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Behavioral ecology of savanna chimpanzees (*Pan troglodytes verus*) with respect to insectivory at Fongoli, Senegal

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**Behavioral ecology of savanna chimpanzees (*Pan troglodytes verus*) with respect to
insectivory at Fongoli, Senegal**

by

Stephanie Lynn Bogart

A dissertation submitted to the graduate faculty
in partial fulfillment of the requirements for the degree of

DOCTOR OF PHILOSOPHY

Major: Ecology and Evolutionary Biology

Program of Study Committee:
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Iowa State University

Ames, Iowa

2009

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ABSTRACT

In this dissertation I examine the behavioral ecology of savanna chimpanzees in Senegal. I test hypotheses related to the effects of the environment on the diet of the chimpanzees at Fongoli, concentrating on their insectivory specifically. Fongoli is the hottest and driest site in which chimpanzees have been habituated for observational data collection. Grassland habitats (68%) dominate, characterizing the site as an open savanna mosaic, which is interspersed with woodland and small patches of closed forests. The environment at Fongoli presents a setting similar to that of Plio-Pleistocene hominans (Bobe & Behrensmeyer 2004, Bromage & Schrenk 1995, Cerling 1992, Reed 1997) and provides the opportunity to examine the behavior of apes in response to selective pressures associated with such an environment.

I examine Fongoli chimpanzee insectivory in the larger context of activity and habitat use, with an emphasis on evaluating potential ecological influences in this environment. Most chimpanzee research over the last 40 years has emphasized behavior, with limited data on the ecological context. Here, I provide detailed data on food distribution and availability, using both plot and plotless methods.

A major question I examined was whether termites were an important food resource for the Fongoli chimpanzees. Chimpanzees are highly frugivorous and usually rely on a few important food species, yet as omnivores, also incorporate animal prey in their diet. My previous research indicated that Fongoli chimpanzees often fished for termites with tools. I predicted that the environment of these savanna chimpanzees affected insect foraging. Thus, I expected that ecological factors at Fongoli influenced their insectivorous behavior and

hypothesized that certain habitats were more important for feeding (open habitats), while other habitat types (closed habitats) were used mainly for resting and social behaviors.

Over 900 hours of observation provided behavioral data on insect foraging, general activity, general diet, and habitat use of chimpanzees. Fongoli chimpanzees consume termites (*Macrotermes subhyalinus*) more often than any other chimpanzee population studied. The chimpanzee diet at Fongoli is composed mostly of fruit (61.3%) and termites (24.1%). Although termites were consumed throughout the year, with a peak during the transitional period to the beginning of the wet season, the inclusion of termites in the diet did not correlate significantly with rainfall or fruit scarcity. Termites are an essential resource for the Fongoli chimpanzees throughout the year, and chimpanzees spend an annual average of approximately 8% of their active time termite fishing. High soil and air temperatures correlated to greater proportion and longer bout length of termite fishing. Fongoli chimpanzees forage for termites most often in woodland habitat types. General foraging and feeding was conducted primarily in woodland and grassland habitat types, where all food resources exhibited the highest densities. While seasonality had no effect on termite foraging, seasonality did influence feeding and foraging behavior in general, in that more time was devoted to these activities in the dry season (November through May) when fruits are more abundant.

The extensive termite feeding of Fongoli chimpanzees adds to the list of distinctive behaviors they display relative to chimpanzees living in more forested habitats (Pruetz 2001, 2007, Pruetz & Bertolani 2007). I incorporate the Fongoli chimpanzees' behaviors in a relational model of hominan evolution. I found that these chimpanzees consume termites more than any other ape community across Africa. The relatively few mammalian prey

species, high temperatures correlating with increased termite fishing, and abundant density of *Macrotermes* in savanna woodland habitat types at Fongoli are all variables indicating environmental influence on termite foraging. Paleoanthropologists can use these data to construct testable hypotheses about the ecology of hominan habitats. Environmental stresses associated with savanna paleo-habitat would likely be comparable to what is found at Fongoli. Hominan species living in similar habitats may have relied on termites as an animal resource when other foods were scarce resembling Fongoli chimpanzees.

