June – October), thereby potentially reducing the period of optimal fruit production and ripening. This reduction at Afi is likely related to the lack of sunlight during these five months. Several studies have suggested that irradiance is also an important factor influencing flower and fruit production and some argue that sunlight may be more important than rainfall (Anderson 2001; Chapman et al. 1999; van Schaik 1986; van Schaik et al. 1993; White 1994; Wright & van Schaik 1994).

Though the amount of sunlight was not measured in the present study, there is some evidence to suggest that the period of maximum irradiance at Afi coincides with peak flower and fruit production (February – May). During the dry season, there is little or no cloud cover though the hazy skies of the ‘Harmattan’ period (December – January) may impede sunlight. The haze begins to clear in the dry month of February and usually disappears by the end of March. The brightest and clearest days at Afi tend to occur in the early wet season months of April and May when ripe fruit availability peaks. During the remaining months of the wet season (June – October), cloud cover is essentially constant and rain fell on all but 1 – 3 days of each month in the present study.

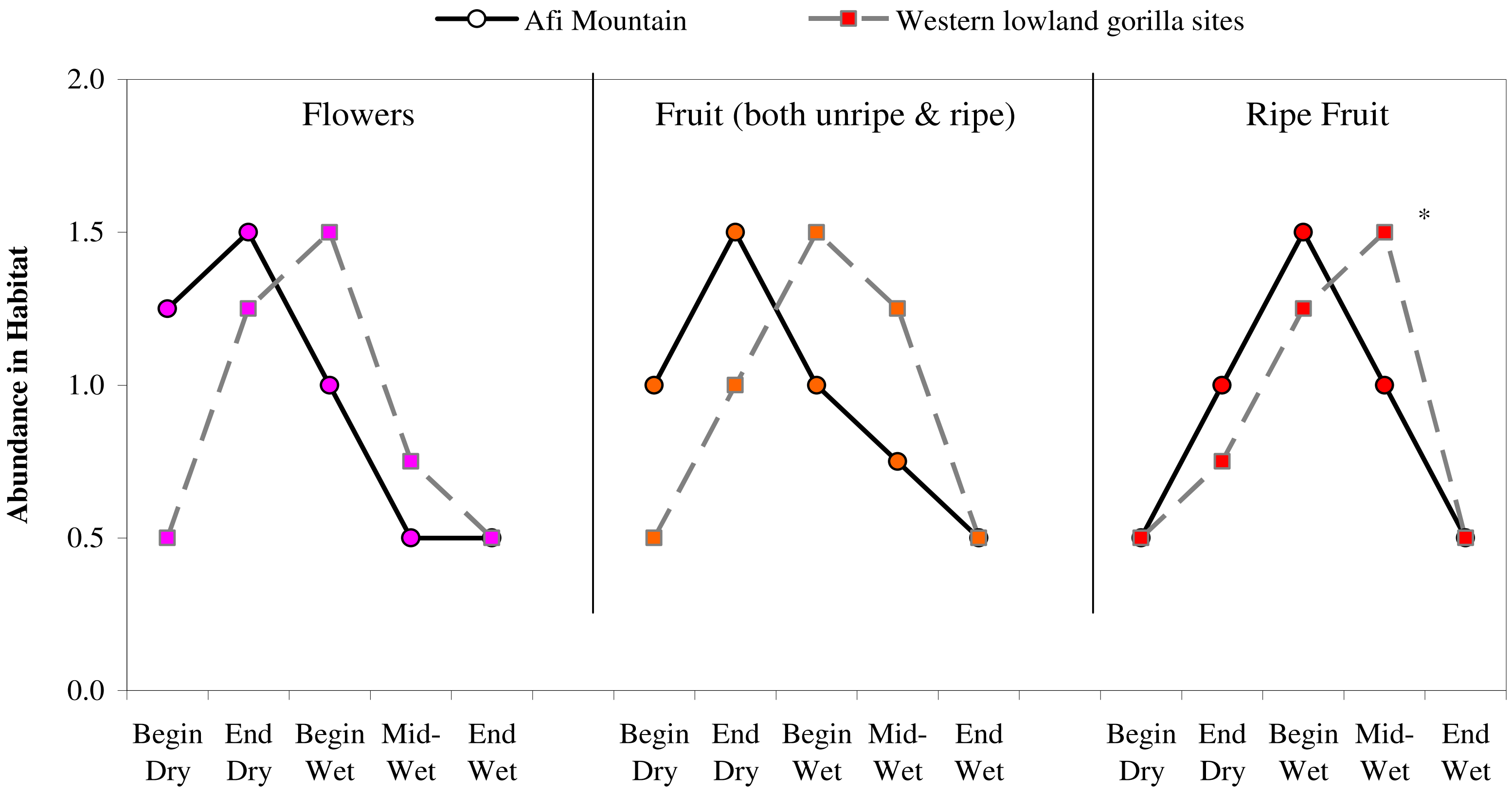

Figure 2.27 Comparison of estimated typical annual cycles of flowering and fruiting at Afi Mountain and western lowland gorilla sites (availability: 0.5 = lowest and 1.5 = highest; see text for details; * At Lope ripe fruit availability is also high in the minor dry season)

Consequently, water is certainly abundant during these months at Afi, but sunlight is not. Under these conditions it may be advantageous for plants to flower and produce fruit earlier in the year to allow sufficient time for fruit development and ripening when irradiance levels are relatively high. Therefore, the more intense wet season at Afi may explain the apparent shift in the annual fruiting cycle observed at Afi compared to other western gorilla habitats.

Herb Availability

Table 2.13 compares herb species diversity, stem density, most and least common genera, occurrence of swamp herbs, and spatial pattern (coefficient of dispersion) at Afi with four other western gorilla study sites, Bai Hokou (Goldsmith 1996), Lopé (Rogers et al. 2004; White et al. 1995), Mondika (Doran et al. 2002) and Ndoki (Malenky et al. 1993; Rogers et al. 2004). Herb species diversity is similar at the three sites where data is available (Afi, Bai Hokou, and Lopé). Overall mean stem density at Afi (1.16 stems/m^2) is most similar to Bai Hokou (1.11 stems/m^2) with both being lower than that at Lopé (at least 1.83 stems/m^2) and Ndoki (2.25 stems/m^2). The density figure shown for Mondika (0.78 stems/m^2) is an underestimate since it is based on five most important gorilla herb food genera within two habitat types only and does not include swamp herbs, which are common at Mondika. Doran et al. (2002) suggest that herb density at Mondika is most likely similar to Lopé and Ndoki.

Table 2.13 Comparison of gorilla herb availability at five western sites, including herb species diversity, density, least and most common genera present, presence of swamp herbs, and spatial pattern at Afi and four western gorilla study sites [Mean density: mean number herb stems per 1 m^2; Spatial Pattern: coefficient of dispersion (CD, variance/mean); n/a: no data available].

	AFI [1]	**BAI HOKOU [2]**	**LOPE [3, 4]**	**MONDIKA [5]**	**NDOKI [4, 6]**
Diversity:					
Total no. species (Mean per 1m^2)	15 (0.21)	12 (0.39)	12	n/a	n/a
Mean density:					
Overall	1.16	1.11		0.78 *	2.25
Marantaceae	0.51	0.56	1.75	0.60	
Zingiberaceae	0.51	0.34	0.13	0.07	
Commelinaceae (*Palisota* spp.)	0.02	0.21	n/a	0.11	
Genera:					
Most Common	*Aframomum* (0.43)	*Haumania* (0.44)	*Haumania* (0.90)	*Haumania* (0.37)	Marantaceae
Least Common (Mean Density)	*Palisota* (0.02)	*Aframomum* (0.05)	*Ataenidia*	*Aframomum* (0.05)	Zingiberaceae
Swamp Herbs	Absent	Rare	Absent	Common	Common
Spatial Pattern **	12.6 / 5.8	4.6	n/a	Clumped	2.3

[1] Present Study; [2] Goldsmith 1996; [3] White et al. 1995; [4] Rogers et al. 2004; [5] Doran et al. 2002; [6] Malenky et al. 1993.

* Includes 5 most important herb food genera within two habitat types only and no swamp herbs.

** Number (n), size, and placement of plots varied between sites - Bai Hokou: n = 1000 plots , size = 1 m^2, placed every 5 m along transect; Ndoki: n = 125, 4 m^2, randomly selected along transects; Afi: n = 1000, 1 m^2, randomly selected at 5 m intervals for comparison with Bai Hokou (first CD) and n = 125, 4 m^2, randomly selected for comparison with Ndoki (second CD).

One of the major differences between herb availability in Afi and other western gorilla habitats is the relative abundance of the Marantaceae and Zingiberaceae herb families. Whereas herbs of both families are equally abundant at Afi, Marantaceae herbs are more abundant than Zingiberaceae at all other sites. *Aframomum* is the most common genus found at Afi and the least common at most other sites. As at Afi, *Aframomum* occurs most frequently within light gaps at Lopé and Bai Hokou but these light gaps are most often associated with logging activities and roads (Goldsmith 1996; White et al. 1995), which are absent at Afi. Afi's complex topography does, however, create a high level of naturally occurring disturbances such as presence of large rock outcrops, rockslides, and falling trees, which frequently occur on steep slopes most likely creating larger light gaps than in the lowlands (Brokaw 1985). In addition, fire burns at least some portion of Afi almost annually; fire is not reported to occur at other sites. The fact that *Aframomum* is most abundant in disturbed areas and is most commonly found at Afi may indicate that levels of disturbance are greater at Afi than other sites, despite the absence of logging and roads at Afi.

Haumania is clearly the most important herb at Bai Hokou, Lopé, and Mondika and is absent from Afi. Gorillas at these other sites eat young shoots of *Haumania* only, which occur at much lower densities than mature stems. For example, only 5.5% of *Haumania* stems recorded were young shoots at Mondika (Doran et al. 2002). Consequently, density of mature *Haumania* stems does not accurately reflect the availability of this food resource. Densities of *Haumania* at Bai Hokou and *Aframomum* at Afi are similar, as is overall herb density, suggesting that herb availability may be higher at Afi than Bai Hokou.

Though herbs are clumped in their distribution at all sites for which data are available, they appear to be more clumped at Afi. Malenky et al. (1993) suggest that magnitude of coefficients of dispersion are influenced by size and number of sample plots, which varied between the present study and those conducted at Bai Hokou and Ndoki (Goldsmith 1996; Malenky et al. 1993). Therefore, two additional coefficients of dispersion were calculated for Afi by randomly selecting plots from the 40,900 plots sampled during the present study. For comparison with Bai Hokou, 1000 1 m^2 plots every 5 m along transects were selected and for comparison with Ndoki, 125 4 m^2 plots were chosen. The resulting coefficients of dispersion for Afi (12.6 and 5.8, respectively) are more than two times greater than coefficients reported for Bai Hokou and Ndoki (4.6 and 2.3, respectively).

SUMMARY

Afi Mountain's unique climate among gorilla habitats and its complex topography appear to influence food availability, both temporally and spatially, and these measures differ from other gorilla study sites in several ways. Compared to other gorilla study sites, the climate at Afi is characterized by greater annual rainfall and an extreme seasonal rainfall pattern with a prolonged and more intense dry season, which is most likely related to Afi's most northwestern location within the range of gorillas. Annual rainfall at Afi is on average at least two times greater than at any other gorilla study site. Its dry season lasting up to five months (November - March), typically with up to four months of no rain at all, is prolonged compared to length of dry seasons at other sites where typically there are only three months with less than 50 – 80 mm per month.

Whereas rainfall rarely exceeds 400 mm per month at other gorilla study sites, during the wet season at Afi (April - October) rainfall averages greater than 450 mm per month with up to 3 months with greater than 500 mm of rain per month.

The extremely intense wet season at Afi likely produces a shift in the annual fruiting cycle, compared to other sites. Fruit availability at Afi was highest at the end of the dry season (February and March) and relatively high at the beginning of the wet season (April and May), differing from other western gorilla study sites where fruit availability tends to be high during the wet season and low during the dry season (Doran et al. 2002; Goldsmith 1996; Remis 1997b; Tutin et al. 1991; Williamson 1989). Thus, unlike other sites the period of fruit scarcity at Afi does not strictly coincide with the dry season but rather occurs during the height of the wet season (August – October) and the beginning of the dry season (November - January). Consequently, there was no correlation between rainfall and fruit availability.

Afi's complex topography, occasional rock slides, frequent tree falls, and periodic fires caused by humans create a highly diverse habitat. Altitude on Afi ranges between 200 and 1300m. Frequency of habitat types varied with altitude. Whereas secondary forest was the most common habitat type at all altitudes, mature forest types (open and closed) are more frequent below 600 m and light gaps (forest gaps and herb patches) more frequent above 600 m. The greater frequency of light gaps at higher altitudes may be due to the presence of large rocks and frequent tree falls, the majority of which occurred on steep slopes and most commonly at altitudes above 600 m.

This relationship between habitat types and altitude may explain gorilla herb food availability, which for the most part varied among habitat types and altitudes in a similar fashion. Herb species diversity as well as overall and individual species stem density was greatest in light gap habitat types, particularly herb patches, with the exception of *Stylochiton*, which occurred most frequently within closed mature and secondary forests. Overall diversity and stem density do not vary among altitudes lower than 600 m but do increase significantly thereafter as altitude increases and light gaps become more common. When considering individual herbs, only three (i.e., *Aframomum, Hypselodelphys,* and *Palisota* sp. 1) exhibited the relationship with altitude described above. Stem densities of three other herbs (*Marantochloa, Palisota* sp. 2 and *Thaumatococcus/Megaphrynium*) peak at 600 m and then decrease as altitude increases. By contrast, *Stylochiton* stem density is greatest at ≤ 400 m corresponding to altitudes where closed mature forest is most common.

When compared to other sites, overall herb stem density at Afi (1.16 stems/m^2) was most similar to Bai Hokou and lower than at Lopé, Ndoki, and Mondika. Whereas *Aframomum* is the most common herb genus at Afi, it is the least common or occurs at relatively low densities at other sites (Doran et al. 2002; Goldsmith 1996; Malenky et al. 1993; Rogers et al. 2004; Rogers & Williamson 1987; White et al. 1995). Afi's complex topography and naturally occurring disturbances (e.g., fallen trees) may account for this difference. At other sites, *Aframomum* is associated with areas disturbed by human activity (e.g., along logging roads) (Goldsmith 1996; White et al. 1995), which are absent at Afi. Logging activities at most of these sites ceased many years ago, however, eliminating further disturbance and the growth of *Aframomum.* On the other hand, naturally occurring disturbances at Afi are continuous and likely frequent enough to create light gaps promoting *Aframomum* growth. As at most other sites, herbs at Afi were clumped in their distribution at all levels measured, including each genus separately and within all different habitat types. Herbs at Afi, however, appear to be clumped to a greater extent than at Bai Hokou and Ndoki where comparable data is available.

Within the Afi study site, altitude, habitat type frequency and food availability differed significantly across three sectors (South, Central, and West) within the study site. Mean altitude was greatest within the Central sector where frequency of herb patch and forest gap habitat types, and herb species diversity, stem density and biomass were greater than within West and South sectors. Altitudes were intermediate in the West where frequency of herb patch and forest gap habitat types was similar to the Central sector but herb species diversity, stem density, and biomass were significantly lower than in the Central sector. Altitudes on average were lowest in the South where there was a significantly greater proportion of closed and open mature forests and lower proportions of herb patch and forest gap habitat types than within the Central and West sectors. In addition, particular important gorilla tree food species appear to be concentrated within certain sectors. How this variation in food availability across different sectors may influence the gorillas' ranging behavior is explored in Chapter Four.

CHAPTER THREE – DIET:

Composition, Temporal Variation and Important Food Species

INTRODUCTION

One of the main objectives of the study was to describe the Afi gorillas' diet, specifically the composition of the diet, variation in the diet including its relationship to temporal variation in fruit availability and identify important food species in the diet. Based on initial observations during the pilot study, the composition of the Afi diet was expected to be similar to that of western lowland gorillas who rely on herbaceous food resources throughout the year (i.e., staple food) but consume large amounts of fruit when it is available (Doran et al. 2002; Goldsmith 1996, 1999; Nishihara 1995; Remis 1997; Rogers et al. 2004; Tutin et al. 1991; Williamson 1989). While western lowland gorillas consume fruit throughout the year, the level of fruit consumption fluctuates monthly and is correlated with fruit availability. During periods of fruit scarcity, western lowland gorillas increase their overall consumption of non-fruit vegetation food resources (e.g., stem pith of herbs, leaves, and bark) and particular species serve as important fallback foods during this time. Thus, the relative contribution of fruit and non-fruit vegetation foods in the western gorilla diet varies on a monthly and seasonal basis in relation to fruit availability (Doran et al. 2002). The Afi gorilla diet was expected to vary throughout the year in a similar manner.

At western lowland gorilla study sites, fruit availability correlates with rainfall so that periods of high and low fruit availability tend to coincide with the wet and dry seasons, respectively. Consequently, previous western lowland gorilla studies investigated seasonal variation in diet by comparing dry versus wet season months and found that the relative contribution of fruit and non-fruit vegetation in the diet did vary between these seasons as predicted by fruit availability (Goldsmith 1996; Remis 1997; Tutin et al. 1991). During my study, however, I learned that fruit availability at Afi was not related to rainfall and the periods of high and low fruit availability both extend across wet and dry months, so that these periods do not strictly coincide with rainfall seasons as at western lowland gorilla study sites. Therefore, consumption of fruit and non-fruit vegetation by Afi gorillas was not expected to differ between rainfall seasons. So in order to investigate variation in the relative contribution of fruit and non-fruit vegetation in the Afi gorillas diet, it was necessary to identify periods of high and low fruit consumption using dietary measures.

The specific aims of this chapter include the following: 1) to describe the overall composition of the Afi gorilla diet and identify the staple foods that they rely on throughout the year, 2) to describe monthly and seasonal variation in the Afi gorilla diet, including examination of the relationship between fruit availability and fruit consumption by gorillas, identification of high and low fruit consumption periods, and investigate how Afi gorillas respond to the period of fruit scarcity, 3) to describe monthly variation in the relative contribution of different food species to the Afi gorillas' diet by identifying important food species within different food categories, and to identify important staple, seasonal and fallback food species. The results of the above analyses provide the background information necessary to examine how variation in diet and food availability influences the Afi gorillas' ranging behavior discussed in Chapter Four. Dietary data were collected using methods that allow comparison of the Afi gorilla diet to that of gorillas at other study sites. In this chapter, however, only general comparisons are made; more specific comparisons are presented in Chapter Six.

METHODS

Determining Diet Using Indirect Methods

Indirect methods of assessing diet, such as analyzing feces and feeding remains, are less desirable than direct methods (i.e., visual observation) that can provide both quantitative and qualitative information. Indirect methods, however, have been found to be the most feasible way of studying unhabituated gorillas (and chimpanzees) in the wild since the mid 1980s and to date have provided the bulk of the dietary information from lowland gorilla studies (Goldsmith 1996; Nishihara 1995; Remis 1994, 1997; Rogers et al. 2004; Tutin & Fernandez 1993b; Williamson et al. 1990; Yamagiwa et al. 1994).

Indirect methods are particularly useful when studying gorillas because gorillas leave behind many and a relatively greater number of signs of their behavior than most other primates. In addition, signs left by gorillas (i.e., feces, nests, and food remains) can usually be readily distinguished from those of sympatric primates, including chimpanzees (Goldsmith 1996; Schaller 1963; Tutin & Fernandez 1993b; Williamson 1989). For example, gorillas most often swallow the seeds and skin of the fruit they consume, which pass through the gut and are deposited in the feces. By contrast, monkeys spit out most seeds and chimpanzees often wad up their food, suck on it like a sponge, and then discard the remains (Goldsmith 1996; Tutin & Fernandez 1993a). Due to their large body size, gorillas travel terrestrially between feeding sites leaving behind footprints, feces, feeding remains, and disturbed undergrowth creating a trail that can be followed, so potentially providing complete day range lengths.

Indirect methods do have limitations, however, resulting in under or over representing particular food items in deduced diet. While seeds and fruit skin found in fecal samples can be identified taxonomically, vegetative foods (i.e., pith, bark, and leaves), flowers, and some invertebrates can rarely be identified. This limitation of macroscopic fecal analysis results in the under representation of non-fruit vegetation and invertebrates on food lists (Tutin & Fernandez 1993b). Feeding remains found along trails, on the other hand, can underestimate arboreal foods (i.e., tree fruit and leaves) relative to terrestrial foods (i.e., herb pith, leaves and fruit). These along with other limitations and biases resulting from the use of indirect evidence are discussed further in subsequent sections where applicable.

Determining Diet in the Present Study

Indirect methods were essentially the only option available for the present study since the Afi gorilla population is highly endangered and Afi gorillas were hunted both in the past as well as during this study (see Chapters 1 and 4 for details). Consequently, habituation of the Afi gorillas was not possible or desirable since it would make the gorillas more vulnerable to hunting. In fact, contact of any kind with the gorillas was avoided. While the Afi gorilla population may now receive a higher level of protection than in the past, the gorillas' extremely close proximity to a dense human population and the precarious nature of local politics makes it inadvisable to attempt habituation even in the future. Keeping this in mind, I strove to modify and expand current indirect methodologies to provide the greatest amount of information possible. At the same time, data were also collected using methods similar to those of previous studies to allow comparison.

To increase the probability of finding gorilla trails and following them successfully, assistants (mostly former hunters) from local villages were employed. In addition, a forestry department staff member was appointed to join the study. A total of 12 assistants was hired to provide four teams consisting of three members, and three teams worked at all times (one team was ‘off’ one week a month). Each team included a tracker and two field assistants. Using information from interviews of new staff members and past working experience of staff employed during the mapping exercise, members of each team were chosen based on their skill level (i.e., hunting experience, education) so that members would possess complimentary abilities. For the first six months, I joined different teams to observe their skills and ability to work together, and to provide training. In addition when a team collected data along gorilla trails or at nest sites without my participation or supervision, we reviewed their work the next day and any omissions or mistakes encountered were discussed. After this initial six-month training period, I was confident in the staff’s ability to collect data unsupervised though I continued to check their work personally when time permitted, and reviewed their field notes daily to monitor their accuracy.

Following feeding trails and collecting fecal samples to investigate the Afi gorillas’ diet (and ranging behavior) was the focus of the study from December 1997 through November 1998. Foods were placed into five categories: 1) Herb pith, 2) Liana bark/pith[2], 3) Tree bark, 4) Leaves - herbs, lianas, vines, shrubs and trees, and 5) Fruit - herbs, lianas, and trees. The term non-fruit vegetation refers to foods other than fruit (i.e., pith, leaves, bark, flowers, and roots). These categories encompass the range of foods gorillas are known to consume and correspond to categories used by previous studies of other gorilla populations, thereby facilitating comparisons.

Fecal analysis

Fecal analysis methods were modified from Tutin & Fernandez (1993b) and Goldsmith (1996). Fecal samples were collected from nest sites and gorilla trails when dung could be assigned with certainty to gorillas based on smell and characteristic lobed form (Schaller, 1963). For each sample, diameter was measured in cm, and then entire samples were collected separately in plastic bags with date, location, and age-class noted. Extraneous debris was brushed from samples before collection. The following age-class categories based on diameter of feces were used: adult males: ≥ 6.5 cm diameter; adult females and adolescent males: 4.5 – 6.4 cm; juvenile: 2.0 – 4.4 cm; infant: < 2.0 cm (Tutin & Fernandez 1993b). Samples were carried back to base camp, where each sample was weighed, and then washed with water through 1 mm mesh metal sieves.

Because gorillas swallow the seeds of the majority of fruit foods, it was assumed that seeds in fecal samples represent most of the fruit eaten by the gorillas. Undigested fiber and leaf fragments represented non-fruit foods (stems, piths, leaves). Due to the extremely wet conditions at Afi, it was not possible to dry samples before analysis as performed in other western gorilla studies (Goldsmith 1996; Remis 1994, 1997). Excess

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[2] This category includes bark/pith from 3 species of shrubs that were a minor part of the gorillas' diet

water was, however, removed from fiber/leaf fragments, seeds, etc. previous to further analysis.

After washing samples, seeds and fruit skins were separated from fiber/leaf fragments. Seeds were identified, counted, weighed (each type separately), and a sample preserved for future reference. Because fig (*Ficus*) fruit contain numerous very small seeds that are usually less the 1 mm in diameter, it was not possible to separate fig seeds from fiber and leaf fragments. Therefore, the number of *Ficus* seeds was estimated using the following scale: ≤ 50, ≤ 100, ≤ 500, ≤ 1,000 or > 1,000. Fruit skin was also identified and weighed separately.

The abundance of fiber and leaf fragments in fecal samples was estimated using two methods to facilitate comparisons with other studies. First, abundance was estimated relative to total fecal mass using a five-point scale (0 = absent, 1= rare, 2 = few, 3 = common, 4 = abundant) for fiber and leaf fragments separately. These two abundance scores were then summed to produce a total foliage score. Secondly, because these scores are subjective, fiber and leaf fragments were weighed together to produce a more quantitative measure. It was not possible to separate leaf fragments from the fiber so their weight corresponds to the total foliage abundance score.

The following measures were calculated monthly. For fruit: the percentage of fecal samples containing seeds; the total number of fruit species eaten; the mean number of different fruit species per sample; and the mean fruit pulp volume eaten per fecal sample (see below). For non-fruit vegetation, the mean fiber, leaf fragment and foliage scores were computed. In addition, the relative contribution of fruit and non-fruit vegetation was estimated using percent fecal weight for fruit and fiber/leaf fragment weight (see below). For the present study, using wet weights should not influence the results since wet weights were used for both seeds/fruit remains and fiber/leaf fragments. The relative contribution of fruit and non-fruit vegetation found in this study, however, cannot be directly compared to those of Goldsmith (1996) who used dry weights.

Fruit pulp volume eaten per fecal sample was calculated in the following manner similar to that used by Williamson (1989). For each identified fruit species found in fecal samples, length and width of seeds and fruits and number of seeds per fruit were obtained from field measurements or botanical references (Keay 1989; Keay et al. 1964). Seed and fruit volumes were calculated using the formula for an ellipsoid (appropriate for a spheroid as well), as most seeds and fruits approximated this shape:

$4/3\ \Pi\ (ab^2)$ or $4.189\ (ab^2)$, where $a = \text{length} \times 0.5$, $b = \text{width} \times 0.5$, $a < b$

The volume of pulp was obtained by subtracting seed volumes from the fruit volumes. The pulp volume per seed was then computed by dividing the total fruit pulp volume by the average number of seeds per fruit. For each fecal sample, the number of seeds for each species was multiplied by that species' pulp volume per seed and then summed to provide the total fruit pulp eaten per fecal sample. Calculation of pulp volume per seed was not possible for 24 seed species since their fruit source was not determined. Seeds of these species, however, represented only 0.2% of the total number of seeds present in samples; consequently, their absence when calculating total fruit pulp eaten per fecal sample likely had little affect on the results.

Relative contribution of fruit and non-fruit vegetation, represented by percent fecal weight, was determined following Goldsmith (1996). For each fecal sample, the weights of all fruit remains (predominantly seeds) were added together to provide a total fruit weight per sample. All non-fruit vegetation (herb, woody material, and leaves) was added together to provide the total weight of non-fruit vegetation per sample. The total weight of a fecal sample was the sum of fruit and non-fruit vegetation weights. The percentage of the total fecal weight represented by fruit and non-fruit vegetation was then calculated for each fecal sample.

Feeding trails

Systematic searches were conducted to locate fresh gorilla trails (see Chapter 4 for details). When encountered, trails were paced for distance and the direction was noted every 50 paces, or more frequently if major changes in direction occurred. Feeding remains were recorded along three types of trails: 1) Complete trails from one night's nest site to the next night's nest site, 2) Partial trails to/from one night's nest site, 3) trails not beginning or ending at a nest site but attributed to gorillas by associated feces and/or footprints. Since it was not possible to differentiate feeding trails of individual gorillas, food remains were recorded along the 'main' path traveled by the gorillas. Secondary paths branching from the 'main' path were followed to determine whether they re-joined the main path or terminated at a different nest site but feeding sites were not consistently recorded along these 'branch' paths.

A feeding site was defined as any identifiable food remains left by gorillas that were at least 1 m away from any other site (Nishihara, 1995; cf. Goldsmith, 1996). Feeding sites were placed in one of five categories: herb pith; leaf (herb, liana, shrub, and tree); liana bark/pith; tree bark; and fruit (herb, liana, and tree). For each feeding remnant, location, species, part eaten (i.e., fruit, leaves, pith, bark, etc.), developmental stage (i.e., young/mature leaves, ripe/unripe fruit), amount eaten (see below), and habitat type (see Chapter 2 for definitions) were recorded. For each month, the total number of species eaten, percentage of feeding sites, and mean amount eaten per feeding site were calculated for each different food category.

Though feeding sites recorded along each trail represent the activities of more than one individual on the day the trail was created, they do not represent the activities of all group members since feeding sites along ‘branch’ paths were not consistently recorded. Each individual feeding site does, however, likely represent the food eaten by only one individual gorilla. Individual feeding sites containing food remains of herbs (pith, leaves, or fruit) and bark/pith of young liana stems were readily identifiable since remains were often left in distinct ‘piles’. Each separate area of bark removed from trees, main liana stems, or shrubs were considered to be different feeding sites even if they occurred on the same stem. Distinguishing individual feeding sites containing tree leaf or fruit remains was not always possible and estimates were made based on, for example, number of broken tree branches. Consequently, tree leaf and fruit frequencies were likely underestimated relative to other foods.

To estimate amount of food eaten per feeding site, measurements taken and amount eaten calculated differed depending on food type:

1. Herb pith: Number of stems and length of pith removed. Using measurements taken to calculate herb biomass, the weight of pith per centimeter (g/cm) was calculated for the different herb species separately. For each herb pith feeding site, the lengths of pith removed were summed and multiplied by pith weight per centimeter to determine amount of herb pith eaten in terms of number of grams eaten per feeding site. When

more than one herb species was eaten at the same feeding site, amount eaten was calculated for each species separately and then summed.

2. Liana bark/pith and tree bark: Length and width of the area removed to calculate area eaten (cm^2). The gorillas often ate many young liana stems, developing from the main stem, at one feeding site. Because measuring the widths of each stripped stem became too time consuming and the average width of bark removed was 1 cm (based on the first month of data collection), only length of the stripped stem was measured during the remainder of the study. Amount (i.e., area) of pith removed was calculated by multiplying length removed by 0.2 cm (average width based on the first month of data collection).
3. Leaves – Number eaten. Since most herb species from which the gorillas ate leaves have one leaf per stem, actual counts of leaves eaten were possible. This was rarely possible for leaves of tree, shrub, and liana species, so for these species estimates were made based on number of broken branches or fresh compound leaf stems with missing leaflets found on the ground. Each leaflet of compound leaves was considered to be a single leaf. Results based on number of leaves eaten along trails are interpreted cautiously for several reasons, including the fact that number of non-herb leaves eaten were estimated, variation in leaf size was not considered, and there was a bias towards herb leaves since they are more easily detected than leaves of other plant forms.
4. Fruit: Estimates were attempted but due to the difficulties making estimates for most fruit species (i.e., those trees that produce large numbers of small fruits), these

estimates were not used for analysis. Instead the amounts of fruit eaten per month are based on fecal measurements only.

Data Analysis

To investigate monthly variation in diet, species diversity, frequency, and abundance measures from fecal samples and/or feeding trails were calculated monthly for each different food category (i.e., fruit, herb pith, leaves, liana bark/pith, tree bark) and for non-fruit vegetation (i.e., leaves, liana and tree bark/pith, and herb pith pooled). Species diversity of fruit in the diet was determined monthly using fecal data only (total fruit species in feces and mean fruit species per fecal sample). Non-fruit vegetation diversity was calculated from feeding remains (i.e., total number of species found along trails) for each non-fruit food category separately and then pooled.

For each of the food categories, frequency of consumption was calculated monthly by summing the number of feeding sites at which a given food category was eaten and dividing by the total number of sites recorded that month (i.e., percentage of feeding sites). The frequency of herb feeding sites may be over represented since herb remains are more easily recognized than fruit, leaf, liana bark/pith, and tree bark remains. In addition, food remains may have represented more than one individual. This likely occurred more often when the gorillas were consuming herbs, which tend to occur in dense patches where distance between foraging individuals was likely reduced compared to when feeding on other plant forms. These biases, however, occur equally for each month and differences between months are valid (Goldsmith 1996).

Both fecal and feeding site data were used to determine the abundance of different food categories in the gorillas diet including the following monthly means:

1. Fruit: percent fecal fruit weight and fruit pulp volume per fecal sample.
2. Non-fruit vegetation: foliage score (fiber + leaf fragment score).
3. Leaves: leaf fragment score and number of leaves eaten per feeding site.
4. Liana and tree bark/pith: amount (cm^2) eaten per feeding site.
5. Herb pith: fiber score and amount (grams) eaten per feeding site.

To investigate seasonal variation in the gorillas' diet, periods of high and low fruit consumption were identified in a manner similar to Goldsmith (1996). Medians were calculated for diversity (number of fruit species per fecal sample), frequency (percentage of feeding sites) and abundance (percentage of fruit fecal weight and pulp volume per fecal sample) of fruit in the diet. Months with measures above their respective medians were considered the period of high fruit consumption and months with measures below their respective medians were considered the period of low fruit consumption. Though the use of medians may artificially divide the year into two periods, the periods identified in the present study clearly reflect a natural break in values of fruit diversity, frequency and abundance measures.

Wilcoxon-Mann Whitney two-tailed tests were performed using monthly measures to determine whether diversity, frequency, and abundance of each different food category and non-fruit vegetation categories pooled in the diet differed between periods of high and low fruit consumption. I also investigated whether consumption of the different food categories differed between rainfall seasons (comparing the November – March dry season with the April – October wet season) to avoid making the assumption that they did not vary between rainfall seasons as predicted by the discontinuous relationship between rainfall seasons and fruit availability (see Chapter Two).

Relationships between fruit consumption, fruit availability, and rainfall were investigated using Pearson correlations. Phenology data were not available for all months in which diet data were collected (December 1997 – November 1998); monitoring began only in May 1998. Consequently, I used phenology data from 2000 for this analysis and therefore results should be viewed with caution. I chose to use phenology data from 2000 based on the following rationale (see Chapter Two for details):

1. The rainfall pattern in 2000 was most similar to that of 1998 (Chapter 2). Short-term fluctuations in rainfall have been suggested to produce deviations from typical cycles of phenophases (Anderson 2001).
2. A greater number of individual trees and species were monitored during 2000, including several important gorilla fruit-food species that were not monitored during 1998 and 1999.
3. The 2000 data provide a more accurate description of ripe fruit availability due to the improved abilities of my assistant and I to distinguish ripe from unripe fruit; we had difficulty distinguishing ripe fruit during 1998 and 1999.

Determining Important Food Species

Important food species were identified for each food category using criteria incorporating frequency and abundance measures modified from those of Goldsmith (1996). Important fruit species were identified using five fecal and feeding trail measures. Fruit species were considered important if in any given month they were present in 20% or more fecal samples or at least two of the following four criteria were met: 1) represented ≥ 10% of total monthly fruit weight, 2) represented ≥ 1.0% of total monthly fruit pulp volume (Williamson 1989), 3) present along feeding trails on ≥ 10% of days sampled, and/or 4) present at ≥ 10% of total monthly fruit feeding sites (regardless of the amount of fruit eaten per feeding site).

Important leaf, liana bark/pith, and tree bark species were identified using three feeding trail measures. A species was determined to be important when one of the following criteria was met for any given month: 1) present along feeding trails ≥ 10% of days sampled, 2) present at ≥ 10% of that food category's total monthly feeding sites, or 3) represented ≥ 10% of that food category's total monthly amount eaten. Important herb pith species were identified using these same three criteria, but a ≥ 20% cut-off was used.

RESULTS

Sample Sizes for the Two Data Collection Methods

Fecal analysis

A total of 1,418 fecal samples, collected on 124 days, was analyzed from the 12-month period December 1997 – November 1998. Table 3.1 presents, on a monthly basis, the number of days sampled, number of fecal samples collected and estimated/presumed age-sex class composition of the individuals sampled. Samples come from a total of 39 different weeks and the number of days sampled per month was distributed throughout ≥ 3 different weeks of each month, except in November when only 2 weeks were sampled.

Table 3.1 The number of days sampled, number of samples and the age-sex class composition of fecal samples colleted at Afi each month (wet season months are in bold).

Month	**No. of Days Sampled**	**No. of Samples Collected**	**AdM**	**AdF or AdolM**	**Juv**	**Inf**	**Unk**
Dec 1997	10	97	10	48	14	0	25
Jan 1998	9	161	22	107	26	0	6
Feb 1998	9	126	17	87	12	0	10
Mar 1998	9	62	5	24	4	0	29
Apr 1998	12	160	31	95	14	0	20
May 1998	14	151	38	87	24	0	2
June 1998	8	100	15	64	18	1	2
July 1998	12	172	28	109	31	3	1
Aug 1998	15	151	29	100	18	1	3
Sep 1998	10	96	15	66	12	1	2
Oct 1998	9	74	12	49	9	0	4
Nov 1998	7	68	10	51	6	1	0
TOTAL	124	1,418	232	887	188	7	104

AdM = adult male silverback; AdF = adult female; AdolM = adolescent male; Juv = juvenile; Inf = infant; Unk = unknown (measurement of fecal diameter not possible).

None of the monthly fecal dietary measures were significantly correlated with number of fecal samples collected monthly (r = +/- 0.157 to 0.436, p > 0.157) or the number of days sampled per month (r = +/- 0.173 to 0.429, p > 0.164). Therefore, sample size is unlikely to have affected the following results based on fecal data.

Feeding trails

Table 3.2 shows, on a monthly basis, the number of days sampled, number of kilometers followed and number of feeding sites recorded on gorilla feeding trails. Between December 1997 and November 1998, a total of 4,181 feeding sites were recorded along 130.2 km of gorilla trails during 142 days. Gorillas often consumed foods of more than one category at a single feeding site and a total of 4,909 feeding sites containing different food categories were recorded. An average of 10.9 km of trails were followed monthly (SD = 4.7, range = 5.2 – 18.8). A total of 44 different weeks were sampled and the number of days sampled per month was distributed throughout ≥ 3 different weeks in all months; four weeks were sampled during eight months. During the majority (59.1%) of weeks ≥ 3 days per week were sampled. Number of non-fruit vegetation, herb pith, leaf, and tree bark species were significantly correlated with number of days and/or feeding sites recorded monthly (r = 0.63 – 0.70, p = 0.01 – 0.03). Monthly variation in frequency of leaf consumption (percentage of feeding sites) was significantly related to number of days sampled per month (r = 0.594, p = 0.041). Therefore, sample size may have affected the following results based on feeding site data accordingly.

Table 3.2 Number of days sampled, number of kilometers followed and number of feeding sites recorded on gorilla feeding trails per month at Afi (wet season months are in bold).

Month	**No. of Days Sampled**	**Total No. of Km Followed**	**Total No. of Feeding Sites Recorded ***
Dec 1997	7	5.2	271 (310)
Jan 1998	10	9.5	215 (225)
Feb 1998	11	18.8	213 (229)
Mar 1998	9	8.5	117 (132)
Apr 1998	18	16.3	438 (500)
May 1998	14	17.2	373 (467)
June 1998	8	10.5	261 (318)
July 1998	12	11.8	324 (362)
Aug 1998	17	12.9	804 (1,046)
Sep 1998	13	5.5	295 (360)
Oct 1998	13	8.4	519 (589)
Nov 1998	10	5.6	351 (371)
TOTAL	142	130.2	4,181 (4,909)

* In parentheses: Number of feeding sites containing different food categories (see text for details).

Composition of Diet

Gorillas at Afi consumed at least 216 different food items (plant species plus part eaten) from 168 species (22 herb, 32 liana and vine, 6 shrubs, 69 tree and 39 unidentified seed species). A total of 70 food species have been identified to at least the genus level and are listed in Appendix II along with the parts eaten from them. Of all different food items eaten, 46.3% are fruits of 100 herb, liana, and tree species, 24.5% are bark (including liana pith) of 53 liana, vine, shrub and tree species, 16.7% are leaves of 36 herb, liana, shrub, and tree species, 10.2% are pith of 22 herb species, 1.4% are roots of 3 tree species, and 0.9% are flowers of 2 tree species. To date, evidence of invertebrate consumption has not been recorded at Afi.

Herb pith, leaves, liana bark/pith, tree bark, and fruit were consumed in all 12 months of the year sampled, though diversity, frequency and abundance varied monthly and seasonally (see next section). Table 3.3 presents the frequency with which the different food categories occurred in fecal samples (i.e., percentage of weeks, days, and fecal samples) and along feeding trails (i.e., percentage of weeks, days, and feeding sites). Since herb pith remains are more easily detected along trails than other foods, the frequency of this item is most likely over represented relative to frequencies of leaves, liana bark/pith, and fruit, which are underestimated using feeding trail evidence.

These data suggest that herb pith, leaves, and liana bark/pith can be regarded as staple foods; they were present in fecal samples during all weeks and on all days sampled (leaves and herb pith) or recorded along trails during all weeks sampled (liana bark/pith). Herb pith was present in 100% of fecal samples and consumed along trails during all weeks, on 97.1% of days sampled and at 50.1% of feeding sites, making it the

Table 3.3 Frequency of different food categories in Afi gorilla fecal samples and at feeding sites along trails.

FOOD CATEGORY	**FECAL ANALYSIS** (percentage, %)			**FEEDING TRAILS** (percentage, %)		
	Weeks	**Days**	**Samples**	**Weeks**	**Days**	**Sites**
Herb Pith	100	100	100	100	97.1	50.1
Leaves						
All	100	100	98.6	88.6	74.3	20.6
Herb	----	----	----	75.0	54.2	9.7
Tree	----	----	----	77.3	50.7	8.5
Fruit	100	98.4	90.2	86.4	67.1	9.2
Liana Bark/Pith	----	----	----	100	75.7	14.7
Tree Bark	----	----	----	77.3	45.0	4.9

Fecal Analysis – Samples: Percentage of fecal samples (n = 1,418) containing herb pith (fiber), leaves (leaf fragments), or fruit (seeds, fruit skin).

Feeding Trails –

Weeks: Percentage of weeks sampled (n = 44) in which each food category was recorded along feeding trails.

Days: Percentage of days sampled (n = 142) on which each food category was recorded along feeding trails.

Sites: Percentage of feeding sites sampled (n = 4,909) at which each food category was recorded along feeding trails.

most frequently recorded food. Leaves were consumed throughout the year and were present in fecal samples in all weeks and days sampled (98.6% of all samples contained leaves; mean per week = 99.0%, SD = 2.4%, range = 90.2 – 100%; mean per day = 98.3%, SD = 7.6%, range = 33.3 – 100%). Based on feeding trail evidence, herb and tree leaves were consumed at similar frequencies. Liana bark/pith was recorded along feeding trails during all weeks and on the majority of days sampled (75.7%, mean % of days per month = 71.4%, SD = 15.7%, range = 37.5 – 100%), and was the third most frequently eaten food (14.7% of feeding sites). Fruit remains were found in 90.2% of fecal samples. Fecal samples contained fruit during all weeks and on 98.4% of days sampled when on average 89.6% of fecals contained fruit remains (SD = 22.1%, range = 0 – 100%).

Other non-food items, such as stones, rubbery substances and charcoal were also present in fecal samples. Small stones (≤ 1 cm diameter) were found in 10.7% of fecal samples during 10 months (January – October) when on average 11.2% samples per month contained stones (SD = 11.7%, range = 1.3 – 39.8%). Whether the gorillas ingested these stones incidentally while eating plant foods or actively is unknown. At least one of two different rubbery substances, suspected to be latex, was present in 6.3% of samples during all 12 months sampled (mean samples per month = 7.9%, SD = 11.1%, range = 0.7 – 39.2%). Charcoal was relatively abundantly available during 1997 – 1998 due to the fires that burned a large portion of the study site during the 1996 dry season. Charcoal was present in 3.6% of all samples collected and present in samples during five months of the year (January, April, June, and August, December; mean samples per month = 7.9%, SD = 8.7%, range = 1.0 – 18.6%).

Temporal Variation in Diet

Fruit consumption

Table 3.4 shows species diversity (total number of fruit species in fecal samples and mean number of fruit species per fecal sample), frequency (percent of feeding sites containing fruit), and abundance (mean percent fruit fecal weight and mean pulp volume eaten per fecal sample) of fruit in the gorillas' diet for each month. Total number of fruit species in fecal samples per month averaged 17.3 species (range = 7 – 31 species) and there was an average of 2.5 fruit species per fecal sample (range = 0.07 – 4.7 species). The frequency of fruit remains along feeding trails averaged 10.7% per month (range = 0.6 – 22.4%). On average fruit represented 28.9% of fecal weights per month (range = 1.2 – 66.8%) and a monthly average of 301.8 cm^3 fruit pulp was consumed per fecal sample (range = 2.0 – 996.2 cm^3).

Monthly variation in fruit consumption by gorillas was related to fruit availability and was not related to rainfall. Despite the fact that the diet and fruit availability measures were from different years [3], the relationship between fruit consumption (species diversity, frequency and abundance of fruit in the gorillas' diet) and availability of fruit eaten by gorillas was highly significant. Mean number of tree fruit species per fecal sample significantly increased with proportion of species with ripe fruit and unripe fruit eaten by gorillas separately ($r = 0.758$ and 0.700, respectively, $p \leq 0.006$, $n = 12$ months). Percent of feeding sites with tree fruit along trails significantly increased with proportion of individual trees with ripe fruit and unripe fruit eaten by gorillas separately ($r = 0.877$

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[3] Phenology data were not available for all months in which diet data were collected (December 1997 – November 1998); monitoring began in May 1998. Consequently, phenology data from 2000 was used for this analysis and results should be viewed with caution (see Methods for details).

Table 3.4 Monthly variation in diversity, frequency and abundance of fruit in the Afi gorilla diet (high fruit consumption months in bold; the fruit category includes tree, liana and herb fruit).

	DIVERSITY		**FREQUENCY**	**ABUNDANCE**	
	Total No. of species in fecal samples	Mean No. of species per fecal sample	Percentage of feeding sites along trails	Mean percentage of fruit fecal weight (g)	Mean pulp volume per fecal sample (cm^3)
Dec 97	12	1.2	1.3	3.8	10.2
Jan 98	18	1.2	6.7	3.7	31.3
Feb 98	22	4.3	20.5	54.7	260.0
Mar 98	24	4.7	19.7	49.5	535.2
Apr 98	31	4.1	22.4	52.6	1002.7
May 98	13	3.3	18.6	66.8	803.3
Jun 98	21	2.9	9.1	35.2	277.6
Jul 98	22	3.0	21.3	45.4	545.9
Aug 98	16	1.6	1.9	7.4	65.0
Sep 98	8	1.3	0.6	2.9	37.8
Oct 98	13	1.6	4.9	23.8	50.4
Nov 98	7	0.7	1.6	1.2	2.0

Fruit diversity: Total: mean = 17.3, median = 17.0
Species per sample: mean = 2.5, median = 2.2
Fruit frequency: Feeding sites: mean = 10.7%, median 7.9%
Fruit abundance: Fruit weight: mean = 28.9% (g), median = 29.5% (g);
Pulp volume: mean = 301.8 cm^3, median = 162.5 cm^3

and 0.856, respectively, $p < 0.001$, $n = 12$ months). Mean fruit pulp volume eaten per fecal sample significantly increased with proportion of individual trees with ripe fruit and unripe fruit eaten by gorillas separately ($r = 0.930$ and 0.772, respectively, $p \leq 0.002$, $n = 12$ months). All measures of fruit consumption by gorillas were not related to rainfall (for diversity, frequency, and abundance measures: $r = -0.03$ to $– 0.24$, $p \geq 0.45$).

Periods of high and low fruit consumption by Afi gorillas were identified, in a manner similar to Goldsmith (1996), using medians calculated for each of the five fruit diversity, frequency, and abundance measures shown in Table 3.4. During six consecutive months of the year (February – July), fruit measures were above their respective medians and these months were considered to be the period of high fruit consumption. During the remaining six months (August – January), fruit measures were below their respective medians and these months were considered to be the period of low fruit consumption. There were only two exceptions to the above pattern; the total number of species in fecal samples was less than the median in May and greater than the median in January. Though the use of medians may artificially divide the year into two periods, the division produced clearly reflects a natural break in fruit measures between months of high fruit consumption (February – July) and low fruit consumption (August – January).

During high fruit consumption months, fruit diversity, frequency, and abundance in the gorillas' diet were significantly greater compared to low fruit consumption months [Diversity: means = 3.7 versus 1.3 fruit species per sample, $z = 2.9$, $p = 0.004$; Frequency: means = 18.6% versus 2.8% of feeding sites, $z = 2.9$, $p = 0.004$; Abundance: means = 50.7% versus 7.1% of fecal weight per sample (g), and 570.8 versus 32.8 pulp per sample (cm^3), $z = 2.88$, $p \leq 0.001$; $n = 12$ months]. In addition, monthly percentages of fecal samples containing fruit remains was significantly greater during high fruit consumption months (mean = 99.6% of samples) compared to low fruit consumption months (74.8% of samples; z = 2.93, p = 0.002, n = 12 months).

Unlike fruit consumption by gorillas at western lowland sites, periods of high and low fruit consumption at Afi do not coincide strictly with wet and dry seasons (Figure 3.1). The period of high fruit consumption at Afi occurs during two dry season months (February – March) and four wet season months (April – July). The period of low fruit consumption at Afi occurs during three wet season months (August – October) and three dry season months (November – January). Fruit diversity, frequency, and abundance did not differ significantly between dry and wet season months [Diversity: means = 2.4 versus 2.5 fruit species per sample, z = 0.57, p = 0.57; Frequency: means = 10% versus 11.3% of feeding sites, z = 0.41, p = 0.69; Abundance: means = 22.6% versus 33.5% of fecal weight per sample (g), z = 0.73, p = 0.47 and means = 167.7 versus 397.5 pulp per sample (cm^3), z = 1.71, p = 0.09; n = 12 months].

Non-Fruit vegetation consumption

Non-fruit vegetation consumption by Afi gorillas was inversely related to fruit consumption and was not related to rainfall seasonality. Monthly variation in diversity (total number species along trails), frequency (percentage of feeding sites), and abundance (percentage fecal non-fruit weight) of non-fruit vegetation in the Afi gorillas' diet were all negatively and significantly correlated with monthly variation in diversity (mean number species per fecal sample), frequency, and abundance of fruit in the diet, respectively ($r = -0.626$ to -0.996, $p \leq 0.05$). None of the non-fruit vegetation diet

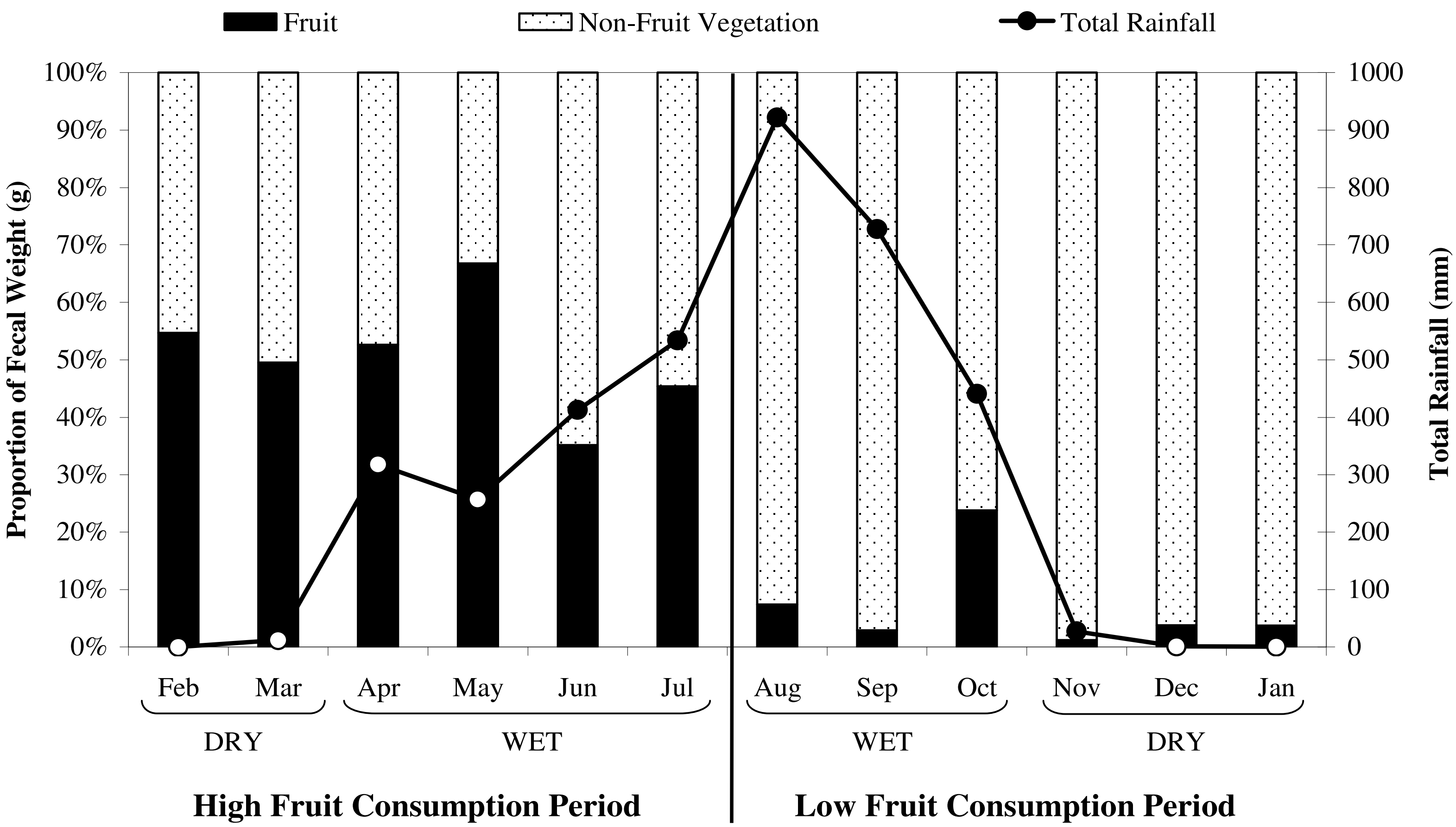

Figure 3.1 Relative contribution of fruit and non-fruit vegetation in fecal samples and rainfall

measures (diversity, frequency, or abundance) were correlated with rainfall ($r = -0.08$ to 0.30, $p \geq 0.35$). Furthermore, no diet measures of non-fruit vegetation consumption, including each of the non-fruit vegetation food categories individually (herb pith, leaves, liana bark/pith, and tree bark), differed significantly between dry and wet season months (diversity: $z = 0.08 – 1.63$, $p = 0.10 – 0.94$; frequency: $z = 0.01 – 1.54$, $p = 0.12 – 1.0$; abundance: $z = 0.41 – 1.54$, $p = 0.12 – 0.69$).

Consumption of non-fruit vegetation foods varied on a monthly basis and between periods of high and low fruit consumption. The number of all non-fruit vegetation food species, as well as herb pith, leaf, liana bark/pith, and tree bark food species separately (Figure 3.2), varied considerably between months sampled[4]; total number of non-fruit vegetation species eaten per month ranged between 17 and 37 species. While the gorillas consumed a greater variety of non-fruit vegetation, and tree bark separately, during the low fruit consumption period, these differences were not significant ($z = 1.37$ and 0.98, respectively, $p \geq 0.17$; Figure 3.3). During low fruit consumption months, however, species diversity of herb pith and liana bark/pith food species in the diet was significantly greater compared to high fruit consumption months ($z = 2.0$ and 1.32, respectively, $p \leq 0.05$).

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[4] These result may be explained by monthly variation in sample size (see Methods for details).

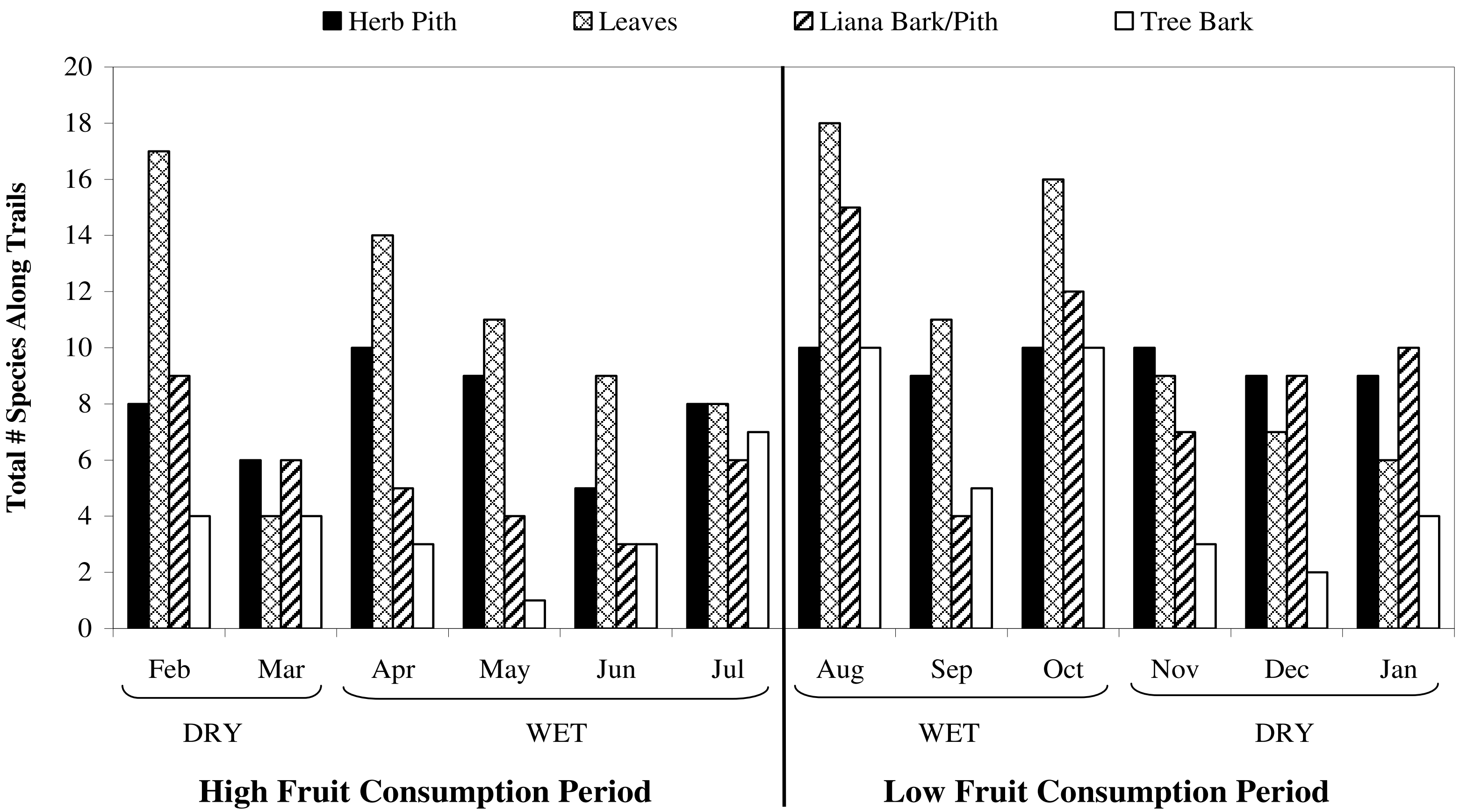

Figure 3.2 Species diversity of different non-fruit food categories along feeding trails

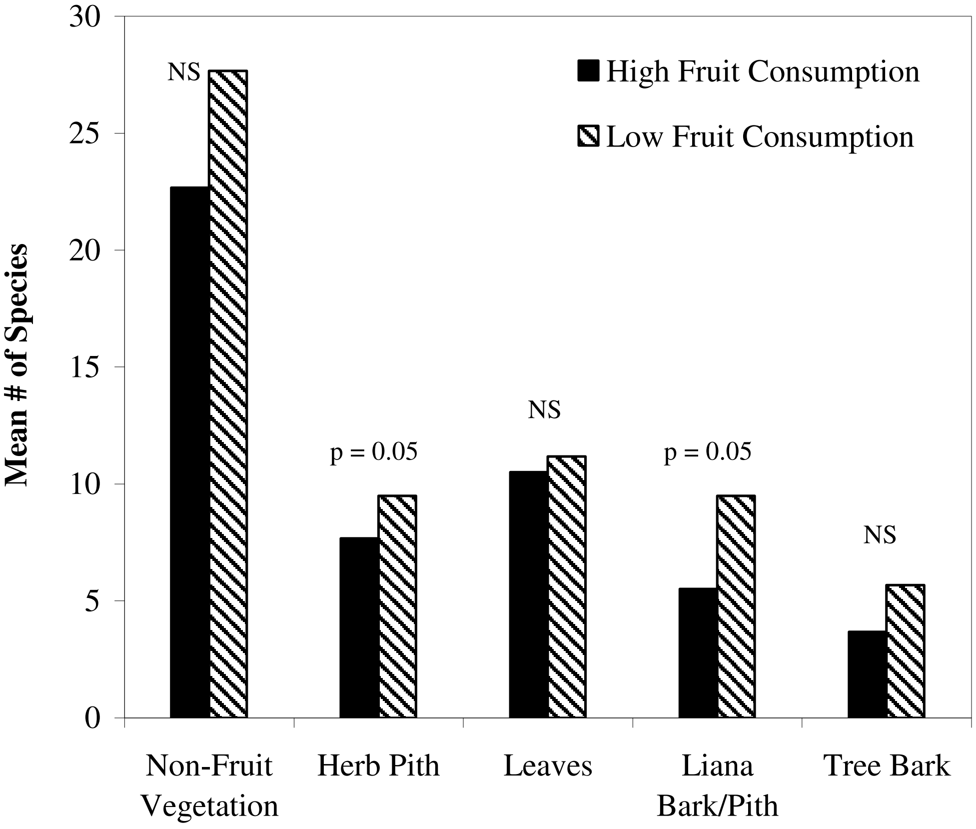

Figure 3.3 Differences in species diversity (mean total number of species along feeding trails per month) of non-fruit vegetation in the gorillas' diet between high and low fruit consumption periods

The frequency with which gorillas consumed non-fruit vegetation foods, and tree bark separately, was significantly greater during the low fruit consumption period (Figures 3.4 and 3.5; z = 2.89 and 2.17, p = 0.004 and 0.03, respectively). Frequency of herb pith, leaf and liana bark/pith consumption varied little between high and low fruit consumption months (z = 0.48 – 1.60, p = 0.11 – 0.63). When considering variation within the low fruit consumption period only (Figure 3.4), the gorillas consumed herb pith significantly more frequently during dry months (November – January) compared to wet months (August – October) within this period (means: 65.4% versus 42.6% of feeding sites; z = 1.96, p = 0.05, n = 6 months). On the other hand, leaves were consumed significantly more frequently during wet months compared to dry months within the low fruit consumption period (means: 12.2% and 26.9% of feeding sites; z = 1.96, p = 0.05, n = 6 months)[5].