Finally, data in this thesis should also be brought to bear on the conservation of chimpanzees' habitats. Emphasis on protecting closed forest habitats is usually a focus in conservation efforts. However, woodland and grassland habitat types contain the majority of the important food resources of the Fongoli chimpanzees and should be conserved to ensure the long-term survival of the West African chimpanzees in southeastern Senegal.

CHAPTER ONE

Introduction: Ecology and behavior of chimpanzees

1.1 Introduction

The study of chimpanzee (*Pan troglodytes*) behavior in an ecological context has been neglected relative to the number of long-term study sites that have provided information on social behavior (Pruetz 2006). More recently, the importance of ecological studies has been recognized in facilitating chimpanzee conservation (Arnhem et al. 2008, Chepstow-Lusty et al. 2006, Pruetz et al. in prep, Tweheyo & Babweteera 2007). The current study focuses on the interrelationships between Fongoli chimpanzees in Senegal and their environment, information that is essential for preserving the areas they inhabit. Additionally, Fongoli is the only active, long-term savanna chimpanzee study site where these apes have been habituated to human presence. It is an environment that is thought to be similar to those inhabited by early hominans¹ during the Plio-Pleistocene (Bobe & Behrensmeyer 2004, Bromage & Schrenk 1995, Cerling 1992, Owen-Smith 1999, Potts 1998, Reed 1997). Studying the ecology of chimpanzees can provide testable hypotheses regarding aspects of hominan behavior (Foley 1999, Reed 1997, Stanford 2006, Unger et al. 2006). Data obtained from this research will be used to examine questions related to the diet and habitat use of these hominans. Results will also be used to develop hypotheses about the role of foraging in the evolution of hominan tool use.

Tool use was historically thought of as “uniquely human,” but chimpanzees have been recognized as tool users since Jane Goodall’s pioneering studies in the 1960s (Goodall

¹ The term “hominan” refers to bipedal apes (humans and their extinct relatives since the split from the chimpanzee lineage) using subtribe classification Hominina from Groves 2001 (see Figure 1.1). Classification includes *Australopithecus* spp., *Paranthropus* spp., and *Homo* spp.

1963). Tool use is defined as: “the external employment of an unattached environmental object to alter more efficiently the form, position, or condition of another object, another organism, or the user itself when the user holds or carries the tool during or just prior to use and is responsible for the proper and effective orientation of the tool” (Beck 1980, p. 10). Tool use to gain an otherwise unattainable food resource such as termites has been widely studied, yet research on the ecology of this behavior is relatively lacking (Bogart 2005, Bogart & Pruetz 2008, Collins & McGrew 1987, Deblauwe & Janssens 2008, McGrew & Collins 1985). My research on the Fongoli chimpanzees’ insectivorous diet and tool use in relation to their environment provides novel information in this respect. I aim to contextualize this behavior within the Fongoli chimpanzee environment, activity, habitat use, and diet. The combination of systematic methods for obtaining these data has not been previously applied to study chimpanzee insectivory to the degree presented here. Data on the environment at Fongoli, and the activity, habitat use, and diet of the chimpanzees will be used to examine the insectivorous diet in more detail. Finally, the findings of this research are discussed in terms of implications for understanding hominan diet as well as regarding conservation issues plaguing chimpanzees today.

1.1.1 Family Hominidae

Due to our genetic relatedness and morphological similarities, non-human primates² have been a major source of information in the attempt to better understand human evolution. This pertains especially to the Superfamily Hominoidea, otherwise known as the lesser apes [gibbons (*Hylobates* spp., *Hoolock* spp., *Nomascus* spp.) and siamangs (*Symphalangus*

² Referred to solely as primates throughout this dissertation.

syndactylus)] (Groves 2005) and great apes [chimpanzees (*Pan troglodytes*), bonobos (*Pan paniscus*), orangutans (*Pongo pygmaeus*), gorillas (*Gorilla gorilla*) and humans (*Homo sapiens*)] (Gagneux et al. 1999, Groves 2001, Morin et al. 1994). Recent genetic evidence has changed our understanding of great ape taxonomy (Ruvolo 1997, Chen & Lee 2001, Morin et al. 1994, Gagneux et al. 1999). Chimpanzees and bonobos were historically placed in the family Pongidae with gorillas and orangutans based on morphological similarities, but through molecular data a new taxonomy was proposed by Groves (2001) (see Figure 1.1). Chimpanzees and humans share a common ancestor and approximately 98% of their DNA (Cheng et al. 2005). This close relatedness offers an examination of chimpanzees as referential models for the last common ancestor of humans and the chimpanzee lineage (Moore 1996, see Section 2.6). Thus, from a phylogenetic perspective, our closest living relative can provide important information for modeling hominan behavior.

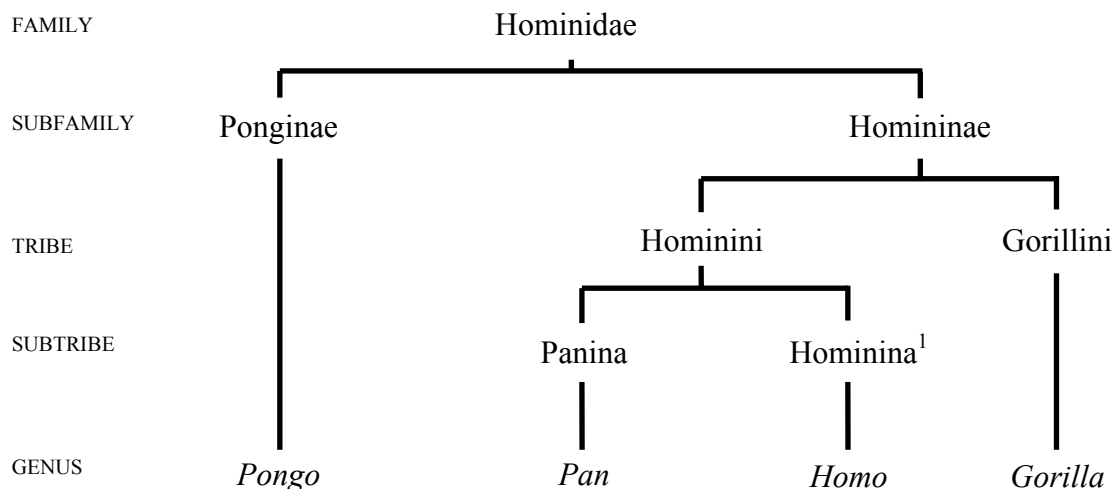


Figure 1.1: Taxonomic classifications of the great apes (after Groves 2001) to demonstrate relatedness (hominan in text refers to Hominina subtribe including all species that stemmed from the last common ancestor of humans and chimpanzees, or *Pan*).

¹Also includes the genera *Australopithecus* and *Paranthropus*

Paleoanthropologists rely on archaeological and fossil evidence, which provides clues to extinct hominin behaviors. Empirical observations of primates and hunter-gatherer societies supplement these data in hypotheses about hominin behavior (Foley 1999, Reed 1997, Stanford 2006, Unger et al. 2006). Knowledge of chimpanzee ecology and behavior is therefore essential for an understanding of human evolution.

The four allopatric subspecies of chimpanzees (defined by genetics and morphology) are dispersed across subSaharan Africa (Figure 1.2) (Morin et al. 1994, Gagneux et al. 1999, Oates et al. 2009). *Pan troglodytes schweinfurthii* is the eastern chimpanzee, found in the countries of Uganda and Tanzania (Morin et al. 1994, Gagneux et al. 1999, Stumpf 2007). The central African chimpanzee, *Pan troglodytes troglodytes*, resides from Gabon to the Democratic Republic of Congo (Morin et al. 1994, Gagneux et al. 1999, Stumpf 2007). The formerly named Nigerian chimpanzee was given the subspecies designation of *vellerosus* (Gonder et al. 1997, Sommer et al. 2004), but that designation is now considered incorrect in terms of the rules of taxonomic nomenclature and should instead be *Pan troglodytes ellioti* (Oates et al. 2009). Finally, the western chimpanzee is categorized as *Pan troglodytes verus*, and their range includes Senegal, Sierra Leone, Guinea-Bissau, Ivory Coast, and Guinea (Morin et al. 1994, Gagneux et al. 1999, Butynski 2003). Abundant research on chimpanzee behavior across sites reveals variation between them (Whiten et al. 1999, 2001). The four subspecies vary in their social behavior (Boesch & Boesch-Achermann 2000), habitat (McGrew et al. 1979, Russak & McGrew 2008), diet (Conklin-Brittain et al. 2001, Garber 1987), and specifically in their tool technology (McGrew 1992). Data on the behavior and

ecology of the West African subspecies in a savanna habitat will be provided here, with a focus on the insectivorous aspect of the chimpanzee diet.