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[5] This result may be explained by monthly variation in sample size (see Methods for details).

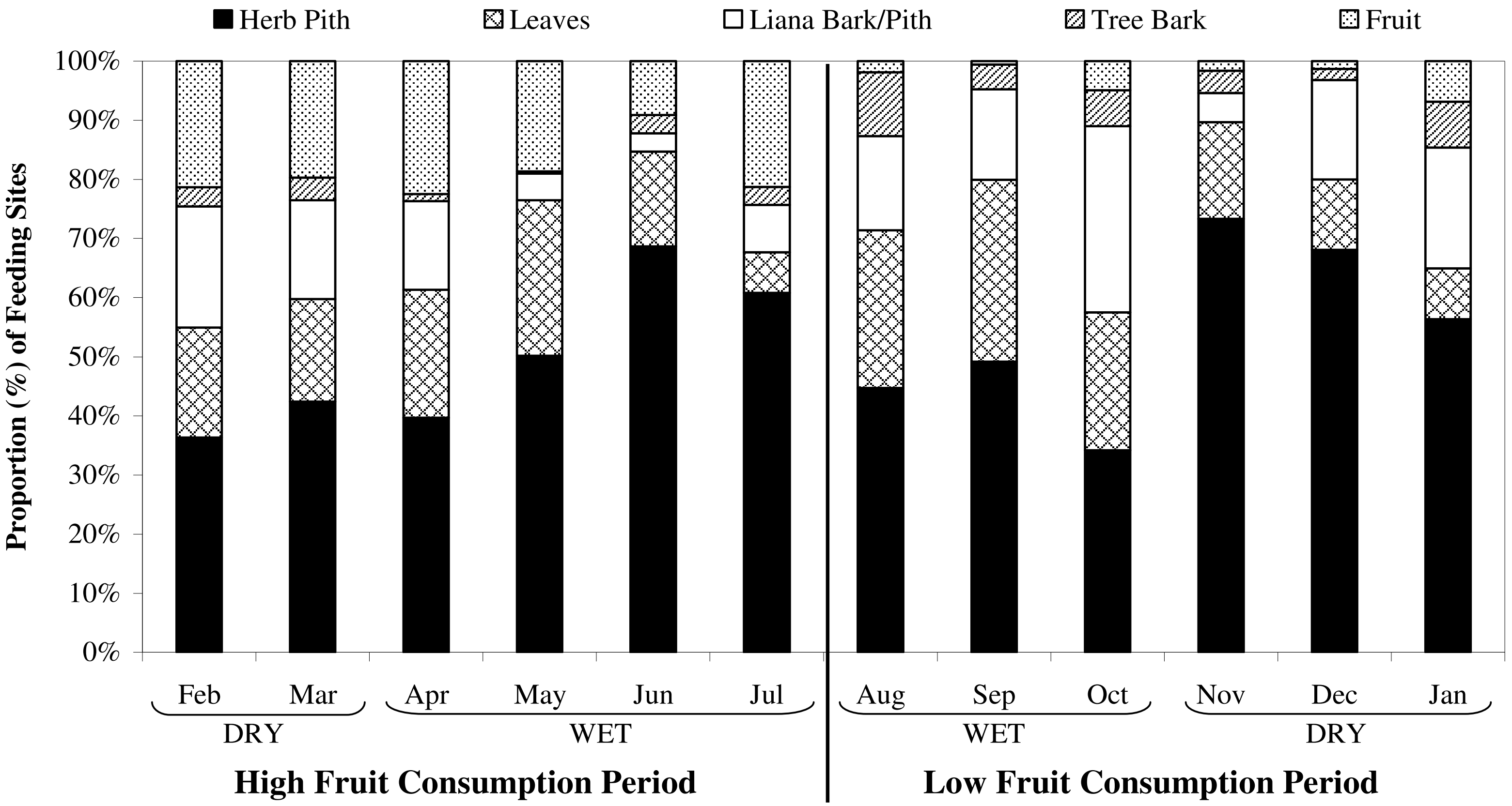

Figure 3.4 Relative frequency of different food categories eaten along feeding trails

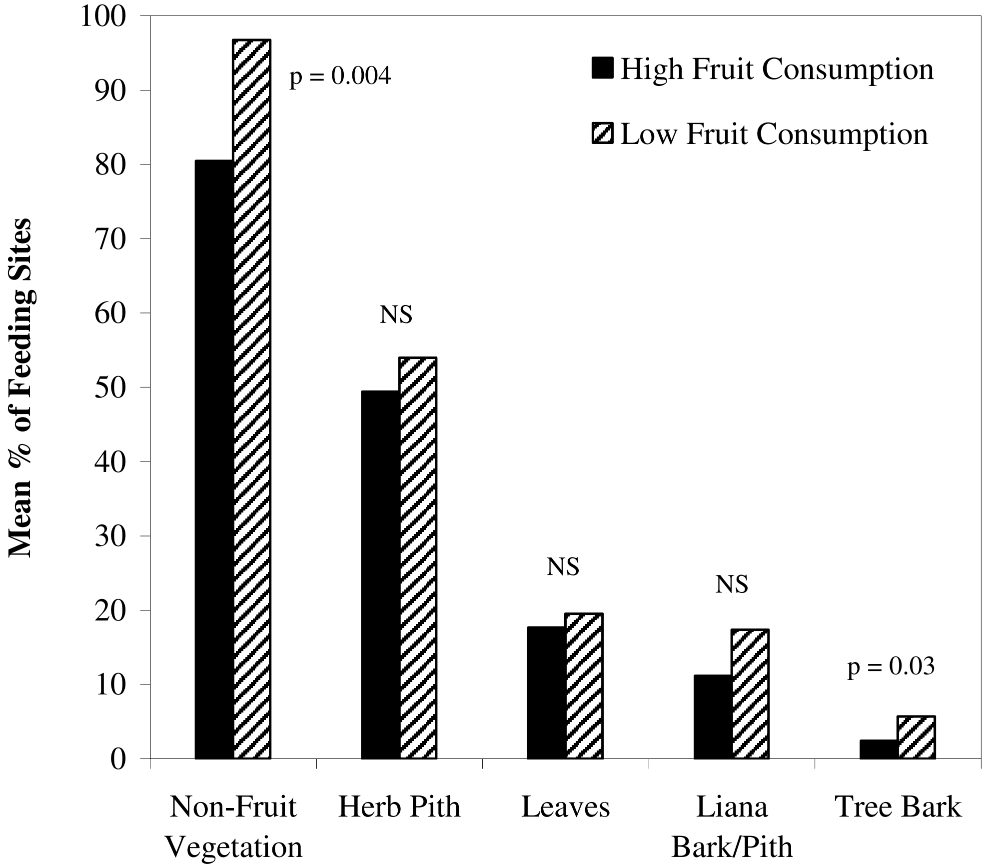

Figure 3.5 Differences in frequency (percentage of feeding sites along trails per month) of non-fruit vegetation in the gorillas' diet between high and low fruit consumption periods

Abundance of non-fruit vegetation in fecal samples was significantly greater during low versus high fruit consumption months [foliage score (fiber + leaf fragment abundance cores): Figure 3.6; percentage of fecal weight: Figure 3.1, means = 92.8% versus 49.3%; z = 2.88, p = 0.004, n = 12 months]. When considering herb pith and leaves separately, both were significantly more abundant in fecal samples during low fruit consumption months (z = 2.90, p = 0.004, n = 12 months; Figure 3.6). The amount of herb pith eaten by gorillas at feeding sites was, however, relatively consistent across months sampled (Figure 3.7). Gorillas consumed on average greater amounts of herb pith per feeding site during low fruit consumption months (means = 140.8 versus 107.4 grams/site) compared to high fruit consumption months, though this difference was statistically non-significant (z = 1.60, p = 0.11). A similar pattern of variation across months and between low and high fruit consumption periods was found for the amount of liana bark/pith eaten per feeding site (Figure 3.7; means = 257.0 versus 210.6 cm^3 per feeding site, z = 1.60, p = 0.11). During low fruit consumption months, the gorillas did consume significantly greater amounts of tree bark per feeding site than during high fruit consumption months (means = 245.2 versus 116.6 cm^3, z = 2.88, p = 0.004).

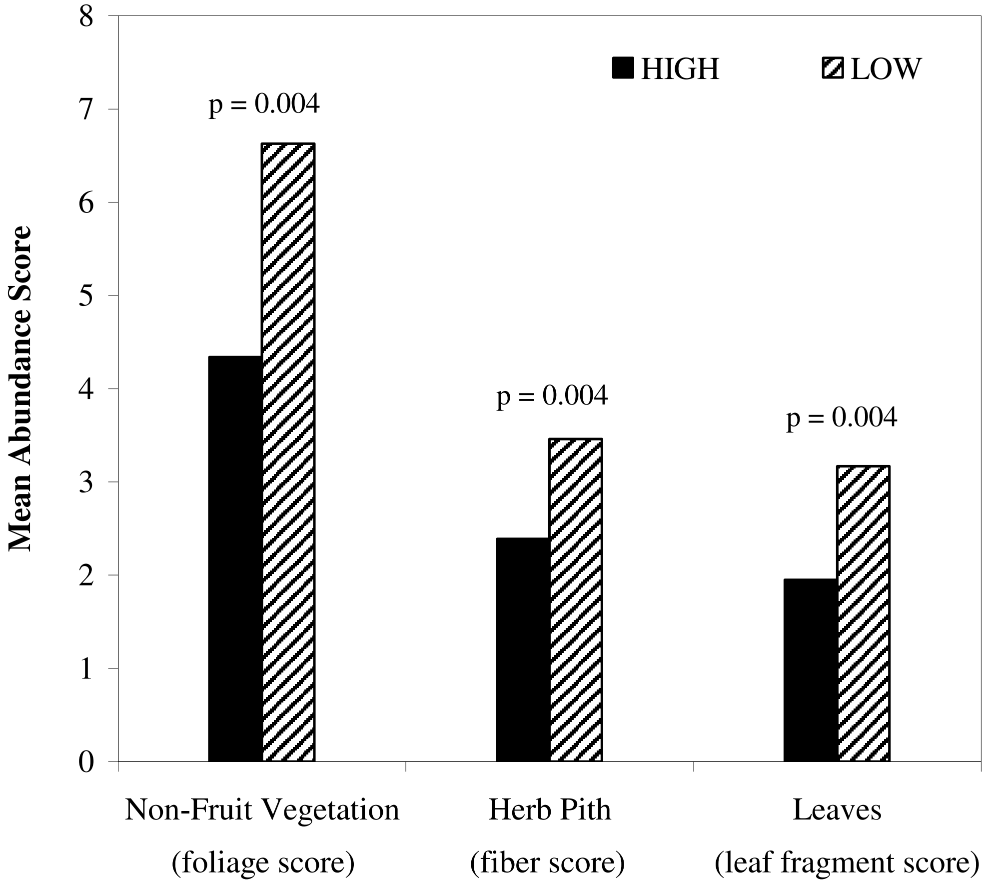

Figure 3.6 Differences in abundance (mean fecal abundance scores per month) of non-fruit vegetation in the gorillas' diet between high and low fruit consumption periods

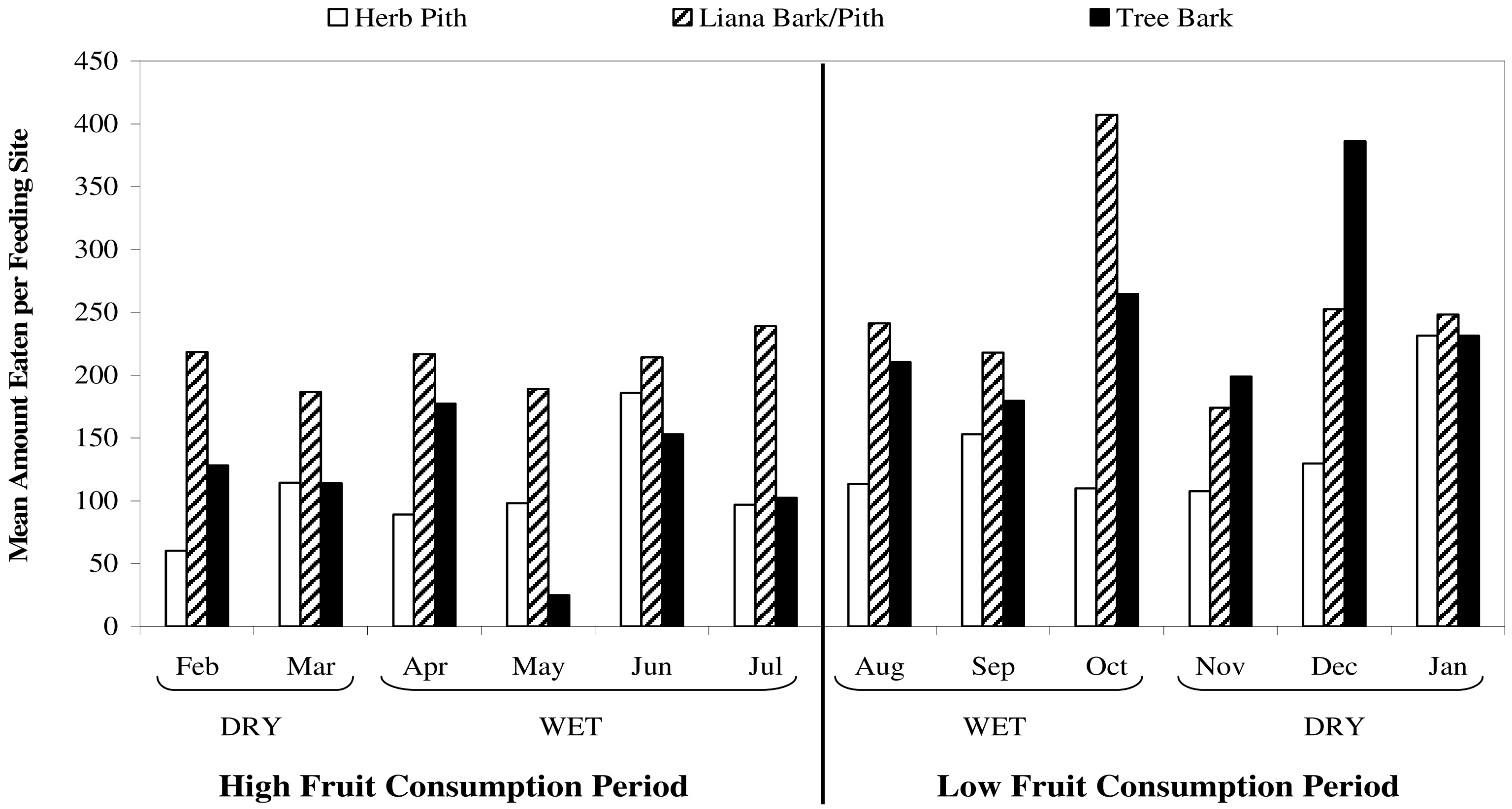

Figure 3.7 Abundance of woody bark/pith, tree bark and herb pith in the gorillas' diet using feeding site measures (amount eaten per feeding site; * herb pith = grams eaten, and liana bark/pith and tree bark = area eaten in cm^2)

To summarize, in response to fruit scarcity the Afi gorillas increased their overall consumption of non-fruit vegetation foods by increasing diversity, frequency, and/or abundance of different non-fruit vegetation foods in their diet to varying degrees. Specifically, during low fruit consumption months, Afi gorillas consumed a greater variety of herb pith food species, consumed herb pith more frequently during dry months of this period, and herb pith abundance in the diet was greater. Leaves were more abundant in the gorillas' diet during low fruit consumption months but were consumed more frequently only during wet months of this period. The gorillas increased their frequency of tree bark consumption as well as the amount of tree bark eaten at feeding sites throughout the low fruit consumption period. The gorillas consumed a greater variety of liana bark/pith food species during low fruit consumption months but frequency of consumption and abundance of liana bark/pith was relatively consistent throughout the year. These results indicate that tree bark was a particularly important supplemental food throughout the period of fruit scarcity, and within this period herb pith was an important supplemental food during dry months (November – January) and leaves were an important supplemental food during wet months (August – October).

Important Food Species

Fruit species were considered important if in any given month they were present in 20% or more of fecal samples or at least two of the following four criteria were met: 1) they represented ≥ 10% of total monthly fruit weight, 2) they represented ≥ 1.0% of total monthly fruit pulp volume (Williamson 1989), 3) they were present along feeding trails on ≥ 10% of days sampled, and/or 4) they were present at ≥ 10% of total monthly fruit feeding sites (regardless of the amount of fruit eaten per feeding site). Leaf, liana bark/pith, and tree bark species were determined to be important when one of the following criteria was met for any given month: 1) they were present along feeding trails ≥ 10% of days sampled, 2) they were present at ≥ 10% of that food category's total monthly feeding sites, or 3) they represented ≥ 10% of that food category's total monthly amount eaten. Important herb pith species were identified using these same three criteria, but a ≥ 20% cut-off was used.

To examine the relative importance of each species within the different food categories, I calculated an importance value (IV) modified from that employed in Chapter Two (tree enumeration) and Williamson (1989). Importance values incorporated relative frequency (proportion of fecal samples or feeding sites per month), relative dominance (proportion of amount eaten per month, for fruit: pulp volume, for non-fruit vegetation: amount eaten along feeding trails) and relative density (proportion of months the species was important, as frequency of consumption per year). To control for the variable number of fecal samples collected and feeding sites recorded per month, relative frequency and dominance were calculated monthly, totaled, and converted to percentages. Relative densities (i.e., number of important months per year) were also totaled and converted to percentages to equalize the measures.

Important fruit food species

Table 3.5 lists the 24 important fruit species in the Afi gorillas' diet in importance rank order and indicates the months in which they were determined to be important. Species of *Landolphia, Aframomum,* and *Treculia* were important during the greatest number of months during the year. At least one *Landolphia* liana species was present in the diet throughout the year (*Landolphia* sp. 1: December – May and October – November; *Landolphia* sp. 2: April – September). Whereas *Landolphia* sp. 1 occurred in the majority of fecal samples during only one month (February, 62%), *Landolphia* sp. 2 occurred in the majority of fecal samples during five months (April – July and September, 65 – 89% of samples). *Aframomum* was present in the diet during all 12 months sampled but was important during only five months (one high fruit consumption month: February and four low fruit consumption months: October – January) and did not occur in the majority of samples during any month (23 – 40%). *Treculia* was important during five months (March – July); however, it only occurred in the majority of fecal samples during April and May (82% and 69%, respectively). Appendix III provides percentage of fecal samples and number of 'other' criteria met per month for each important fruit species.

Since frequency measures are based on presence of seeds only regardless of their numbers, abundance measures were incorporated as well. Goldsmith (1996) used seed weight to reflect the relative abundance of different fruit species. Seed weight, however, rarely corresponds to fruit weight or size. Hence, seed weight does not accurately reflect the amount of fruit consumed and can often under or over represent a species' abundance depending on its seed weight (or size) to fruit weight (or size) ratio. By contrast, fruit pulp volume incorporates both fruit size and proportion of large compound fruits eaten (based on number of seeds); thus, pulp volume more accurately represents abundance.

Table 3.5 Important fruit species in the Afi gorilla diet listed in importance rank order (December 1997 – November 1998; high fruit consumption months in bold; wet months in italics).

Species	**Life Form***	**IV**	**Feb**	**Mar**	***Apr***	***May***	***Jun***	***Jul***	*Aug*	*Sep*	*Oct*	Nov	Dec	Jan
Landolphia sp. 2	L	40.7			**X**	**X**	**X**	**X**	X	**X**				
Landolphia sp. 1	L	34.3	**X**	X	*	*					X	X	X	X
Treculia africana	T	33.4	*	X	**X**	**X**	X	X	*	*				
Myrianthus arboreus	T	33.2					*	**X**	**X**	X	X			
Aframomum spp.	H	22.1	X	*	*	*	*	*	*	*	X	X	X	X
Pseudospondias microcarpa	T	16.0	**X**	**X**	*	*	X							
Parkia bicolor	T	14.4	*	X	X									
Ficus spp. (3)	T	13.8	X	X	*		*	*	X		*		*	X
Sorindeia spp.	T	12.7			X	**X**	*	*						
Dialium guineense	T	12.0		*	X	X	X	X						
Vitex sp.	T	8.9					*		*		X	X		
Tabernaemontana pachysiphon	T	8.3	X	X	*									X
Maesopsis eminii	T	6.9		X	X	*	*							
Unidentified SD-01	U	6.5									*	X	X	
Morus mesozygia	T	6.4	**X**	*										*
Chrysophyllum sp.	T	5.2	*	**X**	*									
Antiaris toxicaria africana	T	5.0	X										X	
Unidentified SD-49	U	3.5		X	*									
Garcinia kola	T	3.3					X	*						
Cola millenii	T	3.0		*	*	*	X		*					
Monodora myristica	T	3.0			*		X	*	*	*				
Uvariodendron calophyllum	T	2.9						X	*					
Unidentified SD-68	U	2.4					X	*						
Unidentified SD-09	U	2.0											X	*

Life Form: H = herb, L = liana, T = Tree, U = unknown; Importance value (IV) = (relative frequency + relative dominance + relative density) x 100, see text for details; status in diet: X = months in which species were important (bold indicates months in which important species were present in ≥ 60% of fecal samples), * = months in which species were present in the diet but were not considered to be an important species.

Figures 3.8 and 3.9 show the relative contribution of the different important fruit species during high and low fruit consumption months in the gorillas' diet using two different fecal abundance measures, percent of total monthly seed weight and percent of total monthly fruit pulp volume. Seed weight likely underestimated the abundance of seven species that contain many small lightweight seeds embedded in a relatively large amount of pulp, particularly *Treculia* (seed weight: < 1.0 – 4.4% versus pulp volume: 16.3 – 53.8%), *Ficus* (< 1.0% vs. 2.4 – 27.7%), and *Aframomum* (0.1 – 5.0% vs. 2.0 – 65.2%). On the other hand, seed weight likely overestimated the abundance of 11 species that have large and heavy seeds relative to amount of pulp available per fruit or seed, particularly *Vitex* (43.1 – 94.3% vs. 11.0 – 31.5%), *Pseudospondias* (22.6 – 69.3% vs. 4.3 – 27.5%), and *Sorindeia* (36.7 – 80.0% vs. 6.8 – 33.7%).

During the high fruit consumption period (February – July 1998; Figure. 3.8), one to two species represented the majority of fruit pulp volume eaten (i.e., ≥ 60%). *Landolphia* sp. 1 represented the greatest proportion of pulp volume during February (44%) with *Pseudospondias* dominating secondarily. *Parkia* represented the greatest proportion of pulp volume in March (67%) and the second greatest proportion in April (32%). Treculia dominated the amount of pulp volume eaten in April and May (54% and 44%, respectively) though in May, *Sorindeia* was a close second (34%). In June, pulp of *Landolphia* sp. 2 and *Garcinia* was consumed more than any other species (61% and 15%, respectively). The abundance of *Garcinia* in the gorillas' diet was most likely underestimated since gorillas may not have swallowed its seeds on many occasions due to their large size (6.1 cm^3, spit out seeds were observed along feeding trails). Finally, *Myrianthus* represented the greatest proportion of pulp volume consumed in July (60%).

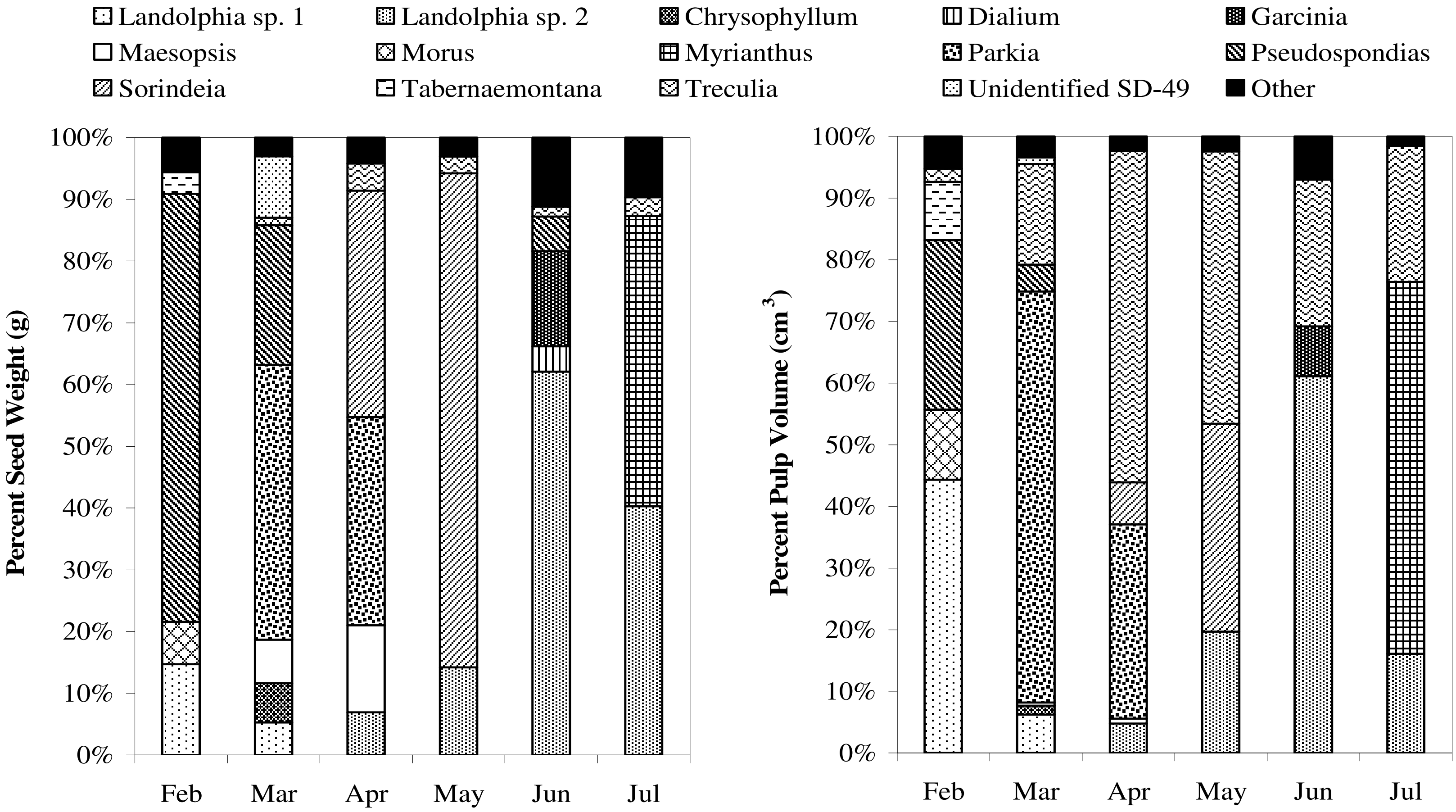

Figure 3.8 Relative contribution of different important fruit species in the gorillas' diet during high fruit consumption months (February - July 1998) using two different fecal abundance measures

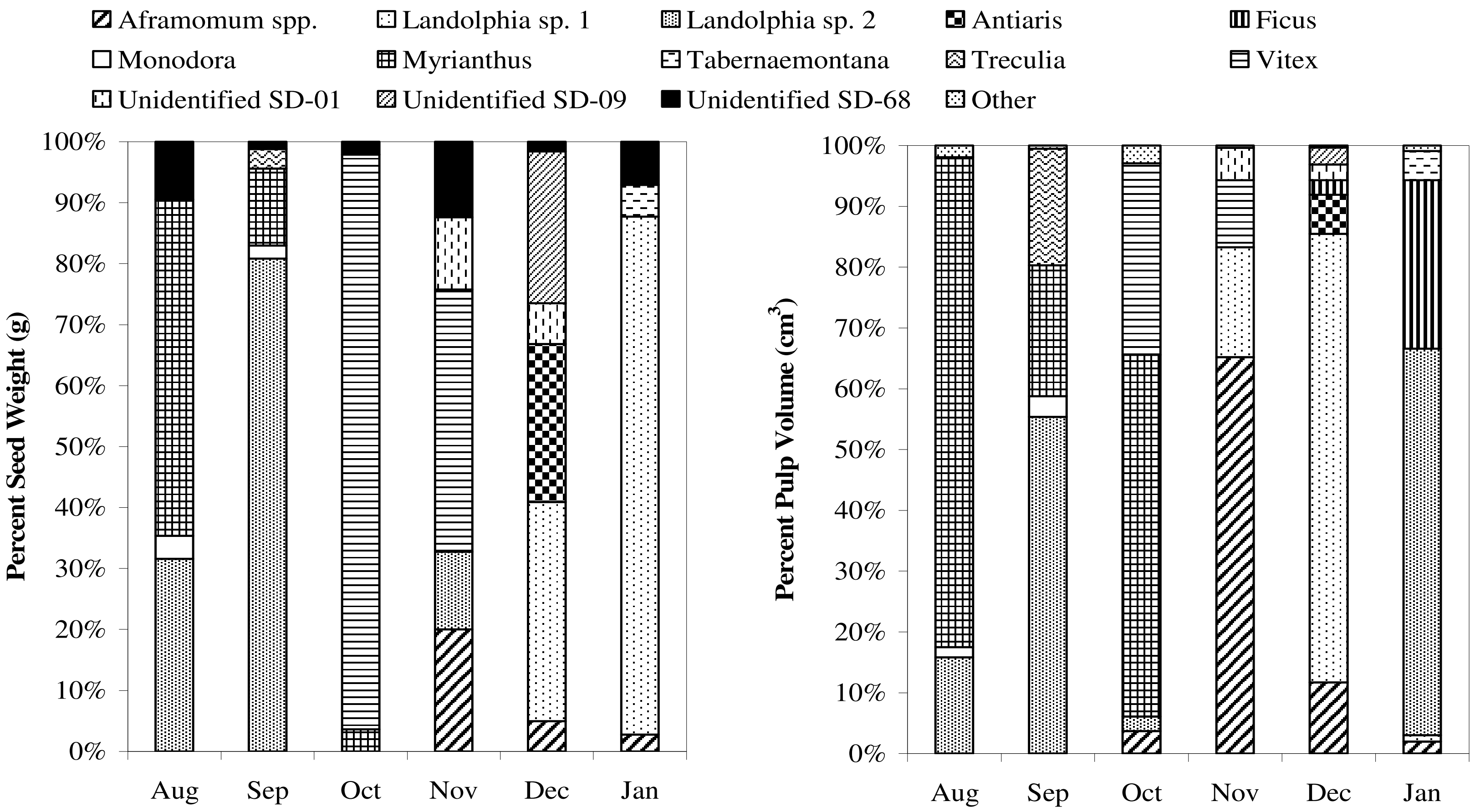

Figure 3.9 Relative contribution of different important fruit species in the gorillas' diet during the low fruit consumption months (Jan, Aug - Nov 1998, Dec 1997) using two different fecal abundance measures

During the low fruit consumption period (December 1997 and January, August – November 1998; Figure 3.9), one species represented the majority of fruit pulp consumed by the gorillas during all months of this period, except September. In August and October, *Myrianthus* fruit once again dominated (81% and 60%, respectively) with *Vitex* fruit dominating secondarily in October (31%). *Landolphia* sp. 2 became dominant again in September (55%). *Aframomum* represented the greatest proportion of pulp volume in November (65%). *Landolphia* sp. 1 represented the greatest proportion of pulp volume consumed during December and January (74% and 65%, respectively) with *Aframomum* dominating secondarily in December and *Ficus* dominating secondarily in January.

Important herb pith food species

Table 3.6 lists the 10 important herb pith species in the gorillas' diet in importance rank order and indicates the months in which they were determined to be important (see Appendix IV for percentage of days sampled and feeding sites per month for each important herb pith species). *Aframomum* pith was the most frequently eaten herb pith food (recorded at 33% of all herb pith feeding sites), was important throughout all 12 months sampled, and was eaten on the greatest proportion of days sampled and/or feeding sites recorded during eleven months of the year (67 – 89% of days sampled, 30 – 69% of feeding sites). *Anchomanes*, the second most frequently eaten herb (25% of all herb pith feeding sites), was important during all months it was available (March – November). *Costus, Stylochiton,* and Unidentified G-01 were important only during the low fruit consumption period (August – January). All but one month in which *Marantochloa* and *Palisota* sp. 1 were important occurred during this period.

Table 3.6 Important herb pith species in the Afi gorilla diet listed in importance rank order (December 1997 – November 1998; high fruit consumption months in bold; wet months in italics).

Species	**IV**	**Feb**	**Mar**	***Apr***	***May***	***Jun***	***Jul***	*Aug*	*Sep*	*Oct*	Nov	Dec	Jan
Anchomanes difformis	71.7		X	X	X	**X**	**X**	**X**	**X**	**X**	X	*	
Aframomum spp.	64.3	**X**	**X**	**X**	**X**	X	**X**	**X**	**X**	**X**	**X**	**X**	**X**
Palisota sp. 1	54.0		*	X	X	*	*	*	X	X	**X**	X	**X**
Palisota sp. 2	28.6	X		*	X	X	X	X	X	*	X	*	X
Hypselodelphys scandens	23.9	X	X	X	X		**X**	X		*	X	X	X
Thaumatococcus/ Megaphrynium spp.	16.3		*	*	X		X	X	*		X	X	*
Costus spp.	12.1	*		*	*	*	*	X	*	X	X	X	X
Marantochloa spp.	10.8	X		*				X	*	*	X	X	X
Stylochiton sp.	10.6	*		*				X	X	X			*
Unidentified G-01	7.5							*	*	X	X	X	

IV = Importance value [(relative frequency + relative dominance + relative density) x 100, see text for details].

X = months in which species were important (bold indicates months in which important species were present in the diet on ≥ 60% of days sampled and were eaten at ≥ 20% of herb pith feeding sites).

* = months in which species were present in the diet but were not considered to be an important species.

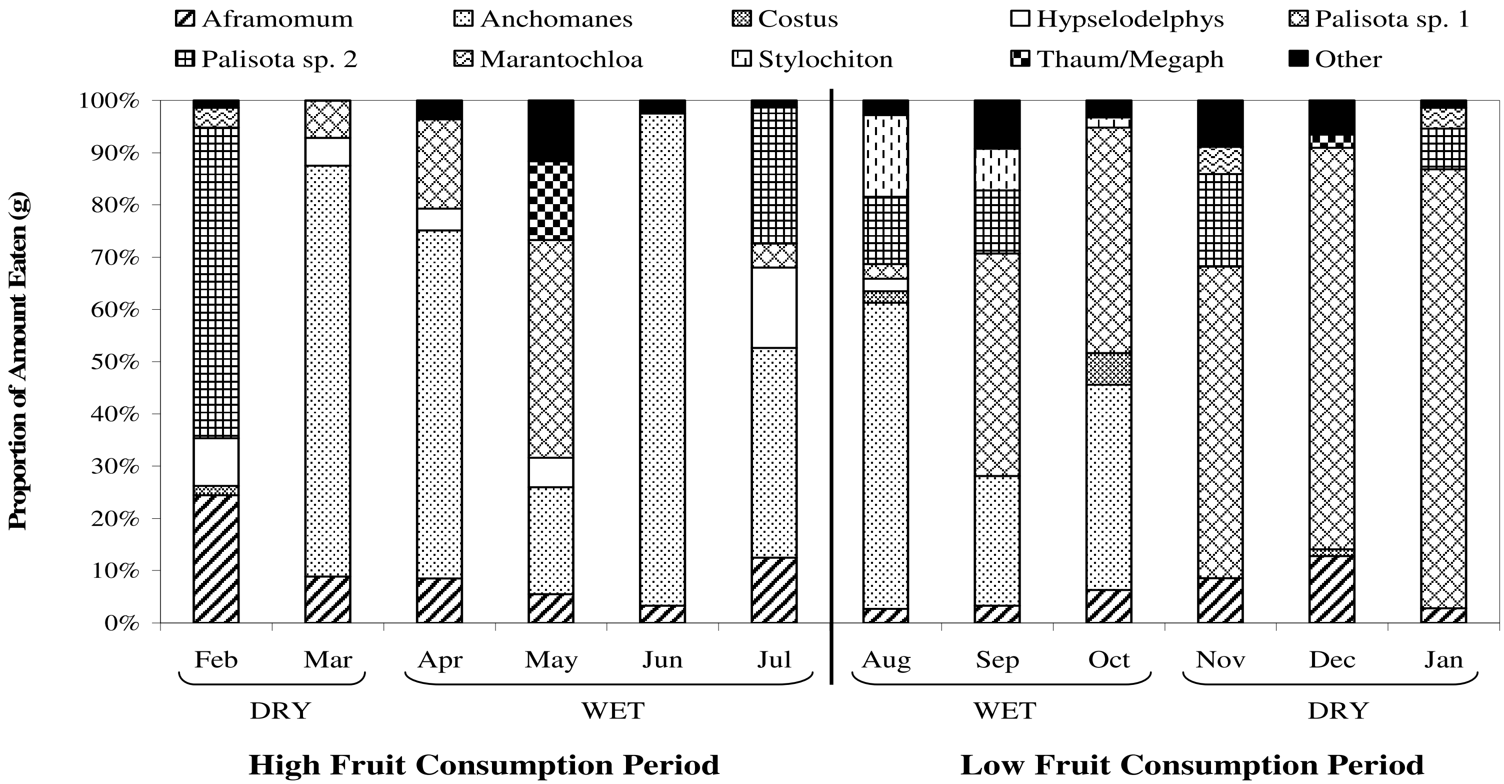

Figure 3.10 Relative contribution of different important herb species to the gorillas' diet from December 1997 and November 1998

Figure 3.10 shows the relative abundance (based on percent of amount eaten at feeding sites per month measured in grams) of the different important herb pith species in the gorillas' diet. Though during most months of the year *Aframomum* pith was consumed more frequently than any other herb species, it did not represent the majority of grams eaten during any months. *Anchomanes* represented the greatest proportion of pith eaten during five months (March, April, and June – July; 40% – 95% of grams eaten per month), including one low fruit consumption month (August, 59%). *Palisota* sp. 1 dominated the amount of herb pith eaten in the low fruit consumption months of September and November – January (43% - 85%). *Anchomanes* and *Palisota* sp. 1 dominated equally in October (39% and 38%, respectively).

Table 3.7 presents characteristics of important herb pith species in the gorilla diet at Afi, including importance values, mean amount eaten per stem and per feeding sites along trails, and mean density. *Aframomum* occurred at the highest density (0.43 stems/m^2) and was the most frequently eaten herb. By contrast, *Anchomanes* occurred at a much lower density (0.01 stems/m along trails)[6], but was the second most frequently eaten herb, even though it is not available throughout the year (March – October). Despite its low availability, *Anchomanes* had the highest importance value because it provides much greater amounts of food per stem than *Aframomum*. The gorillas consumed 17.5 times greater amounts of *Anchomanes* pith per stem than *Aframomum* (Table 3.7). Furthermore, when both species were present in close proximity along feeding trails, *Aframomum* was often ignored. This may be related to differences in nutritional value between these species.

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[6] Since *Anchomanes* stems tend to occur singly and the gorillas rarely failed to consume it when stems were present along trails, its density was estimated based on occurrence along feeding trails (i.e. total number of stems eaten divided by total length of trails followed during months in which it was available).

Table 3.7 Characteristics of important Afi gorilla herb foods listed in importance value rank order (see legend for definitions and units).

SPECIES	**IV**	**MEAN AMOUNT EATEN (g)**		**MEAN DENSITY**
		Per Stem	**Per Feeding Site**	
Anchomanes difformis	71.7	120.6	184.8	0.01 *
Aframomum spp.	64.3	6.9	23.6	0.43
Palisota sp. 1	54.0	79.2 **	396.6	0.05 **
Palisota sp. 2	28.6	170.2	274.7	0.01
Hypselodelphys scandens	23.9	34.4	59.7	0.14
Thaumatococcus/ Megaphrynium	16.3	4.8	30.4	0.01
Costus spp.	12.1	19.1	34.8	0.08
Marantochloa spp.	10.8	36.9	82.6	0.07
Stylochiton sp.	10.6	16.7	82.6	0.08
Unidentified G -01	7.5	4.2	94.0	-----

* Estimated based on occurrence along feeding trails (see text for details).
** Amount eaten per stem and density are for leaf stems (see Chapter 2 for details).

IV = Importance value [(relative frequency + relative dominance + relative density) x 100], see text for details.

Feeding trail evidence:
Mean amount eaten per stem = mean number of grams eaten per stem (total number of stems/total number of grams eaten);
Mean amount eaten per feeding site = mean number of grams eaten per feeding site.

Herb enumeration:
Mean density = mean number of stems per 1 m^2 plot;
Mean biomass = mean number of grams per 1 m^2 plot.

While chemical analyses were not conducted during the present study, Calvert (1985) provides data from Campo, Cameroon, for *Anchomanes difformis* and four *Aframomum* species, two of which are known to occur in the Afi area, *A. daniellii* and *A. subsericeum*. Compared to *Aframomum*, *Anchomanes* stems at Campo were higher in protein (7.1% vs. 2.6 – 5.5% dry matter) and digestibility (pepsin-cellulase digestibility: 81.3% vs. 35.3 – 47.3% dry matter), and lower in overall fiber content (neutral detergent fiber: 34.7% vs. 52.9 – 62.7%; acid detergent fiber: 36.8% vs. 38.1 – 45.9%; Lignin: 6.3% vs. 6.1 – 9.0% dry matter). *Anchomanes* stems were also higher in total phenols (1.9% vs. 1.0 – 1.4% dry matter) but this probably did not deter the gorillas. Calvert found that banana stem cores had 4.6 times more phenols than outer layers, which were ignored. Though nutrient content varies between sites, the results of Calvert's study and the Afi gorillas' behavior indicating a preference for *Anchomanes* suggest that *Anchomanes* at Afi probably contains greater amounts of protein and lesser amounts of fiber, and is more digestible than *Aframomum*.

Herb pith was a particularly important supplemental food during the dry months within the low fruit consumption period (November – January, see previous section). During these fruit scarce months, *Palisota* sp. 1, though not necessarily the most frequently eaten herb pith species, overwhelmingly dominated the amount of pith eaten (Figure 3.10), and provided greater amounts of food per stem (mean = 79.2 g) and feeding site (mean = 396.6 g) compared to *Aframomum*. Like *Anchomanes*, *Palisota* sp. 1 also occurred at a low density (0.05 leaves/m^2; the gorillas eat the pith of leaf stalks only) and was often preferred over *Aframomum* when both occurred nearby along trails; *Anchomanes* is not available during this time (November – December). Calvert (1985) found that stems of two *Palisota* species at Campo were 2 – 3 times higher in protein than *Aframomum* stems (10.3% and 14.0 vs. 2.6 – 5.5% dry matter) but overall fiber content was similar. In addition, the present study found that on average *Palisota* sp. 1 leaf stalks provide 5.5 times greater amounts of water compared to *Aframomum* stems (mean water weight per stem: *Palisota* sp. 1 = 35.0 g and *Aframomum* = 6.4 g).

The Afi gorillas' preferences for *Anchomanes* when available and *Palisota* sp. 1 during dry months within the low fruit consumption period suggest that amounts of pith available per stem, and protein and water content are likely important factors influencing Afi gorillas' herb pith food choice.

Important leaf food species

Table 3.8 lists the 18 important leaf food species in the gorillas' diet in importance rank order and indicates the months in which they were determined to be important (see Appendix V for percentage of days sampled and feeding sites per month for each important leaf food species). *Anchomanes* leaves were the most frequently eaten (recorded at 21% of all leaf feeding sites) and the most important leaf food followed by *Ficus, Thaumatococcus/ Megaphrynium*, *Milicia* and "Okpeje". The gorillas consumed *Anchomanes* leaves during all nine months in which it was available and *Anchomanes* was an important leaf species during eight of these months (March – October). *Anchomanes* was eaten on the greatest proportion of days sampled (22 – 75%) and at the greatest proportion of leaf feeding sites (36 – 63%) during five months, March – July. The second most important leaf species, *Ficus*, was present in the gorillas' diet in all months except March and was an important leaf food species during the greatest

Table 3.8 Important leaf species in the Afi gorilla diet listed in importance rank order (December 1997 – November 1998; high fruit consumption months in bold; wet months in italics).

Species (or Local Name)	**Life Form**	**IV**	**Feb**	**Mar**	***Apr***	***May***	***Jun***	***Jul***	*Aug*	*Sep*	*Oct*	Nov	Dec	Jan
Anchomanes difformis	H	44.3		**X**	**X**	**X**	**X**	**X**	**X**	**X**	**X**	*		
Ficus spp. (2)	T	39.4	*		X	X	**X**	X	X	X	X	X	X	**X**
Thaumatococcus/ Megaphrynium spp.	H	35.2			X	**X**	*	X	X	*	*	**X**	**X**	
Milicia excelsa	T	29.5	*		X		**X**	X	**X**	X	**X**	*		
(“Okpeje”)	T	27.3	X					X	**X**	X	X	X		
Turreanthus africanus	T	25.8	**X**		X			X	X				X	
Musanga cecropioides	T	20.0				*	*	*		X	**X**	**X**		
Stylochiton sp.	H	15.6	*		*				**X**	**X**	X			X
Morus mesozygia	T	8.1	*		X	*			**X**		*			
(“Beleh/Bakur”)	L	7.9			*	*	*		*		**X**	X		
Pycnanthus angolensis	T	7.4					*			X				
Unidentified T-11	T	7.4		X							*			
(“Kibang ushie”)	H	7.2		X										X
Landolphia sp. 2	L	5.9							X	**X**				*
Gongronema latifolium	L	5.8					*		*	*	X			
Dracaena arboreus	T	5.2	*	X	*	*								
(“Kidako”)	V	4.1				X								
Albizia zygia	T	3.9	X		*				*					

Life Form: H = herb, L = liana, T = Tree, V = vine.

IV = Importance value [(relative frequency + relative dominance + relative density) x 100, see text for details].

X = months in which species were important (bold indicates months in which important species were present in the diet on ≥ 30% of days sampled and/or were eaten at ≥ 30% of leaf feeding sites).

* = months in which species were present in the diet but were not considered to be an important species.

number of months, nine. Leaves of liana and vine species were among the least important leaf species.

Figure 3.11 shows the relative abundance (based on the percent of leaves eaten per month) of the different important leaf species in the gorillas' diet. During the 12 months sampled, no one species dominated leaf abundance in the diet, except during January when *Ficus* represented 55.2% of leaves eaten. Though *Anchomanes* was the most frequently eaten leaf species during March through July, it represented less than 25% of leaves eaten during these months. However, because only number of leaves and not leaf size was considered, these results should be interpreted cautiously. For example, *Anchomanes*, *Stylochiton*, *Ficus*, and *Thaumatococcus/Megaphrynium* leaves tend to be approximately 2 – 5 times larger than the leaves (or leaflets) of the other important leaf species; consequently, the abundance of these species in the diet was likely greatly underestimated.

Musanga, Stylochiton, Landolphia sp. 2*, Pycnanthus*, and *Gongronema* were important leaf species only during months within the low fruit consumption period (August – January). In addition, these species were either important during the wet months within the low fruit consumption period exclusively (August – October, *Landolphia* sp. 2*, Pycnanthus*, and *Gongronema*) or the majority of months in which they were important occurred during this time (*Musanga* and *Stylochiton*). Unidentified T-11, "Kibang ushie", and *Dracaena* were important only during dry season months.

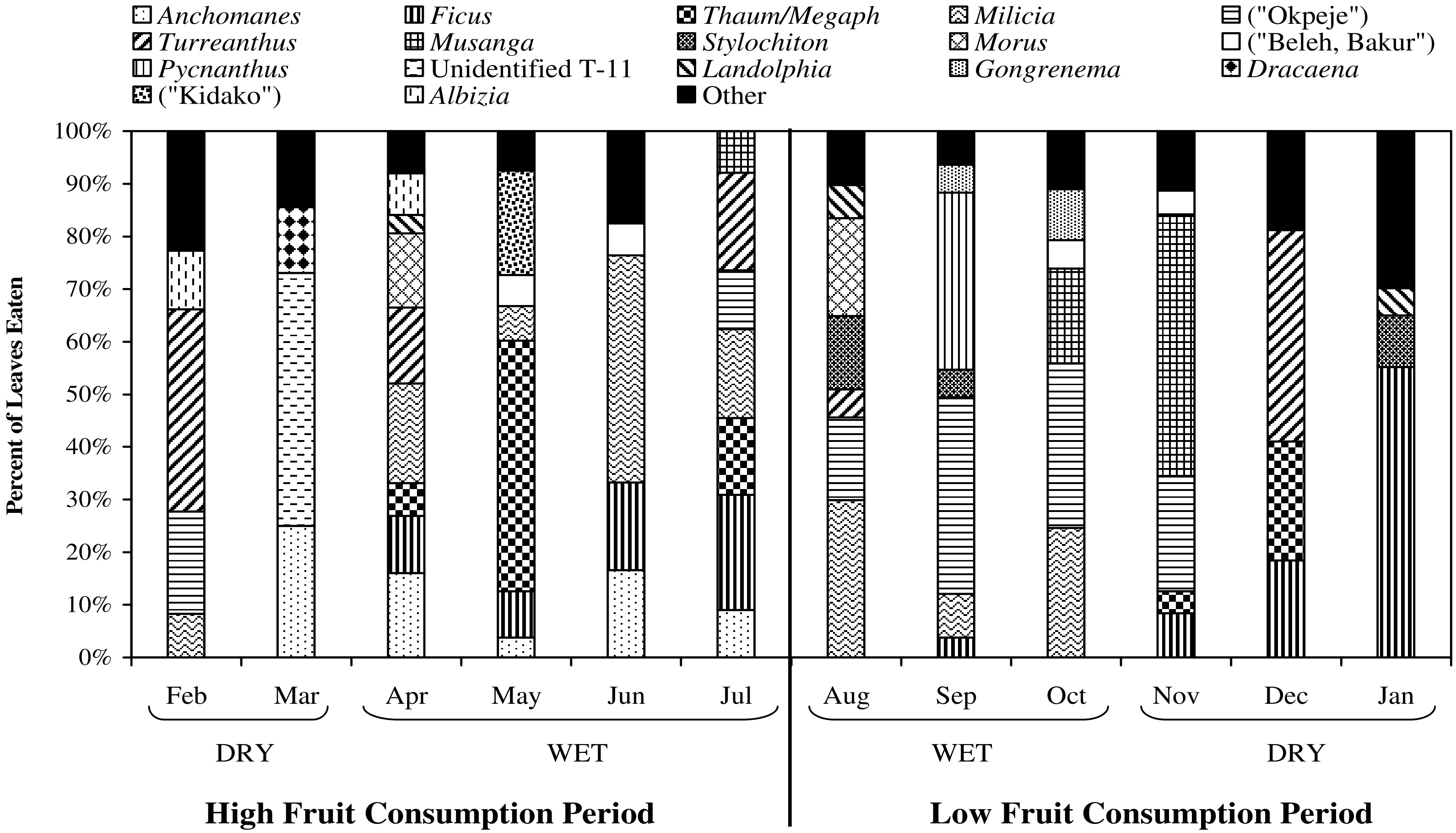

Figure 3.11 Relative contribution of different important leaf species to the gorillas' diet from December 1997 to November 1998

Important liana bark/pith food species

Table 3.9 lists the 9 important liana bark/pith food species in the gorillas' diet in importance rank order and indicates the months in which they were determined to be important (see Appendix VI for percentage of days sampled and feeding sites per month for each important liana bark/pith food species). All but one important liana bark/pith food species are lianas. *Landolphia* sp. 2, a large liana species, was the most frequently recorded liana bark/pith food recorded along feeding sites (47% of all liana bark/pith sites) and was the most important liana bark/pith species followed by *Landolphia* sp. 1. Throughout the year, at least one (of three) *Landolphia* species was present and important in the gorillas' diet. *Landolphia* (3 species pooled) was eaten on the greatest proportion of days sampled (38 – 92%) and at the greatest proportion of liana bark/pith feeding sites for all months (42 – 93%).

Figure 3.12 shows the relative abundance, using percent of amount eaten per month (cm^2), of the different important liana bark/pith species. No one species overwhelmingly dominated the amount of liana bark/pith during most months of the year except in June, July, and September (*Landolphia* sp. 2: 75 – 93%). *Landolphia* sp. 2 did, however, represent the greatest proportion of liana bark/pith eaten during 10 months of the year (40% – 93%; February, April – September, and November – December). "Ofusi" contributed the greatest proportion of liana bark/pith eaten in March and *Landolphia* sp. 4 in October (31% and 39%, respectively).

Table 3.9 Important liana bark/pith species in the Afi gorilla diet listed in importance rank order (December 1997 – November 1998; high fruit consumption months in bold; wet months in italics).

Species (or Local Name)	**IV**	**Feb**	**Mar**	***Apr***	***May***	***Jun***	***Jul***	*Aug*	*Sep*	*Oct*	Nov	Dec	Jan
Landolphia sp. 2	156.6	**X**	**X**	**X**	**X**	**X**	**X**	**X**	**X**	**X**	**X**	**X**	**X**
Landolphia sp. 1	44.6	*	X	**X**	X			*	*	*	X	**X**	X
(“Ofusi”)	29.2	**X**	**X**	**X**				*					*
(“Ole ejuejue“)	16.6	*						X			X		X
(“Ofre etta“)	13.0	*	*					*		X	*		**X**
(“Beleh/Bakur”)	9.0								*	X	X		
Landolphia sp. 4	8.4									X			
Gongronema latifolium	7.2						*	*		X			
(“Ole elem”)	5.8					X		*					

IV = Importance value [(relative frequency + relative dominance + relative density) x 100, see text for details].

X = months in which species were important (bold indicates months in which important species were present in the diet on ≥ 30% of days sampled and/or were eaten at ≥ 30% of liana bark/pith feeding sites).

* = months in which species were present in the diet but were not considered to be an important species.

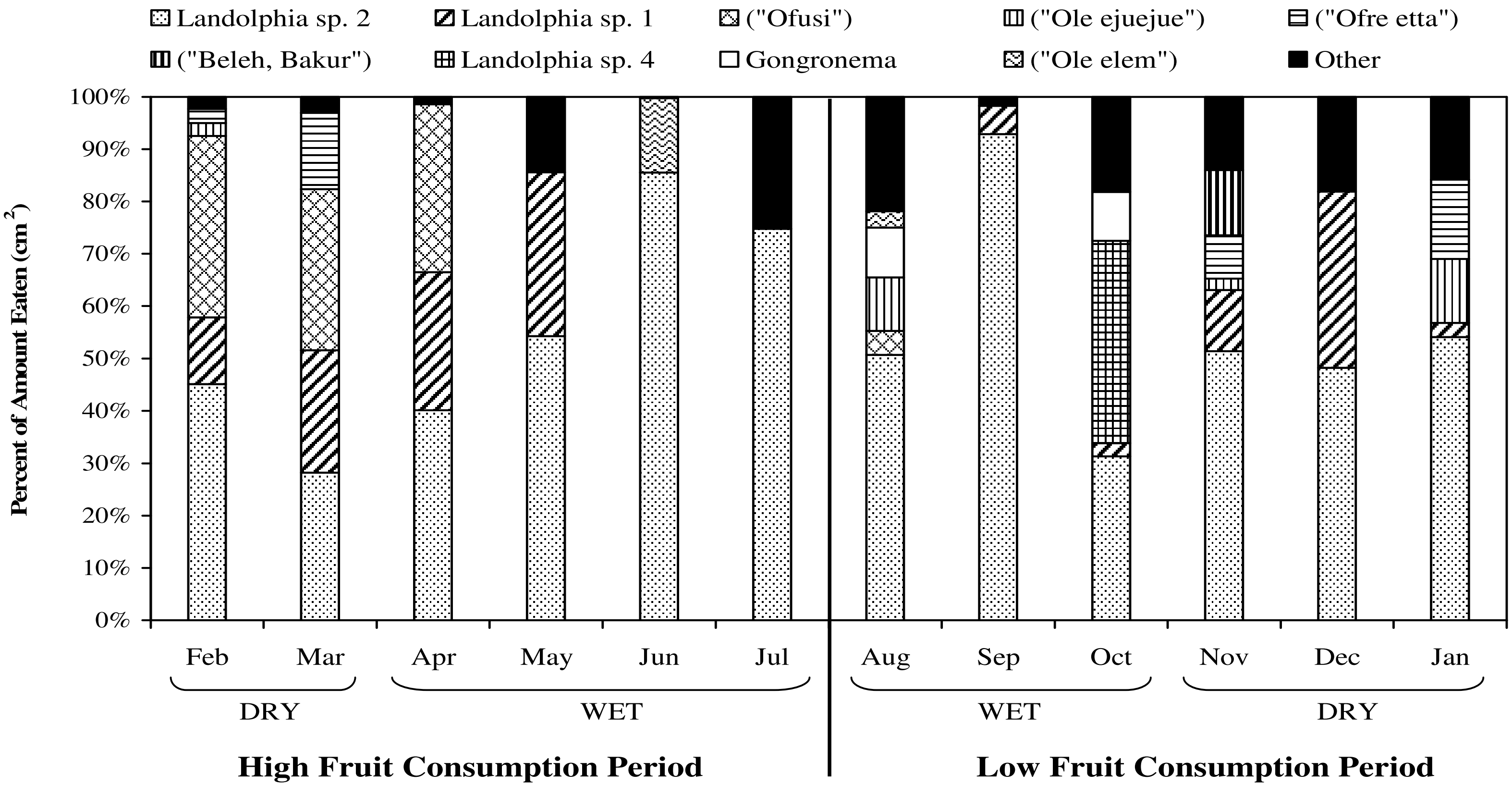

Figure 3.12 Relative contribution of different important liana bark/pith species to the gorillas' diet from December 1997 to November 1998

Five liana species (*Landolphia* sp. 4, *Gongronema latifolium*, "Ofre etta", "Ole ejuejue" and "Beleh/Bakur") were important only during low fruit consumption months (August – January). *Landolphia* sp. 4 and *Gongronema* were important only during the wet month of October within the low fruit consumption period.

Important tree bark species

Table 3.10 lists the 10 important tree bark foods in the gorillas' diet in importance rank order and indicates the months in which they were determined to be important (see Appendix VII for percentage of days sampled and feeding sites per month for each important tree bark food species). The only evidence of tree bark consumption in May was *Ficus* bark recorded at two feeding sites on the same day; consequently, no important tree bark species are listed for May. *Milicia* bark was the most frequently eaten tree bark food (recorded at 28% of all tree bark feeding sites), but *Pterocarpus* spp., the second most frequently eaten (recorded at 13% of all tree bark feeding sites), was the most important tree bark food based on importance values that consider both frequency and abundance in the diet.

Figure 3.13 shows the relative abundance, based on percent of amount eaten per month (cm^2), of the different tree bark species. *Pterocarpus* dominated the amount of tree bark eaten during five months, December – March and November (53 – 93% of monthly cm^2 eaten). *Milicia* represented the greatest proportion of tree bark eaten during four months, June – August (39 – 85%) and October (72%). *Morus* dominated in April (71%) and *Grewia* in September (67%).

Table 3.10 Important tree bark foods in the Afi gorilla diet listed in importance rank order (December 1997 – November 1998; high fruit consumption months in bold; wet months in italics).

Species (or Local Name)	**IV**	**Feb**	**Mar**	***Apr***	***May***	***Jun***	***Jul***	*Aug*	*Sep*	*Oct*	Nov	Dec	Jan
Pterocarpus osun/mildbraedii	78.9	X	X							X	**X**	**X**	**X**
Milicia excelsa	69.6					**X**	X	**X**	X	**X**	X		
Ficus spp. (2)	55.9	X				**X**	X	X	X	**X**			
Morus mesozygia	33.3	X		X				**X**		X			
Grewia mollis	19.3							**X**	X				
Unidentified T-11	12.2							*	X				X
Tabernaemontana pachysiphon	11.2		**X**							*			
Garcinia kola	7.4											X	
Bosqueia angolensis	6.6			X									
("Okpeje")	5.6							X					

IV = Importance value [(relative frequency + relative dominance + relative density) x 100, see text for details].

X = months in which species were important (bold indicates months in which important species were present in the diet on ≥ 30% of days sampled).

* = months in which species were present in the diet but were not considered to be an important species.

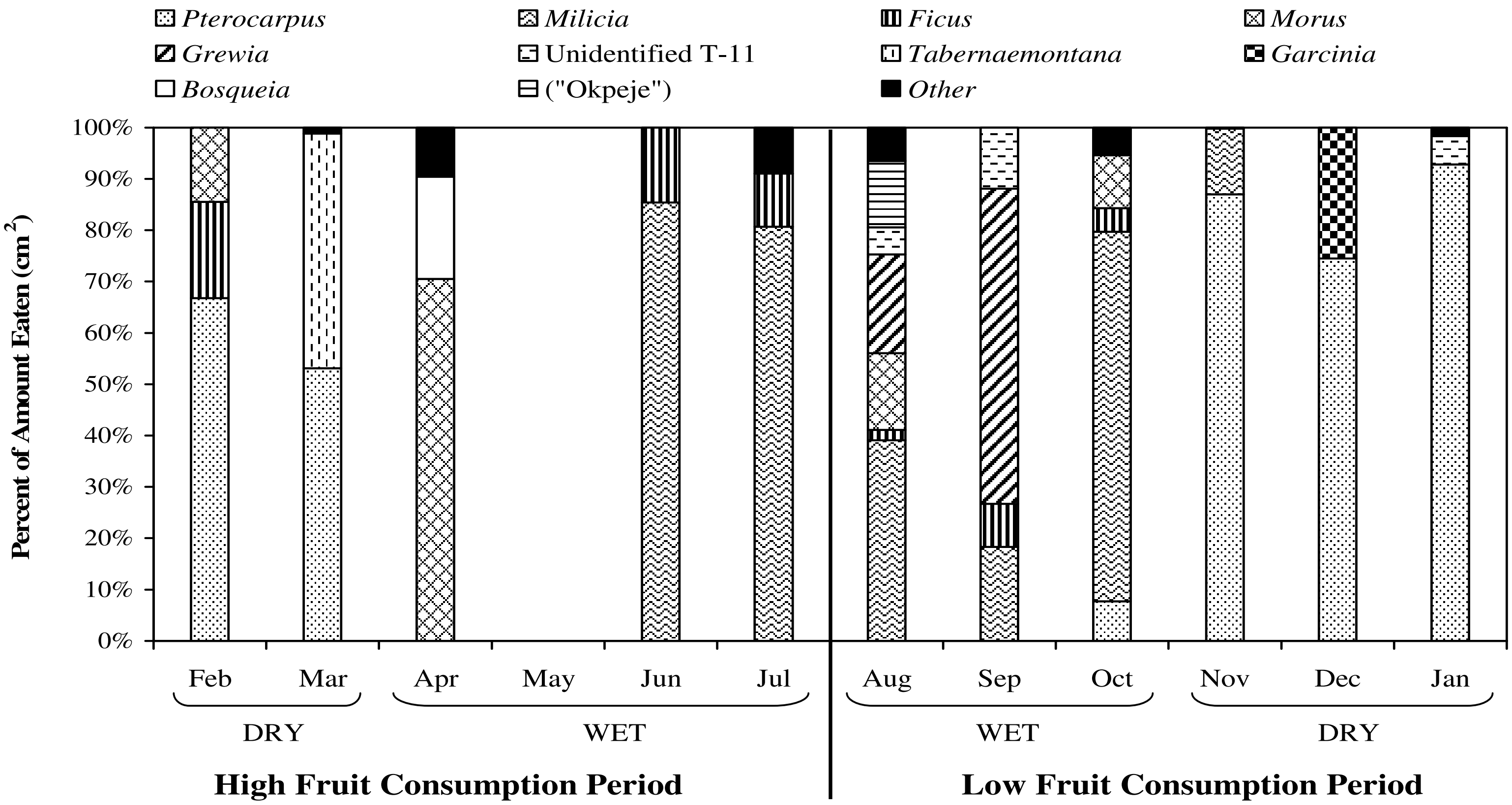

Figure 3.13 Relative contribution of different important tree bark species to the gorillas' diet from December 1997 to November 1998

Four tree bark foods were present and important in the diet only during low fruit consumption months, Unidentified T-11, *Grewia*, *Garcinia* and “Okpeje”, and two were important only during wet months of this period (*Grewia* and “Okpeje” during August and September). The majority of months in which *Milicia* and *Pterocarpus* bark were important foods occurred during the low fruit consumption period.

Important staple, seasonal, and fallback food species

Important food species were designated as staple foods (eaten on a daily or weekly basis throughout the year), seasonal foods (important in the gorillas’ diet when available), or fallback foods (always available, but eaten exclusively or mainly during fruit scarce months; referred to as supplemental foods in previous sections) (Doran et al. 2002; Rogers et al. 2004). Table 3.11 lists the life form and part(s) eaten of the 51 staple, seasonal, and fallback important species including 71 different food items [7]. Two herb pith (*Palisota* sp. 2 and *Hypselodelphys*), one tree bark (*Bosqueia*) and two liana bark/pith (“Ofusi” and “Ole elem”) important food species are not listed in Table 3.11 since they did not fit the above criteria; they are available throughout the year but not consumed on at least a weekly basis and not consumed exclusively or mainly during fruit scarce months.

Species were determined to be staple food species based on frequency along feeding trails (i.e., percentage of months, weeks, and days sampled). Since frequencies based on feeding trail data are underestimates for reasons discussed in the methods, the most frequently recorded species were considered to be staples if they were consumed

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[7] *Trichoscypha* and *Santiria* species were determined to be important fruit species during March and May 1999, respectively.

along trails during at least 11 months of the year, ≥ 50% of weeks sampled, and on ≥ 11% of days sampled per month indicating that they were likely eaten on at least a weekly basis.

Four food species (2 herb, 1 liana, and 1 tree) were determined to be staples in the gorillas' diet. The pith and/or fruit of *Aframomum* species were eaten along feeding trails during all months and weeks sampled, and on the greatest number of days sampled (74%) of all food species (mean percent of days per month = 75%, SD = 14.9%, range = 43 – 100%). *Landolphia* sp. 2 was the second most frequently recorded food species; bark, pith and/or fruit were consumed along trails during all months, 98% of weeks and on 63% of days sampled (mean days per month = 61%, SD = 18%, range = 33 – 89%). Leaves, bark, and/or fruit of *Ficus* species, the fourth most frequently eaten food species, were recorded along feeding trails during all months, 57% of weeks, and 28% of days sampled (mean days per month = 31%, SD = 17%, range = 11 – 64%).

Food species were determined to be important seasonal foods if they were not available throughout the year and were considered to be an important food species (based on fecal and/or feeding site frequency and abundance measures) during at least one month in which it was available. The majority (79%) of the 29 seasonally important foods were fruit of 18 tree, one liana, and four unidentified species. The remaining seasonally important foods were leaves of three tree, two herb and one vine species, and one herb pith food species (Table 3.11). Three fruit species were important exclusively during low fruit consumption months, *Vitex* and Unidentified SD-01 and SD-09.

Table 3.11 Important staple, seasonal, and fallback food species in the Afi gorilla diet.

Family	Species (or local name)	Life Form	Part(s) Eaten	Season eaten*
STAPLE				
Apocynaceae	*Landolphia* sp. 2	L	BP, F, Lv	---
Marantaceae	*Thaumatococcus daniellii / Megaphrynium macrostachyum*	H	YLv, P, F	---
Moraceae	*Ficus* spp. (3)	T, L	Lv, B, F	---
Zingiberaceae	*Aframomum* spp.	H	P, F	---
SEASONAL				
Agavaceae	*Dracaena arboreus*	T	Lv	H
Anacardiaceae	*Pseudospondias microcarpa*	T	F	**H**
	Sorindeia sp.	T	F	**H**
	Trichoscypha sp.	T	F	**H**
Annonaceae	*Monodora myristica*	T	F	H
	Uvariodendron calophyllum	T	F	H
Apocynaceae	*Landolphia* sp. 1	L	F	D
	Tabernaemontana pachysiphon	T	F	H
Araceae	*Anchomanes difformis*	H	P, Lv	W
Burseraceae	*Santiria trimera*	T	F	**H**
Caesalpinioideae	*Dialium guineense*	T	F	**H**
Guttiferae	*Garcinia kola*	T	F	**H**
Meliaceae	*Turreanthus africanus*	T	Lv	---
Mimosoideae	*Albizia zygia*	T	Lv	H
	Parkia bicolor	T	F	---
Moraceae	*Antiaris toxicaria africana*	T	F	**D**
	Morus mesozygia	T	F	H
	Myrianthus angolensis	T	F	**W**
	Treculia africana	T	F	H
Rhamnaceae	*Maesopsis eminii*	T	F	H
Sapotaceae	*Chrysophyllum* sp.	T	F	**H**
Sterculiaceae	*Cola millenii*	T	F	H
Verbenaceae	*Vitex* sp.	T	F	L
Unidentified	Unidentified SD-01	U	F	**L**
	Unidentified SD-09	U	F	**L**
	Unidentified SD-49	U	F	**H**
	Unidentified SD-68	U	F	**H**
	(“Kibang ushie”)	H	Lv	**D**
	(“Kidako”)	V	Lv	**H**

Table 3.11 Continued on next page.

Table 3.11 Continued.

Family	**Species (or local name)**	**Life Form**	**Parts Eaten**	**Season eaten***
FALLBACK				
Apocynaceae	*Landolphia* sp. 4	L	BP	**W-L**
Araceae	*Stylochiton* sp.	H	P, Lv	W-L
Commelinaceae	*Palisota* sp. 1	H	P	D-L
Marantaceae	*Marantochloa* spp.	H	P	D-L
Moraceae	*Milicia excelsa*	T	B, Lv	W-L
	Morus mesozygia	T	B, Lv	W-L
	Musanga cecropioides	T	Lv	L
Myristicaceae	*Pycnanthus angolensis*	T	Lv	W-L
Papilionoideae	*Pterocarpus osun / mildbraedii*	T	B	D-L
Tiliaceae	*Grewia mollis*	T	B	**W-L**
Zingiberaceae	*Costus* spp.	H	P	W-L
Unidentified	*Gongronema latifolium*	L	BP, Lv	W-L
	Unidentified G-01	H	P	**L**
	(“Beleh/Bakur”)	L	BP, Lv	W-**L**
	(“Ofre etta”)	L	BP	D-L
	(“Ole ejuejue”)	L	BP	L
	(“Okpeje”)	T	B, Lv	W-**L**
	Unidentified T-11	T	B	W-**L**

Season Eaten = Season in which the month(s) a species was consumed either exclusively or most frequently (see Tables 3.5, 3.6 and 3.8 – 3.10); L = Low fruit consumption months (August – January), H = High fruit consumption months (February – July), D = Dry months (November – March), W = Wet months (April – October), D-L = dry months within the low fruit consumption period (November – January) and W-L = wet months within the low fruit consumption period (August – October); Bold: eaten exclusively during season noted.

Life Form: H = Herb, L = Liana, T = Tree, V = Vine, U = Unknown.

Parts Eaten: B = Bark, BP = Bark/Pith, F = Fruit, Lv = Leaves, P = Pith, YLv = Young leaves.

Food species were determined to be important fallback foods if they were available throughout the year, considered to be important food species during at least one month, and were eaten exclusively or mainly during the low fruit consumption months of August – January (≥ 70% of feeding sites at which a food species was eaten occurred during these months). Table 3.12 lists the 26 non-fruit food items of 18 important fallback species listed in order of importance value rank within their given food category, percentage of feeding sites and amount eaten for each species during low fruit consumption months. Six fallback foods (2 liana bark/pith, 3 tree bark, and one herb pith) were recorded along trails exclusively during low fruit season months; for an additional 12 fallback foods, percentage of feeding sites and amount eaten were ≥ 90%. Most fallback food species (85%) were exclusively or mainly consumed during dry or wet months within the low fruit consumption period (Table 3.11).

Nine fallback foods were among the most important food species within their corresponding food category (i.e., importance value rank ≤ 5), including two tree (*Milicia excelsa* and "Okpeje"), two liana bark/pith ("Ofre etta", and "Ole ejuejue"), four tree bark (*Pterocarpus osun/mildbraedii, Milicia excelsa, Morus mesozygia,* and *Grewia mollis*), and one herb pith species (*Palisota* sp. 1). Six species provided more than one important fallback food (e.g., both leaves and bark of *Milicia* were important fallback foods). Consequently to determine the top five most important fallback species, total monthly relative frequency, dominance and density were summed for each different food category and then importance values were calculated as previously described. The four most important fallback species in rank order were *Milicia excelsa, Palisota* sp. 1, *Pterocarpus osun/mildbraedii*, and *Stylochiton* sp.

Table 3.12 Important fallback food species for Afi gorillas listed in order of importance value within given food categories.

SPECIES (or Local Name)	**IV Rank**	**For Each Species during Low Fruit Months (Aug – Jan)**	
		% Feeding Sites *	% Amount Eaten **
Leaves			(number)
Milicia excelsa	4	79	79
(“Okpeje”)	5	96	91
Musanga cecropioides	7	95	96
Stylochiton sp.	8	97	99
Morus mesozygia	9	85	88
(“Beleh/Bakur”)	13	70	67
Pycnanthus angolensis	14	92	96
Gongronema latifolium	15	97	97
Liana Bark/Pith			(cm^2)
(“Ofre etta”)	4	79	71
(“Ole ejuejue”)	5	95	96
Gongronema latifolium	6	97	99
(“Beleh/Bakur)	8	100	100
Landolphia sp. 4	9	100	100
Tree Bark			(cm^2)
Pterocarpus osun / mildbraedii	1	81	86
Milicia excelsa	2	85	88
Morus mesozygia	4	73	84
Grewia mollis	5	100	100
Unidentified T-11	6	100	100
(“Okpeje”)	10	100	100
Herb Pith			(grams)
Palisota sp. 1	3	86	86
Costus spp. (2)	7	90	92
Marantochloa spp. (3)	8	90	94
Stylochiton sp.	9	96	98
Unidentified G-01	10	100	100

IV = Importance value, see text for details.

* i.e. 79% of feeding sites at which *Milicia* leaves were eaten occurred during fruit scarce months.

** i.e. 79% of *Milicia* leaves were consumed during fruit scarce months.

The top 10 overall most important food species in the Afi gorillas' diet during the year sampled in importance value rank order were: *Landolphia* sp. 2 (liana), *Anchomanes* (herb), *Aframomum* (herb), *Ficus* (tree), *Landolphia* sp. 1 (liana), *Milicia* (tree), *Palisota* sp. 1 (herb), *Thaumatococcus/ Megaphrynium* (herb), *Treculia* (tree), and *Myrianthus* (tree).

SUMMARY AND DISCUSSION

Afi Gorilla Diet

In general, the Afi gorillas' diet is similar to diets of western lowland gorillas, though they differ in several important ways that are discussed in more detail in Chapter Six. Afi gorillas consume a wide variety of different food items and species (at least 216 items of 168 species), including at least 100 species of fruit. Afi gorillas consumed the pith of herbs, leaves of herbs and trees, the bark/pith of lianas, and fruit of trees, herbs, and lianas throughout the year, though the relative contribution of these foods to the gorillas' diet varied monthly and seasonally (see below). Herbs were a staple food resource for Afi gorillas, including the pith and leaves of Zingiberaceae and Marantaceae herb species similar to those consumed by gorillas at western lowland sites (reviewed in Rogers et al., 2004). *Anchomanes difformis* and *Aframomum* spp. were the most important herb food species in the Afi gorilla diet. Since *Anchomanes difformis* was the only seasonally available herb species at Afi, it was designated as an important seasonal food species. *Anchomanes* stem pith and leaves were certainly staple foods in the gorillas' diet when it was available (March – November) and was found to be the second most important of all Afi gorilla food species.

Frequency of *Aframomum* spp. stem pith consumption occurred as predicted by its availability; it was the most commonly available (0.43 stems/m^2) and frequently consumed herb. Though *Anchomanes* occurred at a much lower stem density (0.01 stems/m^2), it was consumed at similar or higher frequencies than *Aframomum* spp. during some months and when *Aframomum* and *Anchomanes* were both present nearby each other on feeding trails, the gorillas preferred the less common *Anchomanes*. The Afi gorillas' preference for *Anchomanes* is likely related to the fact that it provides much greater amounts of pith food per stem (based on results of the present study) and its higher protein and lower fiber content, and high digestibility compared to *Aframomum* spp. (based on nutrient analyses conducted at Campo, Cameroon by Calvert, 1995).

Unlike studies of western lowland gorilla diets, the present study found that liana foods were an important component of the Afi gorillas' diet throughout the year. Liana bark/pith was consumed on at least a weekly basis throughout the year and consumption of liana bark/pith did not differ significantly between high and low fruit consumption months. The fruit of at least one liana species (*Landolphia* sp. 2 or *Landolphia* sp. 1) was an important fruit resource during all months of the year sampled. One liana species, *Landolphia* sp. 2, was determined to be an important staple food and the most important of all Afi gorilla food species.

The relative contribution of fruit versus non-fruit vegetation in the Afi gorillas' diet varied monthly and seasonally in relation to fruit availability. Though gorillas consumed fruit throughout the year, fruit consumption by the gorillas was significantly greater during six months of the year (February – July). This high fruit consumption period includes two dry months (February and March) and four wet months (April – July) so this period does not strictly coincide with the wet season as at most western lowland gorilla study sites. The relative contribution of different fruit species fluctuated monthly and a total of 24 fruit species were determined to be important seasonal food species.

As at western lowland gorilla sites, Afi gorillas relied more heavily on non-fruit vegetation foods during the period of fruit scarcity (i.e. low fruit consumption period, August – January) but increased consumption of particular non-fruit vegetation foods and/or food species during dry versus wet months within this period. Tree bark was a particularly important supplemental food resource throughout the period of low fruit consumption, but different tree bark fallback foods were important during dry months within this period (*Pterocarpus*) versus wet months within this period (*Milicia*, *Morus*, *Grewia*, Unidentified T-11, and “Okpeje”). Leaves were important supplemental foods particularly during the wet months within the low fruit consumption period, when all but one of the eight leaf fallback foods were either exclusively or more frequent and abundant in the diet. Herb pith was an important supplemental food during dry months within the period of low fruit consumption when two species (*Palisota* sp. 1 and *Marantochloa* spp.) served as important fallback foods. During this time, Afi gorillas preferred the less commonly available *Palisota* sp. 1 (0.01 stems/m^2) to *Aframomum*. This preference for *Palisota* sp. 1 is likely related to its greater water content and amount of pith provided per stem (based on results of the present study), and higher protein content (based on nutrient analyses conducted at Campo, Cameroon by Calvert, 1995).

Whereas gorillas at western lowland study sites rely relatively heavily on a few fruit fallback food species during periods of fruit scarcity (reviewed in Rogers et al, 2004), no fruit food species at Afi met the criteria to be considered a fallback species (either they were not always available or were not consumed exclusively or mainly during low fruit season months). Nine species were important fruit foods in the Afi gorilla diet during low consumption months and three species were important exclusively during this time (*Vitex* spp., and Unidentified SD-01 and SD-09).

Methodology

Although indirect methods are limited and biases are present, they can provide a large amount of dietary information and if collected in a detailed manner (i.e., counting seeds in fecal samples and measuring amount eaten per feeding site) some of these limitations and biases can be reduced. Most previous studies of gorillas that have relied on indirect methods likely did not collect these additional measurements (cf. Williamson, 1989) because they are time-consuming and because habituation was the primary goal of these studies. However, these measurements collected during the present study provided many important insights into the Afi gorillas' diet, which would have been overlook using methods of previous studies. Indeed they might never have been discovered since habituation of Afi gorillas or any other Cross River gorilla subpopulation may never be desirable.

Counting seeds present in fecal samples provided the data necessary to calculate fruit pulp volume eaten per sample, which provided specific insights into the Afi gorillas' seasonal variation in fruit consumption. Pulp volume data were also useful for identifying important fruit species and determining their relative importance. Presence of seeds in samples alone does not indicate their abundance and estimates of seed abundance are subjective. Consequently if important fruit species were determined using frequency only, *Monodora myristica* and *Cola millenia* would not have been considered important fruit species since they were eaten at relatively low frequencies but provided relatively large amounts of pulp. Because seed weight does not necessarily correspond to fruit size or weight, it tends to underestimate the abundance of fruits containing small lightweight seeds relative to amount of pulp available and overestimate those with relatively large heavy seeds compared to amount of pulp available. Thus, without pulp volume data the importance of 18 (of the 24) important fruit species would have been either under or over estimated.

Measuring amount of food eaten along feeding trails was particularly useful for identifying and determining the relative importance of non-fruit foods. While fecal abundance scores can indicate overall abundance of non-fruit plant foods (i.e., leaves and herb pith), estimating the abundance of particular species from fecal remains is rarely possible (cf. Goldsmith, 1996). Consequently, most other gorilla studies use frequency along trails (i.e., present on a certain percentage of days or trails sampled or feeding sites) to identify important non-fruit vegetative foods. But the present study demonstrates that it is critical to also consider amount of food eaten when identifying important non-fruit foods. This was particularly true for herb pith species in the present study (i.e., the importance of *Anchomanes* stem pith).

CHAPTER FOUR – RANGING BEHAVIOR:

Home Range Size and Utilization, and Daily Path Length

INTRODUCTION

The ranging behavior of primates is influenced by many factors including body size, diet, food availability (i.e., density and distribution), intergroup encounters, mating strategies, group size, and avoidance of predators and food competitors (Boinski et al. 2000; Chapman & Chapman 2000; Clutton-Brock & Harvey 1977; Dunbar 1988; Isbell 1991; Janson & Goldsmith 1995; Milton & May 1976; Oates 1987; Watts 2000; Yamagiwa 1999). The influence of diet in particular has been well documented. In general, frugivorous primates, who rely on high-energy foods with variable spatial and temporal availability, tend to have larger home ranges and long day ranges. By contrast those primates that rely on lower quality foods, which are more consistent and uniformly available such as leaves, tend to have smaller home ranges and shorter day ranges (Clutton-Brock & Harvey 1977; Milton & May 1976). Foraging models predict that primates should use their range in an efficient manner in relation to food availability, specifically that they concentrate their foraging efforts in areas with highest food availability (Pyke et al. 1977).

Mountain gorillas rely heavily on perennial herbaceous vegetation that is abundantly available in their high altitude habitat, where edible fruits are rarely available. Consequently, they have short daily path lengths (≈ 500 m) and small annual home ranges (6.0 – 11.5 km^2) (McNeilage 2001; Vedder 1984; Watts 1991, 1998a, 2000).

Whereas herbs are essentially ubiquitous in montane habitats, abundance of high quality foods varies spatially on a small scale as well as among different habitat types. As expected, mountain gorillas use areas with high quality food more frequently and for longer periods of time compared to 'lower quality' areas (Vedder 1984; Watts 1991, 1998a).

Mountain gorilla groups tend to use high quality food areas repeatedly within a fairly short period (up to 30 days) separated by long intervals of approximately 4 months (180 days) (Watts 1998b). Watts (1998b) suggests that this cyclical pattern may be related to herb regeneration rates after gorillas have trampled an area. Re-visits to these areas, however, occur before they have fully regenerated, which can take up to 280 days (Plumptre 1993). Watts (2000) argues that these shorter than expected intervals between visits could allow the gorillas to take advantage of abundant and high-quality new growth foods available during this intermediate regeneration period than when the area had fully matured. Furthermore, trampling at regular and relatively short intervals would prevent succession to woody non-food species.

Compared to the high-altitude mountain gorilla habitat, western lowland gorillas live in forests with lower herb densities and abundant edible fruit. Whereas western lowland gorillas consume herbaceous vegetation on a daily basis throughout the year, they also incorporate large amounts of fruit in their diet (reviewed in Rogers et al., 2004). As expected due to their more frugivorous diet and the lower herb availability in their habitat, western lowland gorillas have larger home ranges and longer day ranges compared to mountain gorillas (Cipolletta 2003, 2004; Doran-Sheehy et al. 2004; Goldsmith 1999, 2003; Remis 1994; Remis 1997a; Tutin 1996; Tutin et al. 1992). In addition, mean daily path lengths are significantly longer during the wet season, when fruit availability is high, compared to the dry season when fruit availability is low (Goldsmith 1999; Tutin 1996); therefore, daily path lengths are positively correlated with temporal fruit availability (Doran-Sheehy et al. 2004; Goldsmith 1999). However, Goldsmith (1999) found no relationships between daily path length and other factors such as density, spatial pattern and patch size of fruit, availability of other food items (e.g. herb, leaves), climate (rainfall and temperature), and group size. Also, presence of predators may influence daily ranging on some occasions (Goldsmith 1996, 1999).

By measuring intensity of quadrat use, previous studies have identified core areas utilized by western lowland gorillas, but range size varied seasonally or monthly (Bermejo 2004; Cipolletta 2004; Doran-Sheehy et al. 2004; Remis 1997a; Tutin 1996). Some evidence suggests that core areas contain high concentrations of herbs and that shifts in range use occur to exploit highly concentrated food resources outside the core area, such as fruit and swamps herbs (Doran-Sheehy et al. 2004; Kuroda et al. 1996; Remis 1994; Remis 1997a; Tutin 1996; White 1994). Since western gorillas range over large areas with widely distributed food resources and most studies involve non or partially habituated groups, little is known about range use in relation to food availability or the presence of predators.

As shown in previous chapters, the Afi gorilla diet is similar to the diets of western lowland gorillas and is characterized by periods of high fruit consumption when fruit is abundant, and heavy reliance on herbaceous vegetation, tree/liana leaves and bark during periods of fruit scarcity (Chapter 3). Densities of important herb and fruit species as well as fallback foods vary across different sectors (i.e., South, Central, West and

North) within the Afi gorillas' home range. As will be shown in this chapter, predator pressure also varies across these sectors. Consequently, the Afi Mountain study site provides a unique opportunity to investigate the influence of food availability and presence of predators on Afi gorilla monthly range utilization.

The overall aims of this chapter are the following: 1) Estimate home range size and describe the Afi gorillas' general pattern of range utilization, 2) Investigate whether the Afi gorillas utilized their range in a non-random fashion by examining variation in overall, monthly and seasonal variation in the frequency with which the gorillas used different sectors within their range; 3) Investigate whether the Afi gorillas' pattern of range use reflects efficient use in relation to food availability and avoidance of predator pressure by comparing the gorillas' frequency of sector use with variation in food availability and predator pressure across sectors; 4) Describe the Afi gorillas' daily ranging behavior, including estimation of mean daily path length, description of monthly and seasonal variation, and investigation of whether different factors such as diet, fruit and herb availability, climate, and presence of predators influenced daily path length.

Predictions

Because of the Afi gorillas' highly frugivorous diet, their ranging behavior was expected to be similar to the ranging behavior of western lowland gorillas rather than to that of the folivorous mountain gorillas. Afi gorilla home range size was expected to be larger and mean daily path length longer than those of mountain gorillas. The Afi gorillas were expected to use different sectors within their range in a non-random fashion related to ecological factors, such as food availability and predator pressure. Based on the temporal and spatial variation in food availability described in Chapter Two and the temporal variation in the relative contribution of fruit and non-fruit vegetation foods, as well as individual important foods, in the gorillas' diet identified in Chapter Three, the following additional predictions were examined.

Relationship Between Range Use and Ecological Factors

Herb pith and leaves were a staple food resource for the Afi gorillas but abundance of herb foods in the gorillas' diet was significantly greater during the period of fruit scarcity (i.e., the low fruit consumption period of August – January; see Chapter 3 for details). Overall herb availability (i.e., stem density) as well as availability of individual herb species varied significantly across the three sectors sampled (South, Central, and West; see Figure 4.1 and Chapter 2 for details). Thus, the gorillas' herb diet and range use throughout the year and particularly during the low fruit consumption period should occur as predicted by variation in herb availability across sectors. Specifically, the frequency of sector use and consumption of different herb species when utilizing these sectors were both expected to correlate with variation in herb stem density across sectors.

Four herb pith and leaf foods and eight tree leaf and bark foods were available throughout the year but were consumed more frequently or exclusively during the low fruit consumption period and were identified as important fallback foods. Different herb and tree fallback foods were specifically consumed more frequently during dry or wet months within this period (November – January and August – October, respectively; see Table 3.12), suggesting that they were more sought out by the gorillas during these times.

Thus, variation in the availability of these foods across sectors should influence the gorillas' frequency of sector use during the low fruit consumption period and during dry and wet months within this period.

Though Afi gorillas consumed fruit throughout the year sampled, fruit consumption was significantly greater during February through July (i.e., the high fruit consumption period) and the relative contribution of individual fruit species in the gorillas' diet varied monthly (see Chapter 3 for details). Fruits of two liana species were important foods during all months of the year, but the majority of important fruit foods (79.2%) came from tree species. Thus, frequency of sector use, both during the high fruit consumption period and each month separately, was expected to correlate with variation in the density of fruiting trees of important tree-fruit food species across sectors.

Predator pressure was expected to be an important factor influencing the gorillas' pattern of range use throughout the year. Humans have been hunting on Afi Mountain for a very long time, and are currently the only predators threatening the gorillas. Though the presence of researchers likely deterred hunting, hunters were active throughout the study period. Hunters usually do not target gorillas, but they usually carry a shotgun, and if the opportunity arises they will shoot gorillas. During the present study, a hunter killed an adult male gorilla in the Afi study group. In addition, a severed gorilla finger was found hanging in a wire snare from a tree branch within the study area. Gorilla feet, hands or fingers can become entangled in wire snares creating possible infection resulting in death as has been shown for mountain gorillas (Mudakikwa et al. 2001). Thus, a negative relationship between level of hunting activity in each sector and frequency of sector use might indicate that hunting pressure influenced Afi gorilla ranging behavior during the present study.

Daily Path Length

Afi gorillas were expected to travel longer distances daily when fruit was abundant in their diet (i.e., the high fruit consumption period of February – July) than when relying on non-fruit vegetation foods (i.e., the low fruit consumption period). Daily path length was expected to positively correlate with fruit availability in the habitat and dietary measures of fruit consumption. Variation in daily path lengths across sectors was examined in order to investigate whether the gorillas' daily ranging behavior was influenced by low herb availability. Compared to the Central sector, the South is characterized by much lower herb stem density, and fewer herb patches that are more widely dispersed (Chapter 2). In addition when using the South during the low fruit consumption period, the gorillas consumed large amounts of the pith and leaves of *Anchomanes difformis*, an herb that occurs as single widely scattered stems rather than densely clumped stems in large patches like other Afi gorilla herb foods. Thus, daily path lengths when the gorillas utilized the South sector were expected to be longer than when they used the Central sector, particularly during the low fruit consumption period. Also, Afi gorillas were predicted to travel longer distances when hunters were present nearby as they certainly pose a serious threat (see above).

METHODS

Searching Techniques

Data on the ranging behavior of Afi gorillas, like data on feeding, were gathered from a study of foraging trails and nest sites. Systematic searches were conducted to locate fresh gorilla trails. Following gorilla trails was the focus of the study from December 1997 through November 1998 and during the census (February – March 1999). Trails were followed intermittently during December 1998, January 1999 and April 1999. Based on analysis of nest site data, it is assumed that the vast majority of the evidence collected is attributable to the same gorilla group (see Chapter 5).

Searches were conducted by up to three field teams, consisting of local research assistants (see Chapter 3 for details), who followed marked hunters' trails branching at various points along different compass bearings forming circular patterns within a particular sector. Hand-held radios were used to coordinate team movements throughout the day. Sectors searched were identified based on many factors, such as trackers' knowledge of past gorilla movements, results of the previous day's search and location of fruiting trees. Temporary camps (e.g., caves) were often used for up to a week when the gorillas traveled far from Base Camp.

While searching, direction was noted approximately every 15 minutes and when major landmarks and marked trails were encountered. Any non-gorilla wildlife signs, such as sightings, calls, footprints, feces, feeding evidence and sleeping sites of other primates (i.e., chimpanzees, monkeys, galagos, and pottos), duikers, porcupines, red river hogs, and other mammals (see Table 2.1) were described noting location, estimated age, number, and evidence of food consumed as encountered while searching and following gorilla trails. Evidence of hunting (i.e., wire snares, spent shotgun shells, gunshots, trails, camps) was also noted. If old gorilla nest sites (≥ 5 days old) were encountered, location, estimated age, habitat type, and number and type of nests were noted. Relatively old gorilla trails (5 – 7 days old) were followed when possible to determine the general direction in which the gorillas were traveling to inform the next day's search.

Fresh gorilla trails (≤ 4 days old) were paced for distance and direction was noted every 50 paces or more frequently if major changes in direction occurred. The locations of feces and footprints were noted and data on feeding remains were collected as described in Chapter Three. Whenever a trail became unclear or was 'lost' it was noted. Teams returned to the last definite sign and searched in a circular pattern to re-establish the gorillas' trail. Trails less than one day old were followed backwards to avoid meeting the gorillas and disturbing their natural movement pattern. Trails estimated to be 1 – 2 days old were followed forward and backward by separate teams. For trails estimated to be 2 – 4 days old, at least one field team searched the area in which the gorillas were heading in hopes of finding a fresher trail. Meanwhile another team continued on the older trail. This method greatly improved our ability to record complete daily path lengths (i.e., one night's nest site to the next night's nest site). In addition, we were often able to record several complete daily path lengths within a short period of time allowing us to eventually reach a less than one-day old trail, consequently ages of previous nest sites were then known.

Determining Range Utilization

Two different datasets were used to describe the Afi gorillas' home range size and utilization. First, a Quadrat Dataset was created to determine the gorillas' home range size and to illustrate their overall pattern of range use. All fresh trails and nest sites ≤ 4 days old, and those 5 – 7 days old for which locations could be determined, encountered between December 1997 and April 1999 were drawn onto a scaled map. Pacing and noting direction from some point along gorilla trails to marked hunter's trails determined the location of each gorilla trail and nest site. A 100 by 100 meter quadrat grid was then superimposed onto the map and entrances of gorillas into particular quadrats were recorded.

Because the Quadrat Dataset contained biases in sample sizes for different sectors (see result for details), a Sector Dataset was created to describe the gorillas' overall, monthly and seasonal variation in the frequency with which they utilized four different sectors within their range (South, Central, West, and North; Figure 4.1). The location of each quadrat entered within one of these four sectors was noted and the gorillas' use of one or more of these sectors was recorded once daily.

Though ranging data were collected over a 17-month period (December 1997 – April 1999), for analyses I pooled records obtained in the same month of different years (i.e., December 1997 and 1998 and January through April 1998 and 1999) so that the Quadrat and Sector datasets represent the gorillas' home range and movement patterns for a one-year period. This procedure appears just for several reasons. I superimposed maps with locations and dates of trails recorded in each of these months (December, January – April) for the different years they were sampled. Interestingly, trails recorded in the same months of different years filled ‘gaps’ between fresh trails that were ‘lost’ and fresh trails encountered several or more days later (see Figures 4.2 a and d). Directions of partial trails followed from fresh nest sites and locations of older evidence (≥ 7 days old) indicate that during December 1997 and January – April 1998, the gorillas likely utilized quadrats and sectors that were recorded more extensively during these months in the following year. While such consistent ranging patterns in different years are unusual at other gorilla study sites (M. Remis, personal communication), the above evidence strongly suggests that the Afi gorillas’ movements were relatively consistent during the five months sampled in different years. For example, in early December 1997 the Afi gorillas consumed the bark of a *Pterocarpus osun/mildbraedii* tree at a nest site and approximately one year later they ate from the same tree and then slept nearby.

Home range size and overall range use pattern

The Quadrat Dataset used to estimate home range size and illustrate the gorillas’ overall range use pattern includes locations of nest sites and trails ≤ 7 days old representing a total of 240 days. The majority of quadrat data were, however, derived from partial and complete trails ≤ 4 days old, representing 158 days. Evidence from the additional days sampled (82) mostly includes locations of nest sites only, but sometimes includes partial trails.

Minimum annual home range was estimated by calculating the area of the smallest shape enclosing all 100 by 100 m quadrats entered. To estimate the maximum annual range, a larger shape was drawn to include quadrats likely entered based on directions of partial trails (i.e., including quadrats between where a trail was lost and where fresh trails were discovered several days later) and location of old evidence (≥ 7 days old). Taking this method further to estimate the gorillas' total home range an even larger shape was drawn based on past experiences of hunters, gorilla sightings reported by hunters during the present study, and adjoining areas of viable gorilla habitat. Quadrats located on rocky peaks, which are difficult to access even for a gorilla and where no food is present, were removed from all shapes created.

To illustrate the gorillas' home range size and overall range use pattern, maps using 200 by 200 m cells were created. On the map showing home range size, the numbers of visits to the four 100 by 100 m quadrats within each 200 by 200 m cell were summed to indicate intensity of quadrat use (i.e., ≤ 4 visits, 5 – 9 visits, ≥ 10 visits).

Use of range sectors

To examine the gorillas' pattern of range use and whether they used their range in a non-random fashion, I examined variation in the gorillas' overall, monthly, and seasonal use of four sectors within their range (South, Central, West, and North; Figure 4.1), which was estimated based on the number of days gorillas were recorded in each of these sectors. The ranging data collected are assumed to represent the gorillas' range during a one-year period; the Sector Data collected for December – April in different years were pooled (see above). In this one-year pooled dataset, the days sampled (n = 240 days) were dispersed throughout the year and within each month sampled. A total of 49 weeks are represented, with days sampled distributed during ≥ 3 different weeks within each month. On average 66% of days per month (SD = 16.7%, range = 46.7 –

100%; see Table 4.1) and 4.2 days per week (SD = 2.0, range = 0 – 7) within the one-year period are represented.

Because the data are distributed relatively evenly throughout each month, it was possible to estimate the gorillas' location (i.e., within one of the four sectors) on the days that data were missing. Estimations were based on the locations (and directions of partial trails) of the evidence before and after gaps in data and unsuccessful searches. With the additional estimates, the gorillas' location within one or more sectors during all days within 10 months of the year was known or estimated with relatively high confidence (n = 353 days, see Table 4.1). Work was suspended from October 29 – November 9 1998 while field staff and I aided in the capture and prosecution of a hunter who killed a gorilla; thus, it was not possible to estimate the gorillas' movements during this time with any confidence.

Overall and monthly variation in frequency of sector use is presented as the percentage of total days sampled per sector the gorillas were recorded in each sector and was calculated in the following manner: number of days a sector was utilized (throughout the year or per month) divided by the total number of days sampled (throughout the year or per month) multiplied by 100. Overall and monthly frequencies of sector use were calculated using the smaller and larger Sector Datasets separately (n = 240 days with known locations and n = 353 days with known and estimated locations, respectively) and were compared using Pearson correlations.

To investigate seasonal variation, I compared frequency of sector use between periods of low and high fruit consumption representing variation in the relative contribution of fruit and non-fruit vegetation foods in the gorillas' diet (August – January versus February – July) and between dry and wet months within the low fruit consumption period (November – January versus August – October). Seasonal variation in frequency of sector use was also examined for each sector separately [e.g., number of days gorillas used the South during the low (or high) fruit consumption period divided by the total number of days the gorillas used the South x 100]. Chi-square tests were performed to determine if frequency of sector use differed overall, monthly, and seasonally from expected if the gorillas utilized each sector equally and if the use of each sector separately differed significantly across different seasons.

The number and average length of 'visits' the gorillas made to each sector were calculated to identify any variation in the manner with which the gorillas utilized the different sectors. A visit to a sector was defined as the period of consecutive days the gorillas remained in one sector before entering another sector. The length of a visit was defined as the number of consecutive days the gorillas spent in one sector. When gorillas visited more than one sector during a day (n = 28 days), I noted their presence in each sector separately.

Relationships Between Ranging and Ecological Factors

Herb Food availability and consumption

Eight of the ten important herb foods in the gorillas' diet were enumerated along transects within the South, Central and West sectors (i.e., *Aframomum* spp., *Costus* spp., *Hypselodelphys scandens, Marantochloa* spp., *Palisota* sp. 1, *Palisota* sp. 2, *Stylochiton* sp., and *Thaumatococcus/ Megaphrynium* spp., see Chapter 2 for details). Mean stem densities of the eight herb foods pooled and each herb food separately were calculated for each sector by summing the number of stems per 1 m^2 plot and dividing by the total number of plots sampled. Densities of an additional herb, *Anchomanes difformis*, that was the gorillas' most important herb food resource, were estimated for each sector using feeding site encounter rates along trails. Stems and/or young leaves of all but one herb species, *Anchomanes difformis*, were available throughout the year. *Anchomanes* stems were available during nine months of the year (March – November) but were most abundantly available during wet season months, April – October.

To examine whether variation in herb stem density across sectors influenced the gorillas' diet when utilizing different sectors, I compared densities and frequencies of herb consumption for the three sectors sampled. Comparisons were made for all herb foods pooled and for each herb food separately. Frequency of herb consumption (pith and/or leaves) by gorillas was determined by calculating the average number of stems found eaten along feeding trails per day sampled in each sector (e.g., total number of herb stems eaten in the South divided by total number of days the South was sampled).

To investigate the relationship between herb availability and the gorillas' pattern of range use, comparisons were made between variation in herb density across sectors and frequencies of sector use. Herb foods were consumed throughout the year but were more abundant in the gorillas' diet during the low fruit consumption period. In addition, four fallback herb foods were consumed most frequently during the low fruit consumption period and different fallback herbs were specifically eaten more frequently during dry or wet months within this period. Consequently, the availability of different herb foods was expected to influence range use during certain times of the year.

Taking this into consideration, the following comparisons between variation across sectors in the mean stem densities of different herb species pooled and the gorillas' frequency of sector use:

1. Density of all herbs (the nine herb foods enumerated) and frequency of sector use throughout the year and during the low fruit consumption period,
2. Mean stem density of all fallback herbs (*Costus* spp., *Marantochloa* spp., *Palisota* sp. 1, and *Stylochiton* sp.) and frequency of sector use during the low fruit consumption period,
3. Density of fallback herbs eaten in dry low fruit months (*Marantochloa* spp. and *Palisota* sp. 1) and frequency of sector use during these months (November – January),
4. Density of fallback herb foods eaten in wet low fruit months (*Costus* spp. and *Stylochiton* sp.) and frequency of sector use during these months (August – October).

Kruskal Wallis Chi-square tests were performed to determine whether herb stem densities and frequencies of herb consumption differed significantly between the sectors. Pearson correlations were performed to determine the relationship between herb stem density and consumption, and herb density and frequency of sector use. Because of the small sample size (1 sample per sector), significance was only obtained when correlation coefficients were very high (≥ 0.997). Therefore, correlations were used mainly to determine the direction of the relationship (i.e., positive or negative) and to compare the different relationships investigated (i.e., the relationship between overall herb stem density and frequency of consumption compared to the relationships between individual herb food densities and frequencies of consumption).

Tree food availability

Trees, including most of the species that were important gorilla fruit, leaf, and bark foods, were enumerated within the South and Central sectors. Tree food densities were estimated using 250 m^2 quadrats along tree enumeration and phenology transects located within these two sectors (see Chapter 2 for details). To examine whether variation in the availability of tree fallback food species across sectors influenced the gorillas' pattern of range use during the low fruit consumption period, I compared the total mean density of all fallback species for each sector to the frequency of sector use during this period. I also calculated the mean density of tree fallback food species that were consumed exclusively or more frequently during dry or wet months within the low fruit consumption period separately and compared them to frequency of use during these months. Mean densities were calculated by summing numbers of fallback food trees per 250m^2 quadrat within the South and Central sectors.

Unlike most herb foods, availability of fruit varies spatially and temporally. Phenology data were not available for all months and/or for all important fruit species eaten during the time period for which ranging data were collected. Presence of seeds in fecal samples, however, demonstrates the availability of fruit species within the gorillas' habitat. Months in which fruit species were most abundant in the dung, usually indicate the period of greatest availability as demonstrated at other gorilla study sites (Nishihara 1995; Remis 1994, 1997b).

To examine spatial variation in tree-fruit food availability at Afi, mean densities of each of the most important tree-fruit species consumed by gorillas during the present study were calculated for South and Central sectors (densities were calculated as described above; see below for how most important tree-fruit foods were identified). To incorporate temporal variation in fruit availability, these mean densities were used to estimate monthly variation in density of trees in fruit across the two sectors. Estimated density of fruiting trees was calculated for South and Central sectors separately by summing densities of the most important tree-fruit species eaten during each month sampled. These estimated densities of fruiting trees were then compared to frequencies of sector use during each month, to investigate whether the gorillas' range use pattern may be related to variation in tree-fruit food availability across sectors.

The most important tree-fruit species were identified using importance values calculated for all important fruit species consumed by gorillas in each month sampled. Importance values incorporated proportion of fecal samples in which species were present, proportion of pulp volume and number of days present in fecals per month (see Chapter 3 for details). Those species with importance values ≥ 20 during a given month were considered to be a most important fruit species for that month. A value of ≥ 20 was used because it represented a natural cut-off between the most and least frequently consumed important fruit species. Only those most important fruit species that were tree species were included in the analyses.

To determine whether densities differed significantly between South and Central sectors, Mann-Whitney U tests were performed using numbers of trees per 250 m^2 quadrat (n = 94 and 57 quadrats, respectively). Due to the small sample available for most of the tree foods, differences between the densities of individual species in the two sectors rarely reached statistical significance even when a species was recorded in one sector exclusively. Therefore, a species' availability was considered to differ between the two sectors when one of the following criteria was met: 1) it was recorded in one sector exclusively or (2) its density in one sector was ≥ 2 times greater than the other sector.

Limitations of food availability data

Herb and tree densities were not available for all of the four sectors within the gorillas' range, though densities were available for those sectors the gorillas utilized most frequently throughout the year and during the low and high fruit consumption periods. Low estimated densities of fruiting trees in South and Central sectors can, however, provide insights as to why the gorillas may have utilized West or North sectors more frequently than expected during particular months. Another limitation of the data is the fact that lianas, which were an important food resource for the gorillas, were not enumerated (see Discussion for further details). Hence, results are preliminary and should be interpreted with caution.

Hunting pressure

While searching and following gorilla trails, evidence of hunting was noted as encountered (e.g., wire snares and gunshots, see Searching Techniques for details). To describe variation in hunting pressure experienced by the gorillas when utilizing different sectors, the rates at which wire snares were encountered and the proportions of total gunshots heard in each sector were estimated. Average snare encounter rate was calculated by summing the number of snares encountered in a sector and dividing by the number of days researchers spent in that sector. Because gunshots could be heard over long distances, most shots fired in South, Central and West sectors could be heard from Base Camp where an assistant was always present and recorded all shots heard (The sector from which each shot originated was noted); 69% of total shots heard were recorded at Base Camp. Since whether or not a shot was heard was not necessarily dependent on the presence of researchers in sectors, the proportion of total gunshots heard (e.g., number of shots fired in the South/total number of shots fired) was used rather than "encounter rate".

Daily Path Length

Daily path length was estimated based on complete nest to nest trails ≤ 4 days old. Trails were paced for distance and direction was noted every 50 paces (or more frequently if major changes in direction occurred, see Searching Techniques for details). A total of 60 complete trails was recorded between January 1998 and April 1999. These complete trails probably underestimate daily path length since the likelihood of successfully following a complete trail was greater when gorillas traveled shorter distances. Consequently, when gorillas were traveling long distances between sectors within their range, trails were most often lost and only rarely were complete trails recorded under these circumstances.

To compensate for this bias, 15 additional partial trails of greater than 1.5 km were included in the analysis. The 1.5 km cut-off was used to adequately represent longer distance trails and provide a more representative sample for different seasons and individual months (see Results for details). Analyses were performed using both the smaller dataset containing complete trails only and the larger dataset including the additional partial trails of ≥ 1.5 km in length, and differences in the results are discussed.

Mean daily path length was calculated for all trails pooled and for each month of the year sampled (n = 12 months). To investigate the relationship between daily path length and the relative contribution of fruit and non-fruit vegetation foods in the gorillas' diet, mean daily and monthly path lengths were compared between high and low fruit consumption periods (February – July versus August – January). T-tests were performed to determine whether differences were statistically significant.

The relationship between the relative contribution of fruit and non-fruit vegetation foods and daily path length was also investigated using dietary variables. Four food categories were used: fruit, leaves, liana/tree bark, and herb pith. The latter three categories were also pooled to form a non-fruit food category. For each food category, the following dietary variables were calculated for each month sampled (see Chapter 3 for further details): 1) Species diversity, measured as the total number of species eaten along trails; 2) Frequency of consumption, measured as percentage of feeding sites along trails; 3) Abundance, measured using weights or abundance scores from fecal samples and amount eaten per feeding site along trails separately. Regression analyses were performed between monthly mean daily path length and the various dietary variables for each of the different food categories. When significant relationships were found for more than one food category, multiple and step-wise regressions were performed to determine the relative importance of each.

Regressions were used to determine the relationship between monthly mean daily path length and temporal availability of fruit in the gorillas' habitat. Phenology data are not available for all months in which diet and ranging data were collected (December 1997 – April 1999); phenological data collection began in May 1998. Consequently, I used phenology data from 2000 for this analysis and therefore results should be viewed with caution. I chose to use phenology data from 2000 because: 1) the rainfall pattern in 2000 was most similar to that of 1998, 2) a greater number of trees and species of important gorilla foods were monitored during 2000, and 3) the 2000 data provide a more accurate description of ripe fruit availability (see Chapter 2 for details). Despite the fact that diet and fruit availability measures were from different years, all fruit dietary variables and phenological measures from the different years were significantly correlated (Chapter 3). Since different fruit phenology measures, such as proportion of species and individual trees and abundance scores, were significantly correlated with one another (Chapter 2), proportion of individual trees with fruit eaten by gorillas was chosen to represent fruit availability. Relationships were separately investigated between path length and the following fruit availability measures: all fruit (ripe and unripe), ripe fruit, and unripe fruit.

Whether the Afi gorillas' daily ranging behavior may have been influenced by low herb availability was examined by comparing daily path lengths when the gorillas utilized South and Central sectors, which differed in their herb availability. Mann-Whitney U tests were preformed to elucidate any significant differences in daily path lengths between these two sectors. Inadequate sample sizes did not allow comparisons for West and North sectors.

Other factors investigated included climate and predator pressure. Regressions were separately performed between the following measures: daily path lengths with daily rainfall (i.e., total, day-time, and night-time) and temperature (minimum and maximum) and mean monthly path lengths with monthly total rainfall and mean temperatures. Mean daily path length of trails associated with evidence of hunting (i.e., hunters presence in vicinity and gunshots from neighboring quadrats were detected) was compared to that of trails with no associated hunting evidence and a t-test was used to determine any significant difference.

RESULTS

Home Range Size and Overall Use Pattern

Figure 4.1 shows the gorillas' estimated total home range based on the quadrats they entered (Quadrat Dataset). The gorillas used a total of 985 quadrats (n = 1692 entrances to individual quadrats) and the smallest shape enclosing these quadrats yields a minimum annual home range of 13.1 km^2. Based on directions of partial trails and location of old evidence (≥ 7 days old), maximum annual home range size is estimated to be 20.0 km^2. The largest shape, taking information from hunters and adjoining sectors of viable gorilla habitat into consideration, yields an estimated total home range size of 30.2 km^2. Figure 4.1 also shows the intensity of quadrat use. The numbers of visits to the four 100 by 100 m quadrats within each 200 by 200 m cell were summed to indicate intensity of use (≤ 4 visits, 5 –9 visits, and ≥ 10 visits). The majority (78.4%) of quadrats utilized most intensely are located within the Central sector.