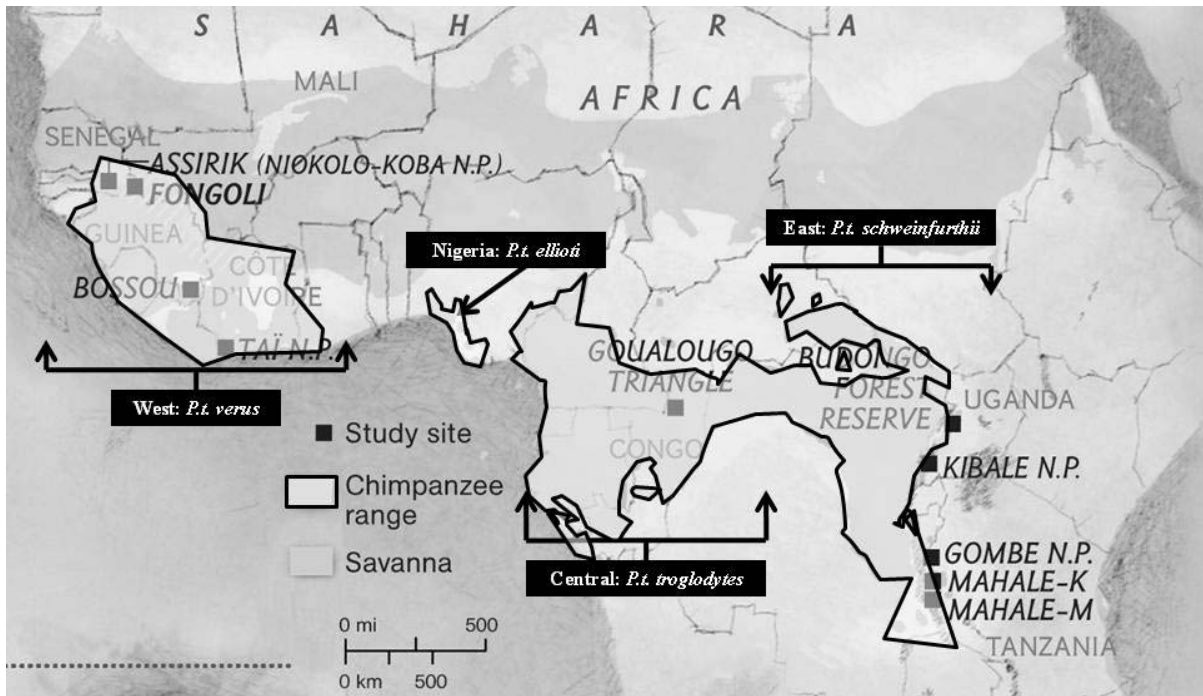


Figure 1.2: Chimpanzee subspecies distribution across Africa.

Map and chimpanzee range by National Geographic Magazine (Lisa Ritter), modified by S. Bogart

This study examines the West African chimpanzee subspecies in the country of Senegal at the Fongoli site. The Fongoli chimpanzee community has been studied since 2001 by Dr. Jill Pruetz of Iowa State University, and ranges from 32-34 individuals annually (Pruetz, unpublished data). Fongoli's environment differs from that of chimpanzees studied elsewhere, in that it is a savanna mosaic as opposed to the forested environments of other long term field studies of chimpanzees.

Chimpanzees are classified as endangered according to the International Union for the Conservation of Nature and Natural Resources (IUCN) Red List³. They have

³ <http://www.iucnredlist.org/details/15933>

experienced a significant population reduction over the last twenty to thirty years (Oates et al. 2008), with a current estimate of fewer than 300,000 wild chimpanzees remaining (Butynski 2003). West Africa has an estimated 21,300 to 55,600 chimpanzees remaining in the wild (Butynski 2003). Many factors have caused the decline of chimpanzees as a species, such as disease, poaching/hunting, habitat destruction and habitat degradation (Hill 2002). Thus, research on chimpanzees and their environments can also aid conservation efforts.