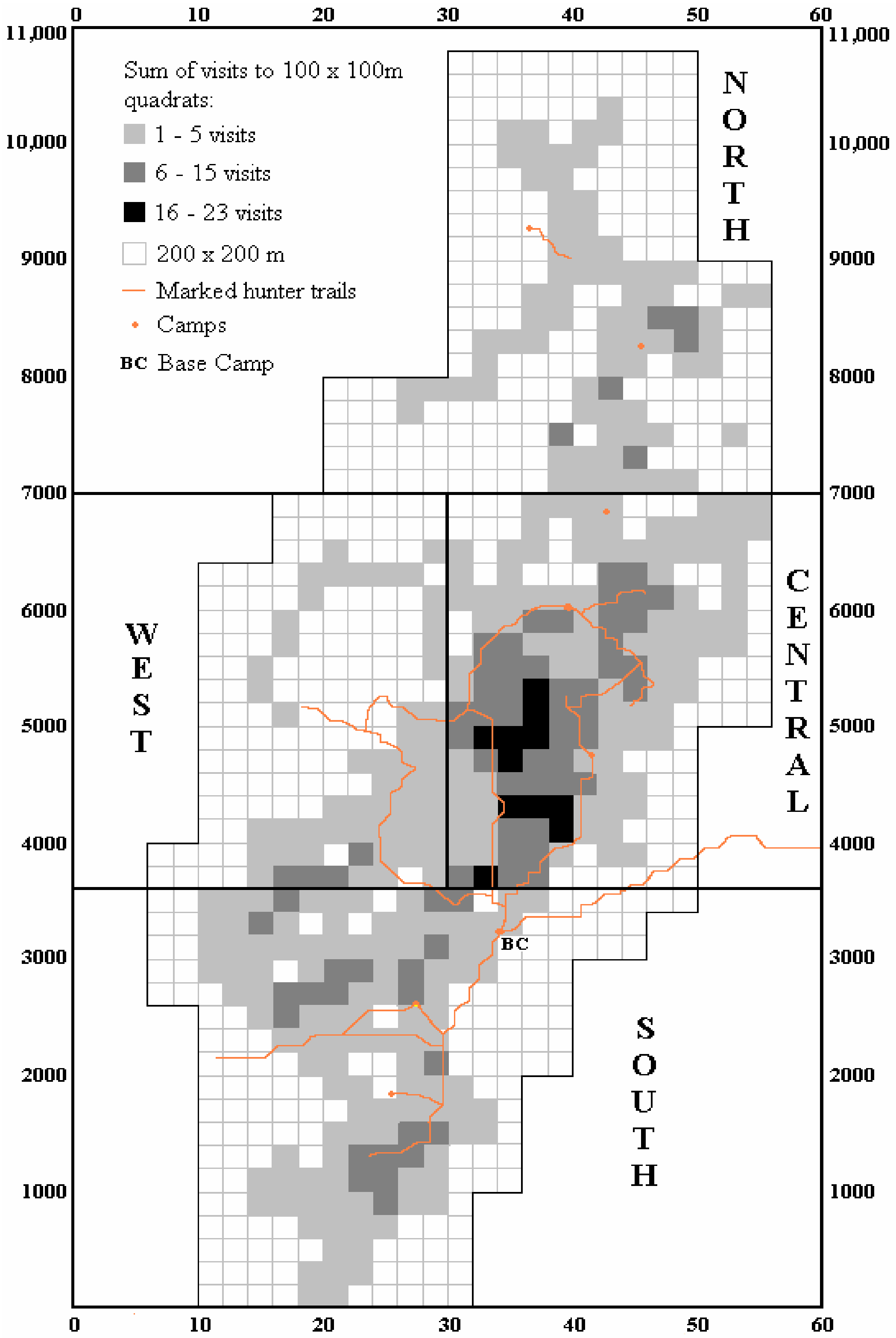


Figure 4.1 Total annual home range (color indicates intensity of use, see text for details)

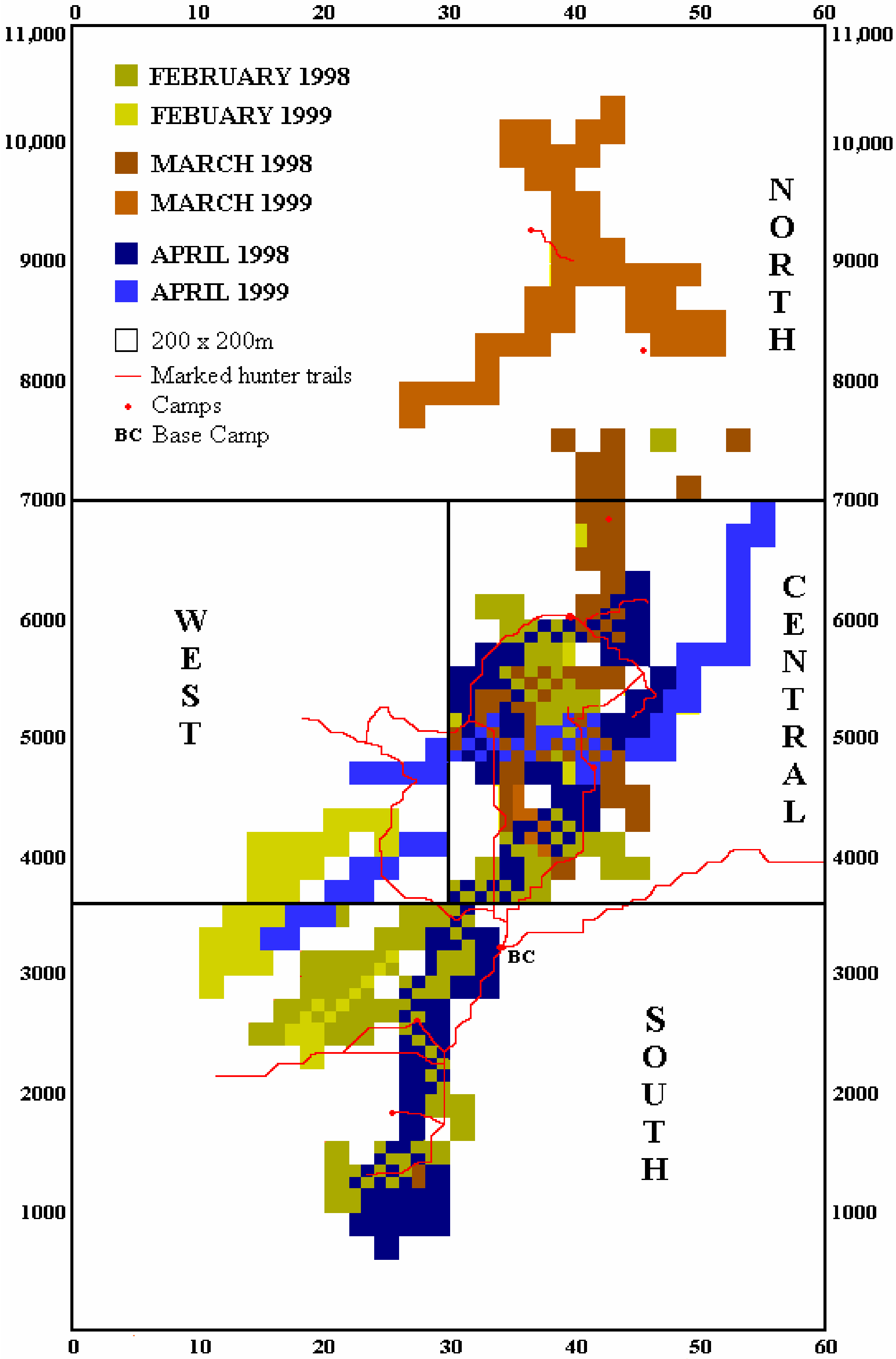


Figure 4.2a Quadrat use by Afi gorillas during the high fruit consumption months of February, March and April

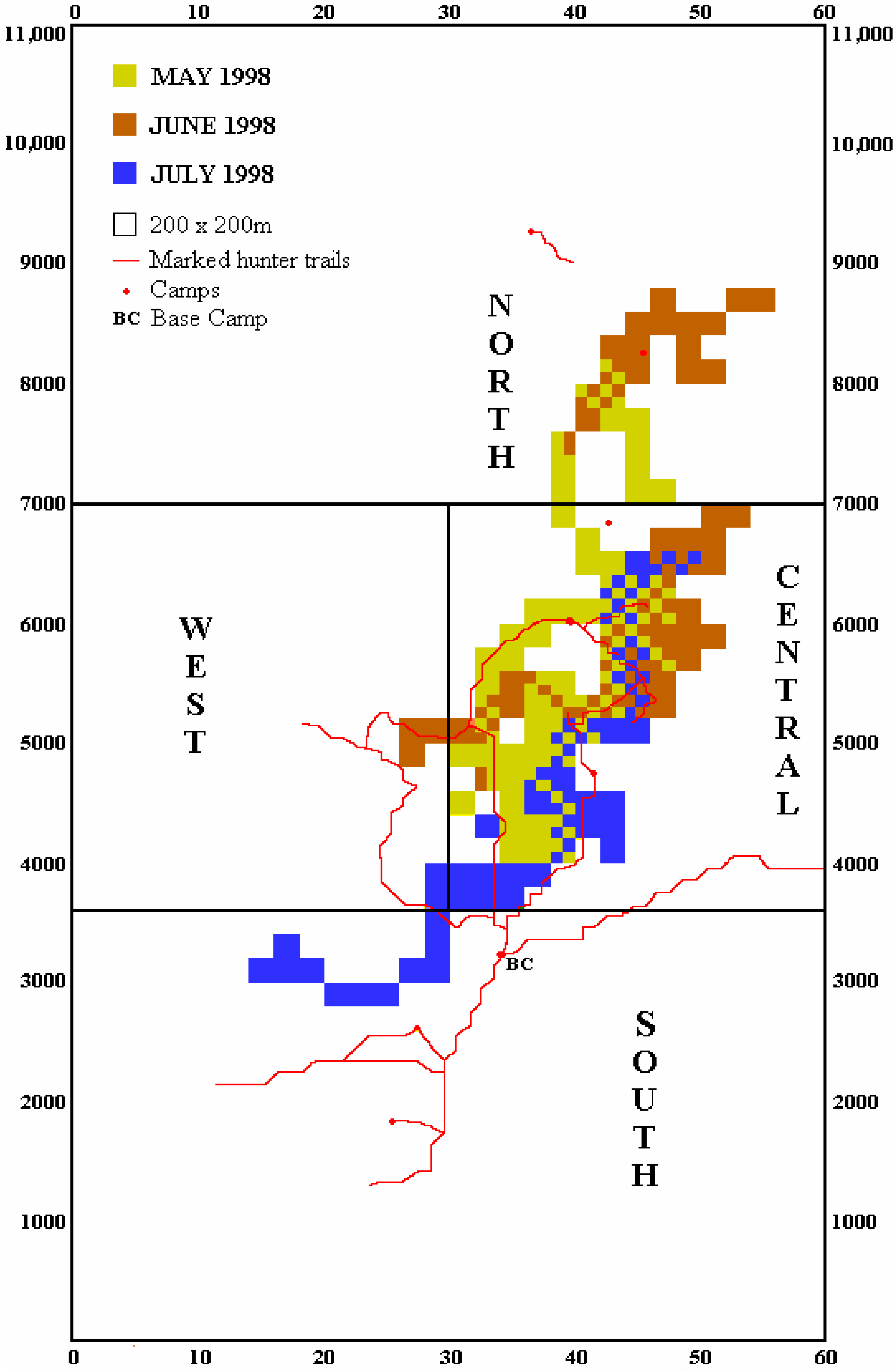


Figure 4.2b Quadrat use by Afi gorillas during the high fruit consumption months of May, June and July

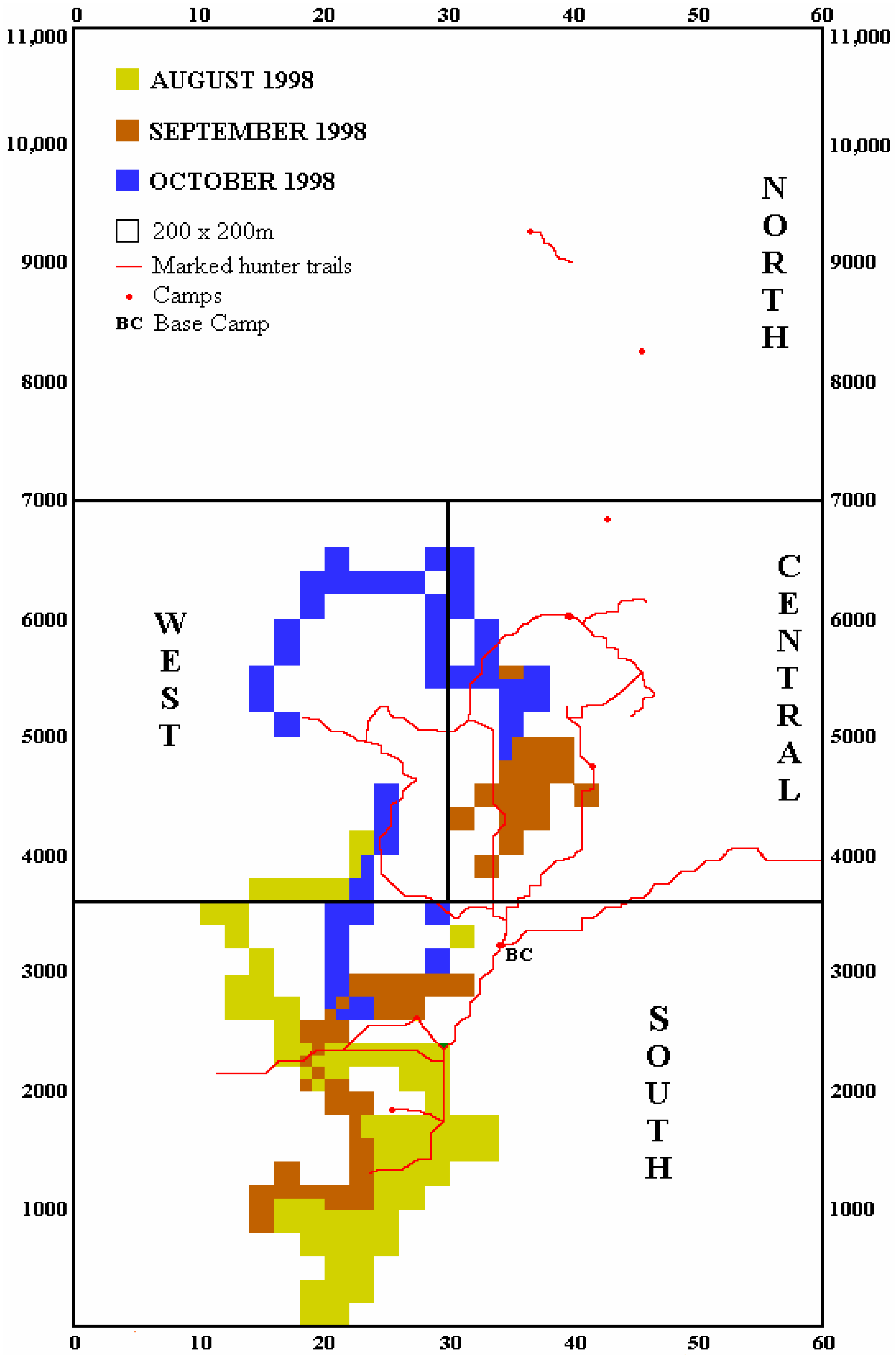


Figure 4.2c Quadrat use by Afi gorillas during the low fruit consumption months of August, September and October

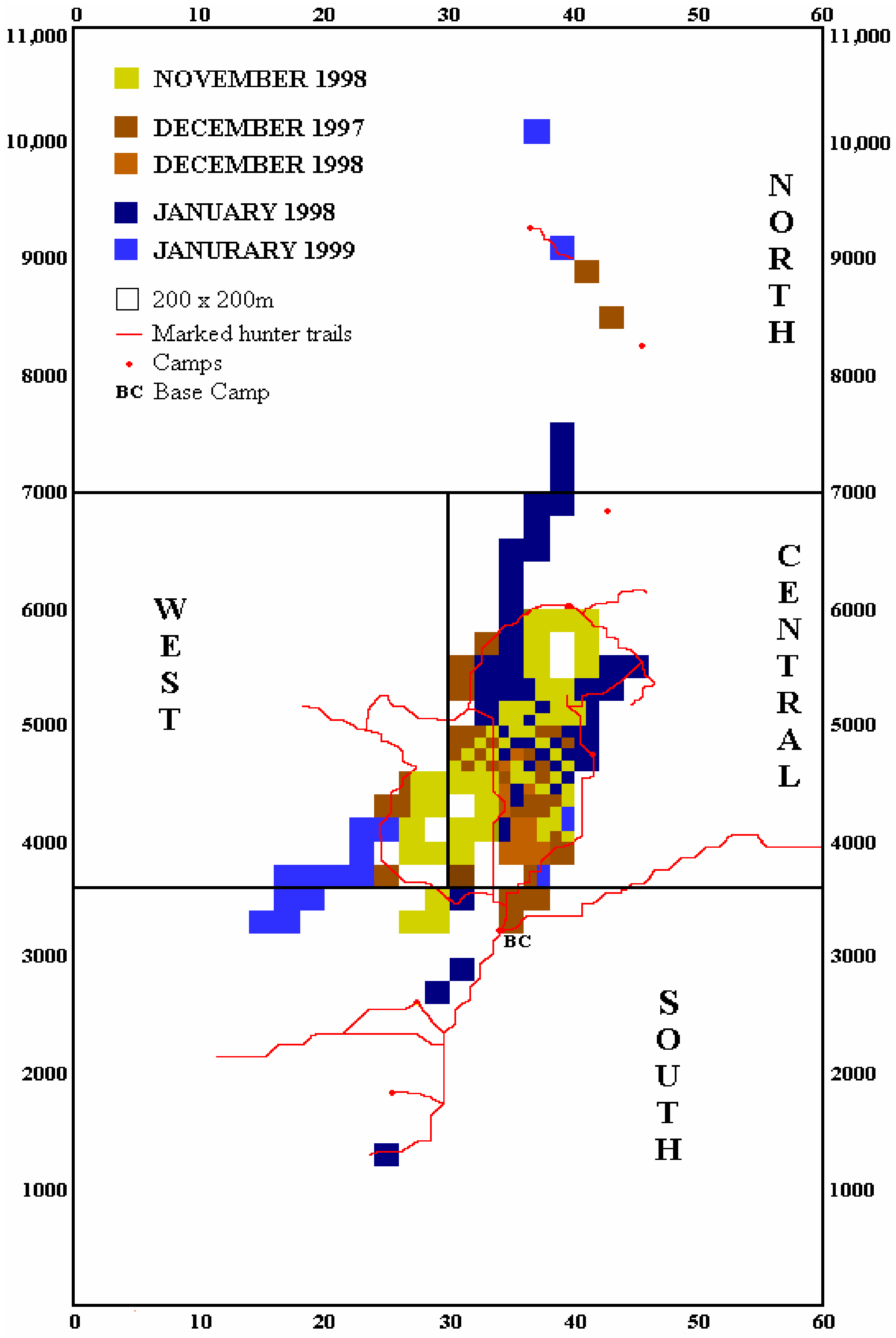


Figure 4.2d Quadrat use by Afi gorillas during the low fruit consumption months of November, December and January

Figures 4.2 a-d show those quadrats the gorillas entered during each month sampled and illustrate the gorillas' general movement pattern between the four main sectors of their range throughout the year. In general, the gorillas moved on a north-south axis, covering a large portion of their range within a 3-month period, except during August – October when the gorillas were not recorded entering the North sector. They tended to remain in one sector for a period of up to several weeks, and then traveled long distances (≥ 3 km) to another sector.

Though sectors are delineated on Figures 4.1 and 4.2 a-d, these maps do not accurately reflect intensity of sector use since the amount of evidence available for each day sampled in the Quadrat Dataset varied across sectors (i.e., number of complete and partial trails, and nest site location only). The majority of trails included in the Quadrat Dataset for the Central sector were partial trails (64.5% of 'Central trails', n = 93 trails) but the greatest number of all trails (59%, n = 158 trails) and complete trails (53.2%, n = 62 complete trails) recorded were located within the Central sector. Partial trails made up half of the trail evidence in the Quadrat Dataset for the South sector (n = 40 trails) and 32.2% of all complete trails recorded were located in the South.

By contrast, only 35% of the data in the Quadrat Dataset for the North sector are partial or complete trails. This is due to the fact that the North, the most rugged of the sectors, is not directly accessible from Base Camp. Consequently, the North sector was searched only when evidence suggested the gorillas entered this sector, though it was thoroughly searched in February – March 1999 during the census (see Chapter 5 for census methods and results). Working in the North required hiking down the mountain and then climbing back up the mountain into the North sector, which required 3 – 4 days of travel from Base Camp to the North sector. By the time we began working in the North, gorilla evidence found was often greater than 4 days old.

Partial trails made up the greatest proportion of trail evidence available for the West sector (80.0% of ‘West trails’ were partial, n = 15 trails) and only 3 complete trails are included in the Quadrat Dataset for the West. This occurred due to the fact that the marked hunter’s trails used when searching for trails in the West and much of the border area between the South and West sectors are located within rocky open forest, making detecting and successfully following trails difficult. In addition, our ability to search the core of the West sector was hampered by the presence of the only ‘career hunter’ on Afi Mountain. This hunter had essentially lived on the mountain within the West sector for more than 10 years and intensively hunted most of this sector and the Central sector to some extent. The hunter threatened to shoot anyone who interfered with his hunting activities. Though his threats did not prevent us from entering the sector all together, it did affect my willingness to search the core of the West unless specific evidence suggested the gorillas entered it, in order to reduce any chance of harm to the staff or myself.

Use of Range Sectors

To determine whether the gorillas utilized their range in a non-random fashion, I examined the frequency with which the gorillas utilized the four sectors within their range throughout the year, on a monthly basis and seasonally in relation to the relative contribution of fruit and non-fruit vegetation in their diet (i.e., low versus high fruit consumption periods). The following results will demonstrate that the Afi gorillas did not use their range randomly. Instead they preferred particular sectors during certain times of the year. How the gorillas' pattern of range use may be related to ecological factors such as temporal and spatial variation in food availability and presence of predators (i.e., humans) is addressed in the next section.

Comparison of the two sector datasets

Pearson correlations were performed to compare frequency of sector use based on known locations ($n = 240$ days) compared to known and estimated locations ($n = 353$ days) of gorillas within one or more sectors for each day sampled. Overall frequencies of sector use calculated separately from each Sector Dataset were positively and significantly correlated ($r = 0.997$, $p = 0.003$). Comparing frequencies of sector use for each month separately, results for most months were also positively and significantly correlated (February – May and July – November: $r = 0.972 – 0.999$, $p \leq 0.028$). Whereas frequencies for June were highly and positively correlated, they were not significant ($r = 0.935$, $p = 0.065$) and this is likely to be the result of the underestimation of the gorillas' utilization of the West based on known locations only and was related to the factors hampering access to this sector described in the previous section.

Frequency of sector use based on known locations compared to known and estimated locations for January and December were the least correlated of the months sampled ($r = 0.762$ and 0.867, respectively, $p \geq 0.133$). This arose from the fact that the gorillas' use of the North during these months was greatly underestimated when using known locations only. Because of the Christmas and New Year holidays demanded by local employees, fieldwork was suspended from December 19 to January 6 both in 1998 and 1999. Much evidence, however, suggests that the gorillas spent most of this time in the North sector. When field-work resumed in January 1998, trails and nest sites ≥ 14 days old were discovered indicating that the gorillas had traveled through the Central sector and entered the North; no new evidence was found in the South and West. On January 13, a 1-day old trail was discovered leaving the North and entering the Central sector. In February 1999 when the North sector was thoroughly searched during the census, nest sites 1 – 2 months old were seen confirming the gorillas' presence in the North at the end of December 1998 and beginning of January 1999.

To summarize, the majority of the results from the two Sector Datasets are highly and significantly correlated but results based on known locations only underestimates the use of West and North sectors during three of the months sampled. Therefore, only results based on the larger data set ($n = 353$ days), including known and estimated locations of the gorillas within the four sectors, are presented.

Overall utilization of four different sectors

Figure 4.3 shows the frequency with which the gorillas utilized the four different range sectors based on known and estimated locations of gorillas within sectors ($n = 353$ days). The gorillas utilized the Central sector with a significantly greater frequency and the South, West, and North sectors significantly less frequently than expected if each sector was used equally (i.e., expected frequency = 25% per sector and is shown as a solid line in Figure 4.3) ($X^2 = 93.7$, $p < 0.001$, $df = 3$). The gorillas used the South, West, and North sectors at relatively equal frequencies, which differs from the impression given in Figure 4.1 that is based on quadrat data.

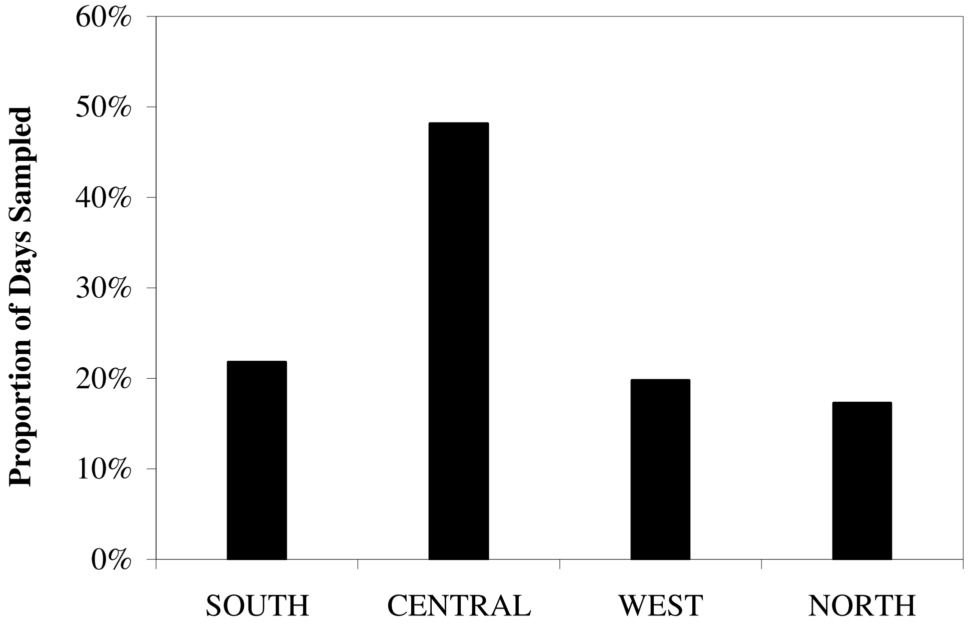


Figure 4.3 Overall frequency with which gorillas utilized four different sectors of their range based the gorillas' known and estimated locations within sectors (n = 353 days)

Based on the number and length of visits to different sectors (i.e., number of consecutive days the gorillas remained in a sector), the gorillas utilized each sector in a different manner. Figure 4.4 shows the percentage of visits per sector in which the gorillas remained for 1 – 3 days, 4 – 7 days and greater than a week, and the average length of visits to each of the four sectors. The Central sector was the most frequently visited sector (n = 23 visits) and on average the gorillas remained there for a week (mean = 7.4, SD = 6.4, range = 1 – 23 days) before entering another sector. The West was the second most frequently visited sector (n = 18 visits); however, the gorillas' visits to the West were on average shorter than visits to other sectors (mean = 4.0 days, SD = 9.3,

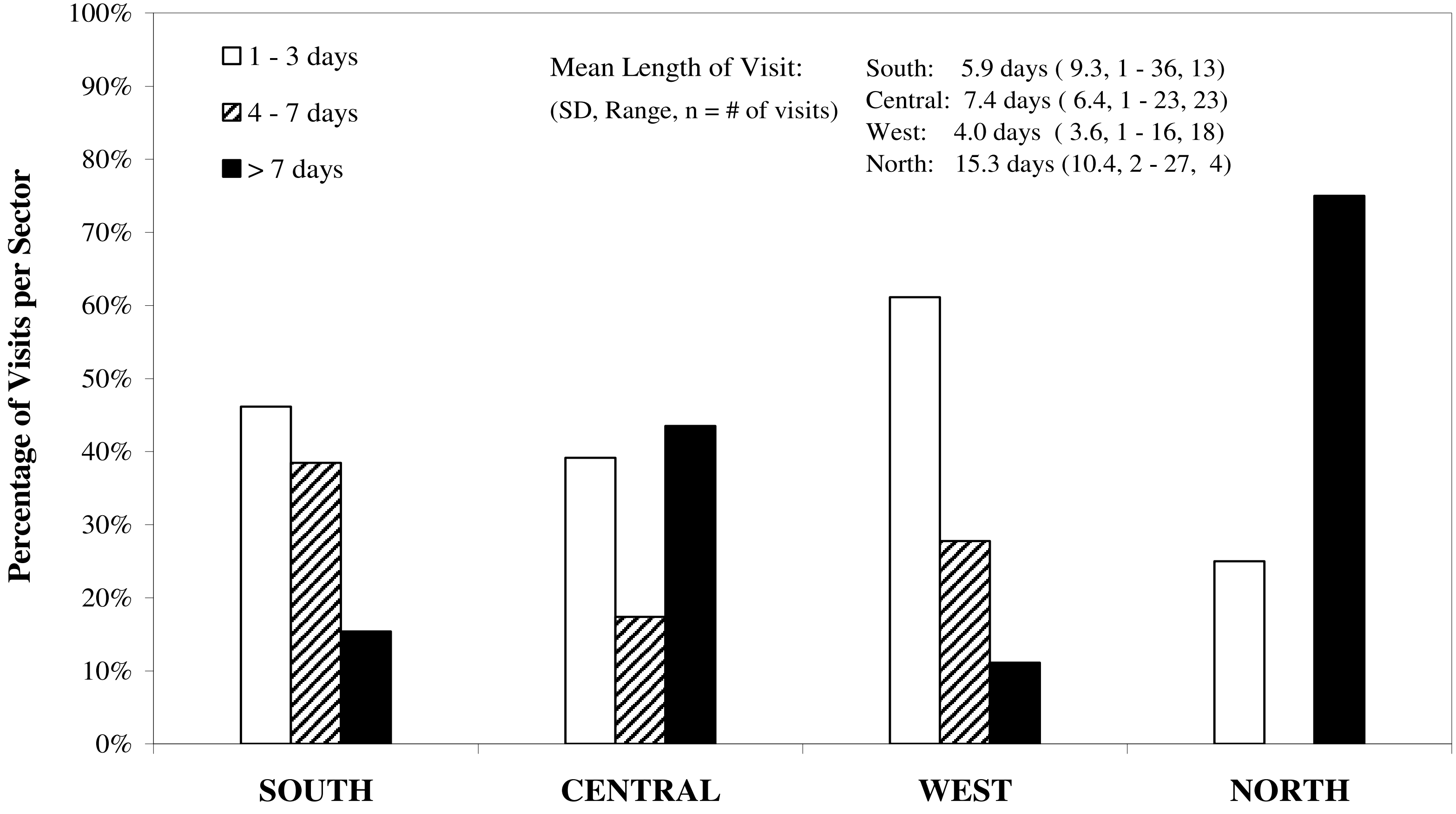


Figure 4.4 Variation in the length of visits to four different sectors

range = 1 – 16 days). When the gorillas entered the West, they tended to only travel through and rarely remained there for longer than a week.

Visits to the South followed a similar pattern to that of the West, though visits to the South tended to be longer (mean = 5.9 days, SD = 6.4, range = 1 – 36 days, n = 13 visits) and the gorillas remained in the South for the longest period recorded (36 days). The North was the least frequently visited sector (n = 4 visits) but when the gorillas did enter the North they most often remained for two or more weeks (mean = 15.3 days, SD = 10.4, range = 2 – 27 days).

Monthly variation in frequency of sector use

Table 4.1 shows the frequency with which the gorillas utilized the four different sectors per month based on their known and estimated locations (n = 353 days). Not all sectors were searched by the research team each month. The South was not searched during May 1998 and the North was not searched during six months (April and July – November 1998). The borders of the South and North sectors were searched during these months and no evidence was found to suggest that the gorillas entered these sectors. Consequently, it was assumed that the gorillas did not utilize the South and North sectors during these months. Central and West sectors were searched during all months sampled.

The gorillas entered between two and four sectors per month but one sector in particular was utilized more frequently than others during each month sampled (Table 4.1). Frequencies of sector use for each month sampled differed significantly from what would be expected if the gorillas had utilized each sector equally (X^2 = 21.2 – 76.8 per month, $p < 0.001$, df = 3). The gorillas entered the Central sector during all but one

Table 4.1 Monthly variation in frequency of sector use by Afi gorillas, including number of days each sector was sampled per month (high fruit consumption months in bold; wet months in italics).

	No. of Days Sampled [1] (n=240)	**No. of Days Sampled** [2] (n=353)	**Frequency of Sector Use** [3] (% of days sampled per month)			
			South	**Central**	**West**	**North**
January 1998 & 1999	20	31	0	48.4	19.4	35.5
February 1998 & 1999	28	28	67.9	32.1	14.3	0
March 1998 & 1999	27	31	0	48.4	6.5	51.6
April 1998 & 1999	25	30	30.0	63.3	20.0	[0]
May 1998	20	31	[0]	67.7	3.2	35.5
June 1998	17	30	0	33.3	16.7	53.3
July 1998	15	31	12.9	77.4	19.4	[0]
August 1998	18	31	83.9	0	19.4	[0]
September 1998	20	30	43.3	46.7	10.0	[0]
October 1998	19	28	17.9	17.9	64.3	[0]
November 1998	12	24		66.7	33.3	[0]
December 1997 & 1998	19	31	3.2	67.7	19.4	22.6

[1] No. of days sampled (n = 240 days): Number of days sampled based on known locations of the gorillas within different sectors.

[2] No. of days sampled (n = 353 days): Number of days sampled based on known and estimated locations of the gorillas within different sectors.

[3] Frequency of Sector Use (% of days sampled per month): Number of days the gorillas entered each sector divided by the total number of days sampled per month (total N = 353 days). Percentages total greater than 100% per month because greater than one sector was entered on 24 of the days sampled. [0] = sector was not searched during that month but there was no evidence to suggest the gorillas entered the sector (see text for details).

month sampled (August), the South during seven months, and the North during five months. The Central sector was utilized more frequently than other sectors during seven months (January, April, May, July, September, November, and December), the South during two months (February and August), and the North during two months (March and June). Though the gorillas entered the West during all 12 months sampled, they utilized the West more frequently than other sectors during only one month of the year, October.

Seasonal variation in frequency of sector use

Figure 4.5 presents variation in frequency of sector use during periods of low and high fruit consumption. During the low fruit consumption period (August – January), the gorillas utilized the Central sector significantly more frequently and the North significantly less frequently than expected ($X^2 = 42.2$, $p < 0.001$); the South and West sectors were essentially used as expected (Figure 4.5a). In the high fruit consumption period (February – July), the Central sector was also utilized significantly more frequently than expected, the South and West were used significantly less than expected, and the gorillas used the North as frequently as expected ($X^2 = 97.7$, $p < 0.001$; Figure 4.5b). When examining differences between low and high fruit periods within each sector separately (Figure 4.5c), the South and West sectors were used significantly more frequently during the low fruit consumption period compared to the period of high fruit consumption ($X^2 = 4.4$, $p = 0.036$ and $X^2 = 16.5$, $p < 0.001$, respectively, df = 1). By contrast, the gorillas utilized the Central and North sectors significantly more frequently during the high fruit consumption period ($X^2 = 9.2$, $p = 0.002$ and $X^2 = 20.3$, $p < 0.001$, respectively, df = 1).

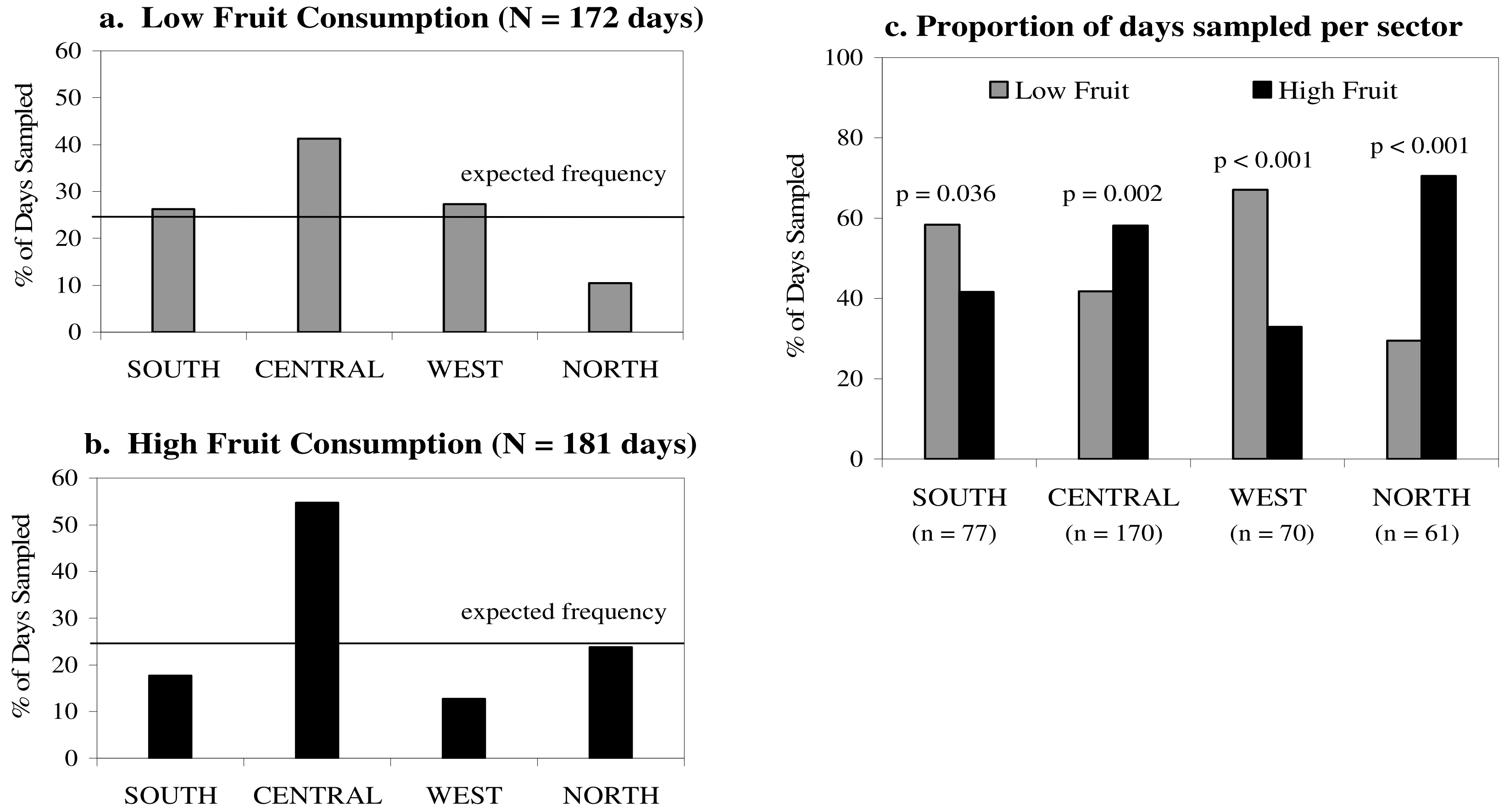


Figure 4.5 Frequency of sector use by Afi gorillas during the (a) low and (b) high fruit consumption periods and (c) differences between frequency of use for each sector separately

Since particular herb and tree foods were consumed exclusively or more frequently during the dry or wet months within the low fruit consumption period (Chapter 3), I also investigated variation in frequency of sector use between these months (November – January versus August – October; Figure 4.6). During dry months within the low fruit consumption period, the gorillas utilized the Central sector significantly more frequently and the South significantly less frequently than expected ($X^2 = 81.9$, $p < 0.001$); the West and North sectors were essentially used as expected (Figure 4.6a). In wet months within the low fruit consumption period, the South sector was utilized significantly more frequently than expected, the North sector was used significantly less than expected, and the gorillas used Central and West sectors as frequently as expected ($X^2 = 59.8$, $p < 0.001$; Figure 4.6b).

When examining differences between these dry and wet months within the low fruit consumption period for each sector separately (Figure 4.5c), the Central and North sectors were used significantly more frequently during dry months compared to wet months within the low fruit consumption period ($X^2 = 28.8$ and 21.1, respectively, $p < 0.001$). By contrast the gorillas utilized the South significantly more frequently during wet months within the low fruit consumption period ($X^2 = 53.0$, $p < 0.001$). Though the West was utilized more frequently during wet compared to dry months within the low fruit consumption period, this difference was not statistically significant ($X^2 = 1.0$, $p = 0.312$).

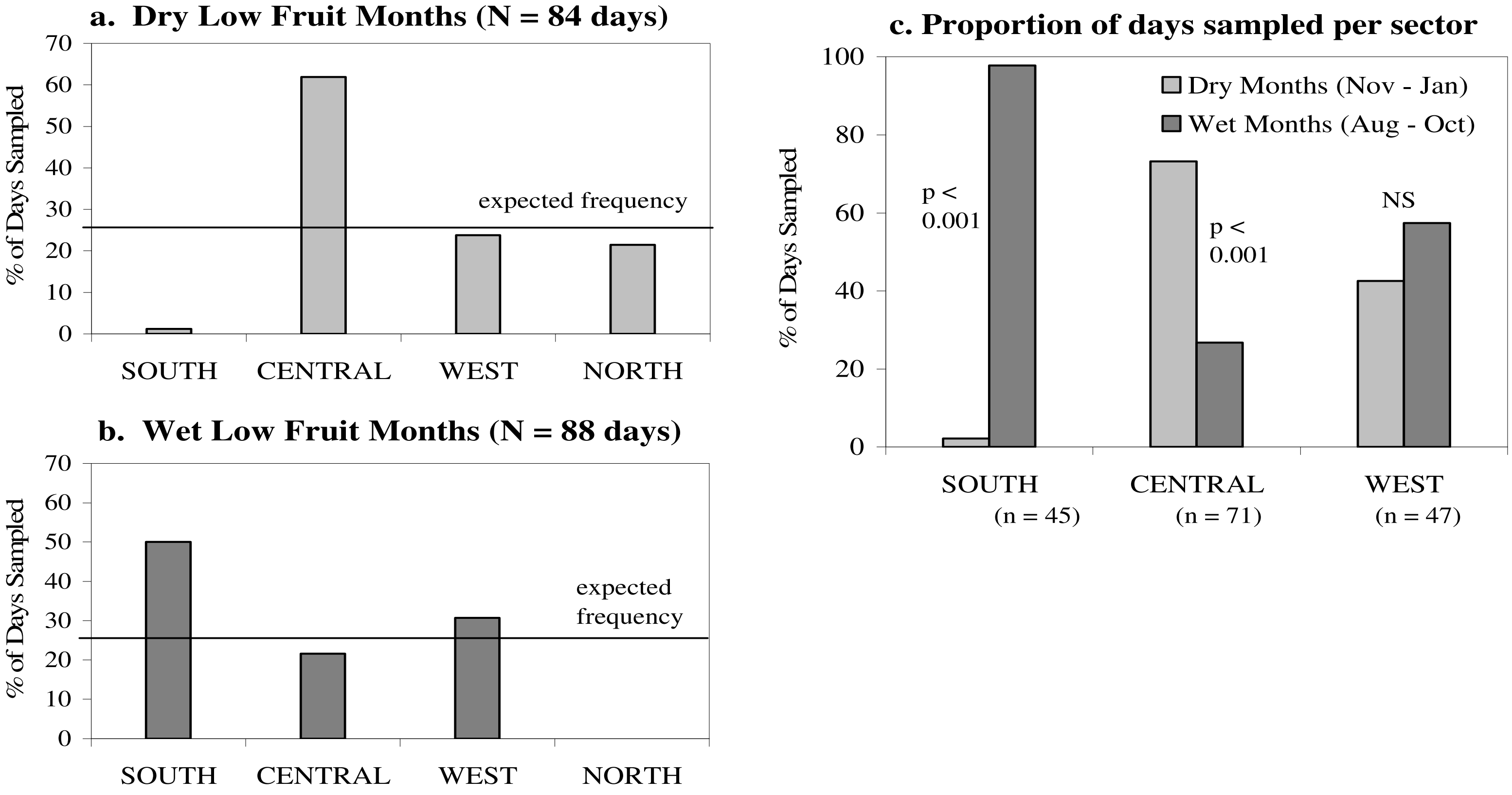


Figure 4.6 Frequency of sector use by Afi gorillas during the (a) dry months of November - January and (b) wet months of August - October within the period of low fruit consumption, and (c) differences between frequency of use for each sector separately

Relationship Between Ranging And Ecological Factors

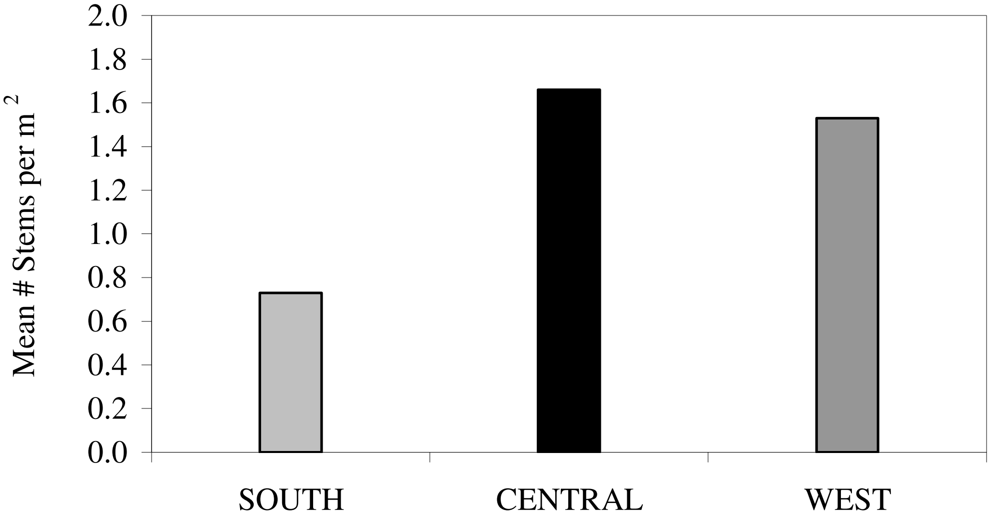
Herb availability and consumption, and range use

Figure 4.7a shows variation in overall herb stem density across the three sectors sampled (South, Central and West). Herb densities were highest in the Central and West sectors, lowest in the South, and differed significantly among all three sectors (Kruskal Wallis: $X^2 = 1444.1$, $p < 0.001$, df = 2; all pair-wise comparison $p < 0.05$). The high overall herb density in the Central sector may be one factor explaining the gorillas' preference for this sector during most times of the year.

Herb stem density and consumption

The frequency of herb consumption by the gorillas throughout the year and during the period of low fruit consumption differed significantly from the expectation that they consumed herb stems at equal frequencies in all three sectors ($X^2 = 8.0$ and 14.1, respectively, $p \leq 0.018$, df = 2; Figure 4.7b). During all months and the low fruit consumption period separately (August – January), frequency of herb consumption was highest in the Central sector, intermediate in the South and lowest in the West and was not significantly correlated with variation in herb stem density across sectors (all months: $r = 0.417$, $p = 0.45$; low fruit consumption period: $r = 0.181$, $p = 0.884$). Whereas both herb density and consumption were highest in the Central sector, Afi gorillas consumed herbs more frequently in the South and less frequently in the West than predicted by herb stem densities in these sectors.

a. Overall mean stem density of nine important herb



b. Herb Consumption

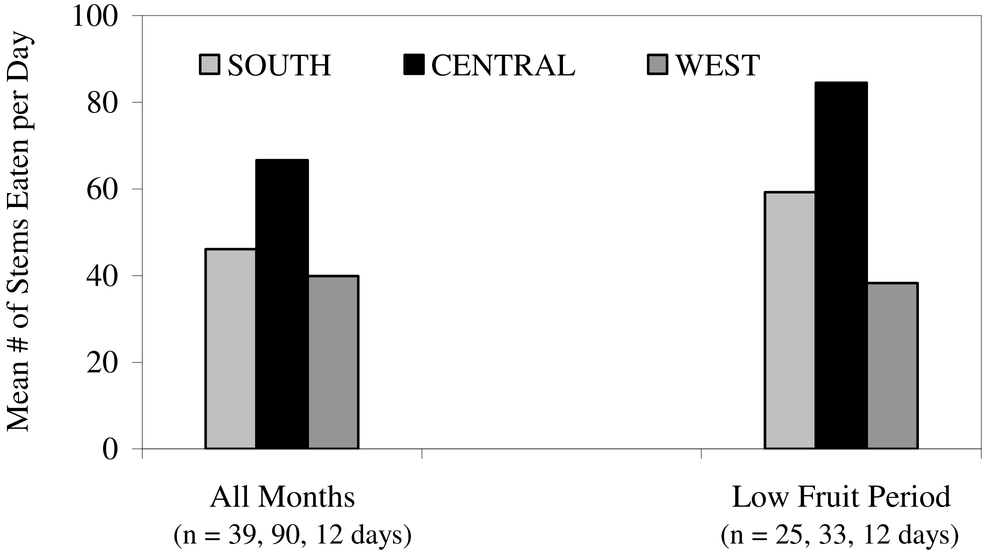
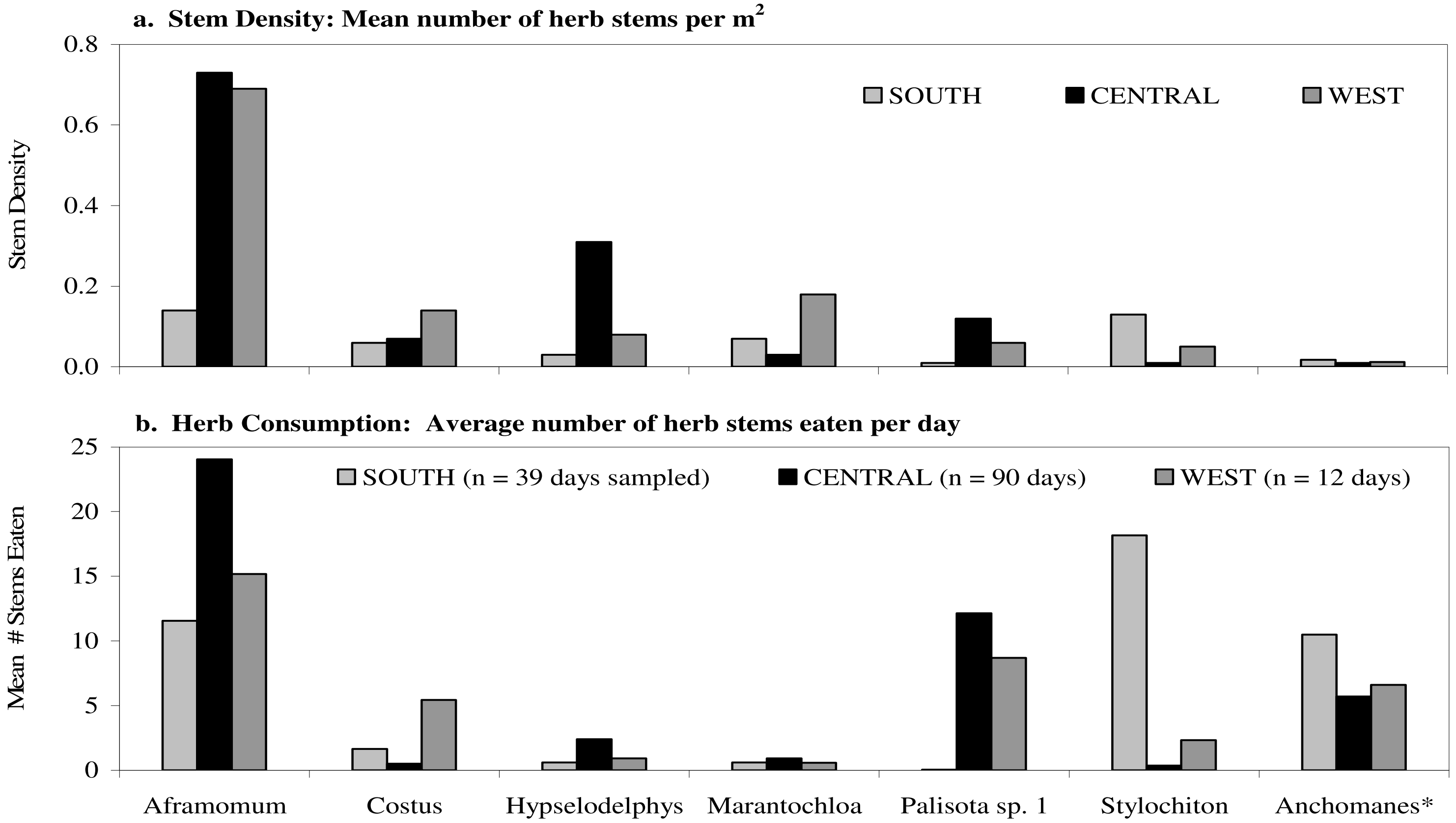


Figure 4.7 Variation across sectors in (a) overall herb stem density in the environment and (b) consumption of herbs by gorillas throughout the year ('all months') and during low fruit consumption months ('low fruit period')

Figure 4.8 examines variation in stem density of different herbs and their consumption by gorillas across sectors. Densities for all but two herbs (*Palisota* sp. 2 and *Thaumatococcus*/*Megaphrynium* spp.) differed significantly among the three sectors (Kruskal-Wallis: $X^2 = 6.6 – 1509.3$, $p = 0.038$ to < 0.001, df = 2, $\alpha = 0.001$; Figure 4.8a). Consumption of all seven herbs differed significantly from expected based on the assumption that stems of these herbs were eaten with equal frequencies in all three sectors ($X^2 = 233.1 – 7.7$, $p = 0.021$ to < 0.001, df = 2; Figure 4.8b). For all but one of the herbs, consumption was highest in the sector where that herb had the highest stem density, resulting in relatively high and positive correlations (*Aframomum* spp.: $r = 0.765$, $p = 0.446$; *Costus* spp., *Hypselodelphys scandens, Palisota* sp. 1, and *Stylochiton* sp.: $r = 0.913 – 0.968$, $p = 0.267 – 0.16$; *Marantochloa* spp.: $r = -0.706$, $p = 0.267$).

Anchomanes difformis density was estimated based on frequency with which it was eaten along feeding trails rather than enumeration; hence density and consumption were inevitably correlated. Since *Anchomanes* tends to occur in forest habitats and the South has a significantly greater proportion of forest cover than Central and West sectors (see Chapter 2, Table 2.3), it is not surprising that estimated *Anchomanes* density was greater in the South than in Central and West sectors.

The above results strongly suggest that variation in density of different herbs across sectors influenced the relative contribution of these herbs to the gorillas' diet. Furthermore, the fact that the relationship between density and consumption of most of the different herb foods ($r = 0.765 – 0.968$) was stronger than that between overall stem density and consumption ($r = 0.417$) suggests that frequency of sector use may reflect preferences for particular herb foods. Alternatively, the gorillas may prefer certain



a. Stem Density: Mean number of herb stems per m^2

b. Herb Consumption: Average number of herb stems eaten per day

Figure 4.8 Variation across three sectors in (a) herb stem density in the environment and (b) consumption by gorillas for each herb food genus separately

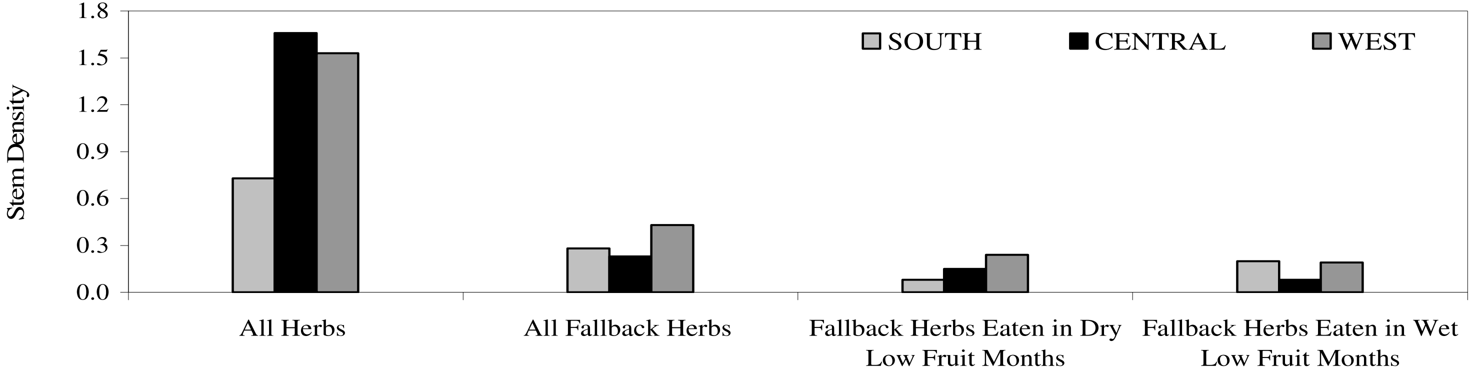
(* *Anchomanes* stem density estimated based on feeding site encounter rates along trails) sectors for reasons other than herb availability so that variation in consumption of different herbs across sectors reflects the frequency with which the gorillas encountered them.

Herb stem density and frequency of sector use

Figure 4.9 compares herb stem density of different herb foods pooled with the gorillas' frequency of sector use (percentage of total days sampled, $n = 353$ days) throughout the year sampled and during the low fruit consumption period (August – January) when these foods were more common in the gorillas' diet. Correlations between density of all herb species and frequency of use throughout the year and during the low fruit season were moderately positive ($r = 0.556$, $p = 0.624$, and $r = 0.658$, $p = 0.543$, respectively). Density of all herb species pooled and frequency of sector use were both highest for the Central sector; however, the gorillas utilized the South and West sectors relatively equally even though herb density in the West was more than twice that of the South.

Stem density of all fallback herb species (*Costus* spp., *Marantochloa* spp., *Palisota* sp. 1, and *Stylochiton* sp.) was significantly greater in the West than in South and Central sectors (Kruskal-Wallis: $X^2 = 122.5$, $p < 0.001$, df = 2; pair-wise comparisons: West vs. South and Central, $p < 0.05$, South vs. Central, $p > 0.05$; Figure 4.9a). During the low fruit consumption period, the gorillas utilized the Central and South sectors more frequently and the West less frequently than expected based on the density of fallback herb species, resulting in a moderate negative correlation between density and frequency of sector use ($r = -0.645$, $p = 0.554$).

a. Stem Density: Mean number of herb stems per m^2 (see text for which species were pooled)



b. Frequency of Use: Percentage of sample days gorillas utilized each area (n = 353 days)

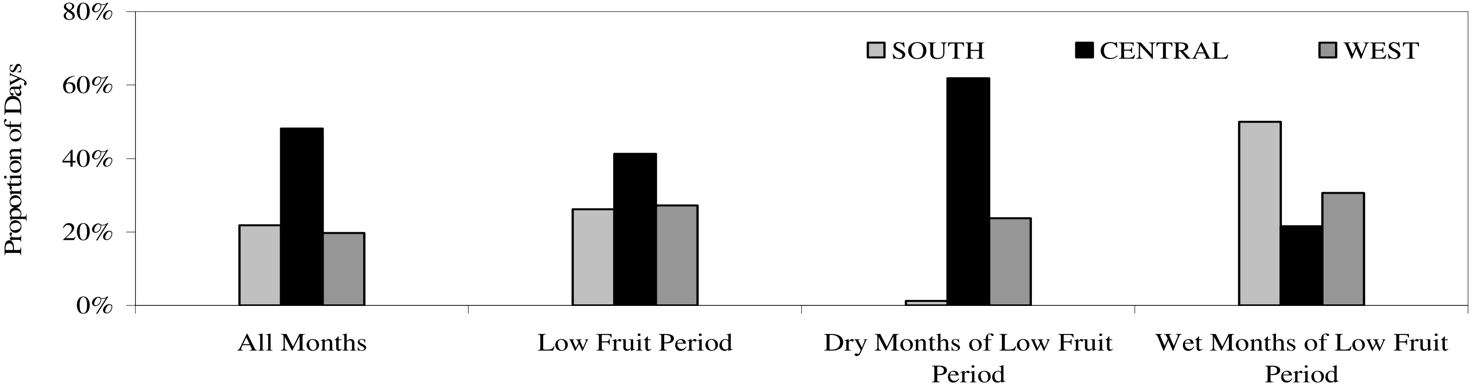


Figure 4.9 Comparison of (a) stem densities of different gorilla herb foods pooled with (b) frequency of sector use throughout the year ('all months') and during the low fruit consumption period

Stem density of those fallback herb species eaten more frequently during dry months of the low fruit consumption period (*Palisota* sp. 1 and *Marantochloa*; November – January) was lowest in the South, intermediate in the Central and highest in the West, and differed significantly among all three sectors (Kruskal-Wallis: $X^2 = 100.5$, $p < 0.001$, df = 2; Figure 4.9a). The gorillas utilized the Central sector much more frequently than predicted by the density of these fallback herbs, resulting in a weak positive correlation between density and frequency of sector use during dry months within the low fruit consumption period ($r = 0.30$, $p = 0.806$). Frequency of sector use during these months was, however, highly and positively correlated with density of *Palisota* sp. 1 stems ($r = 0.996$, $p = 0.06$) and was negatively correlated with *Marantochloa* stem density ($r = -0.396$, $p = 0.741$).

Stem density of those fallback herb species eaten more frequently during wet months of the low fruit consumption period (i.e., *Costus* and *Stylochiton*; August – October) was significantly greater in South and West sectors than in the Central sector (Kruskal-Wallis: $X^2 = 106.1$, $p < 0.001$, df = 2; pair-wise comparisons: Central vs. South and West, $p < 0.05$, South vs. West, $p > 0.05$; Figure 4.9a). Frequency of sector use during this time was moderately high and positively correlated with density of these fallback herbs ($r = .794$, $p = 0.806$); but, was positively and significantly correlated with *Stylochiton* stem density ($r = 1.0$, $p = 0.009$) and *Anchomanes* estimated density ($r = 0.997$, $p = 0.049$).

To summarize, the frequency with which the gorillas utilized South, Central, and West sectors did not strictly correlate with variation in herb stem density across sectors. The gorillas did utilize the Central sector as frequently as predicted by this sectors’ overall high availability of herbs. The Central sector, however, was utilized more frequently during the low fruit consumption period than predicted by the density of fallback herbs. The gorillas utilized the South sector much more frequently, particularly during the wet months of the low fruit consumption period, than predicted by its low herb availability. The gorillas utilized the West sector much less frequently than predicted by this sector's relatively high overall and fallback herb densities. The greater than expected use of the Central and South sectors during the low fruit consumption period may indicate that the gorillas preferred particular herbs during this time that were more abundantly available in these two sectors (*Palisota* sp. 1 in the Central sector during dry months, and *Stylochiton* and/or *Anchomanes* in the South during wet months within this period). This does not, however, fully explain the gorillas' apparent deliberate avoidance of the West despite its relatively high herb food availability.

Tree food availability and range use

The density of all important tree food species pooled was significantly greater in the Central sector (mean = 2.3 trees per 250m^2 quadrat, SD = 1.9, range = 0 – 9) than in the South (mean = 1.5 trees per 250m^2 quadrat, SD = 1.5, range = 0 – 6; Mann-Whitney U-test: Z = 3.0, p = 0.003). This result suggests that the gorillas preferred to utilize the Central sector more frequently than the South due to its greater availability of tree foods.

Tree fallback species availability and frequency of sector use

Table 4.2 lists the six important tree species that were enumerated whose leaves and bark were important fallback foods, together with information on part eaten, season in which they were eaten most frequently or exclusively, and their mean stem densities and abundance in the gorillas' diet within South and Central sectors [8]. Three fallback species had greater densities in the South than in the Central sector (*Grewia mollis, Morus mesozygia,* and *Pycnanthus angolensis*). *Pterocarpus osun/mildbraedii*, were denser in the Central sector. Two fallback species occurred at relatively equal densities within South and Central sectors (*Milicia excelsa* and *Musanga cecropioides*). All species were consumed more frequently in the sector where they were most dense.

Though density of all fallback tree species pooled was greater in the South, the gorillas utilized the Central sector more frequently during the low fruit consumption period. However, densities of fallback species consumed more frequently or exclusively during dry or wet months within the low fruit consumption period did correspond to frequency of sector use during these months. During the dry months of the low fruit consumption period, frequency of sector use and the density of the one tree fallback species consumed during this time (*Pterocarpus osun/mildbraedii*) were both greater for the Central sector. During the wet months within the low fruit consumption period, the gorillas most frequently used the South where those tree fallback species eaten during these months (*Grewia mollis, Milicia excelsa, Morus mesozygia* and *Pycnanthus angolensis*) occurred at greater densities.