1.2 Previous research on chimpanzees

Chimpanzees have been studied systematically since the 1960s (Goodall 1963) and there are many long-term field sites that have provided information on chimpanzees over the years (Tanzania: Gombe, Goodall 1986; Mahale, Nishida 1990; Budongo, Reynolds 1992, Newton-Fisher 1999; Ngogo (Kibale), Mitani et al. 2002; Kanyawara (Kibale), Wrangham et al. 1996; Democratic Republic of Congo: Kahuzi-Biega, Basabose 2002; Congo: Goualougo Triangle, Morgan & Sanz 2003; Gabon: Lope, Tutin & Fernandez 1993; Ivory Coast: Tai, Boesch & Boesch-Achermann 2000; Guinea: Bossou, Sugiyama 1989, Sugiyama and Koman 1992; Nigeria: Gashaka-Gumti, Sommer et al. 2004; and Senegal: Fongoli, Pruetz 2006). Several sites in Africa have produced indirect data on unhabituated chimpanzees (For example: Congo: Goualougo Triangle, Morgan & Sanz 2003; Gabon: Lope, Tutin & Fernandez 1993; Tanzania: Ugalla, Moore 1996; Uganda: Semliki, Hunt & McGrew 2002; Bwindi, Stanford & Nkurunungi 2003; Senegal: Mount Assirik, Hunt & McGrew 2002).

Chimpanzees live in complex social groups composed of multiple females and males that fission and fusion daily into subgroups ranging in size from 2 to 140 individuals (Mitani et al. 2002). Grouping patterns vary depending on food availability (Anderson et al. 2002,

Chapman & Chapman 2000, Chapman et al. 1995), female estrous (Anderson et al. 2002), seasonality (Pruetz & Bertolani, in press), hunting success (Mitani & Watts 1999, Stanford et al. 1994), predator interactions (Boesch 1991) and location within the home range (core or periphery range) (Wrangham 1999). At about 10 years of age females typically disperse from their natal community as they reach puberty (Nishida & Kawanaka 1972, Pusey 1979). In general chimpanzee society consists of a male dominated hierarchy system (Goodall 1986, Wrangham 1986, Boesch & Boesch-Achermann 2000).

Chimpanzees live in a variety of different habitat types. Their range extends from tropical forests to open grasslands, but they have mainly been described as a ‘rainforest-typical’ species (McGrew et al. 1979, Stumpf 2007, Russak & McGrew 2008). In spite of this stereotype, research demonstrates that chimpanzees inhabit a wide range of ecotypes (Russak & McGrew 2008). Goldberg & Ruvolo (1997) used genetic sequencing of *Pan troglodytes schweinfurthii* to examine relatedness of the populations in eastern Africa. They applied this to the forest refugia theory, which predicts that East African chimpanzee populations are related, although now separated, due to forest expansion and reduction overtime (Goldberg & Ruvolo 1997). Genetic material (chimpanzee hairs) were collected from sleeping nests in 19 different populations and provided 268 DNA sequences. The authors found that the East African chimpanzee subspecies has very little variability indicating gene flow was not restricted (Goldberg & Ruvolo 1997). This finding has implications for the geographic distribution of chimpanzees. Goldberg & Ruvolo (1997) concluded that chimpanzees did not evolve in a forest environment, but rather were capable of moving across open spaces between forest patches, through marginal habitats, and consider chimpanzees as a woodland species.

The environment influences chimpanzee behavior on various levels. Thus, the general activity budget and habitat type use was studied here in order to place diet in larger context. How an animal uses the physical or biological components within an area is described as ‘habitat use’ (Hall et al. 1997). Chimpanzees live in a variety of habitat types, and generally their home ranges can contain several different vegetation classifications, defined as habitat type (Daubenmire 1968, Garshelis 2000, McGrew et al. 1979, Russak & McGrew 2008, Stumpf 2007). Habitat use by chimpanzees is suggested as influenced by fruit availability (Furuichi et al. 2001, Itoh & Nishida 2007, Wrangham et al. 1991, 1998, Yamagiwa & Basabose 2006), temperature or season (Pruetz & Bertolani, in press, Takemoto 2004), logging (Arnhem et al. 2008), access to water (Pruetz & Bertolani, in press), and activity patterns (Tweheyo et al. 2003). Fongoli chimpanzees use patches of closed habitat types more often in the dry season, relating to temperature and water issues on a savanna (Pruetz & Bertolani, in press). Seasonality and temperature have been shown to affect activity patterns for various chimpanzee populations (Ngogo: Ghiglieri 1984, Kalinzu: Matsumoto-Oda 2002, Bossou: Takemoto 2002). The Fongoli chimpanzees vary their activity patterns according to the wet and dry seasons (Pruetz & Bertolani, in press). Activity patterns have been demonstrated to correlate with habitat use in chimpanzees in Budongo as well (Tweheyo et al. 2003). At most sites feeding and foraging is the dominant chimpanzee activity during the day [(Kibale (62.1%: Ghiglieri 1984, 59.7%: Wrangham et al. 1991); Budongo (52.7%: Fawcett 2000, 48.8%: Newton-Fisher 1999, 80%: Tweheyo et al. 2003); Tai (45%: Boesch & Boesch-Achermann 2000); Gombe (47%: Goodall 1986, 42.8%: Teleki 1981)]. However, resting is the predominant activity of chimpanzees at Mahale, Tanzania (38.6%: Huffman 1990), as well as at Fongoli (Pruetz & Bertolani, in press). Other behaviors that are

components of the activity budget include traveling, social behaviors such as grooming and playing, and activities such as self-grooming, drinking, and nest building.

Chimpanzees are largely frugivorous, sometimes referred to as “ripe fruit specialists” (Goodall 1968, 1986, Hladik 1977, Nishida 1990, Wrangham et al. 1998). However, they are considered omnivores because they also eat leaves, flowers, bark, insects and vertebrate prey (Conklin-Brittain et al. 2001, Hladik 1977, Garber 1987, Goodall 1986, Pruetz 2006, Tutin et al. 1997, Wrangham 1977, Wrangham et al. 1998). Of the non-human hominids (great apes), however, chimpanzees include the highest proportion of animal prey in their diet (Fossey & Harcourt 1977, Pruetz 2006, Remis 1997, Rodman 1977, Tutin et al. 1997). Food resources vary from site to site where chimpanzees are studied, which appears to correlate with variability in the diets of different communities (see Chapter Two). For example, central chimpanzees consume more fruit than western and eastern communities, while eastern chimpanzees consume more leaves than central and western chimpanzees (see Chapter Two). Studies of the ecological context of feeding behavior in chimpanzees are sparse (e.g., Basabose 2002, Bogart & Pruetz 2008, Hashimoto et al. 2003, McBeath & McGrew 1982, McGrew & Collins 1985, Pruetz 2006, Wrangham 1977) in relation to the number of long-term study sites that have provided general information on chimpanzee behavior (Goodall 1986, Nishida 1990; Reynolds 1992, Newton-Fisher 1999, Mitani et al. 2002, Wrangham et al. 1996, Basabose 2002, Morgan & Sanz 2003, Tutin & Fernandez 1993, Boesch & Boesch-Achermann 2000, Sugiyama 1989, Sugiyama and Koman 1992). Further, most data stem from forested sites such as Kibale and Kalinzu, Uganda and Kahuzi-Biega, DRC (Basabose 2002, Wrangham et al. 1991, Hashimoto et al. 2003). I offer new evidence on the diet of chimpanzees and demonstrate that the Fongoli chimpanzees deviate from general patterns in

the behavior of this species living in other regions of Africa in wetter and cooler, closed-canopy environments.

1.3 Research questions: food availability, feeding behavior, and tool use

A savanna environment is generally thought of as depauperate in terms of the diversity of food resources and the availability of those foods for primates (e.g. Isbell & Young 1996, Moore 1996). Pruetz (2006), however, found that the diversity of fruits in the Fongoli chimpanzee diet is comparable to that of forest chimpanzee communities. Still, the distribution and abundance of foods at Fongoli or any other savanna chimpanzee study site have not yet been provided in detail. Information on the diet of savanna chimpanzees has been largely based on indirect evidence such as fecal remains and feeding traces, with few direct observations (Hunt & McGrew 2002, McGrew et al. 1988, Pruetz 2006, Schoeninger et al. 1999). The local environment of the Fongoli chimpanzees and, specifically, their food resources and diet in relation to insectivory are the focus of this study.