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[8] A species' availability was considered to differ between the sectors if (1) a species was recorded in one sector exclusively or (2) its density in one sector was ≥ 2 times greater than the other sector (see methods for details).

Table 4.2 Characteristics of Afi gorilla important fallback tree leaf and bark foods, including variation in availability across South and Central sectors and abundance in the gorillas' diet when utilizing these two sectors (see legend for definitions and units).

INDIVIDUAL TREE SPECIES	**Part Eaten**	**Season**	**Mean Density**			**Abundance in Diet (% of Feeding Sites)**	
			South	**Central**		**South**	**Central**
Grewia mollis	Bk	W-L	**0.02**	0		100	0
Milicia excelsa	Lvs/Bk	W-L	0.05	0.04		50.7	17.3
Morus mesozygia	Lvs/Bk	W-L	**0.03**	0		92.9	0
Musanga cecropioides	Lvs	L	0.05	0.07		2.7	79.5
Pterocarpus osun/mildbraedii	Bk	D-L	0.03	**0.07**		6.3	81.3
Pycnanthus angolensis	Lvs	W-L	**0.09**	0.02		92.0	8.0
SPECIES POOLED			0.28	0.19		52.4	29.5
Fallback in Dry Months *			0.03	**0.07**		6.3	81.3
Fallback in Wet Months *			**0.19**	0.05		70.9	10.2

Part Eaten: Lvs = leaves, Bk = bark, Lvs/Bk = leaves and bark.
Season: Season in which species were eaten more frequently or exclusively; L = low fruit consumption period (August – January), D-L = dry months within the low fruit period (November – January), W-L = wet months within the low fruit consumption period (August - October)
Mean Density: Mean number of individual trees per $250m^2$ quadrat (Bold indicates highest density, if density of one sector ≥ 2 times greater than the other sector or species recorded in one sector only).
Abundance in Diet: For each species separately, percentage of total number of feeding sites recorded in the South and Central sectors (e.g., Number of feeding sites in which *Grewia* bark was eaten in the South divided by total number of *Grewia* feeding sites x 100).
* Species that were eaten more frequently during dry months or wet months within the low fruit consumption period.

Tree fruit availability and frequency of sector use

Table 4.3 summarizes the availability of 15 of the 16 tree-fruit species determined to be the most important fruit foods in the gorillas' diet during at least one month of the year sampled; unidentified fruit species SD-01 is a tree with a diameter at breast height < 10 cm, consequently it was not enumerated. Table 4.3 shows each species' total mean stem density and its density within South and Central sectors separately, as well as its status in the diet in each month (i.e., most important, important but not most important, or present but not important). Density of all 15 of the most important tree-fruit species pooled was significantly greater in the Central sector (mean = 1.82, SD = 1.95, range = 0 – 10 trees per 250m^2 quadrat) than in the South (mean = 0.78, SD = 1.02, range = 0 – 4 trees per 250m^2 quadrat; Mann-Whitney U Test: $z = 4.2$, $p < 0.001$). Three of the most important tree-fruit species were recorded in the Central sector exclusively and five other species had greater densities this sector. The density of only one of the most important tree-fruit species was greater in the South; it was absent from the Central sector. The remaining six species occurred at relatively equal densities within South and Central sectors.

Densities between the two sectors differed significantly for only three trees: *Sorindeia grandifolia* and *Tabernaemontana pachysiphon*, which were among the four most common tree species on Afi (Chapter 2), and *Trichoscypha* sp. Densities of these species were significantly greater in the Central sector than in the South (Mann-Whitney U Test: $z = 4.1$, 3.0 and 2.6, respectively, $p \leq 0.009$). For species that were recorded in one sector only or their density in one sector was ≥ 2 times greater than the other, differences likely did not reach significant levels due to small sample size.

Table 4.3 Temporal and spatial availability of the 15 most important Afi gorilla tree-fruit foods (high fruit consumption months in bold and wet months in italics; see legend for definitions and units).

INDIVIDUAL TREE SPECIES	**MEAN STEM DENSITY**				**MONTHS PRESENT IN DIET (Feb – Jan)**											
	Total	**South**	**Central**		**F**	**M**	***A***	***M***	***J***	***J***	*A*	*S*	*O*	N	D	J
Chrysophyllum spp. (3)	0.15	0.10	0.23		*	**4**	*									
Dialium guineense	0.01	0	0.02			*	**5**	**4**	x	**5**						
Ficus spp. (4)	0.06	0.07	0.04		**6**	x	*		*	*	x		*		*	2
Garcinia kola	0.01	0	0.02						**3**	*						
Maesopsis eminii	0.02	0.02	0.02			x	**6**	*	*							
Morus mesozygia	0.02	0.03	0		**3**	*										*
Myrianthus arboreus	0.09	0.06	0.14						*	**1**	**1**	**2**	**1**			
Parkia bicolor	0.08	0.09	0.07		*	**1**	**2**									
Pseudospondias microcarpa	0.02	0.01	0.04		**2**	**3**	*	*	x							
Sorindeia grandifolia	0.19	0.06	0.40**				**4**	**1**	*	*						
Tabernaemontana pachysiphon	0.29	0.17	0.49**		**5**	**5**	*									**4**
Treculia africana	0.03	0.03	0.04		*	**6**	**1**	**2**	**2**	**3**	*	*				
Trichoscypha sp.	0.07	0	0.18**			**7**										
Uvariodendron calophyllum	0.09	0.09	0.11							**4**	*					
Vitex spp. (3)	0.05	0.04	0.05								*		**2**	**4**		
SPECIES POOLED	1.17	0.78	1.82**													

Mean Stem Density: Mean number of trees per 250m^2 quadrat (see Chapter 2 for details). Bold indicates highest density (if species present in one sector only or density in one sector ≥ 2 times greater than other), ** = density in Central sector is significantly greater than the South ($p \leq 0.023$). Months Present in Diet: Numbers = importance value rank of most important species during the month (see text for details), x = important but did not meet requirements for most important status, * = present but not important; high fruit consumption months in bold and wet months in italics.

Figure 4.10 shows the estimated mean densities of fruiting trees[9] for the most important tree-fruit species in the South and Central sectors during each of the high fruit consumption months separately and compares them to the gorillas' frequency of sector use during these months (see Table 4.3 for which species were pooled for each month). Frequency of sector use during February did not correspond to estimated densities of trees with fruit in the South and Central sectors; density in the Central was significantly greater (Mann-Whitney U Test: $z = 2.3$, $p = 0.022$), yet the gorillas utilized the South more frequently. The greater estimate of fruiting tree density in the Central sector occurred due to this sectors significantly greater density of *Tabernaemontana pachysiphon*, the fifth most important fruit species in the gorillas diet during February. When this species was removed the analysis, estimated density of fruiting trees was slightly greater in the South than in the Central sector (mean = 0.12 and 0.07 fruit trees per 250m^2 quadrat, respectively).

The second and third most important tree-fruit species eaten in February were *Pseudospondias microcarpa* and *Morus mesozygia*, which were present in greater than 97% of fecal samples during 100% of days sampled in this month (see Table 4.3 and Appendix III). *Pseudospondias* densities in the South and Central sectors were relatively equal, but *Morus* was only present in the South. Thus, the greater availability of *Morus* fruit in the South may explain why the gorillas utilized the South more frequently in February than predicted by estimated fruiting tree densities of all most important tree-fruit species consumed in this month.

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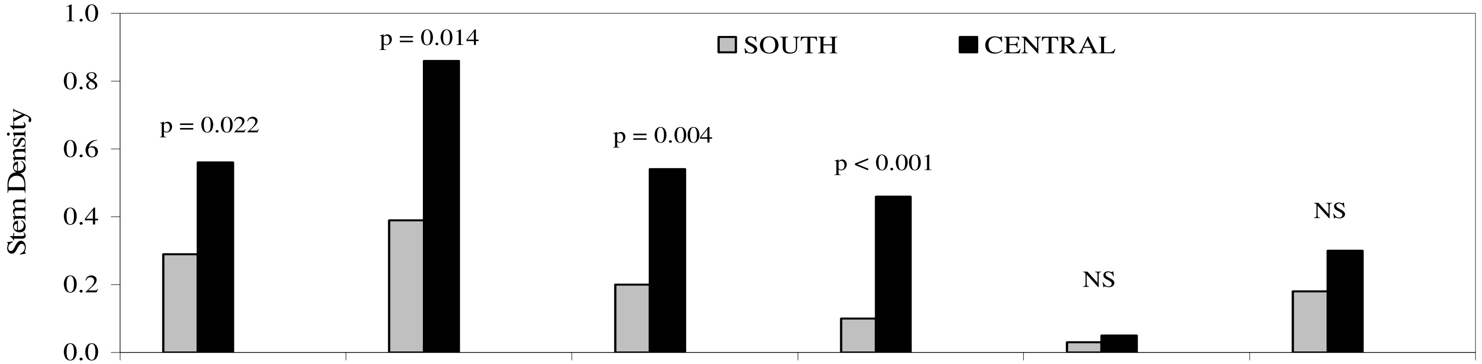
[9] Densities of fruiting trees were estimated by summing the densities of most important tree-fruit species consumed by the gorillas in each month and do not represent actual densities of fruiting trees (see methods for details).

a. Estimated mean density of fruiting trees per 250m^2 quadrat per month (see text for details)



b. Frequency of Sector Use: Percentage of days gorillas utilized different sectors per month

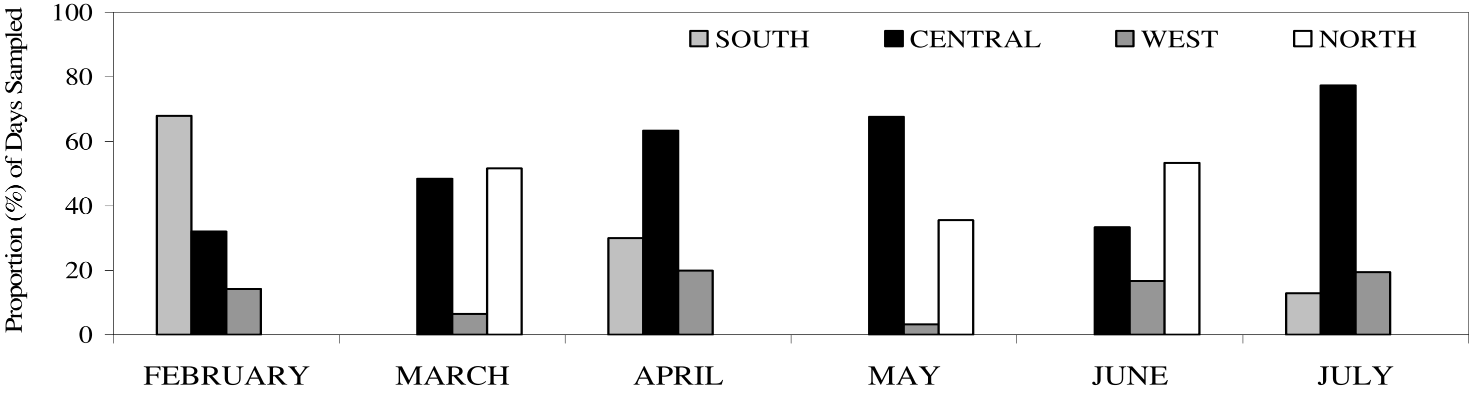


Figure 4.10 (a) Estimated density of fruiting trees for the most important gorilla tree-fruit species eaten per month during high fruit consumption months compared to (b) frequency of gorilla sector use

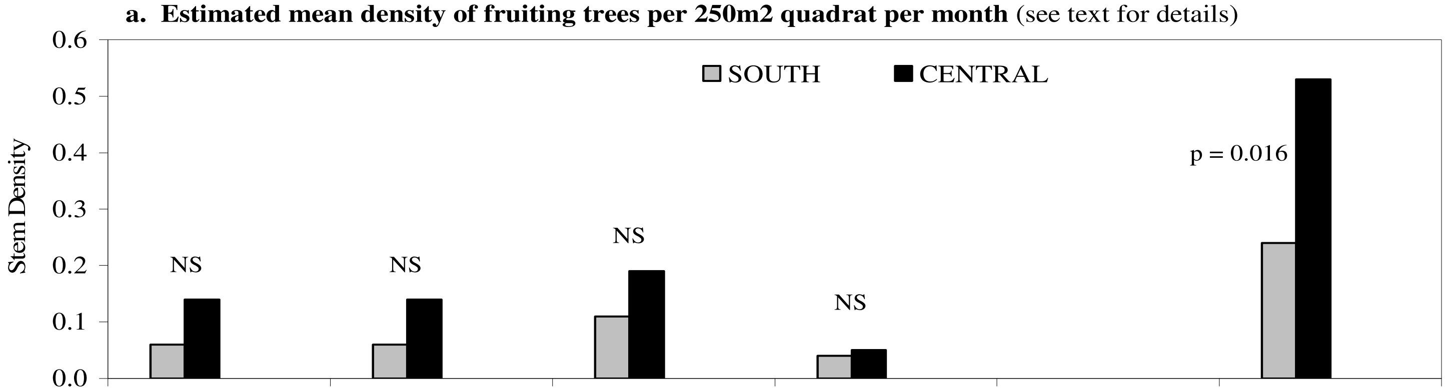
The greater estimated density of fruiting trees in the Central sector during March also occurred largely due to higher densities of *Tabernaemontana pachysiphon*, as well as *Trichoscypha* sp., in the Central sector (see Table 4.3). When these two species were removed from the analysis, however, density in the Central sector was still approximately two times greater than the South (mean = 0.42 versus 0.22 trees per $250m^2$ quadrat). As expected based on the estimated density of fruiting trees, the gorillas utilized the Central sector more frequently than the South during March. The gorillas, however, used the North slightly more frequently than the Central sector. The two most abundant seed species found in fecal samples collected in the North during March were *Tabernaemontana* and *Trichoscypha*. This suggests that the density of fruiting trees for the most important tree-fruit species in the North was likely similar to that of the Central sector during March.

During April and May, estimated densities of fruiting trees were significantly greater in the Central sector than in the South (Mann-Whitney U Test: $z = 2.3 – 3.9$, $p \leq 0.022$). *Sorindeia grandifolia* was the most important fruit species eaten during May and although it was the fourth most important fruit species eaten during April, the significantly greater availability of *Sorindeia* fruit in the Central sector likely explains why the gorillas preferred the Central sector during these two months. When *Sorindeia* was removed from the analysis for April and May, estimated densities of fruiting trees in the South and Central sectors were equal (mean = 0.14 trees per $250m^2$ quadrat).

Estimated densities of fruiting trees were lowest in the South and Central sectors during June and the gorillas utilized the North most frequently during this month. The gorillas likely preferred the North due to the availability of *Garcinia kola* fruit, which is available only during June. Because local village residents eat the seeds of this species, known locally as bitter kola, field assistants often made a point of indicating its presence when encountered. Consequently, the locations of most *Garcinia kola* trees are known. Whereas no trees were encountered in the South and only a few in the Central sector during the entire study, five *Garcinia kola* trees were encountered along gorilla feeding trails within the first two days spent searching the North during June.

Though the availability of the most important tree fruits did not differ significantly between the South and Central sectors during July, the gorillas' clear preference for the Central sector during this month is likely related to fruit availability. *Myrianthus arboreus* was the most important fruit species consumed in July; its seeds were present in 96% of fecal samples during 100% of days sampled in July (see Appendix III). *Myrianthus* was more than two times denser in the Central sector than in the South (mean = 0.14 and 0.06 trees per 250m^2 quadrat, respectively; Table 4.3).

Figure 4.11 shows the densities of fruiting trees for most important tree-fruit species in the South and Central sectors during low fruit consumption months separately and compares them to the gorillas' frequency of sector use during these months (see Table 4.3 for which species were pooled for each month). Availability of tree fruit may have influenced the gorillas' frequency of sector use during two of these months (January and October). During January when the gorillas utilized the Central sector most frequently, the estimated density of fruiting trees was significantly greater in the Central sector than in the South (*Tabernaemontana pachysiphon* and *Ficus* spp.; Mann-Whitney U: $z = 2.4$, $p = 0.016$). October was the only month the gorillas utilized the West more frequently than any other sector. Phenology records show that availability of tree-fruit



a. Estimated mean density of fruiting trees per 250m2 quadrat per month (see text for details)

b. Frequency of Sector Use: Percentage of days gorillas utilized different sectors per month

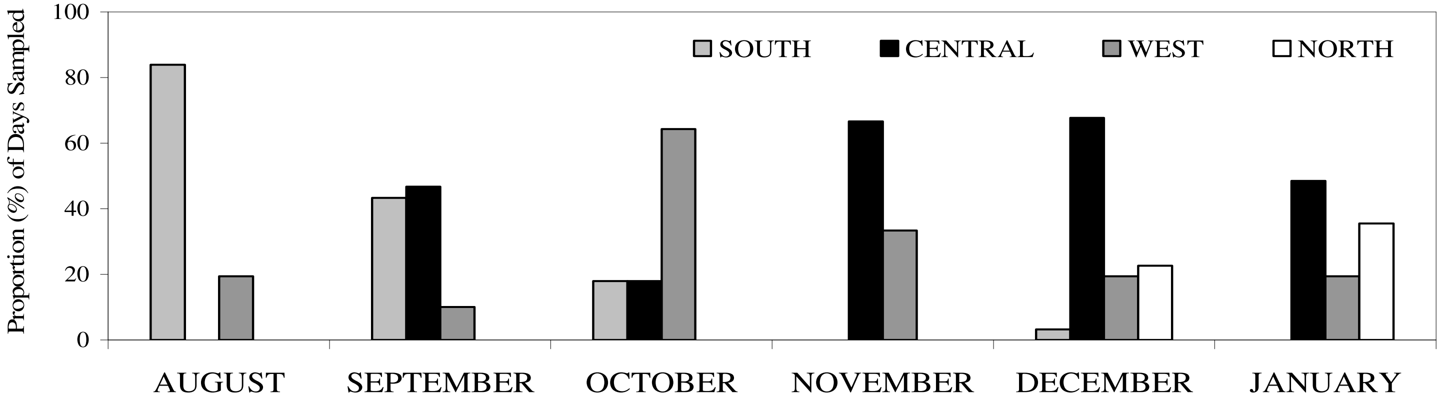


Figure 4.11 (a) Estimated density of fruiting trees for the most important gorilla tree-fruit species eaten per month during low fruit consumption months compared to (b) frequency of gorilla sector use

species consumed by gorillas during October was lowest in the South and Central sectors (see Figure 2.19). Seeds of a *Vitex* species were found in 47% of fecal samples collected and five fruiting *Vitex* trees were recorded along feeding trails followed in the West during October.

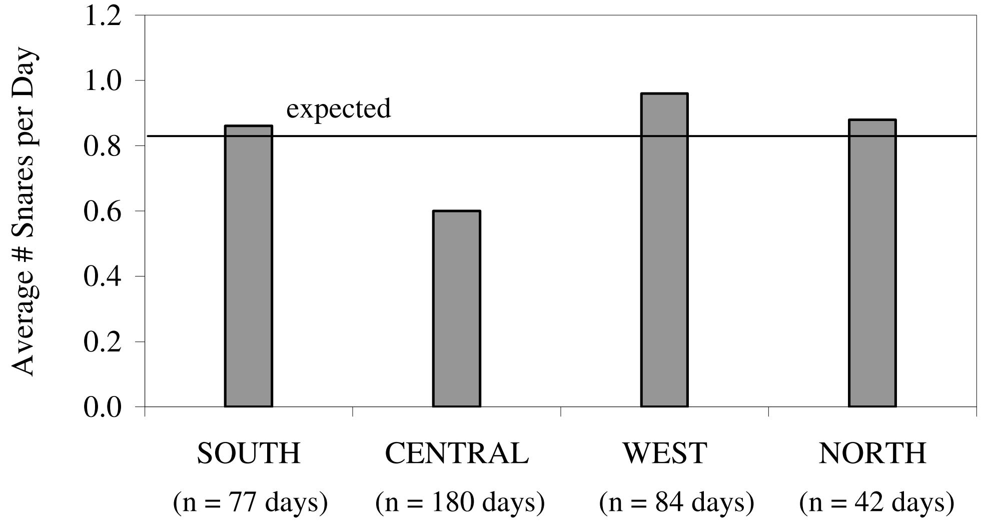
It is unlikely that fruit availability influenced the gorillas' pattern of range use during the other low fruit consumption months. Estimated density of fruiting trees for the one most important tree-fruit species eaten in August and September (*Myrianthus arboreus*) was greater in the Central sector, yet the gorillas utilized the South most often during August, and South and Central sectors relatively equally during September. Estimated fruit tree density of the only most important fruit tree species consumed in November (*Vitex* sp.) differed little between sectors. The only important fruit species eaten during December (i.e., unidentified fruit species SD-01) was not enumerated.

Hunting pressure and range use

Variation in hunting pressure across sectors

Between December 1997 and April 1999, a total of 292 wire snares and 91 gunshots were recorded. Figure 4.12 shows variation in snare encounter rates and proportion of total gunshots recorded across the sectors (expected values are means of averages per sector). Snares were encountered significantly less frequently in the Central sector and slightly more frequently in the West than expected if snares were encountered at equal frequencies within each of the four sectors ($X^2 = 12.8$, p = 0.002, df = 2). In the South and North sectors, snares were encountered as frequently as expected.

a. SNARE ENCOUNTER RATE: Average number snares encountered in each sector per day



b. GUNSHOTS: Percentage of total gunshots heard

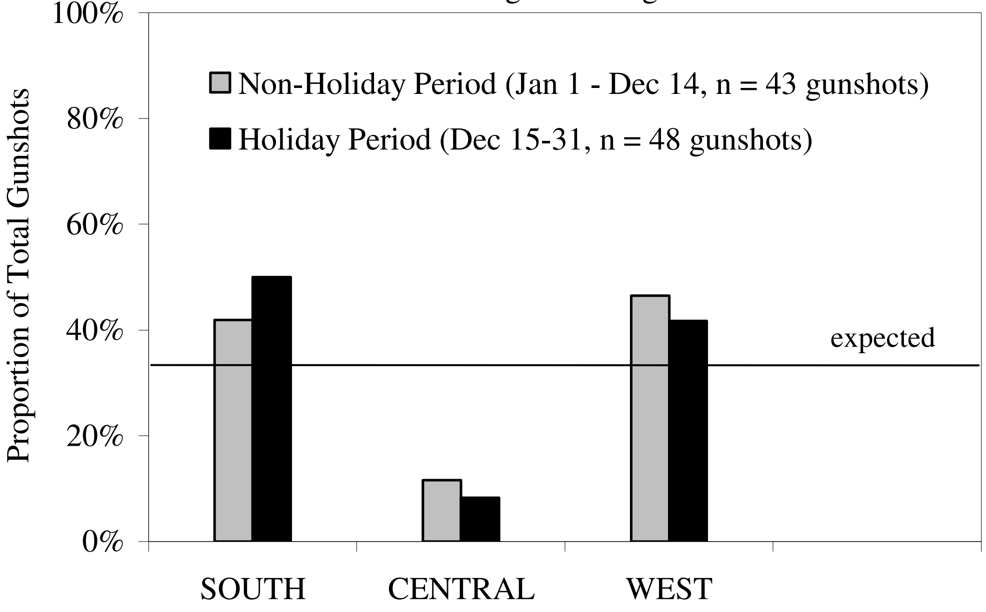


Figure 4.12 Variation in hunting pressure across sectors

More than half of the gunshots heard (53%, n = 48) were recorded during the Christmas and New Year holiday period (December 15 – 31) when bushmeat is an important part of village celebrations. During both the non-holiday and holiday periods, gunshots occurred significantly more frequently in the South and West sectors and significantly less frequently in the Central sector than expected if gunshots occurred at equal frequencies within each of these sectors ($X^2 = 32.1$, $p < 0.001$, df = 2). The fact that no gunshots were heard in the North sector during the present study does not indicate that hunters do not use guns when hunting in this sector; shots fired in the North could not be heard from Base Camp and this sector was not searched regularly (also see below).

Hunting pressure varied across sectors due to several factors, including hunters' ability to access different sectors. Figure 4.13 shows the location of villages in relation to the study site and major rocky peaks (peaks with altitudes ≥ 700m). Because of the South's relatively less complex topography, lower altitudes and the close proximity of villages, hunters can easily enter the South, complete their hunting activities and return to their village within one day. Up to eight young men from the Boje villages hunted throughout the South, mostly using snares and often working as a group. A few older more experienced hunters, who tend to use shotguns more often than less experienced young hunters, intermittently hunted the South during the study.

Based on hunting evidence recorded during the study, hunting pressure in the South and West sectors appeared to be relatively equal. However, hunting pressure was likely higher in the West due to the presence of the only 'career' hunter on Afi Mountain. This hunter from Irruan was responsible for all hunting activity in the West where he lived in various caves and camps from the mid-1980s through October 1998 (except

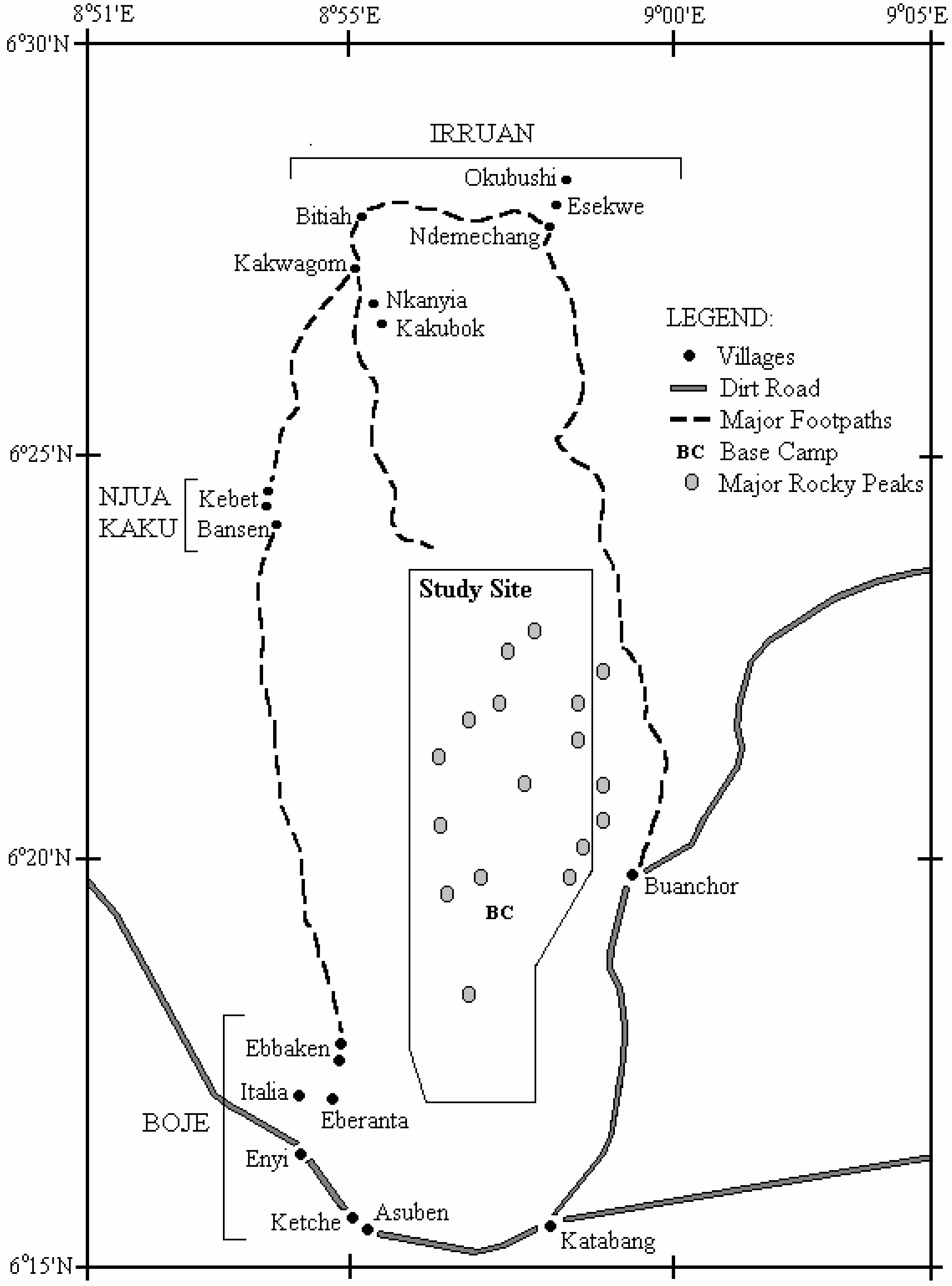


Figure 4.13 Location of villages in relation to the Afi Mountain study site and major rocky peaks (altitudes ≥ 700 m).

during approximately 3 years in the mid-1990s when attempts to provide him with alternative employment were made). Assistants periodically brought food and other supplies to the hunter and transported his catch to Irruan, allowing the hunter to reside and hunt on the mountain continuously. The hunter shot at least two gorillas in the late 1990s. An almost complete adult female gorilla skeleton with a gunshot hole in the scapula and lead shot embedded in several vertebrae and one femur was found in the West in May 1998 (the female likely survived the assault and the hunter was not able to recover the carcass). On October 27 1998, the hunter killed an adult male gorilla. While following a fresh gorilla trail the following day, the research team discovered where the killing occurred, followed the hunter's trail to a cave known to be used by this hunter, and recovered the burnt head, hand, and foot of the gorilla. With the aid of the research team, CRS Department of Forest Development and the police, the hunter was arrested and imprisoned.

Other hunters from Irruan villages were largely responsible for hunting evidence recorded in the North sector. Most Irruan hunters were young and less experienced hunters who relied mainly on the use of snares. A few more experienced hunters were active in the North during the study. Though no gunshots were heard while searching and following gorilla trails in the North, evidence of hunters using shotguns was encountered. For example, during the 42 days working in the North sector, 60 spent shotgun shells were found compared to 38 found in the Central sector over 180 days. However, the majority of evidence found in the North was encountered on the northwestern periphery of the gorillas' range. Due to the relatively great distance between Irruan villages and the North sector, these hunters rarely traversed the several rocky peaks of greater than 1000 m altitude that separated their villages from the main area that the gorillas utilized when in the North sector of their range (Figure 4.13).

Buanchor is the closest village to the Central sector; however, accessing this sector presents a considerable physical challenge due to several very large rocky peaks with altitudes of 820 – 950 m (see Figure 4.13). Consequently, hunters must travel north or south around these peaks in order to reach the Central sector and often remained on the mountain for at least one night. By the start of the present study, most experienced Buanchor hunters had become too old to continue hunting or had found other sources of income; just one experienced Buanchor hunter remained active in the South. Only a few young Buanchor men hunted intermittently in the Central sector during the study. Past hunting pressure in the Central sector, however, was likely greater than current levels. In November 1993, a Buanchor hunter was known to have killed a gorilla and chimpanzee in the Central sector; there have been no reports of gorillas being killed by a Buanchor hunter since this time.

Hunting pressure and frequency of sector use

Frequency of sector use was negatively and significantly correlated with snare encounter rates within the four sectors ($r = -0.957$, $p = 0.043$, $n = 4$). The frequency with which the gorillas utilized the South, Central and West sectors was also negatively and significantly correlated with the proportion of gunshots heard within these three sectors during non-holiday periods ($r = -0.998$, $p = 0.037$, $n = 3$). During the main holiday period (December 18 – 31) when hunting pressure was greatest, the gorillas utilized the

Central sector where gunshots were recorded much less frequently as well as areas of the North sector that hunters rarely enter.

Daily Path Length

In this section, I describe the Afi gorillas' ranging behavior on a daily basis. Specifically, I report mean daily path length, describe monthly and seasonal variation in path length, and examine the relationships between daily path length and the following factors: dietary variables, temporal availability of fruit, herb availability, climate (rainfall and temperature) and presence of predators (i.e., humans).

Mean daily path length

A total of 60 measured complete gorilla group daily path lengths from one night's nest site to the next night's nest site resulted in an average minimum daily path length of 1.06 km (SD = 0.75, range = 0.061 – 3.006). When including partial trails ≥ 1.5 km (n = 75), average minimum daily path length was 1.27 km (SD = 0.828, range = 0.061 – 3.678). Figure 4.14 shows the frequency distribution of different daily path lengths for the two datasets. For complete trails only, the most frequent path length was between 0.5 and 1.0 km (33%), the second most frequent was less than 0.5 km (25%), and the least frequent was between 3.0 and 3.5 km (2%). For the larger dataset, the most frequent path length was also between 0.5 and 1.0 km (27%), but the second most frequent was between 1.5 and 2.0 km (23%) and the least frequent was between 3.0 and 4.0 km (3%). All complete trails and partial trails ≥ 1.5 km were greater than or equal to 4 days old with the majority being ≤ 2 days old (82% and 80%, respectively).

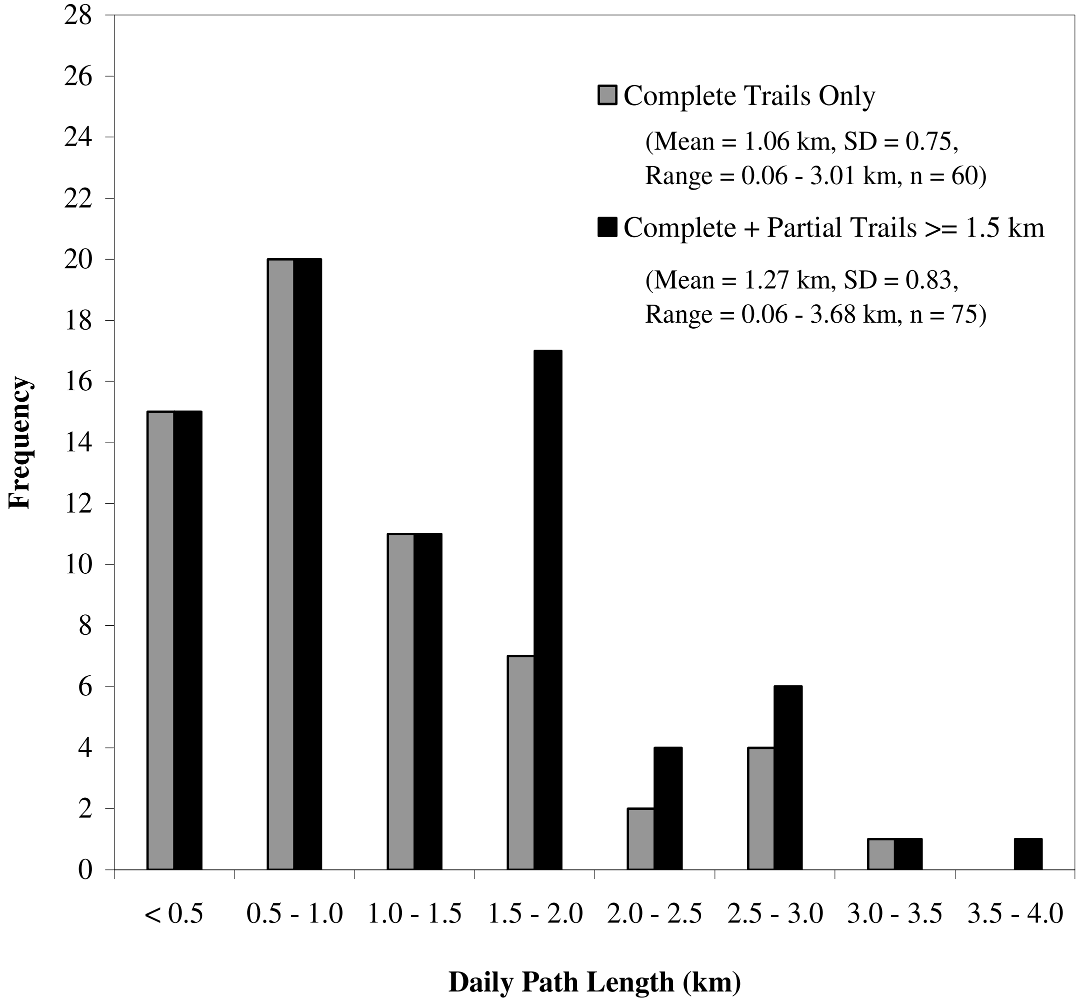


Figure 4.14 Frequency of gorilla daily path lengths for the two different datasets analyzed

Monthly and seasonal variation in daily path length

Figure 4.15 shows monthly variation in gorilla daily path length of complete trails only and complete + partial ≥ 1.5 km trails. When comparing monthly mean path lengths calculated from the two datasets, a major difference occurred for February; the two complete trails recorded in February were much shorter (0.53 and 0.82 km) than the four partial trails included in the larger dataset (1.75 – 3.67 km). Relatively large differences in results of the two datasets also occurred for May and December. Consequently, the larger dataset including partial trails ≥ 1.5 km was used for analyses that employed monthly mean path lengths (e.g., regression analyses).

Distances traveled by gorillas on a daily basis varied in relation to the relative contribution of fruit in their diet. Mean daily path length was significantly greater during the period of high fruit consumption (February – July) compared to the low fruit consumption period (August – January; complete trails only: means = 1.32 km versus 0.87 km, t = 2.24, p = 0.03, df = 42). Mean monthly path lengths were also significantly greater during the high fruit consumption period than the low fruit consumption period (complete + partial trails ≥ 1.5 km: means = 1.61 versus 0.98 km; t = 2.7, p = 0.024, df = 10).

Mean daily path lengths differed from expected based on abundance of fruit in the gorillas' diet during two months (July and January). Daily path length for July were on average shorter than other high fruit consumption months. This occurred because the gorillas remained within a very small area, which had an unusually high concentration of fruiting trees, for three days when they traveled ≤ 100 m per day. When these short path lengths were excluded, mean daily path length for July (1.53 km, SD = 1.0, n = 6) was

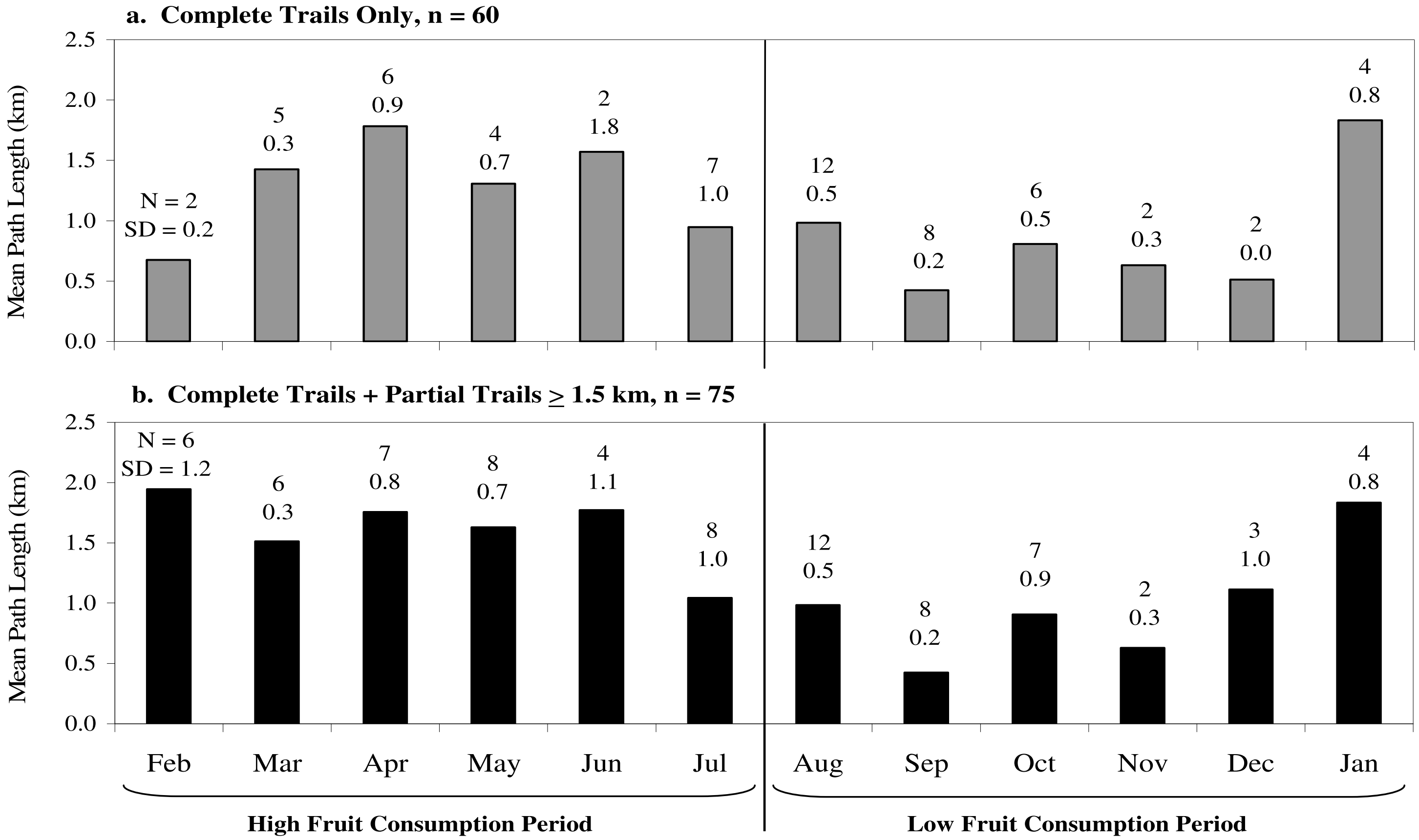


Figure 4.15 Monthly mean gorilla daily path lengths of (a) complete trails only, and (b) complete trails + partial ≥ 1.5 km trails with number of samples (N) and standard deviations (SD)

similar to other high fruit consumption months. Daily path lengths recorded during January were on average longer than other low fruit consumption months and is likely the result of the small sample available for this month (n = 4) and the fact that it includes one (of two) trails recorded for a long distance (3 km) when the gorillas were traveling between two sectors.

Dietary variables

Table 4.4 presents regression results for the relationships between daily path length and dietary variables for different food categories, including species diversity, frequency and abundance of different foods along feeding trails and/or in fecal samples (see Table legend for definitions). Since complete trails underestimated path lengths for some months, regressions were performed using only the larger dataset including partial trails ≥ 1.5 km.

Gorillas traveled significantly farther as species diversity, frequency and abundance of fruit increased in their diet ($F = 8.4$, 7.0 and 5.6, respectively, $p \leq 0.04$, $df = 10$). Gorillas traveled significantly shorter distances as frequency and abundance of non-fruit vegetation increased in their diet ($F = 7.0$ and 5.6, respectively, $p \leq 0.04$), but daily path lengths did not differ as non-fruit species diversity increased ($F = 0.40$, $p = 0.54$, $df = 10$). When non-fruit food categories were considered separately, the gorillas traveled significant shorter distances only as liana/tree bark species diversity increased ($F = 4.8$, $p = 0.05$; $df = 10$); path lengths were not influenced by frequency or abundance of liana/tree bark in the diet ($F \leq 1.5$, $p \geq 0.25$, respectively; $df = 10$). Leaf and herb pith species diversity, frequency, and abundance did not influence path lengths (Leaf: $F \leq 4.6$, $p \geq 0.34$; Herb pith: $F \leq 2.9$, $p \geq 0.47$; df = 10).

A multiple regression showed that species diversity of fruit and liana/tree bark together explained daily path length ($r^2 = 0.49$, $F = 4.4$, $p < 0.05$; df = 10). However, none of the partial regressions were significant on their own. When step-wise regression was conducted the diversity of fruit was the only significant step ($p = 0.016$; liana/tree bark: $p = 0.44$). This suggests that foraging for fruit primarily influences distance the gorillas traveled.

Table 4.4 Results of regressions (r^2) between Afi gorilla mean daily path length and dietary variables for different food categories (n = 12 months, +/- in parentheses indicate direction of relationship, see legend for definitions and units).

	SPECIES DIVERSITY	FREQUENCY	ABUNDANCE	
			Fecals	Trails
Fruit	(+) 0.45*	(+) 0.41*	(+) 0.37*	(+) 0.36*
Non-Fruit Vegetation	(-) 0.04	(-) 0.41*	(-) 0.37*	n/a
Leaves	(-) 0.01	(-) 0.09	(-) 0.31	(-) 0.10
Liana & Tree Bark	(-) 0.33*	(-) 0.01	n/a	(-) 0.13
Herb Pith	(-) 0.22	(-) 0.05	(-) 0.22	(-) 0.10

* $p \leq 0.05$

Species Diversity: Number of species eaten along feeding trails.

Frequency: Percentage of feeding sites in which each food category was consumed.

Abundance – Fecals: For fruit = mean percentage seed weight, leaves = mean leaf abundance score (0 - 4), herb pith = mean fiber abundance score (0 - 4) per fecal sample.

Abundance – Trails: Mean amount eaten per feeding site (for fruit and leaves = number, liana & tree bark = area (cm^2), herb pith = grams).

Temporal availability of fruit

Figure 4.16 shows the relationship between daily path length and temporal availability of fruit eaten by gorillas[10]. Path length increased significantly with the proportion of trees with both unripe and ripe fruit ($r^2 = 0.55$, $F = 12.2$, $p = 0.006$; df = 10). When the availability of unripe and ripe fruit was considered separately, daily path length was significantly influenced by ripe fruit ($r^2 = 0.43$, $F = 7.6$, $p = 0.02$; df = 10) as well as unripe fruit availability ($r^2 = 0.54$, $F = 11.9$, $p = 0.006$; df = 10).

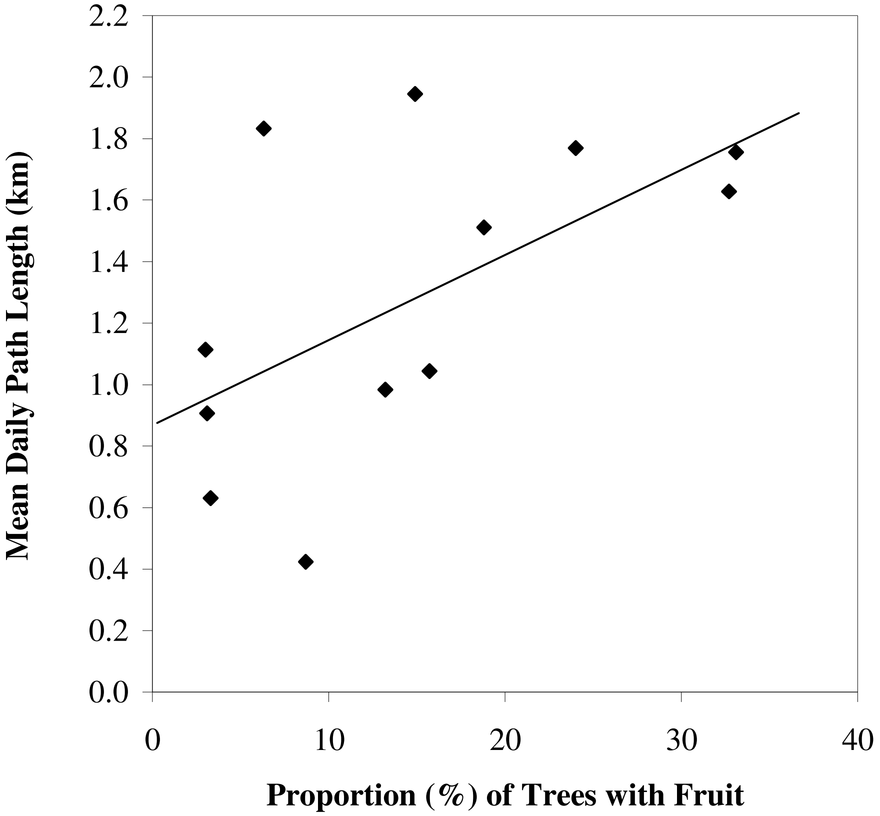


Figure 4.16 Daily path length and temporal availability of fruit (both unripe and ripe) eaten by gorillas

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[10] Phenology data were not available for all months in which diet data were collected (December 1997 – November 1998); monitoring began in May 1998. Consequently, phenology data from 2000 was used for this analysis and results should be viewed with caution (see Methods for details).

Herb availability: variation across sectors

To investigate how herb availability may have influenced distances the gorillas traveled, variation in daily path length across sectors, which differ in their availability of herbs, was examined. Sufficient samples are available for the South and Central sectors only (n = 24 and 42 trails, respectively); relatively few complete and partial trails ≥ 1.5 km were recorded in the West and North sectors (n = 4 and 5 trails, respectively). Table 4.5 compares mean daily path lengths when the gorillas were utilizing the South and Central sectors during different times of the year. Distances the gorillas traveled daily did not differ when they used South and Central sectors throughout the year (z = 0.633, p = 0.527) or during the high and low fruit consumption periods separately (z ≥ 0.151, p ≥ 0.277).

The gorillas, however, utilized the South almost exclusively during the wet months within the low fruit consumption period (August – October; Figure 4.6a). During these months, the gorillas traveled on average approximately two times longer distances when utilizing the South than when using the Central sector (mean = 0.82 versus 0.47 km), though this difference did not reach statistically significant levels (z = 1.65, p = 0.100). The longer distances the gorillas traveled while utilizing the South during this time may be related to this sector's low herb availability and the widely dispersed distribution of a particular herb food, *Anchomanes difformis*, which the gorillas heavily relied upon during this time.

Table 4.5 Mean daily path lengths in South and Central sectors throughout the year (overall), during the high fruit consumption period (February –July), during the low fruit consumption period (August – January), and during wet months within the low fruit consumption period (August – October), including sample size for each sector, standard deviations and ranges in parentheses.

	SOUTH	**CENTRAL**
Overall (n = 24 and 42)	1.16 (0.89, 0.21 - 3.68)	1.29 (0.86, 0.06 - 3.01)
High Fruit Consumption (n = 7 and 27)	1.99 (1.15, 0.53 - 3.68)	1.47 (0.85, 0.06 - 2.8)
Low Fruit Consumption (n = 17 and 15)	0.82 (0.47, 0.21 - 1.98)	0.98 (0.81, 0.28 - 3.01)
Wet Low Fruit Consumption Months (n = 17 and 6)	0.82 (0.47, 0.21 - 1.98)	0.47 (0.21, 0.28 - 0.85)

Climate: rainfall and temperature

Rain fell on 49 days for which complete trails and partial trails ≥ 1.5 km were recorded (range = 0.1 – 116.8 mm). Daily path lengths were not influenced by total, day-time, or night-time rainfall ($r^2 = 0.01 – 0.05$, $F = 0.4 – 1.9$, $p \geq 0.18$, df = 47, 40 and 39, respectively). There was also no relationship between mean monthly path lengths and monthly total, day-time, and night-time rainfall ($r^2 = 0.09 – 0.17$, $p \geq 0.10$; df = 10).

Daily minimum and maximum temperatures were recorded for the 60 complete daily path lengths and the 15 partial lengths ≥ 1.5 km. Whereas minimum temperatures did not influence path lengths ($r^2 = 0.006$, $F = 0.5$, $p = 0.50$), path lengths did increase significantly with maximum temperature ($r^2 = 0.16$, $F = 13.5$, $p < 0.001$; df = 73).

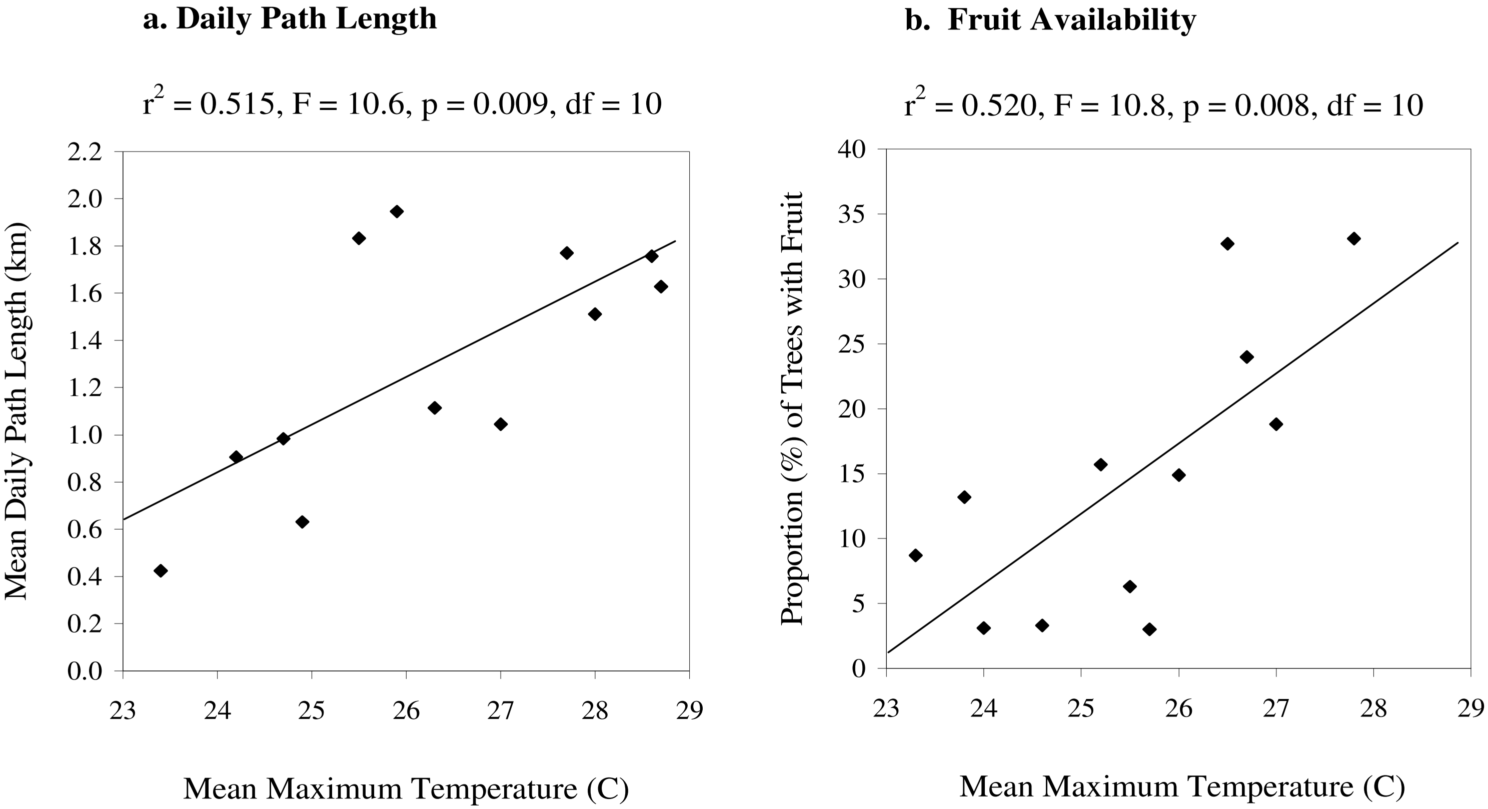

Figure 4.17 Relationship between maximum temperature and (a) gorilla daily path length (complete + partial ≥ 1.5 km) and (b) temporal availability of fruit (both unripe & ripe fruit) eaten by gorillas (n = 12 months)

Mean monthly daily path lengths also increased significantly with mean monthly maximum temperature ($r^2 = 0.52$, $F = 10.6$, $p = 0.009$, df = 10; Figure 4.17a).

As shown in Chapter Two, maximum temperature and fruit availability were significantly and positively related (see Table 2.4). The monthly proportion of trees in fruit increased significantly with mean maximum temperature ($r^2 = 0.52$, $p = 0.008$; Figure 4.17b). A multiple regression showed that the proportion of fruiting trees and maximum temperature together did explain daily path length ($r^2 = 0.58$, $F = 6.3$, $p = 0.019$, df = 10). However, none of the partial regressions were significant on their own. When a step-wise regression was conducted, fruit availability was the only significant step ($r^2 = 0.55$, $p = 0.006$; maximum temperature: $p = 0.41$). This suggests that maximum temperature was indirectly related with path length and its relationship to path length occurred due to its relationship with fruit availability, which was the primary factor influencing path length.

Predators

Evidence of human presence close to six complete and partial (≥ 1.5 km) trails was recorded. Hunters were encountered in the vicinity of two complete trails and gunshots were heard from quadrats adjacent to four complete trails and one partial trail ≥ 1.5 km. Though gorillas tended to travel farther when hunters were present nearby (mean = 1.55, SD = 0.74, range = 0.45 – 2.69 km) than not (mean = 1.24, SD = 0.84, range = 0.06 – 3.69 km) this difference was non-significant ($t = 0.88$, $p = 0.38$, df = 73).

DISCUSSION

Home Range Size And Daily Path Length

As predicted by their frugivorous diet, the Afi gorillas' home range was larger and daily path lengths were on average longer than the folivorous mountain gorillas of the Virungas and both were similar to the frugivorous lowland gorilla populations (see Chapter 6, Tables 6.2 and 6.3, for a more detailed comparison). During the present study, the Afi gorillas ranged over a minimal area of 13.1 km^2, but were estimated to have an annual home range size of 20 km^2 and a total range of 31 km^2. Annual home range size for Afi gorillas is larger than that of Virunga mountain gorillas (6.0 – 11.5 km^2; McNeilage, 2001; Vedder, 1984; Watts, 1991, 1998, and 2000). Though there is considerable variation in annual home range size across different lowland gorilla sites the Afi figures fit well within this range (7 – 31 km^2; Cipolletta, 2003 and 2004; Doran and McNeilage, 2001; Doran-Sheehy et al., 2004; Remis, 1994 and 1997a; Tutin, et al., 1992; Tutin, 1996).

Estimated mean daily path length at Afi (1.27 km) is greater than that of Virunga Mountain gorillas (0.57 km; Watts, 1991) and similar to mean daily path lengths of lowland gorillas (1.11 – 2.59 km; Bermejo, 1997; Cipolletta, 2004; Doran and McNeilage, 2001; Doran-Sheehy et al., 2004; Goldsmith, 1996 and 1999; Remis, 1994 and 1997a; Tutin, 1996; Yamagiwa and Mwanza, 1994; Yamagiwa et al., 1992). Afi mean path length is at the lower end of the range of path lengths of lowland gorillas but this is likely because due to the rugged Afi terrain and open forest floor, which makes gorilla tracking over long distances particularly difficult; hence, path lengths at Afi were likely underestimated to a greater degree than at other sites. The longest daily path length recorded at Afi was a partial trail 3.68 km long, which is within the range of maximum path lengths recorded at lowland gorilla sites (2.79 – 5.50 km).

Results of the present study provide additional evidence that gorillas incur increased foraging costs when consuming widely dispersed food resources such as fruit. Like frugivorous lowland gorillas, Afi gorillas did tend to travel greater distances daily during the period of high fruit availability and consumption, and travel shorter distances when relying on non-fruit vegetation foods that are more uniformly available (Cipolletta 2004; Doran & Greer 2002; Goldsmith 1996, 1999; Remis 1994; Tutin 1996). Variation in the relative contribution of fruit in the Afi gorillas' diet, as indicated by diversity, frequency and abundance dietary measures, and temporal availability of fruit were found to be the primary factors influencing the daily path lengths of Afi gorillas.

Results of the present study suggest, however, that Afi gorilla daily path length may also be influenced by spatial availability of herb foods. During the period of fruit scarcity (i.e., the low fruit consumption period) when the Afi gorillas consumed large amounts of herb pith and leaf foods, daily path lengths recorded in the South and Central sectors differed as predicted by the variation in herb stem densities across these two sectors. Compared to the Central sector, herb availability in the South was characterized by much lower herb stem density and fewer herb patches that were more widely dispersed. In addition, when utilizing the South sector during this time the gorillas relied heavily on the pith and leaves of *Anchomanes* that occur as single widely scattered stems rather than densely clumped stems in large patches like other Afi gorilla herb foods. Afi gorillas traveled on average approximately two times longer distances daily when utilizing the South (0.82 km) than when using the Central sector (0.47 km).

Relationship Between Range Use And Ecological Factors

In general, the gorillas tended to move across their range along a north-south axis entering 2 – 4 sectors each month of the year and covered the majority of their range within a 3-month period. The cyclical pattern with which Afi gorillas utilized different sectors is similar to that of Virunga mountain gorillas suggested to be related to herb regeneration rates (Watts 1998b, 2000). However, variations in food availability and predation risk across the Afi gorillas' range are likely more important factors influencing their ranging behavior.

Afi gorillas utilized their range in a non-random and efficient manner that corresponded to variation in the temporal and/or spatial availability of both herb and tree foods, and hunting pressure. Throughout the year, during different seasons (i.e., low and high fruit consumption periods, and dry and wet months within the low fruit consumption period) and in each month sampled, frequencies of sector use differed significantly from expectation based on equal use. The Afi gorillas utilized the sector (Central) with the highest overall herb and tree food species density more frequently than any of the other sectors throughout the year, during all but one of the seasons investigated and during six months of the year, indicating that the Central sector represents the core of the gorillas' home range. Afi gorillas, however, utilized the South, West, and North sectors more frequently than or as frequently as the Central sector during certain times of the year in order to consume herb and fruit foods that were more abundant in these sectors and avoid high hunting pressure.

Food availability and range use

Availability of important food species should influence ranging behavior (Rogers et al. 2004; Tutin & Fernandez 1993). The fruiting patterns of individual important fruit species clearly influenced the Afi gorillas range use pattern. During the period of high fruit consumption and availability, Afi gorillas ranged widely in order to access sectors of their range where estimated densities of trees in fruit were highest. The availability of one or two tree-fruit species in particular sectors likely explains why the gorillas utilized one sector more frequently than others during each of the six high fruit consumption months (i.e., February: *Morus mesozygia* in the South; March: *Tabernaemontana pachysiphon* and *Trichoscypha* sp. in Central and North sectors; April and May: *Sorindeia grandifolia* in the Central sector; June: *Garcinia kola* in the North; July: *Myrianthus arboreus* in the Central sector). Availability of tree-fruit species may explain the gorillas range use pattern during only two of the six months within the period of low fruit consumption and availability (i.e. January: *Tabernaemontana pachysiphon* and *Trichoscypha* sp. in the Central sector; October: *Vitex* sp. in the West).

Studies of other frugivorous gorillas describe a similar range use pattern in relation to fruit availability (Remis 1994; Remis 1997a; Tutin 1996; White 1994). Western lowland gorillas living in habitats with swamps also range outside their core area in order to consume the mineral rich herbaceous vegetation growing in these swamps (Doran-Sheehy et al. 2004; Kuroda et al. 1996). Western lowland gorilla studies, have not, however, shown directly the influence of other important herb food species, which are the gorillas' staple diet. The present study provides strong evidence that Afi gorilla range use is influenced by variation in the availability of important herb food species.

Variation in the availability of important herb (and tree) fallback foods across their range and preference for particular herb foods during certain months within this period (i.e., dry or wet months within the low fruit consumption period) were likely the most important factors influencing Afi gorilla range use patterns and diet during the period of fruit scarcity. The frequency of sector use by Afi gorillas did not strictly correspond to variation in overall stem densities of all herb or fallback herb foods across sectors.

The gorillas' pattern of sector use during the period of fruit scarcity was, however, significantly related to the availability of specific fallback herbs that were consumed more frequently during dry or wet months of this period and were more abundantly available in South or Central sectors. Variation in the availability of individual herb foods across sectors strongly influenced the relative contribution of different herb foods in the Afi gorillas' diet. For most of the individual herb foods, relationships between variation in the densities and frequencies of consumption across sectors were much stronger ($r = 0.765 – 0.968$) than the relationship between overall herb density and consumption ($r = 0.417$). The above results, as well as those reported in Chapter Three, suggest that the Afi gorillas' pattern of range use may have been influenced by preferences for specific herb foods.

Afi gorillas utilized the South sector more frequently during the fruit scarce period and consumed herbs more frequently than predicted by this sectors' low herb availability; overall herb density in the South was less than half that of Central and West sectors. This is likely related to the gorillas' preference for the pith and leaves of two herbs, *Stylochiton* sp. and *Anchomanes difformis*, during wet months of the low fruit consumption period when the gorillas most frequently used the South where these herbs were more abundantly available. Frequency of sector use during the wet low fruit months was significantly correlated with *Stylochiton* density and *Anchomanes* estimated density separately. *Anchomanes* was the gorillas' most important herb food resource, was preferred over other herb foods likely related to its possible higher protein content and digestibility, and provided the greatest proportion of herb foods consumed during the wet low fruit months (see Chapter 3). Since *Anchomanes* stem densities were estimated based on feeding site encounter rates, it is possible that availability of *Anchomanes* was not greater in the South and the gorillas made an effort to seek it out when utilizing this sector.

Despite the fact that overall herb stem densities were relatively high in both Central and West sectors and fallback herb densities were highest in the West, the gorillas preferred to utilize the Central sector in dry months during the period of fruit scarcity. The gorillas' preference for the Central sector over the West during these dry low fruit months may be related to their preference for *Palisota* sp. 1 over *Marantochloa* spp.; frequency of sector use during these months was positively and significantly correlated with availability of *Palisota* sp. 1, and was negatively correlated with *Marantochloa* spp. availability. As shown in Chapter Three, *Palisota* sp. 1 was the gorillas' third most important herb food resource and was most abundant in their diet during dry low fruit months when it was likely preferred over other herb foods due to its greater water content and possible higher protein content (*Anchomanes* stems were not available during these months).

Based on herb availability, several lines of evidence suggest that Afi gorillas should have used the West more often than the South throughout the year, and more often than South and Central sectors during the period of fruit scarcity. In the West, overall herb availability and stem density of *Aframomum* spp., the gorillas' second most important herb food, was relatively high and similar to that of the Central sector. Densities of two fallback herbs (*Costus* spp. and *Marantochloa* spp.) in the West were greater than densities of the other fallback herb foods (*Palisota* sp. 1, *Stylochiton* sp.) and *Anchomanes difformis* in South and Central sectors. *Marantochloa* and *Costus* spp. are important fallback foods for some western lowland gorilla populations (Rogers et al. 2004; Rogers et al. 1994; Tutin et al. 1997). Afi gorillas likely made an effort to seek out *Marantochloa* stems when utilizing the Central sector; *Marantochloa* stems were eaten most frequently in the Central sector where its density was lowest.

Nevertheless, Afi gorillas utilized the Central sector more frequently than the West throughout the year and during fruit scarce months the gorillas most often used the South and Central sectors. During the wet months of the low fruit period, the gorillas did utilize the West as frequently as expected based on this sectors' density of fallback herbs eaten more often during these months. But this likely occurred because of the availability of *Vitex* fruit in the West during the wet low fruit month of October, the only month in which the gorillas used the West more frequently than other sectors. Preferences for *Palisota* sp. 1, *Stylochiton* sp., and *Anchomanes difformis* described above may explain the lower than expected use of the West during the period of fruit scarcity. These preferences do not, however, fully explain the Afi gorillas' apparent deliberate avoidance of the West throughout the year, which may be related to the high hunting pressure in this sector (see below for details).

Hunting pressure and range use

Spatial and temporal variation in hunting pressure across the Afi gorillas' range clearly influenced their range use decisions. The Afi gorillas utilized different range sectors in a manner indicating that they avoided sectors with high hunting pressure. Frequency of sector use was negatively and significantly correlated with variation in snare encounter rates and proportion of gunshots fired across sectors during the present study. When hunting pressure was highest during the Holiday period, the gorillas avoided the two sectors with the highest hunting pressure (West and South). During this time the gorillas retreated to the difficult to access areas of the North sector.

Hunting pressure was likely the most important factor influencing whether or not Afi gorillas' decided to utilize the West sector. Hunting pressure was highest in this sector throughout the year due to the constant presence of the only 'career' hunter on Afi Mountain; this hunter was most active in the West. The high hunting pressure experienced by Afi gorillas when utilizing the West sector likely explains why the gorillas most often only traveled through this sector without lingering, and used this sector more frequently than other sectors during only one month of the year, October. The gorillas chose not to use the West despite the fact that important herb foods were relatively abundant in this sector. The gorillas likely chose to enter and remain in the West during October in order to consume *Vitex* fruit that appeared to be available only in the West at this time. During this foray into the West, the hunter killed an adult male member of the Afi gorilla study group, demonstrating the considerable predation risk they faced when using this sector. The incident also demonstrates that the gorillas were willing to accept this risk in order to access fruit resources.

CHAPTER FIVE:

Group Size and Composition, and Grouping Patterns

INTRODUCTION

Western lowland and Grauer's gorillas are generally described as forming stable one-male groups similar to most mountain gorilla groups (Doran & McNeilage 1998). The grouping patterns of western lowland and Grauer's gorillas, however, tend to be more flexible than mountain gorilla groups. Gorilla groups at most western lowland and Grauer's study sites have a wide group spread while foraging, including the formation of temporary foraging subgroups (Bermejo 2004; Doran & McNeilage 1998; Doran & McNeilage 2001; Goldsmith 1996, 2003; Kuroda et al. 1996; Remis 1994; Remis 1997a; Tutin 1996; Yamagiwa et al. 2003a; Yamagiwa et al. 2003b). At Bai Hokou, Ndoki, and Kahuzi, there is evidence suggesting that groups containing two adult-male silverbacks often form subgroups that forage and nest separately for one or more days (Goldsmith 1996, 2003; Kuroda et al. 1996; Mitani 1992; Remis 1994; Remis 1997a; Yamagiwa et al. 2003a; Yamagiwa et al. 2003b). "Supergroup" formation (where two groups maintain close proximity overnight) has been observed occasionally at Lossi and Kahuzi (Bermejo 2004; Yamagiwa et al. 2003a; Yamagiwa et al. 2003b). This flexibility in grouping behavior has been suggested to occur due to increased within-group feeding competition related to these gorillas' highly frugivorous diet.

Estimating Group Size and Composition, and Grouping Patterns Using Nests

Generally all weaned gorillas in a group construct a new nest each night and re-use of nests or nest sites is rare. Because gorillas also usually defecate in or near their nests, fecal diameter can estimate the age-class of nest occupants (e.g. Silverback male, adult female or adolescent male, juvenile, and infant). Consequently, nests are particularly useful for estimating group size and composition of unhabituated gorillas. There is some debate, however, as to how reliably nest counts reflect group size (Remis 1993; Tutin et al. 1995). Tutin et al. (1995) found that mean nest group size of one Lopé gorilla group accurately reflected actual group size, but nest counts at each site corresponded to actual group size only one-third of the time (n = 137 sites over 4 years). They suggest two possible sources of the variation in nest counts: 1) One or more individuals may have built multiple nests, either not using one nest or moving to a second nest during the night, producing higher nest counts and 2) Observers failed to detect some nests, particularly bare ground nests, producing lower nest counts.

Whereas nest counts varied widely at Lopé (from ½ to twice that of the actual group size), the great majority (84.5 – 91.1%) of the nest counts were within +/- 2 nests of the actual group size and nest counts differing by ≤ or ≥ 3 nests were rare. Thus, large numbers of nest counts differing from the mean by ≥ +/- 3 might indicate sub or super group formation. Using this criterion, Goldsmith (1996) and Remis (1994, 1997) reported relatively high possible subgroup frequencies at Bai Hokou (31% of nest sites and 58% of consecutive nest sites, respectively) and subgroups foraged and slept apart on 29 and 34 occasions, respectively. In both studies, groups that formed subgroups had two adult male silverbacks and subgroup formation occurred more frequently during the fruiting period, when gorillas consume relatively large amounts of fruit.

Specific Aims

Preliminary results indicated that nest group size at Afi is highly variable, ranging between 8 and 37 nests, and has been tentatively attributed to possible flexible grouping behavior (Oates et al. 2003). The main goals of this chapter are to estimate group size and composition, describe variation in nest group size and evaluate whether this variation can be explained by flexible grouping behavior or other factors including: 1) the data represent more than one gorilla group, 2) multiple nests were built by one or more individuals at a nest site, 3) observers failed to detect some nests, particularly bare ground nests, 4) some juveniles may have built nests of their own on some occasions and chose to share a nest with an adult at other times, 5) groups sometimes remained at or near night nest sites so that day nests were mistaken for night nests.

Whether frequency of nest group size variability was related to intragroup feeding competition associated with consuming fruit or feeding in habitats with low herb availability was also investigated. Based on socioecological theory and previous studies of western lowland gorillas, frequency of group flexibility at Afi was expected to vary as predicted by variation in the relative contribution of fruit and non-fruit vegetation in the gorillas' diet. Specifically, frequency of group instability was expected to be greater when the gorillas consumed large amounts of fruit, a clumped and widely dispersed resource, than when relying heavily on non-fruit vegetation, particularly herb foods which are more evenly and abundantly available. Herb availability, however, differed between sectors within the gorillas' home range. Whereas herb stem density was greatest in the Central sector, herb availability in the South sector was characterized by significantly lower stem density and fewer numbers of herb patches that were more widely dispersed (Chapter 2). In addition, when utilizing the South sector during the period of fruit scarcity, the gorillas consumed large amounts of the pith and leaves of an herb, *Anchomanes difformis*, which occurs as single widely scattered stems rather than clumped in large patches like other herb foods (Chapter 3). During the fruit scarce period, the gorillas traveled on average two times longer distances daily when using the South than the Central sector suggesting that the Afi gorillas may have experienced greater levels of intragroup feeding competition associated with the low herb availability in the South sector (Chapter 4). Hence, group flexibility might also be expected to occur frequently when the gorillas relied heavily on herb foods in the South sector of their range.

METHODS

Estimating Group Size and Composition

Group size (i.e., number of weaned individuals) at Afi was estimated using nest counts at fresh nest sites (≤ 4 days old) found between December 1997 and June 1999; however, the majority of the data were collected between December 1997 and November 1998 when following gorilla trails was the focus of the study. When fresh nest sites were encountered the following information, among other parameters, was recorded: date, location, number of nests, estimated age of nests. For individual nests, nest type, height of nest above ground, presence/absence of feces and hairs, position of feces with respect to the nest (inside, on the rim, or outside), age-class of occupant as determined from diameter of feces (see below for details), and evidence that young also occupied the nest (e.g., presence of infant/juvenile sized feces in nest) were noted (Tutin & Fernandez 1993). See Appendix VIII for a complete description of data collected at nest sites, including nest type definitions.

A total of nine different nest types were recognized, but for the purposes of this chapter they were grouped into the following three categories:

1. Bare Ground: no structure present
2. Ground Nests (< 0.5 m above ground): including zero construction nests (gorilla slept atop vegetation with no construction involved), minimum nests (made with < 4 plant stems), herb nests (made with ≥ 4 stems of Marantaceae and Zingiberaceae herbs), mixed nests (made with herb and woody vegetation) and woody1 nests (made with saplings or other woody vegetation only)
3. Arboreal Nests (≥ 0.5 m above ground): including tree nests (made using tree branches), vine tangle nests (made using lianas with no direct support from tree branches) and woody2 nests (like woody1 but built above ground)

To avoid including nests built but not slept in for any lengthy period, bare ground and other ground nests were included only if feces and/or hairs were present. Because most arboreal nests were inaccessible to the researcher and assistants, all arboreal nests were included, even if feces were not found below the nest. The inclusion of all arboreal nests likely did not significantly overestimate group size of nest sites containing arboreal nests for the following reasons (also see 'Other Factors'). Firstly, only 3.4% of ground nests did not have feces and/or hairs suggesting that few arboreal nests likely also did not have feces and/or hairs. Secondly, the proportion of non-arboreal nests that had feces inside the nest (19.2%) is greater than the proportion of arboreal nests for which no feces were detected (15.7%) suggesting that the arboreal nests with no feces below likely contained feces inside the nest.

Group composition was estimated using diameter of fecal samples associated with nests to identify the age-class of nest occupants (adult males: ≥ 6.5 cm diameter, adult females and adolescent males: 4.5 – 6.4 cm; juvenile: 2.0 – 4.4 cm; infant: < 2.0 cm). These criteria are based on measurements reported by Tutin and Fernandez (1993b) for western lowland gorillas at Lopé, Gabon and have been used to identify gorilla age-class in several other studies of western lowland gorillas (Doran et al. 2002; Goldsmith 1996; Remis 1994, 1997b). Fecal diameter was often not measurable, especially when gorillas were consuming large amounts of fruit and in the wet season when rain fell on all but a few days, 'washing' the feces. Consequently, group composition was estimated based on a subset of nest sites. To estimate numbers of adult female/adolescent male and juvenile sized nests per site, only those sites with ≥ 80% measurable fecal samples (n = 24 sites) were used in order not to greatly underestimate their numbers. To estimate number of adult-male sized nests per site, only those sites that had at least one measurable adult-male sized fecal sample (diameter ≥ 6.5 cm) were included in the analysis (n = 81 sites). Since fecal diameter may not always accurately reflect gorilla age-class, data were also analyzed using fecal diameters of ≥ 6.7 cm to identify adult-male nests (n = 55 sites) in order to reduce the probability of overestimating their numbers.

Number of Groups and Census

Whether the data represent more than one gorilla group was investigated in two ways. Firstly, to explore if core areas of two groups of differing sizes could be identified, mean nest group size was compared across four sectors within the Afi study area (South, Central, West, and North; see Figure 5.3) and 1 km by 1 km grid cells (n = 27; Figure 2.2). Due to small sample sizes for most grid cells, they were pooled into east-west rows (n = 10 rows) within the gorillas' home range starting in the south and moving north, and two consecutive rows were also pooled (n = 5 rows) and tested separately. Secondly, a sweep census of the study area and an adjacent area contiguous with Afi Mountain was conducted during February and March 1999.

While tracking gorillas, it became clear that the originally planned census method, including systematic and thorough searches of 1 km by 1 km grid cells, would not be feasible and transect methods would produce insufficient data. In addition, the variation in nest group sizes observed indicated that the question of how many groups inhabited the study area was important. Thus, the census was conducted in a manner that would optimize the detection of the presence of more than one gorilla group. Searches for fresh gorilla signs were conducted simultaneously in three areas. Fresh signs recorded in different areas at the same time would indicate the existence of different gorilla groups.

The following three areas were searched and are shown in Figure 5.1 (and Figure 5.3):

1. Main Afi (30 km^2): includes South, Central, and West sectors of the Afi Mountain study site where the majority of gorilla signs were recorded.
2. North Afi (10 km^2): includes the North sector of the Afi Mountain study site where fresh gorilla signs were recorded in June 1998; however, this sector had not been fully investigated prior to the census.
3. Olum Hills (20 km^2): includes an area northeast of Afi Mountain separated by a lowland valley and footpath. Previous reports indicated gorillas inhabit this area, but it had not been thoroughly investigated previously.

In February, the Main and North Afi areas were searched, and in March all three areas were searched, simultaneously. Up to three teams of two to three workers each systematically searched areas in circular patterns radiating from various mobile camps. When fresh signs were found, they were followed to nest sites and trails to subsequent nest sites were followed as long as possible. Information at nests sites was collected as described above.

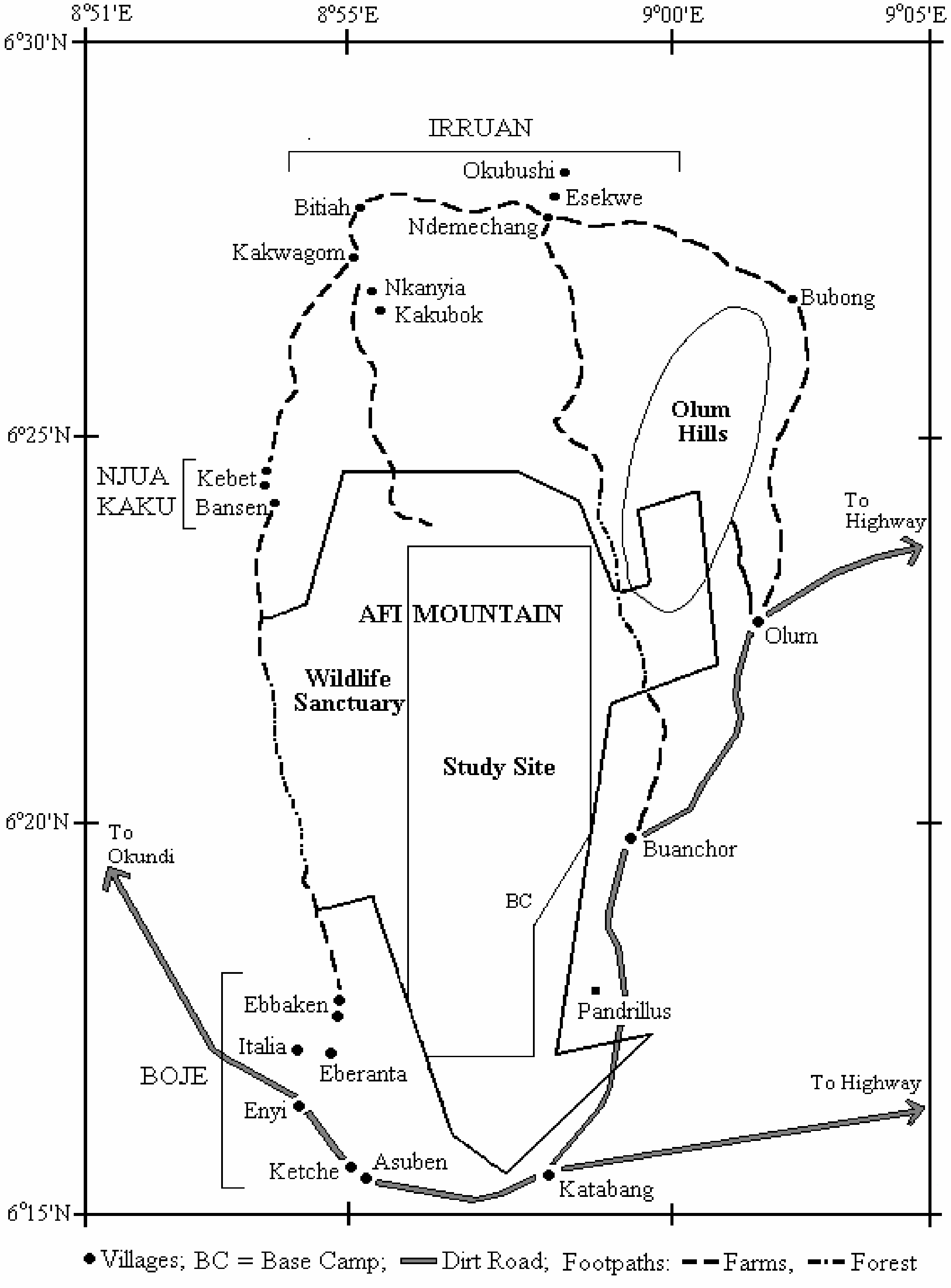

Figure 5.1 The two areas of Afi Mountain and the Olum Hills area searched during a census conducted February – March 1999

Group Size Variation Among Consecutive Nest Sites

The formation of temporary subgroups by gorillas has been suggested based on several types of evidence: 1) presence of small nest counts in areas where large groups are known to occur (Mitani 1992; Remis 1994; Remis 1997a), 2) when individuals of a known group size are contacted but their nest site reflects a smaller group count (Remis 1994; Remis 1997a), and 3) when a significant difference in nest counts occurs on consecutive day follows of groups (Remis, 1994; Goldsmith, 1996). Using the first type of evidence was possible at Bai Hokou because only a very small portion of the main study group's range overlapped with other groups. Consequently, mistaking small nest counts as subgroups of the main study group, rather than as a different group, was much less likely at this site (M. Remis, personal communication). But at other sites home ranges of different gorilla groups often overlap extensively (Bermejo 1997; Tutin 1996), making the use of the first type of evidence to detect subgrouping behavior difficult. The second type of evidence relies on the ability to recognize individual group members, which was not possible in the present study. Until the identity of individual groups is possible either through habituation or DNA analysis, the third type of evidence is likely the most accurate indication of temporary group formations for unhabituated populations (Goldsmith 1996).

In the present study, whether flexible grouping behavior occurred was explored using consecutive nest sites, recorded during 15 months between December 1997 and April 1999, as was done by Goldsmith (1996). When nest group size between consecutive nest site pairs decreased or increased by ≥ 3 nests, the group was considered to have been temporarily unstable (i.e., sub or super grouping may have occurred, respectively). A variation of three individuals was used as a cut-off since stable groups often have nest sites that vary by one or two nests as described by Tutin et al. (1995) and discussed in the introduction. When differences of 0 – 2 nests occurred between consecutive site pairs, the group was considered to remain stable.

To investigate whether nest group size variation may be a response to intragroup feeding competition associated with consuming fruit or feeding in habitats with low herb availability, relative frequencies of stable and unstable group sizes were compared between high fruit consumption months (February – July) when fruit was abundant in the gorillas' diet and low fruit consumption months when they relied heavily on non-fruit vegetation, particularly herb foods (August – January, see Chapter 3 for details). Frequency of group instability was also compared between two sectors, Central and South (see Figure 2.7), where herb availability differed.

Other Factors

Removal of ground nests containing no feces and/or hairs from the analyses likely reduced the probability that multiple nests built by one or more individuals at a nest site produced nest group sizes larger (≥ 3 nests) than the mean. All arboreal nests were, however, included when determining nest group size. Whereas this likely did not overestimate nest group sizes as discussed above, proportion of arboreal nests per site was compared when nest group sizes were within +/- 2 nests of the mean group size and larger (≥ + 3 nests) than the mean to determine whether the inclusion of all arboreal nests may have produced larger nest group sizes.

Proportion of arboreal nests per site was also compared when nest group sizes were within +/- 2 nests of the mean group size and smaller (≥ - 3 nests) than the mean. Based on analysis of nest characteristics, bare ground nests were most often associated with sites made mostly of arboreal nests in forest habitats. Consequently, this comparison should indicate whether smaller nest group sizes tend to be sites composed mostly of arboreal nests suggesting that undetected tree and/or bare ground nests may have produced some of the group size variation observed. It is difficult to decipher whether observers failed to detect other types of nests. While monitoring nest age, I discovered that an additional nest at two nest sites were undetected when the sites were originally encountered in the first two months of data collection. Subsequently, a greater amount of time and effort was made to search the area surrounding sites to ensure that all nests were discovered, especially when smaller numbers of nests were present.

Preliminary results suggested that juvenile nesting behavior varied during the present study. On some occasions juveniles appeared to have shared a nest with an adult as indicated by the presence of adult and juvenile sized feces in a large nest and at other times juveniles built and slept in their own nests. The relationship between nest group size and numbers of juveniles sharing adult nests was examined by comparing mean nest group sizes when different numbers of juveniles slept with adults. If variation in juvenile nesting behavior produced any of the group size variability observed, nest group sizes were expected to be smaller when there were a greater number of indications that juveniles shared adult nests (i.e., a negative relationship was expected).

On several occasions when a less than one-day old nest site was found in the late afternoon, gorillas were detected within 200 m of the nest site, at which feeding evidence was abundant, suggesting that the gorillas remained at the nest sites for a large portion of the subsequent day and may have constructed day nests very near the night nest site. It is possible that these day nests may have been mistaken for night nests. Removal of ground nests without feces and/or hairs from analyses likely eliminated the possibility of mistaking a day nest for a night nest in most cases (Remis 1993). Whereas feces are rarely found in day nests, hairs may be present (Schaller, 1963; Williamson, 1989; this study). Consequently, nests at consecutive sites that had hairs but no feces were removed from the data (Mehlman & Doran 2002) and variation among consecutive nest sites was re-analyzed as described above. If the status of the majority of consecutive nest site pairs affected by the removal of these nests changed from being unstable to remaining stable or vice versa, then mistaking day nests for night nests may explain at least some of the variation in nest group size observed.

Statistics

Means were compared using non-parametric tests, Mann-Whitney U tests or Kruskal-Wallis chi-square tests, including pair-wise comparisons (Siegel & Castellan Jr. 1988). All correlations are Pearson correlations.

RESULTS

Estimated Group Size

Group size was estimated based on nest counts from 122 fresh nest sites (≤ 4 days old) for which nests without feces and/or hairs were excluded. Mean nest group size was 18.2 but was highly variable ranging from 8 – 37 nests (SD = 4.5, see Table 5.1). Figure 5.2 shows the frequency distribution of the different nest group sizes recorded. Overall, group sizes of 18, 19, and 14 were the most frequent. Only 45% of sites had group sizes of ± 2 nests from the mean group size (i.e., 16 – 20 nests). Nest group sizes differing from the mean by ≥ +/- 3 nests were more common (55% of sites); 30% of sites had ≤ 15 nests and 25% had ≥ 21 nests.

No fresh nest sites of lone males were encountered, but this does not indicate that no lone or all male groups inhabit Afi. Two 10-day old nest sites containing one nest were likely lone male nests. In addition, two nest sites approximately one-week old containing 2 and 4 individual nests were found. Due to difficulties detecting gorilla signs and following trails on Afi Mountain, it is not surprising that trails of larger groups were most frequently detected.

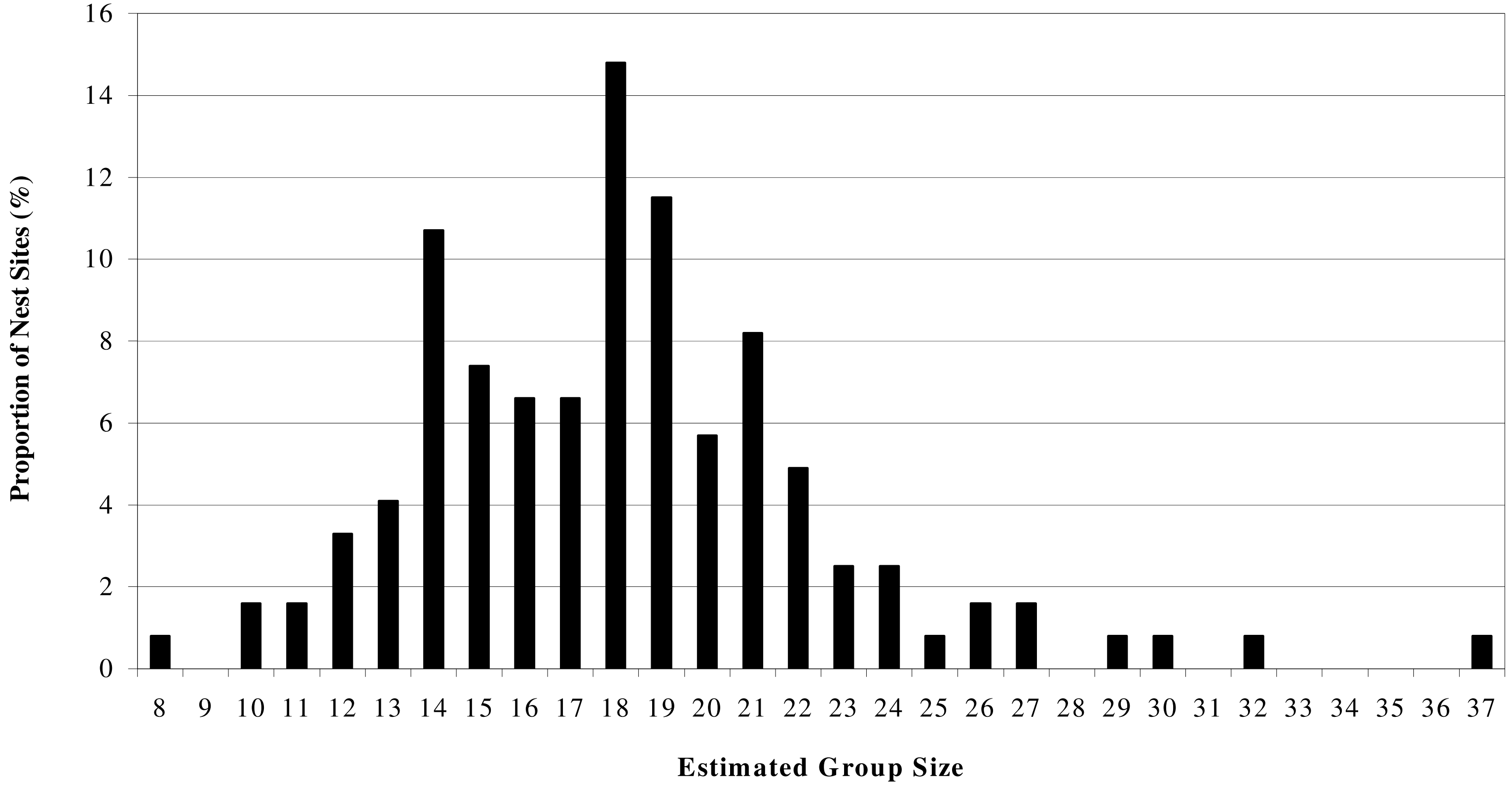

Figure 5.2 Frequency distribution of different gorilla group sizes (estimated from nest counts) at Afi Mountain between December 1997 and April 1999

Number of Groups Inhabiting Afi Mountains

Whether the highly variable group sizes might be explained by the presence of more than one gorilla group on Afi Mountain was examined by comparing nest group sizes across the study site and by conducting a sweep census. Mean estimated group sizes varied little across four sectors within the Afi study group's range (Table 5.1; $X^2 = 5.5$, $p = 0.136$, $df = 3$) and did not significantly differ when considering rows of 1 km by 1 km grid cells singly (means = 16.8 – 19.4 individuals; $X^2 = 4.3$, $p = 0.89$, $df = 9$) or in two consecutive rows (means = 17.2 – 19.1 individuals; $X^2 = 2.4$, $p = 0.67$, $df = 4$). These results suggest that the nest data collected during the present study likely represent the activities of only one gorilla group.

Table 5.1 Afi gorilla nest group size throughout their range (overall) and across different sectors, including standard deviations (SD) and ranges (nest data from December 1997 – April 1999).

	N (nest sites)	MEAN	SD	RANGE
OVERALL	122	18.2	4.5	8 – 37
SECTORS				
SOUTH	34	17.5	3.4	12 – 24
CENTRAL	66	18.8	5.4	8 – 37
WEST	11	15.8	3.2	10 – 22
NORTH	10	18.9	1.2	18 – 22

Table 5.2 and Figure 5.3 summarize the fresh nest sites and trails encountered during the sweep census conducted in February and March 1999. Two areas of Afi Mountain were searched simultaneously: Main Afi covering South, West and Central sectors where most of the gorilla evidence collected during the present study occurred and North Afi covering the North sector, which was not previously thoroughly searched. In February, fresh nest sites (≤ 4 days old) were only recorded in the Main Afi area. At this time no fresh signs were detected in North Afi, though five sites estimated to be approximately 30 or more days old were found, demonstrating that the gorillas were likely present in North Afi during the end of December and beginning of January as described in Chapter Four.

On March 3, a relatively fresh gorilla feeding trail was recorded in the northern portion of the Central sector and was heading toward the North Afi area. The Main Afi area field teams searched the Central sector but found no evidence that gorillas had remained in, or reentered from the North into, the Main Afi area. On March 10, the first relatively fresh signs were encountered in the North, which eventually led to the discovery of the six fresh sites constructed between March 13 and 19; nest group size of these sites was 18 or 19 and was consistent during this time. No fresh signs were recorded in the Main Afi area during this time. Fresh signs in the Main Afi area were later recorded (March 23 – 25) only after the group followed in the North Afi area traveled south into the Main Afi area.

The Olum Hills area was also searched during March 1999 (see Figure 5.1). Even though gorilla feces were found on Olum Hills in 1996 and in spite of thorough and systematic searching, no gorilla signs (old or fresh) were encountered in the Olum area.

This may be due to a fire that devastated more than half of the area in 1997 and appears to have destroyed a significant amount of gorilla food resources. Evidence of chimpanzees, drills and guenons were, however, encountered on Olum Hills.

To summarize, the census provided no definite evidence that more than one gorilla group inhabits the Afi Mountain study area or that gorillas inhabited Olum Hills at this time (though see Discussion for results of more recent censuses).

Table 5.2 Summary of fresh gorilla nest sites (≤ 4 days old) encountered during a census conducted in February – March 1999 on Afi Mountain.

Location (sector)	Age (days)	Estimated Date Made	Nest Group Size
South	2	2/7/99	14
West	2	2/8/99	13
South	4	2/15/99	17
South	2	2/16/99	15
South	2	2/17/99	13
South	4	2/18/99	14
North	2	3/13/99	19
North	1	3/14/99	19
North	2	3/15/99	18
North	1	3/17/99	19
North	2	3/18/99	19
North	3	3/19/99	19
Central	1	3/24/99	13

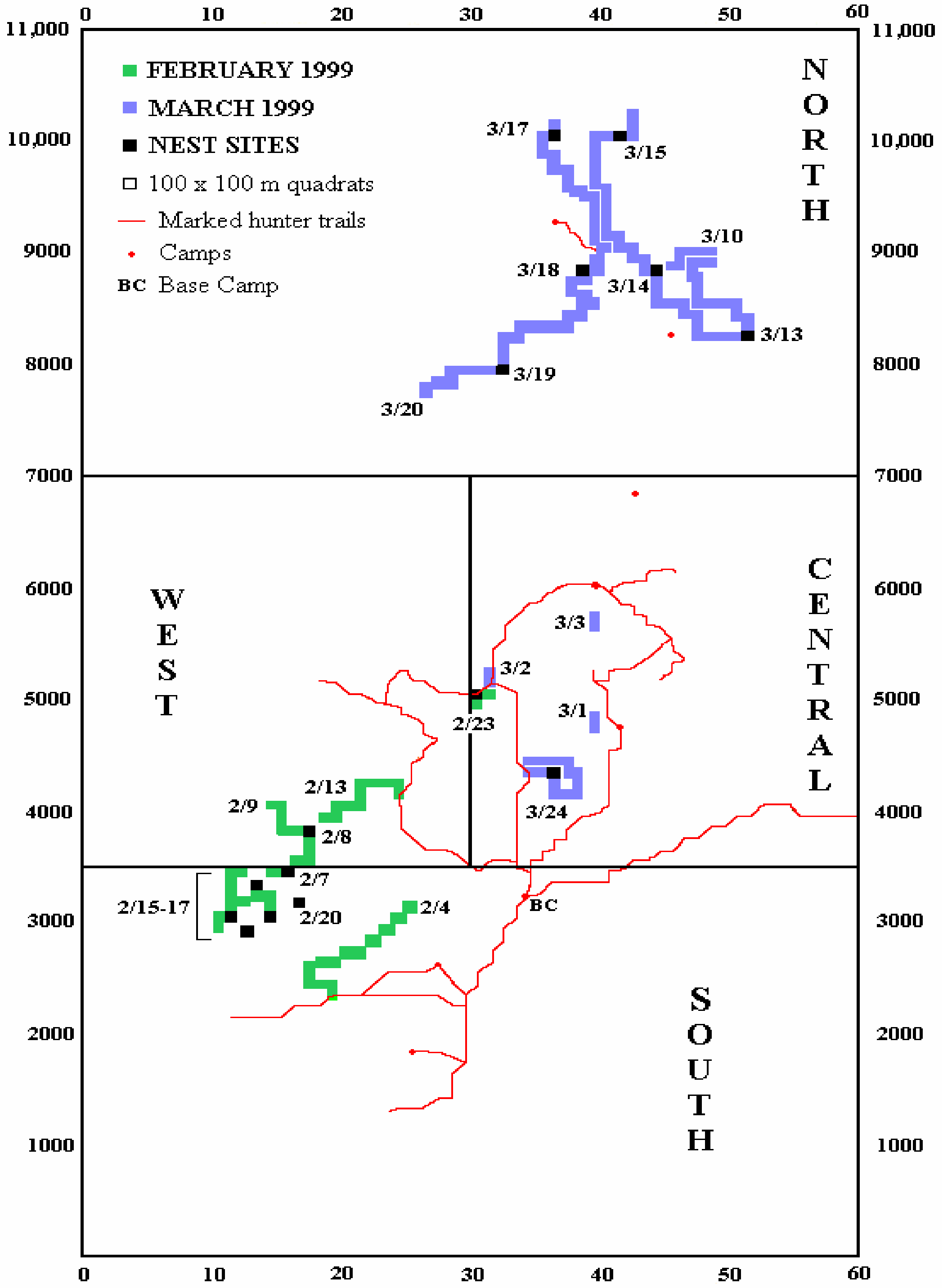

Figure 5.3 Locations of fresh gorilla trails and nest sites (≤ 4 days old) recorded on Afi Mountain during a sweep census conducted in February and March 1999

Group Composition

To estimate the number of silverback males in the Afi study group, only those nest sites that had at least one measurable adult-male sized fecal sample were included in analyses and two different fecal diameters were used to identify adult-male sized nests. Using the criterion employed by western lowland gorilla studies (diameter ≥ 6.5 cm), there was a mean number of 2.7 nests with adult-male sized feces per nest site (SD = 1.6, range = 1 – 7 nests per site, n = 81 sites). The majority of sites (70%) had greater than one adult-male sized nests (2 - 3 adult males at 41% and ≥ 4 adult males at 37% of sites; Figure 5.4). Multiple adult-male nest sites may have occurred more frequently since not all fecal remains present at each site were measurable (mean number of measurable samples per site = 63% SD = 23.7, range = 10 – 100%, n = 81 sites). The above results indicate that there may have been an unusually high number of adult males present in the Afi study group.

To reduce the probability that adult-male numbers were overestimated, data were reanalyzed using a slightly stricter criterion (diameter ≥ 6.7 cm) to identify adult-male nests. Results using this stricter criterion are similar to those based on the smaller fecal diameter (≥ 6.5 cm). Mean number of nests containing adult-male sized feces was 2.0 nests per site and the number varied between 1 and 7 per nest site (SD = 1.3, n = 55 sites). In addition, sites with greater than one adult-male nest were relatively frequent (53% of sites; Figure 5.4). Two and three adult-male sized nests were found at 26% and 15% of sites, respectively, and 11% of sites had greater than four adult-male sized nests.

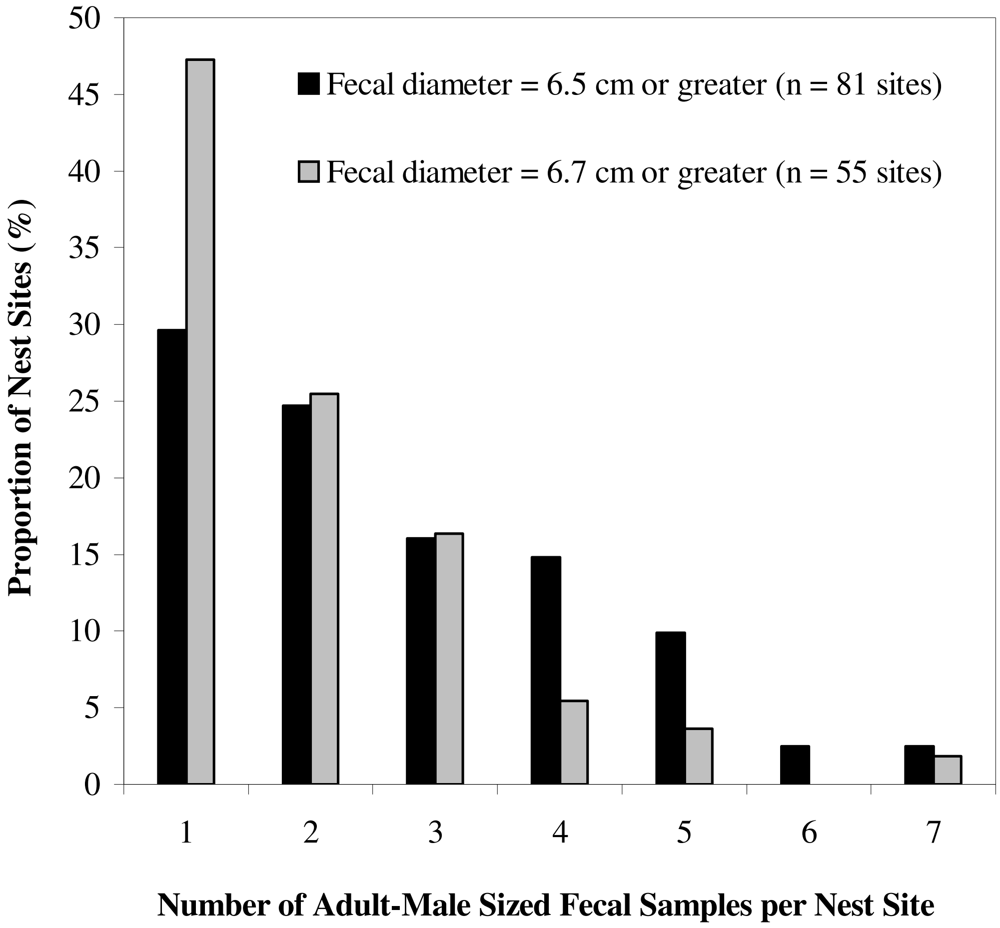

Figure 5.4 Frequency of number of adult-male gorillas per nest site based on fecal samples associated with nests using two different fecal diameter criteria

Figure 5.5 shows monthly variation in number of adult-male sized (diameter ≥ 6.7 cm) nests per site for those months in which adequate samples were available (n ≥ 3 nest sites per month; see figure for sample sizes and standard deviations). During nine months sampled (December 1997, January 1998 and April – October 1998), mean numbers of adult-male sized nests per site were consistently ≥ 2.0, though that of July 1998 was slightly lower (1.75 nests). On October 27 1998, a hunter killed an adult male member of the Afi study group. The number of adult-male sized nests per site was on average less than 2.0 during two months sampled after this incident (November 1998 and March 1999) and was significantly lower than during the months prior to the killing (means = 1.6 and 2.2 nests, respectively; z = 2.17, p = 0.03, n = 11 months). After the adult male's death, the Afi study group remained intact suggesting that another adult male was present and was able to maintain the group's integrity.

Mean estimated group size when 1, 2, or 3 adult-male sized nests were found (19.1, 17.8, and 17.9 individuals, respectively) did not differ significantly from each other ($X^2 = 0.30$, p = 0.87, n = 27, 14, & 8 sites, respectively). But mean group size of sites with 4 – 7 adult-male sized nests pooled (24.2 individuals, SD = 6.6, range = 18 – 37, n = 6) was significantly higher than sites with ≤ 3 adult-male sized nests (18.5 individuals, SD = 4.1, range = 8 – 32, n = 49; z = 47.5, p = 0.007). Number of adult-male nests at a site was positively and significantly correlated with nest group size (r = 0.251, p = 0.009). These results suggest that the number of adult males in the study group may have fluctuated and this may explain some of the variation in nest group size observed.

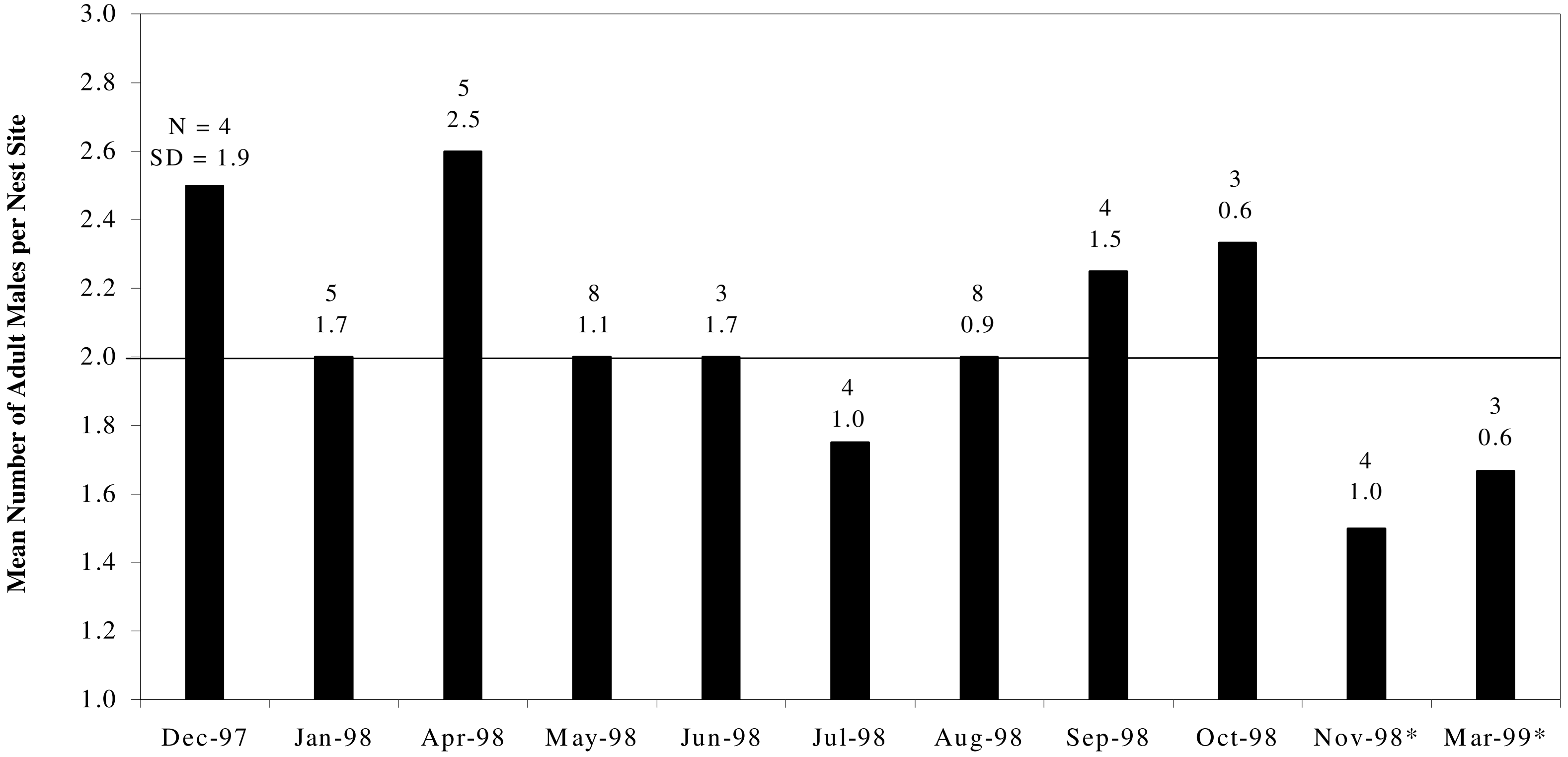

Figure 5.5 Monthly variation in number of adult-male gorilla nests (fecal diameter > 6.7 cm) per site including sample sizes and standard deviations (months with sample sizes of > 2 nest sites are shown only, * months after an adult-male was killed by a hunter)

To estimate numbers of adult females/adolescent males and juveniles, only those nest sites with ≥ 80% measurable fecal samples (n = 24 sites) were used in order not to greatly underestimate their numbers. On average there were 13.2 adult female/adolescent male sized nests (SD = 2.8, range = 6 – 18) and 2.2 weaned juvenile nests (SD = 1.4, range = 1 – 5, n = 14 sites) present at nest sites. During the one time I was able to directly observe the study group, one silverback male, three black-back males, two females and one infant were identified. Thus, based on the above estimates and observation, the Afi group during the present study likely most often contained 18 individuals, including at least two adult males, three black-back males, ten adult females/adolescent males, two juveniles and one infant (though group membership likely varied at times as described below).

Variation Among Consecutive Nest Sites

This analysis examines evidence from consecutive night nest sites to investigate the extent to which the Afi gorillas exhibited flexible grouping behavior. A total of 97 consecutive nest sites (i.e., sites made on consecutive nights) was recorded, producing 73 pairs of consecutive nest group sizes. For the majority of pairs (57 sites, 78.1%) complete nest-to-nest follows were recorded. Complete trails could not be followed for an additional 16 sites; however, based on age and partial trails to/from these sites, they were judged as very likely consecutive. Mean difference between consecutive nest group sizes for complete trails only versus partial trails only was very similar and did not differ significantly (Complete: mean = 3.0, SD = 3.2, range = 0 – 13; Partial: mean = 3.4, SD = 3.4, range = 0 – 11; z = 0.32, p = 0.75). Consequently, the following results are based on consecutive sites with both complete and partial trails between them (n = 73 pairs of sites). Table 5.3 summarizes the frequency distribution of the number of consecutive nest site pairs. A single pair (i.e., two consecutive nest sites) was the most common, followed by 2 consecutive pairs. Three to five consecutive pairs were less common but 6, 7, and 11 consecutive pairs were record once each.

Table 5.3 Frequency of the number of consecutive nest site pairs recorded at Afi during December 1997 and June 1999.

Number of Consecutive Pairs (Number of consecutive nest sites)	**Frequency**
1 (2 nest sites)	9
2 (3 nest sites)	6
3 (4 nest sites)	2
4 (5 nest sites)	3
5 (6 nest sites)	2
6 (7 nest sites)	1
7 (8 nest sites)	1
11 (12 nest sites)	1

Overall mean difference between nest group sizes of consecutive sites was 3.1 nests (SD = 3.2, range = 0 – 13). Figure 5.6 shows the frequency distribution of differences between consecutive nest group sizes. For the majority of consecutive nest sites (n = 43 nest site pairs, 58.9%) group sizes remained relatively stable (i.e., differences between nest group sizes were ≤ 2). For 41.1% of nest site pairs differences between group sizes were ≥ 3 nests, with a mean difference of 6.1 nests (SD = 2.9, range = 3 – 13 nests, n = 30 site pairs), and possibly represent formation of temporary groups (differences of 3 – 6 nests: 27.4% of sites and ≥ 7 nests: 13.7% of sites).

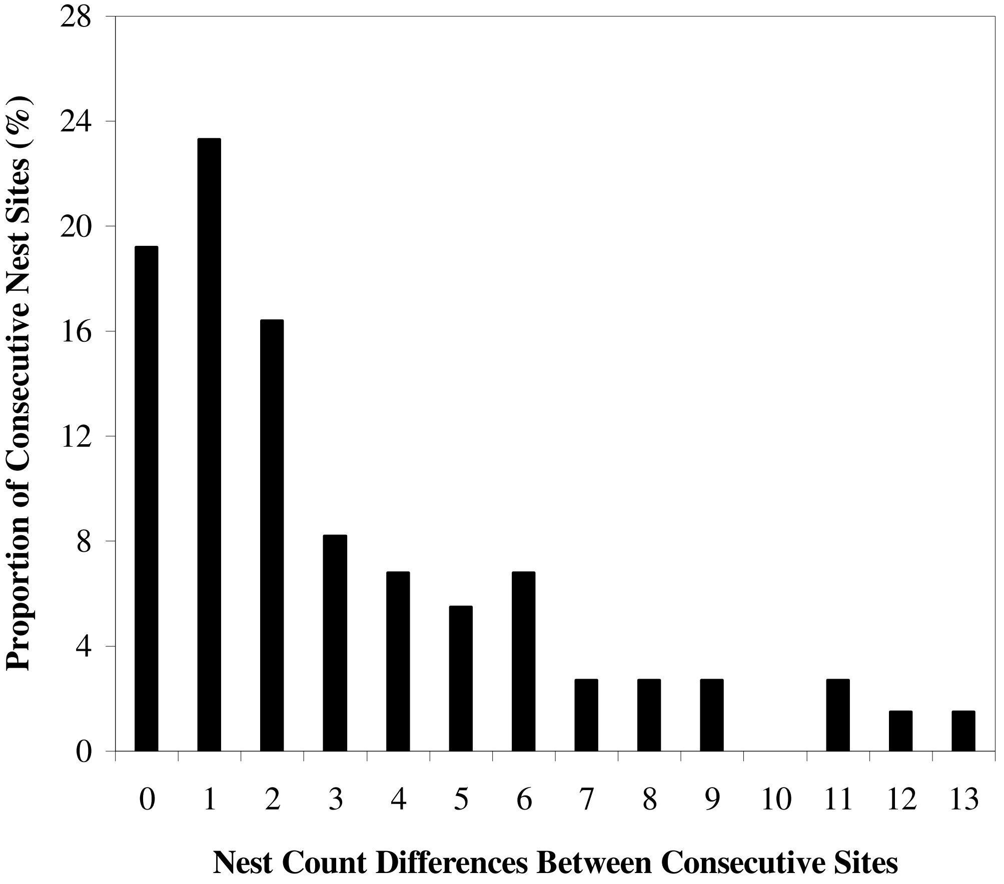

Figure 5.6 Frequency distribution of differences between consecutive gorilla nest group sizes on Afi Mountain based on nest site counts (n = 73 pairs of nest sites)

Table 5.4 shows nest group sizes of consecutive site pairs when the group remained stable and when larger and smaller groups had formed (i.e., differences between consecutive group sizes were ≥ +/- 3 nests). At times nest group size variation was quite erratic, oscillating between larger and smaller sized nest groups from one day to the next or every other day (i.e., August 15 – 21 & August 25 – September 4), and the difference between the largest and smallest group sizes were considerable (9 and 14 nests, respectively). Larger and smaller nest group sizes were maintained for up to 3 and 4 consecutive days on some occasions (i.e., July 5 – 11 & August 25 – September 4). At other times, however, the group remained relatively stable, with nest group size at or near the mean for 4 – 7 days (e.g., January 13 – 18 & September 27 – October 3). When considering nest counts at sites for which ≥ 3 consecutive days were recorded, the average difference between the largest and smallest nest group sizes was 8 nests (SD = 3.7, range = 3 – 14 nests, n = 10 sequences of ≥ 3 consecutive site pairs).

There was one clear instance of the group splitting into smaller subgroups. Two consecutive nights of sites with 23 and 22 nests were followed, on the third night, by two sites of 10 and 12 individuals, 300 m apart (July 28, Table 5.4). Unfortunately, the feeding trail was subsequently lost. On another occasion, two sites with 18 and 8 individuals occurred within 330 m of each other suggesting that supergroup formation had occurred (August 25, Table 5.4). The trail leading from the site of 8 nests intersected the larger group's trail several times and was subsequently lost. The trail from the nest group of 18 led to a site the next night containing 14 nests followed by two consecutive sites of 21 and 20 nests suggesting that some individuals may have temporarily split from the larger group and possibly joined the smaller group.

Table 5.4 Nest group size variability between consecutive site pairs recorded between December 1997 and December 1998 (high fruit consumption months in bold and wet months in italics; * partial trails between sites, ** two nest sites approximately 300 m apart; see Table 5.2 for February and March 1999).

DATE	Nest Group Size	DATE	Nest Group Size	Difference
Dec 15, 16	17, 17	Dec 17	25	+ 8
Jan 13, 14, 15, 16	18, 19, 17, 19	Jan 17 *	24	+ 5
		Jan 18	21	- 3
Mar 19, 20	16, 16			
Apr 01	19	***Apr 02***	15	- 4
Apr 24, 25, 26	12, 13, 11	***Apr 27***	14	+ 3
May 08, 09, 10	23, 23, 21	***May 11 ****	32	+11
May 16	21	***May 17***	30	+ 9
		May 19, 20	17, 17	(-13)
Jun 10	18	***Jun 11 ****	22	+ 4
Jun 21	29	***Jun 22***	16	- 13
		Jun 23 *	27	+11
		Jun 24	21	- 6
Jul 05	21	***Jul 06, 07, 08***	26, 27, 26	+ 5
		Jul 09, 10, 11	18, 18, 19	- 8
Jul 24	17	***Jul 25***	20	+ 3
		Jul 26, 27	23, 22	+ 3
		Jul 28	10 / 12 **	
Aug 15, 16	15, 15	*Aug 17, 18*	20, 18	+ 5
		Aug 19	24	+ 6
		Aug 20	18	- 6
Aug 24	21	*Aug 25*	8 / 18 **	+ 5
		Aug 26	14	- 12
		Aug 27, 28	21, 20	+ 7
		Aug 29, 30	14, 15	- 6
		Aug 31	21	+ 6
		Sep 01	12	- 9
		Sep 02, 03	15, 16	+ 3
		Sep 04	12	- 4
Sep 09	14	*Sep 10, 11*	18, 16	+ 4
Sep 26	14	*Sep 27, 28 29, 30*	21, 19, 19, 21	+ 7
		Oct 01, 02, 03	20, 19, 20	
Oct 17	19	*Oct 18, 19*	16, 18	- 3
Oct 25	18	*Oct 26*	14	- 4
Nov 29, 30, Dec 01, 02	14, 14, 14, 12			

When larger groups formed, nest group sizes were significantly greater than nest group sizes of the previous night (mean = 22.7 and SD = 4.7 nests versus mean = 16.9 and SD = 3.2 nests; $z = 3.3$, $p = 0.001$; $n = 18$ site pairs). When subgroups may have formed, nest group sizes were significantly smaller than those of the previous night (mean = 15.9 and SD = 3.1 nests versus mean = 22.4 and SD = 4.2 nests; $z = 3.6$, $p < 0.001$; $n = 12$ site pairs). When the group was stable, consecutive nest group sizes did not differ significantly (mean = 18.0 and SD = 3.4 nests versus mean = 17.7 and SD = 3.5; $z = 0.32$, $p = 0.75$; $n = 43$ site pairs).

To summarize, whereas the Afi study group often remained stable with consecutive nest group sizes of 16 – 20 nests, its membership also likely varied as indicated by the fluctuations between larger and smaller nest group sizes observed. The results suggest that the Afi gorillas may exhibit a flexible grouping pattern where at times additional individuals, possibly members of a smaller group and/or adult males, flowed in and out of the larger study group and/or some members of the study group (3 – 7 individuals) split from the group forming a temporary subgroup. Other possible explanations for the variation in nest group sizes observed are explored below.

Frequency of Grouping Patterns: Variation Across Seasons and Sectors

This section investigates whether the Afi gorillas' flexible grouping pattern suggested above may be related to intragroup feeding competition associated with fruit consumption and/or low herb availability. Nest group size varied throughout the year, but relative frequency of stable and unstable consecutive nest group sizes varied across periods of high and low fruit consumption and two sectors within the gorillas' range that differed in availability of important gorilla herb foods (Central and South)[11]. Number of unstable consecutive nest group sizes was highly and significantly correlated with number of consecutive nest site pairs recorded monthly ($r = 0.864$, $p < 0.001$). A greater number of consecutive nest sites were recorded and more importantly there was on average a greater number of consecutive pairs recorded at a time during low versus high fruit consumption months ($n = 40$ vs. 33 site pairs and 4.0 vs. 2.2 pairs in a row, respectively). Consequently, there was a greater probability of observing group instability during low fruit consumption months. Therefore, the following results should be interpreted with caution (see below for further details).

Figure 5.7 presents the percentage of consecutive nest site pairs that remained stable (differences between nest group sizes were +/- 2 nests) and those that were unstable (differences between nest group sizes were ≥ 3 nests) during periods when the gorillas consumed large amounts of fruit compared to when they relied heavily on non-fruit vegetation (high versus low fruit consumption periods). At first sight, these results suggest that the Afi group was unstable more frequently during the low fruit consumption period (45.0% of consecutive nest site pairs) compared to during the high fruit consumption period (36.4%). These results, however, are likely misleading due to differences in sample sizes described above. The probability of observing instability was particularly low during the high fruit consumption months of February and March when no group instability was recorded. A relatively small sample was available for February and March ($n = 3$ and 5 site pairs, respectively) and number of consecutive pairs recorded at a time ranged between 1 and 2 days only; hence, the data are likely not representative for these two months.

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[11] Small sample sizes for West and North sectors did not allow analysis for these sectors

When February and March were removed from the analysis, frequency of unstable nest group sizes during high fruit consumption months (April – July, 48.0%) was similar to the frequency during low fruit consumption months (45.0%; Figure 5.7). Grouping patterns did, however, vary when the gorillas utilized Central and South sectors. The frequency of group instability occurred as predicted by the relative contribution of fruit and non-fruit vegetation in the gorillas diet when they utilized the Central sector. When utilizing the Central sector during high fruit consumption months, frequency of unstable nest group sizes was greater than when the gorillas used this sector during the period of low fruit consumption (47.8% versus 21.1%, Figure 5.7).

By contrast, when the gorillas utilized the South sector during low fruit consumption months, consecutive nest group sizes were frequently unstable (66.7%) and group instability was greater than when the gorillas used the Central sector during this time (21.1%) as well as during the period of high fruit consumption (47.8%, Figure 5.7) [12]. The high frequency of group instability when using the South sector likely explains the higher overall frequency during the low fruit consumption period and may be related to this sectors lower herb availability compared to the Central sector. The above results suggest that the variable grouping pattern Afi gorillas may exhibit may be related to high intragroup feeding competition associated with consuming widely dispersed fruit and herb resources.

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[12] Small sample size did not allow analysis for the South sector during high fruit consumption months.

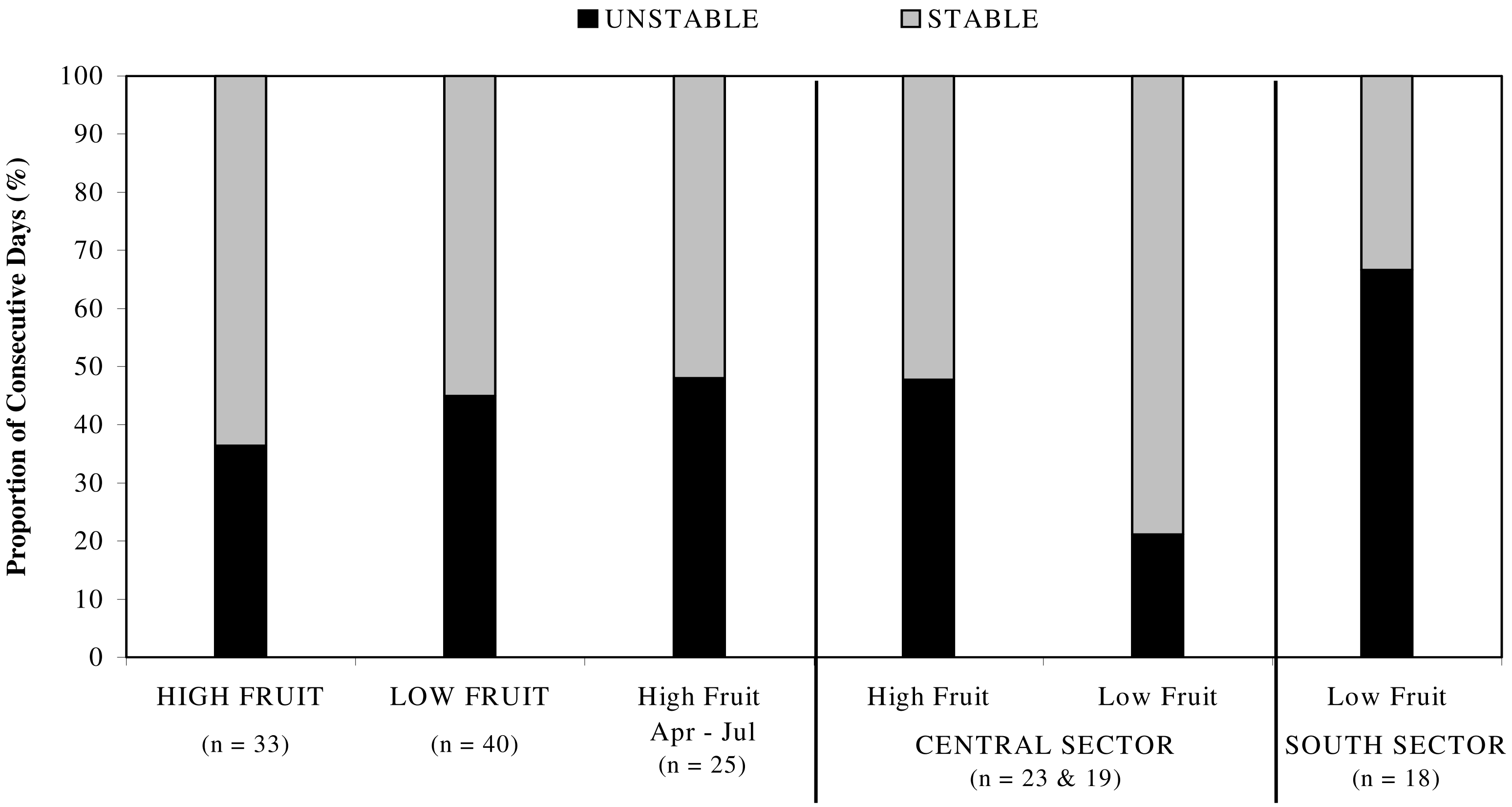

Figure 5.7 Variation in relative frequency of unstable and stable Afi gorilla nest group sizes across periods of low and high fruit consumption months and sectors (n = 73 consecutive site pairs)

Other Possible Factors Producing Nest Group Size Variation

It is unlikely that the building of multiple nests can explain the group size variability observed, especially as I excluded ground nests that did not contain feces and/or hairs. In addition, proportions of arboreal nests per site did not significantly differ between nest group sizes that were larger (≥ 21), smaller (≤ 15), or within +/- 2 of mean group size (means = 44.1%, 59.4%, and 55.1% arboreal nests per site, respectively; Kruskal-Wallis: $X^2 = 3.8$, $p = 0.15$, df = 3). This indicates that including all arboreal nests in the analysis, even when feces were not present below, likely does not explain relatively large nest group sizes. This result also suggests that nest group size did not vary due to observers failing to detect arboreal or bare ground nests, since at Afi bare ground nests are most often associated with sites made mostly of arboreal nests in forest habitats. It is difficult to know whether other types of nests were undetected, but when smaller numbers of nests were present, greater efforts were made to search the area surrounding the nest sites.

Juvenile nesting behavior varied during the present study. At 49.5% of nest sites at least one juvenile-sized fecal sample was found along with that of an adult within relatively large nests, suggesting that juveniles slept in adult nests rather than constructing their own on some occasions. One juvenile was recorded to have slept in an adult nest at 30.7% of sites and 2 – 5 juveniles at 18.8% of sites. To determine if this may explain any of the group size variation observed, mean estimated nest group sizes when different numbers of juveniles slept with adults were compared. Due to small sample sizes, sites at which 2 – 5 juveniles slept with adults were pooled.

Mean group sizes differed significantly among sites with 0, 1, or 2 – 5 juveniles in adult nests ($X^2 = 14.7$, $p = 0.001$; n = 51, 31, & 19, respectively). Pair-wise comparisons demonstrate that group sizes at sites with 2 – 5 juveniles within adult nests (mean = 21.6 individuals, SD = 6.3, range = 10 – 32) was significantly greater than when no or only one juvenile slept in adult nests (0 juveniles: mean = 17.4 individuals, SD = 4.5, range = 10 – 37; 1 juvenile: mean = 17.9, SD = 4.3, range = 13 – 30 individuals). In addition, the number of indications that juveniles slept in adult nests was positively and significantly correlated with group size ($r = 0.238$, $p = 0.001$). These results are contrary to what would be expected if juveniles building their own nest on some occasions, and sharing an adult nest at other times, produced the observed nest group size variation among consecutive sites.

To investigate whether mistaking day nests for night nests explains any of the group size variability observed, variation among consecutive nests was re-analyzed after nests containing hairs only were removed from the database. Hairs but not feces were present in a total of 46 individual nests, at 21 different consecutive nest sites, including those sites where gorillas remained in the surrounding area for most of the subsequent day. Eliminating these nests from the analysis did not produce a significant change in whether nest group sizes between consecutive site pairs remained stable, increased or decreased. For the majority of nest site pairs affected (71.4%), whether nest group sizes remained stable or were unstable did not change. Only three site pairs (14.3%) changed from being unstable to stable, but this was counteracted by the fact that three different site pairs changed from being stable to unstable. In addition, differences between the nest group sizes of yet another three site pairs increased from 3 to 7 nests. These results suggest that while mistaking day nests for night nests may have occurred occasionally, it likely does not explain the majority of group size variation among consecutive nest sites.

DISCUSSION

Afi Gorilla Group Size

The nest data collected during the present study likely represent the activities of one gorilla group. Analyses of mean nest group sizes across different sectors and different numbers of 1 km by 1 km grid cells showed no indication that nest sites with differing numbers of individual nests were concentrated in any particular sectors and nest group size was highly variable throughout the study area. Most nest sites included 14 – 22 nests and the mean estimated group size was 18.2 nesting individuals (range = 8 – 37). Bergl (2006) conducted genetic analyses of DNA extracted from feces collected at nest sites of the Afi study group in 2002 and confirmed the presence of at least 18 unique individuals (Bergl & Vigilant 2007).

The Afi study group size is exceptional compared to most other Cross River gorilla groups; on average these include 3.6 to 5.4 nesting individuals and nest sites rarely contain greater than 13 nests (Nwufoh 2001; Oates et al. 2003; Oates et al. 1990; Obot et al. 1997; Sarmiento & Oates 2000). Group size at Afi is also at the upper end of group size ranges at western lowland, Grauer's, and mountain gorilla sites, where mean (nest) group size ranged between 6.6 and 14 individuals (see Table 6.4). Group sizes at Lossi within the Odzala National Park, Republic of Congo, are also relatively large (mean = 14, range = 6 – 32) (Bermejo 1997) and groups larger than 15 individuals are more common for mountain gorillas than gorilla groups of other subspecies (Steklis & Gerald-Steklis 2001).

Bermejo (1999) suggests that large groups found at Odzala National Park likely occur due to higher herb densities at this site compared to other lowland sites. Other investigators have also suggested a positive relationship between herb densities and gorilla biomass (Nishihara 1991; White 1994). Preliminary impressions of different Cross River gorilla habitats suggests that herb densities are relatively high at Afi and may be one explanation for the larger group size found at Afi and at least one Cameroon subpopulation (J. Sunderland-Groves, personal communication).

Composition of the Afi Study Group

Based on diameter of feces associated with nests and one instance of direct observation, the Afi study group was estimated to most often include at least two adult males, ten females, three black-back males, two juveniles and one infant (though group membership likely varied at times). Several lines of evidence suggest that the Afi gorilla study group contained at least two adult-male silverbacks and number of adult-males may have fluctuated. Based on adult-male sized feces associated with nests, two or more adult-male nests were present at most sites sampled. Numbers of adult male nests per site were highly variable (range = 1 – 7) and were positively correlated with nest group size suggesting that at times additional males were present. Gorilla groups containing only one adult male silverback typically disintegrate after the male’s death and females subsequently join established groups or lone males (Robbins 2001; Stewart & Harcourt 1987; Stokes et al. 2003) (cf. Yamagiwa and Kahekwa, 2001). On the other hand, gorilla groups containing multiple adult males tend to remain intact following the death of one of the adult males. Females likely seek out the protection of adult males as a strategy to avoid infanticide and predation (Harcourt 2001; Harcourt & Greenberg 2001; Sterck et al. 1997; Stokes et al. 2003; van Schaik 1989; Watts 1996, 2003; Yamagiwa & Kahekwa 2001). The fact that the Afi study group did not disintegrate following the death of an adult male further supports the likelihood that it contained at least two adult males.

The numbers of adult-male nests at sites were relatively high and variable when employing the criterion to identify adult-male nests used at other western gorilla study sites (fecal diameter ≥ 6.5 cm) (Goldsmith 1996; Remis 1994; Tutin et al. 1995) and when using a slightly stricter criterion (≥ 6.7 cm). In addition, the death of an adult male was detected using fecal diameter measurements; mean number of adult-male sized nests was significantly lower during months after the adult male was killed. This suggests that the results may reflect a real phenomenon rather than the unreliability of using fecal diameter to determine age-class of individual gorillas.

Do Afi Gorillas Exhibit a Flexible Grouping Pattern?

Several lines of evidence suggest that the nest group variability observed at Afi is best explained by flexible grouping behavior. Nest group size between consecutive sites was highly variable, with differences between consecutive site pairs ranging between 0 and 13 nesting individuals. Afi nest group size often remained stable (differences of ≤ 2 nests between site pairs) between consecutive sites that contained 16 – 20 nests, but also fluctuated between larger and smaller group sizes (≥ 21 and ≤ 15 nests, respectively) relatively frequently. Consecutive nest group sizes differed by ≥ +/- 3 nests on 41% of occasions and differed by ≥ 7 nests on 14% of occasions.

Nest group size variability continued to be observed at Afi during the years following the present study. Various researchers collected nest data while conducting gorilla monitoring exercises between July 1999 and May 2002, and yearly censuses during 2004 through 2006 (Coleman 1999, 2000; Inaoyom 2005, 2006; Kortenhoven 2002; Ransom 2004; White 2001). Results for these additional years, were similar to those of the present study; nest group sizes of the Afi study group were 18.3 nesting individuals on average but varied between 8 and 29 nests (SD = 3.9 nests, n = 70 nest sites). Based on ten consecutive nest site pairs recorded during 1999 through 2002, differences between nest group sizes varied between 0 and 8 nests and on the 60% of the occasions that nest group sizes differed by ≥ +/- 3 nests, mean differences were 5.7 nests (SD = 2.1, range = 3 – 8 nests). This additional evidence suggests that group size variability is a typical characteristic of the Afi study group.

Frequency of nest group variability at Afi during the present study (41%) was much greater than that found for a stable group of western lowland gorillas at Lopé, where 9% and 15.5% of sites had nest counts ≥ +/- 3 nests of actual group size during two 2-year periods of time (Tutin et al., 1995). Nest group size variability at Lopé was attributed to the production of multiple nests by single individuals and undetected nests by researchers. Based on analyses conducted during the present study, these factors as well as others, such as variability in juvenile nesting behavior and mistaking day nests for night nests, may have occasionally produced variability. However, it is unlikely that these factors explain the majority of the nest group size variability observed at Afi.

Consequently, the possibility that Afi gorillas exhibit flexible grouping patterns remains a strong possibility.

Frequency of relatively high nest group size variability at Afi during the present study (41%) was similar to frequencies recorded (58% and 31%) during two studies of gorillas at Bai Hokou, which attributed this variability to possible subgrouping behavior (Goldsmith 1996; Remis 1994; Remis 1997a). Possible subgrouping behavior at Bai Hokou was recorded only for gorilla groups containing two adult silverback males so that each subgroup included one adult male. At gorilla study sites where multi-male groups are absent or rare, no clear evidence of subgrouping behavior has been observed as predicted given that adult-males are a focal point in gorilla societies as described above (also see Chapters 1 and 6). The presence of at least two adult males in the Afi study group provides for the opportunity to form two separate subgroups similar to the Bai Hokou groups.

The pattern of nest group size variability at Afi, however, differs from that found at Bai Hokou where clear instances of the study group(s) splitting and rejoining were observed (34 and 29 occasions; Remis, 1994 and Goldsmith, 1996, respectively). For example, when variability between consecutive nest group sizes of the Bai Hokou gorilla group studied by Remis (1994 and 1997, Group C) occurred, sites contained fewer nests than the typical group size of 13 individuals and when it was possible to locate both subgroups, sites were separated by distances of 500 m to more than one kilometer. Only one such clear instance of subgrouping was observed at Afi and consecutive nest group sizes often oscillated between sizes greater than and smaller than the typical Afi group size of 18 individuals; nest sites of the Bai Hokou group rarely contained greater numbers of nests than the typical group size. The Afi data suggest that members of a small-sized gorilla group may have joined the Afi study group at times and on other occasions members of the study group may have temporarily traveled separately or joined this other smaller group. This pattern, however, is incongruent with the census results that did not detect the presence of any additional gorilla groups within the Afi Mountain study area.

Nonetheless, evidence collected while tracking the Afi study group during the present study and other censuses conducted more recently indicate that at least one additional smaller gorilla group of 6 – 8 individuals may indeed inhabit Afi Mountain. When the Afi study group size was highly variable during the present study, consecutive nest group sizes differed on average by 6 nests and differences between smallest and largest nest group sizes of consecutive sequences of ≥ 3 site pairs was on average 8 nests. Two fresh nest sites containing 8 nests can likely be attributed to a gorilla group other than the study group. One such nest site occurred 300m from a site of the same age containing 18 nests and nest group sizes during the subsequent 10 consecutive days were highly variable (August 25 – September 4, Table 5.4). The second site of 8 nests did not occur nearby a larger nest site; no additional nests were found after several hours were spent searching the area surrounding this smaller nest site or along the feeding trail from the site followed for approximately one kilometer. In addition, two one-week old sites containing two and four nests were also found during the present study.

Small nesting groups were also encountered during the sweep censuses conducted yearly between 2004 and 2006 [Ransom 2004: 3 nests (2 – 3 days old) and 5 nests (1 week old); Inaoyom 2005: 4 nests (1 day old) and 5 nests (3 weeks old); Inaoyom 2006: 3 nests (2 – 3 weeks old) and two sites with 8 nests (1 – 2 weeks old)]. These censuses were conducted six or more years after the present study; consequently the smaller nest groups may represent newly formed group(s). But this is unlikely since similar small-sized nest groups were recorded during the present study and the Afi study group appears to have subsequently remained relatively stable or may have increased slightly; the majority of nest sites recorded during the recent censuses contained 19 nests on average (range = 14 – 29 nests). Small nest groups were probably not recorded between 1999 and 2003 because conservation activities were the main focus of the Afi project during this time so gorilla tracking occurred only sporadically and only three search teams conducted censuses compared to the 5 – 6 teams of the recent censuses (Coleman 1999, 2000; Kortenhoven 2002; White 2001).

Though the present study cannot conclusively demonstrate that the Afi group exhibits a flexible grouping pattern, the evidence for such a pattern is highly suggestive. Nest group size variation at Afi is probably in significant part the result of temporary supergroup and/or subgroup formation and/or fluctuating numbers of adult males. The frequency of possible flexible grouping behavior at Afi was relatively high when the gorillas consumed large amounts of fruit and is congruent with results of other primate studies, which suggest that flexible grouping patterns are a response to high intragroup feeding competition associated with consuming foods with a clumped distribution such as fruit (Goldsmith 1996; Remis 1994; Remis 1997a; Symington 1990; White 1992; Wrangham 1979; Wrangham 1986). Results of the present study suggest that flexible grouping patterns at Afi may also be related to high intragroup competition associated with consumption of herb foods that have widely scattered distributions (i.e., *Anchomanes difformis*) or occur in widely dispersed patches. How intragroup feeding competition as well as other factors, such as predator pressure, dispersal patterns and isolation, may be influencing grouping patterns of the Afi group are discussed further in Chapter Six.

CHAPTER SIX – CONCLUSION:

How Do The Gorillas Of Afi Compare With Other Populations?

INTRODUCTION

Much of the observed subspecific variation observed in gorilla diet, ranging behavior and grouping patterns can be attributed to differences in habitat, particularly the spatial and temporal distribution of food resources. Several aspects of the Afi gorillas' habitat, diet, and ranging behavior are generally similar to western and Grauer's gorillas inhabiting lowland forests. Herbaceous vegetation at Afi is less abundant and evenly distributed, and fruit is more abundant, than in the montane habitats of mountain gorillas and of Grauer's gorillas at Kahuzi. The Afi gorillas' staple diet consists mostly of herbaceous vegetation, but they also consume large amounts and a wide variety of fruit when available. Fruit consumption by Afi gorillas varies positively with temporal availability of fruit and influences ranging behavior in a manner similar to what has been reported for lowland gorillas. During periods of fruit scarcity, Afi gorillas rely more heavily on non-fruit foods, such as herbaceous vegetation, leaves, and bark. Several aspects of Afi gorillas' diet, ranging behavior, and grouping patterns do, however, differ from lowland gorillas and these differences are likely related to Afi's unique habitat.

The Afi gorilla habitat differs from the habitats of western lowland, Grauer's and mountain gorilla populations in several important ways (see chapter two). Compared to other gorilla habitats, Afi receives two times more annual rainfall yet the Afi dry season, lasting five months, is prolonged and more severe; dry seasons at all other gorilla study sites last no longer than three months. This extreme rainfall pattern appears to influence temporal availability of fruit, which at Afi does not strictly coincide with seasonal variation in rainfall and thus, differs from the habitats of western lowland and Grauer's gorillas. Periods of high and low fruit availability in western lowland gorilla and Grauer's lowland gorilla habitats generally coincide with wet and dry seasons, respectively (Doran et al. 2002; Goldsmith 1996; Nishihara 1995; Remis 1997b; Tutin et al. 1991; Yamagiwa et al. 1994). For Grauer's gorillas living in the montane habitats of Kahuzi, on the other hand, fruit availability is predominantly high during the dry season (Yamagiwa & Basabose 2006; Yamagiwa et al. 2005).

Herb availability, specifically the spatial distribution and relative abundance of individual species, was found to differ between Afi and western lowland gorilla study sites. Overall herb stem density is similar at Afi and lowland gorilla habitats where herbs tend to have a clumped distribution; however, herbs are concentrated in dense patches to a greater extent at Afi. Whereas the most commonly available herb at western lowland gorilla sites, for which data are available, is *Haumania* (Family Marantaceae), the most common herbs at Afi are species of *Aframomum* (Family Zingiberaceae), which occur at low densities at western lowland gorilla sites. These differences in herb availability between Afi and western lowland gorilla habitats are likely related in part to Afi's complex topography.

Afi Mountain contains a series of ridges with rocky peaks at altitudes of 900 to 1,300m and steep slopes that converge forming deep valleys (800 – 200 m) between each ridge. This complex topography produces relatively frequent naturally occurring disturbances (e.g., fallen trees, rock slides) that create large forest canopy gaps providing an opportunity for the growth of herbs, particularly *Aframomum*. Most western lowland and Grauer's lowland gorilla populations occur at altitudes below 500m. The altitudes at which some Grauer's lowland gorilla populations live are similar to Afi (Itebero: 600 – 1,300 m), but Grauer's montane gorillas at Kahuzi occur at higher altitudes than Afi gorillas (2,050 – 2,350 m; see Table 6.1).

Afi's complex topography also appears to produce variation in herb food availability within the Afi study site. The frequency of light gaps and the overall density of herbaceous vegetation are positively related to altitude, though this relationship differed for individual herb species. Some herb species, particularly *Aframomum*, are most abundant at relatively high altitudes, but other herb species are more abundant at intermediate or lower altitudes. In addition, availability of Afi gorilla herb and tree foods (e.g., density, relative abundance of individual species) differed between sectors within their range (i.e., South, Central, West, and North) and these differences are likely related to variation in altitude across these sectors.

The following sections provide a summary of the Afi gorillas' diet, ranging behavior, and grouping patterns and their relationship to characteristics of the Afi Mountain's unique habitat. At the same time, comparisons with other gorilla populations are provided to better understand where Afi gorillas fit within the currently known range of gorilla socioecological variation.

COMPARISON OF GORILLA DIETS

Table 6.1 compares aspects of gorilla diets at Afi, four western lowland, two Grauer's, and two mountain gorilla study sites. Data for gorilla populations at all study sites represented, except mountain gorillas in the Virungas, are based on indirect evidence gathered from fecal samples and feeding remains (methods employed at western gorilla studies are summarized in Rogers et al., 2004). Figures for the Bwindi mountain gorilla population are from two studies of one gorilla group living at relatively high altitudes (2,100 – 2,500m) (Ganas et al. 2004; Stanford & Nkurunungi 2003) and one study including information for two additional groups living at lower altitudes (1,450 – 1,800 m) (Ganas et al. 2004). Results from the two studies differ so they are presented separately.

The following comparisons are based on Rogers et al. (2004), sources cited in Table 6.1, and unpublished study site summaries compiled for the Western Gorilla Conference, which took place at the Max Planck Institute in Leipzig, Germany, May 2002. Additional sources are cited below where appropriate.

Overall Composition

The overall composition of the Afi gorillas' diet (in terms of total number of food items and plant species eaten) is similar to that of gorilla diets at western sites. Diets of Afi, western and Grauer's gorillas tend to be more diverse than mountain gorilla diets, though there is a marked effect of study length (Rogers et al. 2004). The actual number of species in the diet is probably larger than reported at sites where studies have been relatively short (Afi, Mondika, Ndoki, Bwindi, and especially Itebero). Studies of other western and Grauer's gorilla populations have occurred over many years and numbers are not likely to increase with further sampling.

Table 6.1 Comparison of gorilla diets at nine sites, including the total number of food items, number of plant, invertebrate and fruit species, percent of fecal samples containing fiber, leaves and fruit, and mean number of fruit species per month and per fecal sample (data from Rogers et al. (2004) and as specified, and based on indirect evidence unless specified; ---, no data available; P = present).

Study Site	***Altitude* (m)**	**No. of Food Items**	**Number of Species Eaten**			**Percent of Fecal Samples Containing**			**Mean No. of Fruit Species**	
			Plant	**Insect**	**Fruit**	**Fiber**	**Leaves**	**Fruit**	**Per Month**	**Per Sample**
Cross River gorillas										
Afi Mountain, Nigeria [1]	200 - 1300	216	168	0	100	100	98.6	90.2	17.3	2.5
Western lowland gorillas										
Lopé, Gabon [2] *	200 - 700	223	157	7	100	98.3	90.1	96.7	14.1	3.1
Bai Hokou, CAR [3] *	300	230	129	9	87	97	91	97.7	14.4	3.4
Mondika, CAR/Congo [4]	Lowland	127	100	P	70	----	----	99.9	10	3.5
Ndoki, Congo [5]	200 - 400	182	152	4 +	115	----	----	n/a	17.0	3.0
Grauer's gorillas										
Itebero, DRC [6]	600 - 1300	194	121	7	48	----	----	89.0	----	----
Kahuzi, DRC [7]	2050 -2350	236	116	3	44	----	----	53.2	----	0.80
Mountain gorillas										
Bwindi, Uganda [8] **	1450 -2500	133	140	1	36	----	----	47.2 [70 / 82]	(3.1) (6.6 / 7)	2.2 (0.85) (1.1 / 1.0)
Virungas, Rwanda [9] (observations only)	2600 -3700	106	62	1	5	----	----	----	----	----

[1] (Present Study; Oates et al., 2003); [2] (Rogers et al. 1988; Tutin & Fernandez 1993b; Williamson 1989; Williamson et al. 1990); [3] (Goldsmith 1996; Remis 1997b); [4] (Doran et al. 2002); [5] (Kuroda et al. 1996; Nishihara 1995); [6] (Yamagiwa et al. 1994); [7] (Yamagiwa & Basabose 2006; Yamagiwa et al. 2005; Yamagiwa et al. 1996); [8] (Ganas & Robbins 2004; Ganas et al. 2004; Stanford & Nkurunungi 2003); [9] (Watts 1984, 1989)

* Percent of fecal samples containing fruit, and mean number of fruit species per month and sample, are averages of results from studies cited.

** Parentheses: data for the high altitude group from Ganas et al., 2004. Brackets: data for two lower altitude groups (1,450 – 1,800m) and are percentages of observation days gorillas consumed fruit.

Insectivory

One major difference between the Afi gorillas' diet and that of other gorilla populations is the lack of invertebrate consumption at Afi (Table 6.1, column 4). By contrast, gorillas are known to deliberately search out and consume invertebrates at western lowland, Grauer's, and Bwindi mountain gorilla study sites (Carroll 1996; Deblauwe et al. 2003; Ganas & Robbins 2004; Nishihara & Kuroda 1991; Remis 1997b; Tutin & Fernandez 1983, 1992; Williamson et al. 1990; Yamagiwa et al. 1991). Virunga mountain gorillas and Grauer's gorillas inhabiting montane forests at Kahuzi also consume insects but do so rarely (Harcourt & Harcourt 1984; Watts 1989; Yamagiwa & Basabose 2006). No evidence that Afi gorillas consume insects was found in fecal samples or along feeding sites during the present study.

Fruit Consumption

Fruit availability and level of frugivory (the diversity of fruit species eaten and the frequency of fruit consumption) vary across sites and are inversely related to altitude. Fruit availability and fruit consumption is lowest for mountain gorilla groups in the Virungas where altitudes are highest (2,600 – 3,700m), intermediate for Bwindi mountain gorilla and Kahuzi Grauer's gorillas that live at intermediate altitudes (1,450 – 2,500 m) (Nkurunungi et al. 2004), and highest for western and Grauer's gorillas inhabiting lowland forests with altitudes lower than 1,300 m. Among lowland gorillas, altitudes and frequency of fruit consumption are most similar for Afi gorillas and lowland Grauer's gorillas at Itebero. The percentage of gorilla fecal samples containing fruit at Afi and Itebero (90.2% and 89.0%, respectively) is lower than found for western lowland gorillas at Lopé, Bai Hokou, and Mondika (96.7 – 99.9%; Table 6.1, column 8). Whereas the mean number of fruit species eaten per month is highest at Afi (17.3), the mean number of fruit species per fecal sample at Afi (2.5) is lower than western lowland gorilla populations (3.0 – 3.5); no comparable data are available for Itebero gorillas. This evidence suggests that Afi, and possibly Itebero, gorillas consume fruit less frequently than western lowland gorillas.

Fruit consumption (based on mean number of fruit species per fecal sample) of western lowland gorillas at Lopé, Bai Hokou, Mondika and Ndoki positively correlates with fruit availability, which positively correlates with rainfall, and is inversely related to measures of non-fruit vegetation consumption (Doran et al. 2002; Goldsmith 1996; Nishihara 1995; Remis 1997b; Tutin et al. 1991). Though considerable variation in fruit availability has been observed (Remis 1994, 1997b; Tutin & Fernandez 1993b, c; Tutin et al. 1991; Tutin et al. 1997), the period of lowest fruit availability and consumption at these western lowland gorilla sites tends to occur during dry season months. Consequently, seasonal variation in the diet of western lowland gorillas is traditionally described in terms of dry versus wet seasons that correspond to low and high periods of fruit consumption, respectively.

Whereas fruit consumption was positively correlated with fruit availability at Afi, periods of low and high fruit availability and consumption do not strictly correspond to seasonal variation in rainfall. The period of fruit scarcity at Afi lasts six months (i.e., low fruit consumption period, August – January) during which time fruit consumption is significantly lower than in the remaining months of the year (i.e., high fruit consumption period, February – July). During the fruit scarce period compared to the high fruit consumption period, Afi gorillas consumed a lower number of fruit species (mean number of fruit species per fecal sample = 1.3 versus 3.7), ate fruit less frequently (percentage of fruit feeding sites = 2.8 vs. 18.6%), and consumed lower amounts of fruit (mean percent of fruit fecal weight per fecal sample = 6.6 vs. 51.7% and mean fruit pulp volume eaten per fecal sample = 36.1 vs. 608.2 cm^3).

The Afi gorillas experience a prolonged and more severe period of fruit scarcity compared to western lowland gorillas. Monthly variation in mean number of fruit species per fecal sample was employed to compare the length and severity of fruit scarcity across sites. This measure is available from most study sites where gorillas consume fruit and generally correlates with the various fruit abundance scores used in these studies. At Afi, the mean number of fruit species per fecal sample was less than 2.0 during all six months of the fruit scarce period (range = 0.7 – 1.6; Table 3.4). By contrast, the number of months in which the mean number of fruit species was less than 2.0 ranged between four months at Ndoki (Nishihara 1995), two – three months at Lopé and Bai Hokou (Goldsmith 1996, 1999; Remis 1994, 1997b; Tutin et al. 1991) and no months at Mondika (Doran et al. 2002).

During the period of fruit scarcity, Afi gorillas also consume fruit less frequently than western lowland gorillas at Lopé, Bai Hokou, and Mondika and this accounts for the overall lower frequency of fruit consumption observed for Afi gorillas described above. Most fecal samples collected during fruit scarce months at Lopé and Bai Hokou contained fruit remains (91% and 95%, respectively; Rogers et. al, 1988; Remis, 1997; Goldsmith, 1996); almost all fecal samples (99.9%) at Mondika contained fruit remains (Doran et al. 2002). By contrast, only 75% of Afi gorilla samples collected during fruit scarce months contained remains of fruit. Frequency of fruit consumption during months of high fruit availability and consumption at Afi (> 99% of samples) is similar to these three western lowland gorilla sites (≥ 98%).

Afi's prolonged period of fruit scarcity occurs due to its unique climate, particularly its extreme rainfall pattern (see Chapter 2). The greater severity of Afi's fruit scarce period is also likely due to the absence of *Duboscia* fruit, which is an important fallback food at Lopé, Bai Hokou, Mondika and Ndoki. Since *Duboscia* trees produce fruit asynchronously, this fruit is available and consumed by gorillas at these sites throughout the year, but mainly during the dry season when fruit availability is low and the majority of fecal samples contain *Duboscia* fruit remains (Doran et al. 2002; Goldsmith 1996; Nishihara 1995; Remis 1997b; Remis 2003; Rogers et al. 1988; Tutin & Fernandez 1993a; Tutin et al. 1991). Whereas *Duboscia* is present at western lowland gorilla study sites at relatively high densities (Lopé: 120 individuals per km^2 in closed canopy forest; Bai Hokou: 6 trees/km^2; Mondika: 1.6 trees/ha) (Doran et al. 2002; Goldsmith 1996; Nishihara 1995; Tutin et al. 1994), to date it has not been observed within the Afi study site area.

Duboscia macrocarpa is present in forests surrounding Afi Mountain; a local Boki name ("Okashie") exists and it tends to occur in lowland forests (Keay 1989). Consequently, its absence is likely due to Afi's relatively high altitudes. Interestingly at the eastern Itebero study site, where altitudes (600 – 1300 m) are similar to Afi and *Duboscia* is not listed as a gorilla food, Grauer's gorillas also consume fruit less frequently during low fruit season months compared to western lowland gorilla sites (%

of samples with fruit during: dry season = 84% and minor-fruiting season = 79%; n = 11 months) (Yamagiwa et al. 1994).

Grauer's gorillas living in the montane forests of Kahuzi experience even longer periods of fruit scarcity than gorillas at Afi. The mean number of fruit species recorded per fecal sample is less than 2.0 during most months sampled (89%, n = 92) and fruit consumption is very low for up to nine consecutive months (Yamagiwa & Basabose 2006; Yamagiwa et al. 2005). Fruit availability and fruit consumption are positively correlated at Kahuzi but are not related to rainfall; periods of high fruit availability and consumption most often occur during dry months.

Non-Fruit Vegetation Consumption

At all sites, gorillas consume the pith of herb stems throughout the year and herb species are considered important staple food resources. The percentage of fecal samples containing fiber at Afi (100%) is similar to, though higher than, western lowland gorillas at Lopé and Bai Hokou (97.5 and 98.3%, respectively; Table 6.1). The relative contribution of individual herb species also varies across western gorilla sites. At Lopé and Bai Hokou, *Aframomum* is the most frequently consumed herb and is considered the most important staple food with *Haumania* being secondarily important (Goldsmith 1996; Remis 1997b; Williamson et al. 1990). At Ndoki and Mondika, *Haumania* is the most frequently eaten herb; *Aframomum* is the third most frequently eaten herb at Ndoki and was considered a fallback species at Mondika (Doran et al. 2002; Nishihara 1995). *Haumania* does not occur within the Afi gorillas' habitat.

Whereas Afi gorillas consume *Aframomum* most frequently, *Anchomanes difformis* was considered the most important herb pith food and the second most important of all Afi gorilla food species. *Anchomanes* pith and leaves are certainly staple foods for Afi gorillas during wet season months when this plant is most abundantly available (April – October). Even though *Anchomanes* is present and consumed at Lopé, Gabon and at Campo, Cameroon, it is not considered to be an important food resource for gorillas at these two sites (Calvert 1985a, b; Williamson et al. 1990). In addition, an important fallback herb species for Afi gorillas, *Stylochiton*, is not consumed by gorillas at any other study site.

Leaves of some herb species are also important staple foods for gorillas at all sites and leaves of liana and tree species are important food resources during at least some months of the year. The diversity of leaf species eaten is relatively low at Afi (leaves represent 15% of food species) compared to western lowland gorilla populations (Lopé, 22%; Bai Hokou, 26%; Mondika, 33%; Ndoki, 18%; Lossi, Gabon, 29%) and Kahuzi montane Grauer's gorillas (34%). Percentage of fecal samples containing undigested leaf fragments at Afi (99%), however, is greater than that at the two western lowland sites, Lopé (90%) and Bai Hokou (91%), for which comparable data are available (Table 6.1, column 7). Doran et al. (2002) found that 99.7% of fecal samples of western lowland gorillas at Mondika contained fiber and/or leaves but frequencies for fiber and leaves separately are not reported. During the present study, Afi gorillas consumed leaves on 100% of days sampled by feces and 74% of days sampled along feeding trails. Yamagiwa et al. (2005) report that Kahuzi gorillas consumed leaves of at least one woody species on 95% of days sampled by feces, feeding remains or direct observation.

This evidence suggests that Afi gorillas consume leaves more frequently than western lowland gorillas and the level of leaf consumption at Afi is similar to Kahuzi.

The level of bark consumption also differs greatly between western lowland, Afi, and Kahuzi gorilla study sites. Afi and Kahuzi gorillas incorporate a greater variety of bark (25% and 22% of food species, respectively) and consume it more frequently throughout the year than western lowland gorilla populations (present study; Yamagiwa et al., 2005). Afi gorillas consume the bark and/or pith of lianas relatively consistently throughout the year; woody bark/pith feeding remains were found along trails on an average of 73% of days sampled per month (range = 38 – 100%). At Kahuzi, bark of at least one woody species was consumed on 94% of days sampled (Yamagiwa et al. 2005).

By contrast, few bark species are eaten at western lowland gorilla sites (Lopé: 0.5% of food species, Bai Hokou: 12%, Mondika: 8%, Ndoki: 2.2%, and Lossi: 5.2%) and most are considered to be fallback foods only. At Lopé and Ndoki, bark is almost exclusively eaten during fruit scarce months (Nishihara 1995; Rogers et al. 1994; Tutin et al. 1997). Though Bai Hokou gorillas consume bark at low rates during most months of the year, bark consumption is greatest during months when fruit is scarce (Goldsmith 1996; Remis 1994, 1997b). Bwindi and Virunga mountain gorillas rarely consume bark (McNeilage 2001; Stanford & Nkurunungi 2003).

Furthermore, based on dietary overlap in important staple, seasonal and fallback food plant species of gorillas at six western gorilla study sites, Rogers et al. (2004) conclude that the Afi gorilla diet is the most distinctive among these sites. In particular, Afi is the only site where non-herb plant species are considered to be staple food resources (one liana, *Landolphia* sp. 2, and one tree, *Ficus* spp.); Afi gorillas consume the bark and leaves of these two species on a regular basis throughout the year as well as large amounts of their fruit when available. This difference is likely the result of the Afi gorillas' greater reliance on bark, particularly woody bark/pith, and possibly leaves, throughout the year compared to western lowland gorillas (though differences in criteria used to identify important species across sites may be an influential factor; for details see Rogers et al., 2004).

Possible Morphological Implications of Increased Bark Consumption

Several studies have shown that Cross River gorillas are morphologically distinct from western, Grauer's, and mountain gorillas (Groves 1967, 1970; Stumpf et al. 1998; Stumpf et al. 2003). These studies are based on skull measurements from a database originally produced by Groves. Sarmiento independently measured skulls of 36 male and 29 female Cross River gorillas in museum collections in Berlin, London and New York, as well as a skull from Afi Mountain, Nigeria (Sarmiento & Oates 2000). Compared with the same measurements on the skulls of western lowland gorillas, the Cross River sample has significantly smaller values for a range of dimensions (including skull length, vault length, cheek-tooth surface area, incisor row width, maximum palate width, premolar-molar row length, biglenoid diameter and vault volume); an additional four measures were also significantly smaller for Cross River males (glenoid-incision, palate, bizygomatic and facial lengths). An additional 17 qualitative cranial characteristics were identified that individually exist as normal variation but together their frequent occurrence and common association in Cross River gorillas results in a distinctive skull morphology.

The Cross River gorillas' distinctive skull and gnathic characters suggest that they can generate greater magnitudes of masticatory forces than western lowland gorillas and commonly have several characteristics associated with lower jaw stabilization (Sarmiento & Oates 2000). Additionally, Sarmiento suggests that Cross River gorilla foods require greater incisive preparation "possibly making up a greater percentage of feeding time compared to other western gorillas, or includes harder and more abrasive foods" (p. 40). These conclusions are consistent with the findings of the present study indicating that Afi gorillas consume bark more frequently than gorillas at western sites as described above. When consuming bark, Afi gorillas use their incisors either to gnaw on tree trunks and limbs as well as large woody lianas, or strip bark from smaller branches.

Subspecific variation in the mandibular morphology of orangutans, which consume bark in a manner similar to Afi gorillas, may be related to differences in level of bark consumption (Taylor 2006). Two subspecies of Bornean orangutans (*Pongo pygmaeus morio* and *P. p. wurmbii*) consume bark more frequently than Sumatran orangutans (*P. abelii*) and exhibit most of the mandibular characteristics that are predicted to provide increased resistance to masticatory and incisal loads. Compared to *abelii*, mandibles of *morio* and *wurmbii* have deeper and thicker corpora and symphyses and larger condylar articular surfaces (condyle width and length), though not all of these characteristic differed significantly for *wurmbii*.

Sufficient comparative data are not available to determine whether Cross River gorillas exhibit mandibular morphology associated with increased bark consumption similar to Bornean orangutans. Whereas Cross River gorilla skull morphology is distinctive compared to other gorilla subspecies, whether their mandibular morphology is similarly distinct is unclear. Taylor and Groves (2003) found that the morphology of western, Grauer's, and mountain gorilla mandibles are clearly distinct, but no distinction between Cross River gorilla ('Nigerian') and western gorilla mandibular morphology was detected (Taylor & Groves 2003). This result should, however, be interpreted with caution for several reasons. Comparisons between western, Grauer's, and mountain gorillas were based on measurements made by Taylor, including all six traits that are predicted to be associated with increased resistance and incisal loads as described for orangutans (i.e., corpus depth and width, symphyseal depth and width, and condylar width and length). By contrast, comparisons of Cross River gorillas with the above three subspecies are based on a different set of measurements from Groves' original data set that includes only two of the six traits listed above. Considering the results of the present study regarding the Afi gorillas' diet and Sarmiento's skull morphology analyses, the mandibular morphology of Cross River gorillas may be more distinct than suggested by Taylor and Groves (2003). Further investigation is needed to clarify this issue and will provide important information to better understand subspecific variation in gorilla morphology and its relationship to diet.

COMPARISON OF GORILLA RANGING BEHAVIOR

Home Range Size and Daily Path Length

There is considerable subspecific variation in gorilla annual home range size and day ranges (Table 6.2 and 6.3) but generally these parameters vary with level of frugivory. Home ranges of gorilla populations that consume fruit (western, Grauer's, and Bwindi mountain gorillas), including Afi gorillas, are larger than the primarily folivorous Virunga mountain gorilla (Table 6.2). During the present study, the Afi gorillas were recorded to range over a minimum area of 13.1 km^2, but were estimated to have an annual home range size of 20 km^2 and, based on hunters' reports, to use a total area of 31 km^2. Afi figures fit well within the range of figures for other western gorillas and are most similar to gorillas at Bai Hokou and Mondika (Table 6.2).

Mean day ranges increase with level of frugivory and are longest for western and Grauer's lowland gorillas, intermediate for montane Grauer's gorillas at Kahuzi and Bwindi mountain gorillas, and are shortest for Virunga mountain gorillas (Table 6.3). Afi gorillas have day ranges similar to lowland gorillas. Afi mean path length is at the lower end of the range of path lengths of lowland gorillas, but this is likely due to the rugged Afi terrain and open forest floor, which makes gorilla tracking over long distances particularly difficult; hence, path lengths at Afi were likely underestimated to a greater degree than at other sites.

Table 6.2 Comparison of home range sizes across different gorilla study sites.

SITE	**Study Type***	**Group Size**	**RANGE SIZE** (km^2)	
			Annual	**Total**
Cross River gorillas				
Afi Mountain, Nigeria (This Study)	T/250	1 group 18 ind	Min: 13.1 Max: 20	≈ 30.2 (12 months)
Western lowland gorillas				
Lopé, Gabon				
(Tutin et al. 1992)	P/100	3 groups (8,11,4 ind)	Min: 3.9 – 8.1 Max: 7.3 – 14.4	
(Tutin 1996)	P/100	1 group (7 - 8 ind)	10 (core area)	≈ 22 – 25 (3 years)
Bai Hokou, CAR				
(Remis 1994; Remis 1997a)	P/250	1 group (12 - 15 ind)	Min: 13.7 & 18.1 (2 years)	23 (27 months)
(Cipolletta 2003)	P/250	1 group (6 ind)	11.4	
(Cipolletta 2004)	H/250	1 group (3 ind)	16.5	18.3 (42 months)
Mondika, CAR (Doran & McNeilage 2001; Doran-Sheehy et al. 2004)	P/250	1 group (10 ind)	15.4	≈ 20 (16 months)
Lossi, Congo (Bermejo 2004)	P/100	1 group (20 ind)		11 (38 months)
Grauer's gorillas				
Kahuzi-Biega, DRC (Yamagiwa et al. 2003b)	H/250	1 group (18 - 23 ind)	14.1	42.2 (8 years)
Mountain gorillas				
Bwindi, Uganda (Ganas & Robbins 2005; Robbins & McNeilage 2003)	H/500	4 group (8 - 30 ind)	11.3 – 24.8	≈ 40.2 (3 years)
Virungas, Rwanda				
(Watts 1998)	H/250	5 groups (6 - 18 ind)	Mean: 6 – 11.5	12 – 25 (6 years)
(Vedder 1984; Watts 1991)	H/250	1 group	8.2 & 8.6	

* H = habituated, P = process of habituation is on going, T = tracking gorilla feeding trails and contact is avoided. Numbers refer to size of quadrats used to determine range sizes including 100 x 100 m, 250 x 250 m, and 500 x 500 m.

Table 6.3 Comparison of day ranges across different gorilla study sites.

SITE	Study Type *	Mean (m)	Range (m)	No. of complete trails
Cross River gorillas				
Afi Mountain, Nigeria (Present study)	T	Min = 1270 ± 828	61 – 3678	60 (+ 15 partial ≥ 1500 m)
Western lowland gorillas				
Lopé, Gabon (Tutin 1996)	P	1105 ± 553	220 – 2790	80 (5 groups)
Bai Hokou, CAR (Remis 1994; Remis 1997a)	P	Max = 2,300 (Min = 1,500)	1000 – 3250 (250 – 4750)	8 (119 partial)
(Goldsmith 1996, 1999)	T	2590 ± 1001	342 – 5237	95
(Cipolletta 2004)	H	1527 ± 575	250 – 3300	431 (1 group, 6 - 3 ind)
Mondika, CAR (Doran & McNeilage 2001)	P	1553 ± 841	200 – 4040	94 (all groups)
(Doran-Sheehy et al. 2004)	P	2014 ± 900	400 – 4860	334 (1 group, 10 ind)
Lossi, Congo (Bermejo 1997)		1853 ± 807	30 – 5500	63 (1 group, 10 ind)
Grauer's gorillas				
Itebero, DRC (Yamagiwa & Mwanza 1994; Yamagiwa et al. 1992)	T	1531 ± 408	142 – 3439	2 (groups) 8 (solitary males)
Kahuzi-Biega, DRC (Yamagiwa et al. 2003a)	P	850.8	239 – 3570	225 (1 grp, 18 - 23 ind)
Mountain gorillas				
Bwindi, Uganda (Goldsmith 2003)	H	867 ± 291		40 (1 group)
(Ganas & Robbins 2005)	H	547 – 1034		x = 18/mo/grp, 1 yr (4 grps, 8 - 30 ind.)
Virungas, Rwanda (Watts 1991)	H	570 ± 427	190 – 3300	145 (1 group)

* H = habituated, P = process of habituation on going, T = tracking gorilla feeding trails and contact avoided.

At all sites where fruit is available, day ranges differ between periods of low and high fruit consumption. Like other frugivorous gorillas, the present study found that Afi gorillas traveled further when consuming fruit, and fruit consumption and temporal fruit availability were the most important predictors of daily path length. Conversely, Afi gorillas traveled significantly shorter distances during the period of fruit scarcity (i.e., the low fruit consumption period) when non-fruit vegetation consumption increased. These results are consistent with those for western lowland gorillas at Bai Hokou, Mondika, and Lopé (Cipolletta 2004; Doran-Sheehy et al. 2004; Goldsmith 1999; Tutin 1996), montane Grauer's gorillas at Kahuzi (Yamagiwa et al. 2003a) and Bwindi mountain gorillas (Ganas & Robbins 2005).

Specific aspects of fruit availability, such as patch size and/or density, have been found to influence day ranges of some primate groups (Chapman & Chapman 2000; Janson 2000), including gorillas. Some gorilla studies, however, indicate that these factors of fruit availability do not always influence gorilla day ranges in the same manner. Fruit patch size and/or density negatively influenced the daily path lengths of western lowland gorillas at Mondika and Bwindi mountain gorillas (Doran-Sheehy et al. 2004; Ganas & Robbins 2005). By contrast, Bai Hokou gorillas' day ranges were longer when fruit was most dense and overall biomass was highest (Goldsmith 1996, 1999).

Studies investigating the influence of herb availability on day ranges, however, are lacking (cf. Goldsmith, 1996). Differences in herb availability between two sectors within the Afi gorillas' home range provided an opportunity to examine the relationship between herb availability and daily path length. Compared to the Central sector, herb availability in the South is characterized by lower overall stem density and species diversity, and presence of fewer herb patches that were more widely dispersed (Chapter 2). Afi gorillas tended to travel twice as far on average in the South (0.82 km) compared to the Central sector (0.47 km) during the wet months of the fruit scarce period. This difference was not statistically significant due to small sample size for path lengths. Furthermore during the wet months within the period of fruit scarcity, the gorillas' most important herb food species while utilizing the South sector was *Anchomanes*, which occurs as single widely distributed stems rather than densely clumped stems in large patches like other herb food species (see Chapters 2 and 3). This evidence suggests that herb availability is an important factor influencing Afi gorilla daily path length.

Some studies show that gorilla day ranges are influenced by factors other than those related to fruit availability and consumption, such as group size, climate, predation, and male mate-search strategies (Cipolletta 2004), but the influence of these factors on daily path lengths is not consistent across sites. Studies of western gorillas at Lopé and Bai Hokou found no relationship between group size and daily path length (Goldsmith 1996, 1999; Tutin 1996), but daily path length was positively and significantly related to group size for Bwindi mountain gorillas (Ganas & Robbins 2005). Bwindi mountain gorilla and western gorillas at Bai Hokou travel significantly shorter distances on days when rainfall was relatively high (Ganas & Robbins 2005; Goldsmith 1996, 1999). No relationship between daily path length and rainfall, however, was found during the present study at Afi or for western gorillas at Mondika (Doran-Sheehy et al. 2004). Bai Hokou gorillas traveled longer distances on days after putative incidences of leopard predation attempts (Goldsmith 1996) and Afi gorillas tended to travel farther on days when hunters were present nearby (though no significant difference was found due to small sample size; also see below).

Home Range Use Patterns

Studies at all sites where gorillas consume fruit have found that gorillas range outside their core area for one day to several weeks in order to access fruit resources, aquatic herbaceous vegetation in swamps, or bamboo in the case of Kahuzi gorillas (Bermejo 2004; Doran-Sheehy et al. 2004; Ganas et al. 2004; Goldsmith 1996; Kuroda et al. 1996; Remis 1994; Remis 1997a; Tutin 1996; Williamson 1989; Yamagiwa et al. 2003a). Few studies, however, directly relate range use patterns to variation in food availability within their range (Remis, 1994, 1997; Doran-Sheehy et al., 2004). Because food availability varies across different sectors within the Afi gorillas' range, it was possible to investigate the relationship between the Afi gorillas range use pattern and variation in food distribution. In addition, the level of hunting pressure also varied across sectors during the present study providing a unique opportunity to investigate the impact of potential predation on gorilla ranging behavior. Though hunters were not actively targeting gorillas during the present study, there is a long history of gorilla poaching on Afi.

Afi gorillas utilized their range in a non-random and efficient manner related to variation in temporal and/or spatial availability of food resources and predator pressure. They preferred to utilize range sectors with the greatest food availability and avoided sectors with high hunting pressure. The Afi gorillas' core area, the Central sector, had greater densities of herbs than the South and West, greater densities of important tree food species than the South, and the lowest hunting pressure [13]. South, West, and North sectors were likely used less frequently than the Central sector due to their lower food availability and/or high levels of hunting. Certain important food species were, however, available at higher densities in South, West or North sectors and may explain why these sectors were utilized more frequently than the Central sector during certain seasons or months of the year.

Temporal and spatial variation of fruit across sectors was the most important factor influencing the Afi gorillas range use decisions during February through July when fruit availability and consumption by the gorillas was greater (i.e., the high fruit consumption period). The Afi gorillas' range use pattern during this time corresponded to monthly variation in estimated densities of fruiting trees of a few important fruit food species across sectors. During the period of fruit scarcity when both fruit availability and consumption was lowest, the Afi gorillas' pattern of range use can best be explained by variation in the availability of preferred herb foods and important tree bark and leaf fallback foods.

The Afi gorillas decision to utilize the Central sector more frequently than other sectors during the dry months of the fruit scarce period (November – January) was likely due to the gorillas preference for the pith of *Palisota* sp. 1 during these months. The gorilla's probably preferred *Palisota* sp. 1 during these months due to its greater water content. During wet months within the fruit scarce period (August – October), the gorillas likely chose to utilize the South most frequently due to preferences for two herbs (*Stylochiton* sp. and *Anchomanes difformis*) and four tree fallback species (*Grewia mollis,*

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[13] Comparisons of herb and tree food availability across all sectors were not possible. Herb enumeration data were not available for the North sector and tree enumeration was not conducted in West and North sectors.

Milicia excelsa, Morus mesozygia, and *Pycnanthus angolensis*) that were more abundantly available in the South. The gorillas consumed these species more frequently or exclusively during this season and rarely ate them when utilizing the South at other times of the year. *Anchomanes difformis* was determined to be the Afi gorillas' most important herb food resource and was likely preferred for its possible higher protein content and digestibility compared to other herb foods [based on nutritional analyses conducted by Calvert (1985) at Campo, Cameroon; see Chapter 3). Afi gorillas may have avoided the South at other times due to its lower overall herb density compared to all other sectors and relatively high hunting pressure.

Fruit availability and avoidance of hunting pressure were important factors influencing the Afi gorillas' use of the North sector. Afi gorillas utilized this sector more often than others during two high fruit season months, March and June, when particular species were fruiting in the North that occur rarely in other sectors. In addition, the gorillas may have retreated to the difficult-to-access valleys of the North during the end of December and early January (the Holiday period) when hunting pressure is particularly high.

High hunting pressure in the West likely explains why the gorillas appeared to deliberately avoid this sector during most months of the year, despite its relatively high overall abundance of herbs, particularly fallback herb species. Hunting pressure was highest in the West throughout the year due to the presence of the only 'career hunter' active on Afi Mountain. The gorillas chose to use the West extensively only in October, when fruit availability was lowest in the South and Central sectors but *Vitex* fruit appeared to be abundant in the West. During this visit to the West, the hunter killed an adult male member of the Afi gorilla study group.

Are Gorillas Opportunistic Frugivores?

Due to the large body size of gorillas and their staple diet of herbs, they are often described as herbivore-folivores. This classification has been re-examined in light of the fact that gorillas incorporate large of amounts fruit in their diet (Doran & McNeilage 1998; Doran & McNeilage 2001; Remis 2003). Gorillas have been characterized by some to be opportunistic frugivores based on the following evidence (Kuroda et al. 1996; Nishihara 1995). The high diversity of fruit species consumed by gorillas indicates low selectivity and relatively low preference for particular fruits. The fact that gorillas often leave a fruit patch before it has been depleted and their ability to rely on non-fruit vegetation foods during times of fruit scarcity also indicate a low insistence on fruit. This evidence suggests that gorillas consume fruit opportunistically rather than deliberately seeking out fruit like chimpanzees that rely primarily on fruit even during periods of fruit scarcity (Kuroda et al. 1996).

Other researchers argue that whereas gorillas are not true ‘fruit pursuers’ like chimpanzees, ‘opportunistic frugivore’ is not an appropriate description for gorillas (Doran & McNeilage 1998; Remis 2003). Studies of western lowland gorillas show that they prefer fruit when it is available and are selective in the fruits they consume (primarily opting for succulent sweet fruits and avoiding high levels of digestive inhibitors) (Goldsmith 1999; Remis 2002; Remis et al. 2001; Remis & Kerr 2002; Rogers et al. 1992; Yamagiwa et al. 2003a). In addition, intergroup contests over fruit have been observed indicating that contest feeding competition occurs to some extent (Olejniczak 1996; Tutin 1996).

If gorillas consume fruit opportunistically there should be little difference between western lowland and mountain gorilla ranging and social organization (Doran & McNeilage 1998). However, western gorilla ranging patterns, including those of the present study, are strongly influenced by their fruit seeking behaviors. Western gorillas range widely in order to access areas with concentrated fruit resources and travel further daily when consuming fruits, thus incurring additional foraging costs (Doran & McNeilage 1998; Doran & McNeilage 2001; Goldsmith 1996, 1999; Remis 1994; Remis 1997a). The fruit seeking behavior of Afi gorillas is particularly striking given the finding that they sought out fruit even when the risk of being hunted was considerable (see above). In addition, gorilla groups are less cohesive when consuming fruit and the possible flexible grouping patterns, such as subgrouping behavior, suggested for some gorilla groups, including the Afi study group, is associated with fruit consumption (see next section for details).

Consequently, the ranging and grouping behavior of highly frugivorous gorillas does differ from the strictly folivorous mountain gorillas. Based on socioecological theory, the fruit seeking behavior and flexible grouping patterns of western gorillas indicate that they experience increased intragroup feeding competition. The gorillas' large body size provides them with the ability to rely more heavily or exclusively on non-fruit vegetation foods thereby alleviating at least some of the feeding competition incurred when consuming fruit (Remis & Dierenfeld 2004; Remis et al. 2001; Tutin & Fernandez 1993a). The ability of highly frugivorous chimpanzees to reduce feeding competition in a similar manner is limited by their smaller body size so that additional responses are required such as fission-fusion grouping behavior. The fact that frugivorous gorillas and chimpanzees respond differently to increased feeding competition does not, however, necessarily indicate that gorillas are ‘opportunistic frugivores’.

In conclusion, the current evidence available suggests that gorillas are not ‘opportunistic frugivores’ but the term ‘fruit pursuer’ used to describe chimpanzees cannot be appropriately applied to gorillas either. Whereas gorillas that consume large amounts of fruit (i.e., western lowland, Grauer’s lowland, and Cross River gorillas) may be described as ‘fruit seekers’, this designation does not incorporate the importance of herbaceous vegetation in the gorillas’ diet and its influence on their ranging and social behavior. These gorillas may best be described as herbivore-frugivores.

COMPARISON OF GORILLA SOCIAL ORGANIZATION

Group Size and Composition of Western, Grauer’s and Mountain Gorillas

In contrast to the great variation in diet and ranging behavior observed across western, Grauer’s and mountain gorilla populations, group sizes in these populations are relatively similar (Doran & McNeilage 1998; Doran & McNeilage 2001; Gatti et al. 2004a; Yamagiwa et al. 2003b). Table 6.4 compares group sizes of various Cross River, western lowland, Grauer’s, and mountain gorilla populations; there are no clear distinctions between mean group sizes of these populations. Maximum group size does, however, vary among these three subspecies. Large groups (> 20 individuals) are

Table 6.4 Variation in group size and composition across different gorilla study sites (* includes unweaned individuals; ** medians).

	Mean	**Range**	**No. Nest Sites or groups**	**Multi-male Groups[1]**	**References**
Gorilla g. diehli					
Nigeria Afi	18.2	8 - 36	122	Present	This study
Mbe	5.5	2 - 13	n/a	n/a	Obot et al. 1997
Boshi	6.5	2 - 12	84	n/a	Nwufoh 2001
SW Cameroon	3.6	1 - 23	87	n/a	Sunderland-Groves et al. 2003
Gorilla g. gorilla					
CAR Bai Hokou	8	4 - 18	163	Present	Remis 1993
Bai Hokou	9.4	2 - 19	232	Present	Goldsmith 1996
Mondika	7.4	2 – 23	512	Present	Mehlman & Doran 2002
Congo Ndoki	7.3	4 - 12	7 grps	14%	Mitani et al. 1993
Odzala NP	6.6	1 - 26	427	n/a	Bermejo 1999
Lossi	14	6 - 32	7 grps	Absent	Bermejo 1997
Mbeli Bai	6.6	2 - 13	14 grps	Absent	Parnell 2002
Lokoué	8.2 *	3 - 15	45 grps	Absent	Gatti et al. 2004b
Maya Nord	11.2 *	2 - 22	31 grps	Absent	Magliocca et al. 1999
Gabon Lopé	10 **	4 - 16	8 grps	25%	Tutin et al. 1992
Gorilla g. graueri					
DRC Itebero	7 **	2 - 17	10 grps	Absent	Yamagiwa et al. 2003b
Kahuzi	10 **	5 - 31	14 grps	7%	Murnyak 1981
Kahuzi	7 **	2 - 21	25 grps	8%	Yamagiwa et al. 1993
Kahuzi	6.4	1 - 31	38	n/a	Hall et al. 1998
Gorilla g. beringei					
Uganda Bwindi	10 **	2 - 23	28 grps	46%	McNeilage et al. 1998
Virungas 1959 - 60	16.9	4 - 21	10 grps	30%	Schaller 1963
1976 - 78	8.8	3 - 15	19 grps	44%	Weber & Vedder 1983
1986	9.2	2 - 25	29 grps	14%	Vedder 1989
1989	9.1	2 - 23	32 grps	25%	Sholley 1991

[1] Multi-male groups: % = proportion of gorilla groups, Present = at least one multi-male group observed, Absent = no multi-male groups observed, n/a = no data available.

relatively rare at most western lowland and Grauer’s lowland gorilla sites. At sites where herbaceous vegetation is more abundant, such as for mountain gorilla at Bwindi and Virunga, Grauer’s montane gorillas at Kahuzi, and western lowland gorillas at Lossi, large groups are more common (Bermejo 1997, 1999; Steklis & Gerald-Steklis 2001; Yamagiwa et al. 2003a; Yamagiwa et al. 2003b).

Western lowland and Grauer’s gorillas are generally described as forming stable one-male groups similar to most mountain gorilla groups (Doran & McNeilage 1998; Doran & McNeilage 2001; Yamagiwa et al. 2003b); however, the proportion of multi-male groups varies dramatically across gorilla populations. Multi-male groups are relatively common at Virunga and Bwindi mountain gorilla study sites, where the proportion of multi-male groups recorded during different censuses has been found to range between 14% and 46% (McNeilage 2001; Sholley 1991; Weber & Vedder 1983; Yamagiwa 1999) (Table 6.4). By contrast, multi-male groups have either not been reported at Grauer’s and western lowland gorilla study sites or have been observed less often than at mountain gorilla sites.

All groups recorded at the Itebero Grauer’s lowland gorilla site contained only one adult silverback (Yamagiwa et al. 2003b). Up to two multi-male groups (7% and 8% of groups), however, have been observed at the Grauer’s montane gorilla site at Kahuzi (Murnyak 1981; Yamagiwa et al. 1993). Multi-male groups have also not been observed at various bais visited by western lowland gorilla in the Congo Republic and occur only temporarily when black-back males are transitioning to adulthood and before they emigrate (Gatti et al. 2004b; Magliocca et al. 1999; Parnell 2002; Robbins et al. 2004). At least one multi-male group has been recorded at some western lowland gorilla sites including Lopé (2 groups; Tutin et al., 1992 and Tutin, 1996), Ndoki (1 group; Mitani et al., 1993), Mondika (mean number of silverbacks per nest site = 1.2; Mehlman and Doran, 2002), and Bai Hokou (Goldsmith 1996; Remis 1997a). Proportions of multi-male groups found at Lopé and Ndoki (25% and 14%, respectively) are at the lower end of the range of proportions of multi-male mountain gorilla groups. However, sample sizes for Lopé and Ndoki (n = 8 and 7 groups, respectively) are smaller than sample sizes for most of the other gorilla populations (mean sample size = 22 groups, range = 7 – 32) and this may indicate that proportions of multi-male groups at these two sites might be overestimated.

Afi Gorilla Study Group Size and Composition

Nest counts collected during the present study and genetic analyses conducted by Bergl et al. (2007) suggest that the Afi gorilla study group contained 18 individuals (Chapter 5). The relatively large size of the Afi group appears to exceptional for Cross River gorillas. Surveys conducted in Nigeria and Southwestern Cameroon indicate that Cross River gorillas usually live in relatively small groups. Afi gorillas appear to be the exception to this pattern. On average most Cross River gorilla groups are estimated to include between 3.6 and 6.5 nesting individuals, and nest sites containing greater than 13 nests are rare (Nwufoh 2001; Oates et al. 2003; Oates et al. 1990; Obot et al. 1997; Sarmiento & Oates 2000). Afi group size is also at the upper end of group sizes reported for lowland western and Grauer’s gorilla populations (mean group sizes: 6.6 – 14 individuals; Table 6.4).

Based on diameter of feces associated with nests and one direct observation, the Afi study group likely most often contained at least two adult males, three black-back males, ten adult females/adolescent males, two juveniles and one infant (though group membership likely varied at times as described below). Even though fecal diameters do not always accurately reflect gorilla age-class, several lines of evidence strongly suggest that at least two adult silverback males were present in the Afi study group. At most nest sites sampled, there were two or more adult-male sized feces even when a stricter fecal diameter criterion (≥ 6.7 cm) than that of other western gorilla sites (≥ 6.5 cm) was used. However, the strongest evidence indicating that at least two silverbacks were present is the fact that the Afi gorilla group remained cohesive following the death of an adult male, rather than disbanding like gorilla groups containing one silverback.

Afi Gorilla Nest Group Size Variability

Though the vast majority of nest sites recorded during the present study included 14 – 22 individual nests (mean nest group size = 18.2 nests), nest group size at Afi was highly variable (range = 8 – 36) even among consecutive nest sites; differences in number of nests between two consecutive nest sites ranged between 0 and 13 nests (Chapter 5). Whereas nest group size of the majority of consecutive sites remained relatively stable (differences of +/- 2 nests between consecutive nest site pairs), group sizes among consecutive sites often differed by ≥ 3 individuals (41.1%) and differed by ≥ 7 individuals 13.7% of the time. This variability suggests that Afi gorillas may exhibit a more flexible grouping pattern than most gorilla groups at other sites. Factors other than flexible grouping behavior that could have produced the observed group size variation explained very little, if any, of this variation. These other factors included: 1) the data represent more that one gorilla group, 2) multiple nests were made by one or more individuals at a nest site, 3) researcher failed to detect some nests, 4) variation in juvenile nesting behavior and 5) some day nests built nearby night nest sites were mistaken for night nests.

Consequently, flexible grouping patterns are currently the best explanation for the nest group size variation observed at Afi. The pattern of nest group variation suggests that members of a small-sized gorilla group likely joined the Afi study group at times and on other occasions members of the study group temporarily traveled separately or joined this other smaller group. The fact that the Afi group contained two or more adult males allows for the opportunity to form subgroups so that females are able to maintain a permanent association with at least one adult male. Afi gorilla flexible grouping patterns are discussed further in the next section.

Flexible Grouping Patterns

Frugivorous western lowland and Grauer's gorillas exhibit more flexible grouping patterns than the strictly folivorous mountain gorillas. When foraging, western lowland and Grauer's gorilla groups are less cohesive with individuals or subgroups often separated by up to 500 m, particularly when feeding on fruit (Doran & McNeilage 1998; Goldsmith 1996; Remis 1994; Remis 1997a; Tutin 1996). Preliminary evidence suggests that group spread is also often large for the Afi group. Western lowland gorilla groups are known to tolerate the presence of other groups at rare but abundant food resources such as swamps (or bais) and large fruiting trees (Bermejo 1999, 2004; Doran-Sheehy et al. 2004; Olejniczak 1996; Parnell 2002; Stokes et al. 2003; Tutin 1996). At Lossi and Kahuzi, 'supergroups' occasionally form when groups maintain close proximity (within 50 m) overnight (Bermejo 2004; Yamagiwa et al. 2003a).

At sites where multi-male groups have been recorded and/or studied, subgrouping behavior has been suggested, including Bai Hokou (Goldsmith 1996; Remis 1994; Remis 1997a), Ndoki (Kuroda et al. 1996; Mitani et al. 1993), Kahuzi (Yamagiwa et al. 2003a; Yamagiwa et al. 2003b) and Afi (present study). Evidence of subgrouping at these sites is based on nest group size variability between consecutive night nest sites or within the home range of a group of known size. Though nest group size does not always accurately reflect actual group size (Tutin et al. 1995), nest group size variability at some western gorilla study sites, including at Afi, occurs more frequently than variability resulting from gorillas building multiple nests or researchers failing to detect nests. At Lopé, nest group size rarely varied from actual group size by greater than ± 2 nests (Porthos group, 15.5% and 9% of nest sites during 1989/90 and 1991/92, respectively). Group size variability, indicating subgrouping behavior (i.e., differences of ≥ 3 nests between consecutive sites), for groups at Bai Hokou, Afi and Kahuzi (31 – 58%, 41%, and 57%, respectively) occurred approximately three or more times frequently than for the Lopé group (Goldsmith 1996; Remis 1994; Remis 1997a; Yamagiwa & Kahekwa 2001).

Flexible grouping patterns in primates have been suggested to be a response to high intragroup feeding competition, particularly when consuming foods with a clumped distribution such as fruit (Symington 1990; White 1992; Wrangham 1979; Wrangham 1986). Kuroda et al. (1996) argue that flexible grouping patterns and wide group spread in gorillas may be better explained as an adaptation to high-quality herbaceous vegetation, such as young shoots of *Haumania* and *Megaphrynium*, and the aquatic *Hydrocharis*. Subgrouping behavior at Bai Hokou and Kahuzi, however, is most likely related to increased intragroup feeding competition associated with consuming fruit. Subgrouping occurred throughout the year at Bai Hokou, but was more frequent during the period when fruit availability and consumption was greatest (Goldsmith 1996; Remis 1994; Remis 1997a). At Kahuzi, subgrouping behavior was observed almost exclusively during the period of highest fruit consumption (Yamagiwa et al. 2003a).

Results of the present study suggest that the flexible grouping pattern exhibited by the Afi group may be the result of high intragroup feeding competition associated with the consumption of both fruit and herb foods. The Afi group was most stable dry fruit scarce months when fruit consumption was lowest and all consecutive nest sites recorded occurred in the Central sector where herb availability is high (see Chapters 2 and 3), suggesting that intragroup competition was relatively low during this time. The Afi group was frequently unstable (48% of consecutive sites) during the high fruit consumption period, as expected if the gorillas were responding to high intragroup competition associated with fruit consumption.

But, the Afi group was most frequently unstable (66.7%) during wet fruit scarce months when they most often used the South sector where herb availability is much lower than the Central sector. In addition, during this time the Afi gorillas relied heavily on the pith and leaves of the herb, *Anchomanes difformis*. Though this herb was likely more abundant in the South, *Anchomanes* was estimated to have one of the lowest densities of the Afi gorilla herb foods and occurs as single scattered stems. This evidence strongly suggests that low herb availability produced increased feeding competition and influenced Afi gorilla grouping patterns.

Flexible grouping patterns may be a response to predation pressure as well (Boesch 1991; Kano 1992; Sakura 1994; Tutin et al. 1983). Despite the large body size of gorillas, they are still at high risk of predation from leopards and humans (Fay et al. 1995; Goldsmith 1996; Remis 1994; Remis 1997a; Tutin & Benirschke 1991). The silverback is usually the defender of the group and multi-male groups may be able to better fend off predators and outsider male challenges (Goldsmith 1996; Robbins 1995). Based on the hunter's description, the Afi silverback male killed during the present study was protecting the group, allowing other group members to escape unharmed. The presence of more than one adult male provides the opportunity for one male to protect the group while the other male(s) remain with the females in the event the first males' attempts fail. Furthermore, if one male is killed the other(s) can maintain group cohesion preventing disintegration of the group.

For the Afi group, demographic and social factors may also influence their grouping pattern. Afi Mountain is one of the most isolated of the Cross River gorilla localities (Bergl 2006) due to the high human density surrounding Afi Mountain and a road between it and the nearest Cross River gorilla locality (Mbe Mountain; see Figures 1.2 and 2.1). Consequently, this isolation likely limits Afi males' ability to acquire mates other than those already present on Afi Mountain and migration has likely been difficult for many years, though not impossible. Through genetic analyses of DNA extracted from feces of different Cross River gorilla localities, Bergl et al. (2007) identified one migrant present at the Mbe Mountain locality that likely came from Afi Mountain.

Considering the dispersal barriers and high predator pressure present at Afi, it may be more advantageous for males to remain in their natal group for long periods after reaching maturity and/or make forays in search of other females but return to the group when unsuccessful (Robbins & Robbins 2005; Robbins 1999; Watts 2000). Furthermore, the degree of relatedness among males and females of the Afi group is likely higher than for gorillas at other study sites. Consequently, the dominant male would more likely tolerate the presence of other adult males in the group and females would benefit from additional protection (Watts 2000). This may explain the high numbers of adult males (3 – 7 male in some cases) detected at some nest sites and the rarity of lone male nests observed at Afi.

CONCLUSION: WHERE DO AFI GORILLAS FIT?

The Afi gorillas' diet, ranging behavior and grouping patterns are most similar to those of western lowland and Grauer's gorillas living at low altitudes but differ in important ways related to habitat differences in rainfall, altitude, herb availability, hunting pressure, and isolation. The Afi gorilla diet represents an intermediate between lowland gorillas and montane Grauer's gorillas at Kahuzi. Afi's prolonged and more severe period of fruit scarcity, which occurs because of Afi's extreme rainfall pattern and absence of fallback fruit resources such as *Duboscia*, accounts for most differences between Afi and western lowland gorilla diets. Whereas fruit consumption is similar at Afi and other western lowland gorillas during periods of high fruit availability, the level of fruit consumption at Afi is lower than at western sites during periods of fruit scarcity.

Afi and western lowland gorillas respond similarly to low fruit availability by increasing consumption of non-fruit vegetation; however, leaf and especially bark consumption is greater at Afi and is more similar to the less frugivorous Grauer's montane gorillas at Kahuzi. The Afi gorillas' diet also differs other western gorilla diets in the following ways: 1) To date no evidence of invertebrate consumption has been recorded at Afi; 2) Two important herb food species for Afi gorillas, *Anchomanes* and *Stylochiton*, are either not available or rarely consumed by western lowland gorillas and *Haumania*, an important herb food species for lowland gorillas is absent at Afi.

Afi gorillas may experience greater intragroup feeding competition than other gorillas. Afi and other frugivorous gorillas respond similarly to increased intragroup feeding competition associated with fruit consumption including having larger home ranges, longer day ranges, wide group spread, and exhibit flexible grouping behavior. However, Afi gorillas also traveled longer distances daily and exhibited flexible grouping behavior when consuming herb foods that occur at low densities and have a widely scattered distribution, particularly *Anchomanes difformis*. This suggests that Afi gorillas experience increased feeding competition associated with consuming fruit and herb foods.

Temporal and spatial availability of fruit, the availability of herbs in space, and hunting pressure all clearly influenced the Afi gorillas' range use pattern. Their use of different sectors corresponded to variation in the density of fruiting trees and the availability of different herb species across these sectors. Particularly high hunting pressure in one sector of their range, the West, resulted in reduced access to important food resources, particularly fallback herb foods. Preliminary studies suggest that the ranging behavior of gorillas at Dzanga-Sangha Reserve (including the Bai Hokou study site) and in southeastern Cameroon is also influenced by human activities, such as hunting and logging (Arnhem et al. 2005; Remis 2000).

The flexible grouping pattern exhibited by Afi gorillas is likely a response to high hunting pressure, intragroup feeding competition and isolation. Afi's large group size may reflect an anti-predator strategy as suggested for gorillas at Dzanga-Sangha Reserve where gorilla group sizes are larger in areas with high hunting levels (Remis 2000). The isolation of the Afi group from other Cross River gorilla groups may limit male dispersal options resulting in the formation of a multi-male group, which provides better predator protection and facilitates temporary subgroup formation. The large Afi group can be maintained when food resources are large enough to accommodate all group members and on some occasions additional individuals. When feeding on fruit and widely distributed herbs, however, Afi gorillas may form subgroups thereby reducing intragroup feeding competition and females can continue to benefit from the presence of an adult male.

Whereas the present study cannot conclusively show that the Afi group exhibits a flexible grouping pattern, the evidence is compelling. Though evidence of gorilla flexible grouping behavior has not been directly observed, current evidence from Bai Hokou, Kahuzi and now Afi strongly suggest that under certain conditions gorillas are capable of responding to intragroup feeding competition by being socially flexible.

APPENDICES

Appendix I. List of tree species enumerated along transects and phenology trails, including number of individual trees monitored during 1998 – 1999 and 2000, presence in the Afi gorilla diet during the present study, mean density per 250 m^2 quadrat, and importance within the Afi gorilla home range (IV = importance values for tree enumeration plots only, range = 0.08 – 27.5, see Chapter 2 for details; * X = known food; ? = suspected food, based on hunter reports and/or previous western lowland gorilla studies).

FAMILY	**SPECIES**	**LOCAL NAME** (Boki or Common Name)	**No. of Trees for Phenology**		**Afi Gorilla Food ***	**Mean Density**	**IV**
			1998 -	**2000**			
Agavaceae	*Dracaena arborea*	Olum/Kaychuchu	5	6	X	0.03	1.7
	Dracaena sp.		0	2		0.02	0.8
Anacardiaceae	*Antrocaryon micraster*	Ojifuno	3	3	X	0.03	---
	Pseudospondias microcarpa	Ushie (Ufe) erue	0	3	X	0.05	5.9
	Sorindeia grandifolia	Kochiche/Kambri	0	15	X	0.20	23.7
	Trichoscypha sp.	Pope Hat Fruit	0	1	X	0.07	7.6
Annonaceae	*Anonidium mannii*	Kichie equere/Kichie uche	11	19	?	0.11	7.5
	Dennettia (*tripetala*?)		0	1		0.02	0.8
	Dennettia sp.		---	---		0.38	19.3
	Monodora myristica	Big Fruit	1	10	X	0.06	5.9
	UK-WWW	Ojuat Kache?	0	1		0.02	0.8
	Uvariastrum (?)		0	2		0.03	1.7
	Uvariodendron angustifolium		0	1		0.02	0.8
	Uvariodendron calophyllum	Alacoburo-eshua	0	13	X	0.09	8.7
	Xylopia (*staudtii*?)	Caseng kidzo	0	6	X	0.08	6.6
Apocynaceae	*Alstonia* (*boonei*?)	Uku/Bokuk	0	1		0.02	1.9
	Funtumia (*elastica*?)	Nkuma/Mkwe/Nkawame	0	2		0.03	1.7
	Rauvolfia vomitoria	Katong	1	2		0.02	0.8
	Tabernaemontana pachysiphon	Kemekoto	18	34	X	0.31	27.5
	UK-CC		0	6		0.10	5.1
Araliaceae	*Polyscias* (*fulva*?)		0	1		0.03	1.8

Appendix I. Continued.

FAMILY	SPECIES	LOCAL NAME (Boki or Common Name)	No. of Trees for Phenology 1998 -	2000	Afi Gorilla Food *	Mean Density	IV
Bignoniaceae	*Kigelia africana*		0	1		0.02	0.9
	Markhamia tomentosa		0	9		0.17	13.3
	Newbouldia laevis	Mbe kikwen	1	2	X	0.01	0.8
	Spathodea campanulata	Kenshie	0	3		0.05	2.6
Bombacaceae	*Ceiba pentandra*	Bokum	0	2		0.05	2.4
Burseraceae	*Canarium schweinfurthii*	Koset	3	4	X	0.03	0.9
	Dacryodes edulis	Ofie (Bush pear)	2	2	?	0.01	---
	Santiria trimera	Purple FR	1	10	X	0.07	3.3
Caesalpinioideae	*Anthonotha* (*lamprophylla*?)		0	5		0.31	19.8
	Anthonotha macrophylla		0	1		0.02	0.9
	Daniellia sp.	Ubeh	7	8		0.09	---
	Dialium guineense	Komionko	0	1	X	0.02	0.8
	Gossweilerodendron balsamiferum	Emonga	0	5		0.08	6.0
	Guibourtia ehie	Kaluk ofuon (?)	0	3		0.05	3.9
	Hylodendron gabunense	Uka kekwen	0	3		0.05	2.5
	UK-SS		0	2		0.08	4.0
Caesalpinioideae?	UK-R		0	1		0.02	0.8
	UK-QQQ		0	1		0.02	2.2
Chrysobalanaceae	*Dactyladenia* (*barteri*?)		---	---		0.02	0.8
	Maranthes or *Licania*		---	---		0.05	2.4
Ebenaceae	*Diospyros* sp.	Ebony	0	3		0.01	---
Euphorbiaceae	*Bridelia atroviridis*	Kensange	0	1		0.02	0.9
	Bridelia ferruginea	Okpani kinsa/Kensange	2	2		0.02	---
	Bridelia (*micrantha*?)	Okpani kinsa/Kensange	1	2		0.02	2.0
	Croton penduliflorus		---	---		0.02	0.8

Appendix I. Continued.

FAMILY	SPECIES	LOCAL NAME (Boki or Common Name)	No. of Trees for Phenology		Afi Gorilla Food *	Mean Density	IV
			1998 -	2000			
Euphorbiaceae cont.	*Discoglypremna caloneura*		0	3		0.05	2.5
	Macaranga schweinfurthii	Kingma kinsa	0	1		0.03	1.7
	Maesobotrya sp.	Kechechua	20	20	?	0.20	---
	Mallotus oppositifolius	Katiah karuru	0	2		0.03	1.6
	Ricinodendron heudelottii	Okpasi	11	12	X	0.03	4.1
	Uapaca (*guineense*?)	Odang	4	5	?	0.01	0.8
Flacourtiaceae	*Caloncoba glauca*	Konka-like Fruit	2	3	X	0.03	2.8
Guttiferae	*Garcinia kola*	Ojie	0	1	X	0.02	0.8
	Garcinia smeathmannii	Oshie ojie	20	21	?	0.29	23.5
	Symphonia globulifera	Kantu onong kichie	0	3		0.08	4.3
Icacinaceae	*Leptaulus daphnoides*	Nquarang/Unquapet	5	5		0.05	
Irvingiaceae	*Klainedoxa gabunensis*		0	2		0.03	1.6
Lauraceae	*Beilschmiedia* (*mannii*?)	Ogbamu	0	9		0.16	8.2
Melastomataceae	*Memecylon* sp.		---	---		0.08	4.0
Meliaceae	*Carapa procera*	Mkpre nkoo/Ube kidzo	4	11		0.05	0.8
	Entandrophragma sp.	Mahogany (1)	0	3		0.06	6.1
	Guarea cedrata	Oyekichie	3	10	?	0.06	4.1
	Guarea thompsonii	Oyekichie	0	1	?	0.01	
	Khaya sp. 1	Mahogany (2)	0	5		0.08	4.2
	Khaya sp. 2	Mahogany (3)	0	1		0.02	0.8
	Trichilia prieuriana	Ogo	0	2	?	0.03	1.7
	Trichilia sp. 1	Ogo	0	4	?	0.06	3.7
	Trichilia sp. 2	Ogo	0	2	?	0.03	1.6
	Turreanthus africanus	Ushie eche	3	14	X	0.08	5.4

Appendix I. Continued.

FAMILY	SPECIES	LOCAL NAME (Boki or Common Name)	No. of Trees for Phenology		Afi Gorilla Food *	Mean Density	IV
			1998 -	2000			
Mimosoideae	*Albizia andianthifolia*	Jua Njua (1)	0	4		0.08	4.1
	Albizia gummifera	Jua Njua (2)	0	1		0.02	0.8
	Albizia zygia	Kampen / Mkpre	12	19	X	0.10	7.4
	Calpocalyx cauliflorus	Otuen	0	18		0.30	17.0
	Cylicodiscus gabunensis	Kendum / Ulem	0	2		0.03	6.4
	Parkia bicolor	Kakpaja	19	19	X	0.08	2.3
	Pentaclethra macrophylla	Kingere	---	---		0.02	0.9
	Piptadeniastrum africanum	Kalilo	7	12		0.07	4.0
	Tetrapleura tetraptera	Kinkpe kinong / Mbe	0	3	?	0.10	5.0
Moraceae	*Antiaris toxicaria africana*	Ukwe	19	23	X	0.09	5.7
	Bosqueia angolensis	Kafu kidzo / Nkpa koni	6	10	X	0.06	3.5
	Ficus sp. A	Kantu	0	1	X	0.02	0.8
	Ficus sp. B	Kintu	1	1	X	0.01	---
	Ficus sp. C	Kintong	2	2	X	0.02	---
	Ficus Strangler (sp. 1-5)	Onkom	9	9	X	0.06	---
	Milicia excelsa	Nsen / Inshie / Iroko	16	17	X	0.11	1.0
	Morus mesozygia	Komwura	7	7	X	0.08	---
	Musanga cecropioides	Okabie / Ukrue	4	9	X	0.06	6.7
	Myrianthus arboreus	Kekekre / Kekeka	9	14	X	0.09	5.2
	Treculia africana	Kichie ofe	2	6	X	0.04	3.5
	Treculia obovoidea	Oken	11	11	?	0.09	---
Myristicaceae	*Coelocaryon botryoides*		0	4		0.06	6.1
	Pycnanthus angolensis	Utsa / Awaylep	4	6	X	0.02	2.0
Myrtaceae	*Syzygium guineense*		---	---		0.02	0.8
	Syzygium rowlandii		---	---		0.02	1.1

Appendix I. Continued.

FAMILY	**SPECIES**	**LOCAL NAME** (Boki or Common Name)	**No. of Trees for Phenology**		**Afi Gorilla Food ***	**Mean Density**	**IV**
			1998 -	**2000**			
Olacaceae	*Strombosia* sp. 1	Ofeng enyia	20	30	?	0.30	27.3
	Strombosia sp. 2	Katiah Ofeng enyia	3	5		0.01	0.8
	Strombosia sp. 3		---	---		0.02	0.9
Olacaceae?	*Olax* (?)	Kanino	6	7		0.04	0.8
Palmae	*Elaeis guineensis*	Uyep / Bojep	6	8	X	0.03	1.9
Pandaceae	*Microdesmis puberula*	Kawa/Kanpodike	0	16		0.11	11.8
Papilionoideae	*Amphimas pterocarpoides*		2	14		0.22	11.9
	Baphia gracilipes		---	---		0.06	3.6
	Baphia nitida	Oshie-female	2	21		0.12	14.1
	Platysepalum violaceum	Ose-male/Katep oshie	20	23	?	0.22	11.1
	Pterocarpus mildbraedii	Kaku pupu (or mpipi)	0	6	X	0.11	10.4
	Pterocarpus osun	Kaku/Ukoo	1	7	X	0.11	10.4
Rhamnaceae	*Maesopsis eminii*	Onyonko/Kimpre okre kidzo	5	8	X	0.02	1.7
Rubiaceae	*Cuviera acutiflora*	Kivo kitom kibwae	0	1		0.02	1.1
	Morinda lucida	Kokpobwa	0	1	?	0.02	0.8
	Pauridiantha sp.		---	---		0.02	0.8
	Rothmannia urcelliformis	Obe kidzo/Olama/Kimpia obe	9	17	?	0.09	6.6
	UK-F	Guava/Coffee kidzo	0	6		0.14	8.0
	UK-Q		0	2		0.03	1.7
	UK-FFF		0	1		0.02	0.8
Rubiaceae?	*UK-RR*		---	---		0.02	0.8
	UK-TT		---	---		0.19	10.8
Rutaceae	*Zanthoxylum* sp.	Kenchicha	0	1		0.02	0.8

Appendix I. Continued.

FAMILY	SPECIES	LOCAL NAME (Boki or Common Name)	No. of Trees for Phenology		Afi Gorilla Food *	Mean Density	IV
			1998 -	2000			
Sapindaceae	*Blighia* sp. 1	Kikukabe	2	9	X	0.05	6.4
	Blighia sp. 2	Kikukabe	0	1		0.02	0.8
	Lecaniodiscus cupanioides	Real Kochiche	0	8	?	0.07	7.6
	Placodiscus glandulosus	Fruit on Trunk	8	29	X	0.18	16.1
Sapotaceae	*Chrysophyllum pentagonocarpum*	Konka	0	3	?	0.05	2.8
	Chrysophyllum sp. 1	Kinkeng kidzo/Konka	7	8	X	0.07	4.4
	Chrysophyllum sp. 2	Konka	0	1	X	0.02	0.8
	Chrysophyllum sp. 3	Konka	0	7	?	0.14	7.8
	Omphalocarpum sp.	Kalela	3	3		0.03	---
	UK-YY	Konka?	---	---		0.02	0.9
Simaroubaceae	*Hannoa klaineana*	Ubeh/ Ober/Bobet	2	9		0.11	6.4
Sterculiaceae	*Cola latiritia*	Kichishen	3	9	X	0.05	5.1
	Cola millenii	Obe Ekong	6	6	X	0.02	---
	Cola verticillata	Kijue kibe (draw cola)	0	2		0.02	1.8
	Pterygota macrocarpa	Kichishen	---	---		0.02	0.8
	Sterculia rhinopetala		0	1		0.02	0.9
	Sterculia tragacantha	Kemuae	0	5		0.03	3.6
Tiliaceae	*Grewia mollis*	Oseng / Ocie	0	2	X	0.03	1.6
Ulmaceae	*Celtis* (*durandii*?)		0	1	?	0.02	1.3
	Celtis zenkeri		0	4	?	0.08	5.9
	Trema guineense	Ofie	---	---	X	0.03	1.6
Verbenaceae	*Vitex simplicifolia*	Different Ocheche ekwan	0	2		0.03	1.7
	Vitex sp. 1	Ufeh/Ocheche ekwan	6	6	X	0.03	---
	Vitex sp. 2 (*ferruginea*?)	Ocheche ekwan	0	1	?	0.03	2.1

Appendix I. Continued.

FAMILY	**SPECIES**	**LOCAL NAME** (Boki or Common Name)	**No. of Trees for Phenology**		**Afi Gorilla Food ***	**Mean Density**	**IV**
			1998 -	**2000**			
Violaceum	*Rinorea oblongifolia*		0	1		0.02	0.8
Unidentified	UK-Phen014	Kinfu akang	3	3		0.03	---
	UK-Phen015	Katiah mbonti	0	2	?	0.02	---
	UK-Phen016	Osampo	4	4	X	0.02	---
	UK-A (SD-01)	Kigbo	21	25	X	0.15	4.0
	UK-S		0	2		0.03	1.6
	UK-U		0	1		0.02	0.8
	UK-V		0	1		0.02	0.8
	UK-W		0	1		0.02	0.8
	UK-X		0	1		0.02	0.9
	UK-FF		0	1		0.03	1.7
	UK-GG		0	3		0.05	2.4
	UK-JJ		0	1		0.14	7.3
	UK-KK		0	1		0.02	0.8
	UK-LL	Ufa	0	1		0.02	0.8
Unidentified	UK-NN		---	---		0.05	2.5
	UK-QQ		---	---		0.02	0.8
	UK-UU		---	---		0.03	1.6
	UK-XX		---	---		0.02	0.8
	UK-ZZ		---	---		0.02	0.8
	UK-BBB		---	---		0.02	0.8
	UK-CCC		0	1		0.03	1.6
	UK-HHH		0	1		0.02	1.1
	UK-III		0	1		0.02	0.8

Appendix I. Continued.

FAMILY	SPECIES	LOCAL NAME (Boki or Common Name)	No. of Trees for Phenology 1998 -	2000	Afi Gorilla Food *	Mean Density	IV
Unidentified cont.	UK-JJJ		0	1		0.02	0.8
	UK-KKK		0	1		0.02	0.8
	UK-LLL		0	1		0.02	0.8
	UK-NNN		0	1		0.02	0.9
	UK-OOO		0	1		0.02	0.9
	UK-PPP		0	1		0.02	0.8
	UK-RRR		0	1		0.02	0.8
	UK-SSS		---	---		0.03	1.6
	UK-TTT		---	---		0.03	1.7
	UK-UUU		---	---		0.10	5.4
	UK-VVV	Osi ojorri	2	3	?	0.02	0.8

Appendix II. List of Afi gorilla food species recorded during the present study, including local name, life form and part(s) eaten. [Life form: H = herb, L = liana, S = shrub, T = tree, V = vine, U = unknown; Part eaten: FR = fruit, LVS = leaves, BK = bark (includes woody pith), PTH = herb pith, RT = root, FL = flower; * Local names often varied between villages, so several local names are listed for some species].

FAMILY	**SPECIES** (or identification number)	**LOCAL NAME** (Boki) *	**LIFE FORM**	**PART(S) EATEN**					
				FR	**LVS**	**BK**	**PTH**	**RT**	**FL**
Agavaceae	*Dracaena arborea*	Kaychuchu, Olum	T		X				
Asclepiadaceae	*Gongronema latifolium*	Otashi (Bitter leaf)	L		X	X			
Anacardiaceae	*Antrocaryon micraster*	Ojifuno	T	X					
	Pseudospondias microcarpa	Ushie (Ufe) erue	T	X					
	Sorindeia (*grandifolia*?)		T	X					
	Trichoscypha sp.		T	X					
Annonaceae	*Monodora myristica*		T	X					
	Cleistopholis patens	Otoh, Otong	T	X					
	Uvariodendron calophyllum	Alacoburo eshua	T	X					
	Xylopia sp.	Caseng kidzo	T	X					
Apocynaceae	*Landolphia owerensis*	Nda akpang (male)	L			X			
	Landolphia sp. 1	Ole (female)	L	X	X	X			
	Landolphia sp. 2	Kanwu, Ole (male)	L	X	X	X			
	Landolphia sp. 3	Kiemu nda (female)	L	X	X	X			
	Tabernaemontana pachysiphon	Kemekoto	T	X					
Araceae	*Anchomanes difformis*	Kukonyolum	H	X	X		X	X	
	Stylochiton (*wareckei*?)		H	X	X		X	X	
Bignoniaceae	*Newbouldia laevis*	Mbe kikwen	T		X	X			
Bombacaceae	*Bombax buonopozense*	Cottonwood	T						X
Burseraceae	*Canarium schweinfurthii*	Koset, Ufe	T	X					
	Santiria trimera		T	X					
Caesalpinioideae	*Dialium guineense*	Komionko	T	X					

Appendix II. Continued.

FAMILY	**SPECIES** (or identification number)	**LOCAL NAME** (Boki) *	**LIFE FORM**	**PART(S) EATEN**					
				FR	**LVS**	**BK**	**PTH**	**RT**	**FL**
Commelinaceae	*Palisota* sp. 1		H		X		X		
	Palisota sp. 2		H				X		
Compositae	*Vernonia* sp.	Kichie omu	T		X	X			
Ebenaceae	*Diospyros* (*crassiflora*?)	Kakukan	T	X					
Euphorbiaceae	*Ricinodendron heudelottii africanum*	Okpasi	T	X		X			
Flacourtiaceae	*Caloncoba glauca*		T	X					
Guttiferae	*Garcinia cola*	Ojie	T	X					
	Symphonia (?)	Kanto no kichie	T		X				
Irvingiaceae	*Irvingia gabonensis*	Uzep (bush mango)	T	X					
Marantaceae	*Hypselodelphys scandens*	Okoo, Okoodadkay	H	X			X		
	Marantochloa congensis	Ogou, Ongong	H				X		
	Marantochloa leucantha	Ogou, Ongong	H	X			X		
	Marantochloa purpurea	Ogou, Ongong	H	X			X		
	Megaphrynium macrostachyum	Floor mat	H	X	X		X		
	Thaumatococcus daniellii	Floor mat	H	X	X		X		
Meliaceae	*Turreanthus africanus*	Ushie (Ufe) eche	T	X	X				
Mimosoideae	*Albizia zygia*	Kampen	T		X				
	Parkia bicolor	Kakpaja	T	X					
Moraceae	*Antiaris toxicaria africana*	Ukwe	T	X					
	Bosqueia angolensis	Kafu kidzo	T	X	X	X			
	Ficus sp. A	Kantu	T	X	X	X			
	Ficus sp. B	Kintu, Kentoo	T	X	X	X			
	Ficus sp. C (Strangler)	Onkom	L	X	X	X			
	Milicia excelsa	Iroko, Nsen, Inshie	T	X	X	X		X	

Appendix II. Continued.

FAMILY	**SPECIES** (or identification number)	**LOCAL NAME** (Boki) *	**LIFE FORM**	**PART(S) EATEN**					
				FR	**LVS**	**BK**	**PTH**	**RT**	**FL**
Moraceae cont.	*Morus mesozygia*	Komwura	T	X	X	X			
	Musanga cecropioides	Okabie	T		X	X			
	Myrianthus arboreus	Kekekre, Kekeka	T	X					
	Treculia africana	Kichie ofe, Kolum ofie, Ulauera	T	X					X
Myristicaceae	*Pycnanthus angolensis*	Uchang, Utsan	T		X				
Olacaceae	*Strombosia* sp. 1	Ofeng enyia (eshua)	T	X					
Palmae	*Elaeis guineense*	Uyep	T	X				X	
Papilionoideae	*Platysepalum violaceum*	Ose (male)	T			X			
	Pterocarpus mildbraedii	Kaku mpipi	T			X		X	
	Pterocarpus osun	Kaku (red)	T			X			
Piperaceae	*Piper umbellata*	Obu			X				
Rhamnaceae	*Maesopsis eminii*	Kimpia okre kidzo, Onyonko	T	X					
Rubiaceae	*Rothmannia* sp.	Oshie ebe	T		X				
	Rothmannia urcelliformis	Obe kidzo	T	X					
Sapindaceae	*Placodiscus glandulosus*		T	X					
	Blighia sp.	Akukabe, Akukichie	T	X					
Sapotaceae	*Chrysophyllum* sp. 1	Kinkeng kidzo (Konka)	T	X					
	Chrysophyllum sp. 2	Konka	T	X					
Sterculiaceae	*Cola latiritia*	Kichishen	T	X					
	Cola millenia	Obe ekong	T	X					
Tiliaceae	*Grewia mollis*	Oseng	T			X			
Ulmaceae	*Trema guineense*	Ofie, Ufie	T			X			
Verbenaceae	*Vitex* sp.	Otsiakwan	T	X					

Appendix II. Continued.

FAMILY	**SPECIES** (or identification number)	**LOCAL NAME** (Boki) *	**LIFE FORM**	**PART(S) EATEN**					
				FR	**LVS**	**BK**	**PTH**	**RT**	**FL**
Zingiberaceae	*Aframomum* sp. 1	Eno, Kensenor	H	X			X		
	Aframomum sp. 2		H	X			X		
	Aframomum sp. 3	Alligator pepe	H	X			X		
	Costus sp. 1	Bush sugar cane	H				X		
	Costus sp. 2	Bush sugar cane	H				X		
Unidentified	(C-04)	Ofre etta	L			X			
	(C-05)	Ole ejuejue	L	X		X			
	(C-09)	Bebiagbo, Oruru orikaku	L	X					
	(C-15)	Ofusi	L			X			
	(C-17)	Kingya abu	L		X				
	(C-20)	Ole bajueh	L			X			
	(C-22)	Olru ebu	L			X			
	(C-26)	Beleh, Bakur, Bakekeh	L		X	X			
	(C-27)	Ole elem	L			X			
	(C-35)	Olikpe	L			X			
	(C-36)	Koja	L			X			
Unidentified	(H?-2)	Kibang ushie	H		X				
	(H?-6)	Obonacha	H				X		
	(V-02)	Ube	L			X			
	(V-06)	Kidako	V		X				
	(S-01)	Osampo	S		X	X			
	(S-09)	Nfue, Kinfue	L			X			
	(S-11)	Kanino	T	X					

Appendix II. Continued.

FAMILY	**SPECIES** (or identification number)	**LOCAL NAME** (Boki) *	**LIFE FORM**	**PART(S) EATEN**					
				FR	**LVS**	**BK**	**PTH**	**RT**	**FL**
Unidentified cont.	(T-16)	Osi ojorri	T	X					
	(T-20)	Okong	T			X			
	(T-27)	Uma usha	T		X				
	(T-40)	Okpeje	T		X	X			
	(T-46)	Kinfu etta	T	X					
	(T-49)	Kigbo	T	X					
	(T-50)	Kima ucha	T	X					
	(T-36)	Otieh kochingcha	T		X				
	(Sd-01)	Bebua onyolum	T	X		X			
	(Sd-49)	Kifa	T	X					
Other Unidentified (recorded rarely along feeding trails unless specified otherwise)	39 species (seeds in feces)		U	X					
	2 species		U	X					
	3 species		H				X		
	7 species		L			X			
	2 species		L		X	X			
	1 species		S			X			
	1 species		S		X	X			
	3 species		S		X				
	2 species		T		X	X			
	3 species		V		X				

Appendix III. Important Afi gorilla fruit foods per month sampled between December 1997 and November 1998 (high fruit consumption months in bold; wet months in italics; life form = tree unless specified otherwise; see legend for definitions and units).

Fruit Food Species	**February**		**March**		***April***		***May***		***June***		***July***	
	% F	Other	% F	Other	% F	Other	% F	Other	% F	Other	% F	Other
Aframomum spp. (herb)	40	3		*		*		*		*		*
Landolphia sp. 1 (liana)	62	4	34	2		*		*				
Landolphia sp. 2 (liana)					65	3	88	4	89	4	81	4
Antiaris toxicaria africana	26	0										
Chrysophyllum sp.		*	76	2		*						
Cola millenii				*		*		*	5	2		
Dialium guineense				*	36	0	48	0	27	2	22	0
Ficus spp. (3)	32	3	31	2		*				*		*
Garcinia kola									25	4		*
Maesopsis eminii			34	0	37	2		*		*		
Monodora myristica						*			13	3		*
Morus mesozygia	98	2		*								
Myrianthus arboreus										*	96	4
Parkia bicolor		*	29	4	34	3						
Pseudospondias microcarpa	98	4	87	4		*		*	23	1		
Sorindeia spp.					43	4	100	4		*		*
Tabernaemontana pachysiphon	17	2	27	1		*						
Treculia africana		*	44	3	82	3	69	3	27	2	36	2
Uvariodendron calophyllum											30	0
Vitex sp.										*		
Unidentified SD-49			47	2		*						
Unidentified SD-68									20	0		*

Appendix III. Continued (high fruit consumption months in bold; wet months in italics; life form = tree unless specified otherwise; see legend for definitions and units).

Fruit Food Species	*August*		*September*		*October*		November		December		January	
	% F	Other	% F	Other	% F	Other	% F	Other	% F	Other	% F	Other
Aframomum (herb)		*		*	23	3	26	4	27	3	37	2
Landolphia sp. 1 (liana)					16	2	3	4	25	4	28	4
Landolphia sp. 2 (liana)	45	2	67	2								
Antiaris toxicaria africana									3	2		
Cola millenii		*										
Ficus spp. (3)	3	2				*				*	23	3
Monodora myristica		*		*								
Morus mesozygia												*
Myrianthus arboreus	60	4	18	3	30	1						
Tabernaemontana pachysiphon											4	3
Treculia africana		*		*								
Uvariodendron calophyllum		*										
Vitex sp.		*			47	4	6	2				
Unidentified SD-01						*	7	2	44	1		*
Unidentified SD-09									3	2		*

% F = percentage of fecal samples (see Table 3.1 for sample sizes).

Other = number of the possible four ‘other’ criteria met (i.e. fecal measures: percent seed weight ≥ 10% and/or percent pulp volume ≥ 1%; feeding trail measures: percent of days present along trails ≥ 10%, and/or percent of feeding sites ≥ 10%; see Chapter 3 for details).

* = species present in fecal samples and/or along trails but was not an important species in the month (i.e., no or only one criterion was met).

Appendix IV. Important Afi gorilla herb foods per month sampled between December 1997 and November 1998 (high fruit consumption months in bold; wet months in italics; see legend for definitions and units).

Herb Food Species	**February**		**March**		***April***		***May***		***June***		***July***	
	% D	% FS	% D	% FS	% D	% FS	% D	% FS	% D	% FS	% D	% FS
Aframomum spp.	73	69	89	55	67	41	86	31	38	23	83	40
Anchomanes difformis			22	27	44	34	57	12	100	75	58	22
Costus spp.	*				*		*		*		*	
Hypselodelphys scandens	36	8	22	13	22	13	36	8			75	19
Marantochloa spp.	27	4			*							
Palisota sp. 1			*		22	4	29	10	*		*	
Palisota sp. 2	46	13			*		21	1	25	1	50	10
Stylochiton sp.	*				*							
Thaumatococcus/Megaphrynium spp			*		*		64	31			50	7
Unidentified G-01												
Herb Food Species	*August*		*September*		*October*		November		December		January	
	% D	% FS	% D	% FS	% D	% FS	% D	% FS	% D	% FS	% D	% FS
Aframomum spp.	65	14	69	18	69	30	100	45	86	53	60	33
Anchomanes difformis	94	42	62	27	85	27	30	2	*			
Costus spp.	59	8	*		54	19	20	1	29	3	20	2
Hypselodelphys scandens	24	3			*		40	3	43	6	20	5
Marantochloa spp.	29	3	*		*		50	8	29	2	30	3
Palisota sp. 1	*		23	15	54	12	70	19	43	24	90	49
Palisota sp. 2	53	6	31	6	*		40	6	*		20	5
Stylochiton sp.	35	20	54	16	46	4					*	
Thaumatococcus/Megaphrynium spp	35	3	*				60	14	29	10	*	
Unidentified G-01	*		*		23	5	30	3	29	2		

% D = percentage of days found on gorilla trails (see Table 3.2 for sample sizes);
% FS = percentage of herb feeding sites along gorilla trails;
* = present along gorilla trails but not an important species for that month.

Appendix V. Important Afi gorilla leaf foods per month sampled between December 1997 and November 1998 (high fruit consumption months in bold; wet months in italics; see legend for definitions and units).

Leaf Food Species (or "local name")	**Life Form**	**February**		**March**		***April***		***May***		***June***		***July***	
		% D	% FS	% D	% FS	% D	% FS	% D	% FS	% D	% FS	% D	% FS
Anchomanes difformis	H			22	61	39	51	57	17	75	63	25	36
Stylochiton sp.	H	*				*							
Thaumatococcus/ Megaphrynium spp.	H					22	12	43	57	*		25	36
("Kibang ushie")	H			22	13								
Albizia zygia	T	x				*							
Dracaena arboreus	T	*		22	13	*		*					
Ficus spp. (3)	T	*				17	7	14	7	38	10	17	8
Milicia excelsa	T	*				11	5			38	10	x	
Morus mesozygia	T	*				x		*					
Musanga cecropioides	T							*		*		*	
Pycnanthus angolensis	T									*			
Turreanthus africanus	T	46	44			x						x	
Unidentified T-11	T			11	13								
("Okpeje")	T	x										x	
Gongronema latifolium	L									*			
Landolphia sp. 2	L												
("Beleh/Bakur")	L					*		*		*			
("Kidako")	V							x					

Life form: H = herb, L = liana, T = tree, V = vine;
% D = percentage of days found on gorilla trails (see Table 3.2 for sample sizes);
% FS = percentage of leaf feeding sites along gorilla trails; x = important species that represented ≥ 10% of leaves eaten per month but percentage of days sampled and feeding sites were < 10%;
* = present along gorilla trails but not an important species for that month.

Appendix V. Continued (high fruit consumption months in bold; wet months in italics; see legend for definitions and units).

Leaf Food Species (or “local name”)	**Life Form**	*August*		*September*		*October*		November		December		January	
		% D	% FS	% D	% FS	% D	% FS	% D	% FS	% D	% FS	% D	% FS
Anchomanes difformis	H	71	18	54	14	62	12	*					
Stylochiton sp.	H	35	31	46	18	23	2					10	16
Thaumatococcus/ Megaphrynium spp.	H	24	5	*		*		30	15	29	54		
(“Kibang ushie”)	H											20	11
Albizia zygia	T	*											
Dracaena arboreus	T												
Ficus spp. (2)	T	18	1	23	5	23	3	20	8	14	11	30	47
Milicia excelsa	T	35	12	15	5	31	17	*					
Morus mesozygia	T	41	10			*							
Musanga cecropioides	T			15	4	39	26	40	50				
Pycnanthus angolensis	T	*		15	20								
Turreanthus africanus	T	18	3							14	22		
Unidentified T-11	T					*							
(“Okpeje”)	T	41	9	15	21	8	10	10	10				
Gongronema latifolium	L	*		*		8	13						
Landolphia sp. 2	L	18	5	31	7							*	
(“Beleh/Bakur”)	L	*				39	9	20	7				
(“Kidako”)	V												

Life form: H = herb, L = liana, T = tree, V = vine;
% D = percentage of days found on gorilla trails (see Table 3.2 for sample sizes);
% FS = percentage of leaf feeding sites along gorilla trails; **x** = Important species that represented ≥ 10% of leaves eaten per month but percentage of days sampled and feeding sites were < 10%;
* = present along gorilla trails but not an important species for that month.

Appendix VI. Important Afi gorilla liana bark/pith foods per month sampled between December 1997 and November 1998 (high fruit consumption months in bold; wet months in italics; see legend for definitions and units).

Liana Bark Food Species (or “local name”)	**February**		**March**		***April***		***May***		***June***		***July***	
	% D	% FS	% D	% FS	% D	% FS	% D	% FS	% D	% FS	% D	% FS
Gongronema latifolium											*	
Landolphia sp. 1	*		22	23	33	33	29	29				
Landolphia sp. 2	64	42	33	37	44	28	50	62	38	80	58	69
(“Ofusi”)	46	36	44	32	28	36						
(“Ole ejuejue”)	*											
(“Ofre etta”)	*		*									
(“Ole elem”)									13	10		

Liana Bark Food Species (or “local name”)	*August*		*September*		*October*		November		December		January	
	% D	% FS	% D	% FS	% D	% FS	% D	% FS	% D	% FS	% D	% FS
Gongronema latifolium	*				15	11						
Landolphia sp. 1	*		*		*		10	6	43	42	10	2
Landolphia sp. 2	82	48	62	93	77	42	40	44	43	21	80	44
Landolphia sp. 4					23	18						
(“Beleh/Bakur”)			*		23	2	20	11				
(“Ofusi”)	*										*	
(“Ole ejuejue“)	24	17					10	11			20	18
(“Ofre etta“)	*				23	2	*				30	13
(“Ole elem”)	*											

% D = percentage of days found on gorilla trails (see Table 3.2 for sample sizes);
% FS = percentage of woody bark/pith feeding sites along gorilla trails;
* = present along gorilla trails but not an important species for that month.

Appendix VII. Important Afi gorilla tree bark foods per month sampled between December 1997 and November 1998 (high fruit consumption months in bold; wet months in italics; see legend for definitions and units).

Tree Bark Food Species (or "local name")	**February**		**March**		***April***		***May***		***June***		***July***	
	% D	% FS	% D	% FS	% D	% FS	% D	% FS	% D	% FS	% D	% FS
Bosqueia angolensis					6	17						
Ficus spp. (2)	18	29							50	50	25	27
Milicia excelsa									38	50	17	46
Morus mesozygia	18	29			6	67						
Pterocarpus osun / P. mildbraedii	9	43	11	20								
Tabernaemontana pachysiphon			11	40								

Tree Bark Food Species (or "local name")	*August*		*September*		*October*		November		December		January	
	% D	% FS	% D	% FS	% D	% FS	% D	% FS	% D	% FS	% D	% FS
Ficus spp. (2)	18	3	23	20	31	11						
Garcinia kola									14	20		
Grewia mollis	35	35	8	27								
Milicia excelsa	47	22	23	40	39	56	20	36				
Morus mesozygia	35	13				x						
Pterocarpus osun / P. mildbraedii					15	11	30	57	43	80	40	71
Tabernaemontana pachysiphon					*							
Unidentified T-11	*		8	13							20	18
("Okpeje")	29	13										

% D = percentage of days found on gorilla trails (see Table 3.2 for sample sizes);
% FS = percentage of leaf feeding sites along gorilla trails;
x = important species that represented ≥ 10% of tree bark eaten per month but percentage of days sampled and feeding sites were < 10%;
* = present along gorilla trails but not an important species for that month.

Appendix VIII. Data collected at nest sites.

Nest data were collected between December 1998 and June 1999 using methods similar to Tutin and Fernandez (1993). When fresh nest sites (≤ 4 days old) were encountered, the following were recorded: date, location, number of nests, estimated age of nests, and habitat type. Six different habitat types were used (closed mature forest, open mature forest, secondary forest, vine tangle, forest gap and herb patch; the latter two were at times pooled into a light gap category) and are defined in Chapter Two. When individual nests within a nest site were located in more than one habitat type, they were listed in descending order based on the proportion of nests in each habitat type.

For individual nests, nest type, height of nest above ground, position of feces with respect to nest (inside, on the rim, or outside), age-class of occupant as determined from diameter of feces (adult males: ≥ 6.5 cm diameter; adult females and adolescent males: 4.5 - 6.4 cm; juvenile: 2.0 - 4.4 cm; infant: < 2.0 cm; Tutin and Fernandez, 1993), species of plants used in nest construction, whether the nest was sheltered by canopy overhead, and evidence that young also occupied the nest (e.g., presence of infant/juvenile sized feces in nest) were noted and hairs collected. Measuring distance and noting direction from each nest to the next nearest nest determined positions of individual nests within the nest site. For nests in trees, the estimated height of tree, its diameter at breast height (dbh; 1.3 m above ground), height of its lowest branch, and position of nest on tree branch (1 = near trunk, 2 = mid-branch, 3 = end of branch) were recorded.

Nine different nest types were recognized as follows. Relationships to nest categories used by Tutin et al. (1995), Remis (1993) and Mehlman and Doran (2002) are noted in parentheses.

1. <u>Bare Ground</u>: gorilla slept on ground and no structure present. The area is characterized by a flattened depression sometimes with a few ‘pressed’ dead leaves and presence of feces and/or hairs (same as bare ground of Remis, zero nest of Tutin et. al. and bare earth of Mehlman & Doran).
2. <u>Zero Construction</u>: gorilla slept atop vegetation, usually non-woody ‘soft vines’ and/or grasses, that provided minimal insulation between occupant and ground (i.e., no ground can be seen through nest); but, no construction was involved. Nest can be

recognized by a circular impression in the vegetation and presence of feces and/or hairs.

3. Minimum: nests constructed with < 4 plant stems indicating a minimal effort to provide some insulation (same as minimum in Tutin et. al. and Mehlman & Doran).
4. Herb: nests constructed with ≥ 4 herbaceous stems (e.g. Marantaceae and Zingiberaceae) that are bent and often interwoven to provide a substantial platform (same as herb of Tutin et. al. and included in Remis' ground constructed and Mehlman & Doran's fully constructed nest categories).
5. Mixed: nests similar to herb nests but woody vegetation (lianas, shrubs, saplings, or detached branches of small trees) are also incorporated (same as mixed of Tutin et. al. and included in Remis' ground constructed and Mehlman & Doran's fully constructed nest categories).
6. Woody 1: nests built on the ground made entirely of woody vegetation (same as woody in Tutin et. al. and included in Remis' ground constructed and Mehlman & Doran's fully constructed nest categories).
7. Woody 2: similar to woody 1 nests but built > 0.5 m above ground.
8. Tree: nests constructed above ground in trees by bending and breaking branches to form a sleeping platform (same as tree of Tutin et. al. and included in Remis' above ground and Mehlman & Doran's arboreal nest categories).
9. Vine Tangle: nests constructed above ground in vine tangles (lianas) with no direct support from tree branches (included in Remis' above ground and Mehlman & Doran's arboreal nest categories).

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