1.3.1 Fongoli chimpanzee insectivory

Animal prey is represented in the diet of chimpanzees more than in any other non-human great ape (Fossey & Harcourt 1977, Pruetz 2006, Remis 1997, Rodman 1977, Tutin et al. 1997). Animal prey accounts for an average of 8% of the Fongoli chimpanzee diet based on preliminary evidence from fecal samples, but only 2.5% of animal prey consists of vertebrates (Pruetz 2006). This provides further confirmation of the importance of invertebrates in the diet. All of the great apes consume insects and use specialized techniques to obtain them (Beck 1980, McGrew 1992). However, the chimpanzee and Sumatran orangutan (*Pongo pygmaeus abelii*) are the only known non-human primate to habitually use

multiple types of tools to acquire insects (McGrew 1992, van Schaik et al. 1996).

Chimpanzees use elementary technology for simple problem solving in order to obtain invertebrate prey (McGrew 1992). The methods employed by these apes for the consumption of invertebrates include manipulating plant material into tools to obtain otherwise unattainable insects en masse. Tool use of this nature has been observed across Africa over the many years that chimpanzees have been studied in the wild (Bogart & Pruetz 2008, Fay & Carroll 1994, Goodall 1963, McBeath & McGrew 1982, McGrew & Collins 1985, Suzuki et al. 1995). Chimpanzees mainly feed on social insects, such as Hymenoptera (ants, wasps and bees) and Isoptera (termites) (McGrew 1983).

According to fecal analyses, the Fongoli chimpanzees consume termites during all months of the year (Pruetz 2006). The consumption of termites throughout the year has not been observed at many other chimpanzee sites. Chimpanzees in central Africa, such as Ndoki (Suzuki et al. 1995), Goualougo (Sanz et al. 2004), and Rio Muni (McGrew et al. 1979), are reported to consume termites throughout the year, but those in East Africa are seasonal regarding this behavior (McGrew et al. 1979, McGrew & Collins 1985). The other Senegalese site of Assirik was reported to have seasonal termite fishing based on indirect evidence (McGrew et al. 1979). Insect proportion in the Fongoli chimpanzee diet is stated as the percentage of fecal samples containing them. This measure does not give a reliable indicator as to how much time chimpanzees spend on insects relative to other dietary foods and in comparison to other chimpanzee sites that have used direct behavioral data. Since Fongoli chimpanzees consume termites all year long, I suggest that the Fongoli chimpanzees spend more time consuming insects throughout the year than other chimpanzee sites in more forested environments (Table 1.1).

Knowledge of the general diet of the Fongoli chimpanzees will provide a foundation for understanding how insectivory is represented in their overall diet. How much time chimpanzees spend feeding on termites as compared to the other foods in the diet indicates their importance in the diet, i.e. if chimpanzees spend very little estimated time on termites, they are probably not a main food resource in the chimpanzee diet. Previous published research on the diet of the Fongoli chimpanzees was based mostly on fecal samples and a limited number of observations (Pruetz 2006). Following successful habituation, it is possible to more specifically examine the chimpanzees' diet at Fongoli. The chimpanzees have a diet consisting of at least 60 different plant items from 47 species (Pruetz 2006). Another five species of vertebrates and invertebrates are among the known diet (Pruetz 2006). The Fongoli chimpanzee diet appears narrow regarding the amount of plant species and parts they consume as compared to chimpanzees at other more forested sites (Pruetz 2006). The general diet of Fongoli chimpanzees should follow previous research at Fongoli and be similar to other chimpanzee communities in composition; thus, fruit will compose the majority of the diet, followed by leaves. Chimpanzees here may consume more unripe fruit than at other sites (Pruetz, unpublished data, personal observation). Preliminary research indicated a seasonal influence in terms of rainfall on fruit abundance (Pruetz 2006). Thus, fewer plant species will fruit in the wet season when "fallback foods" are used. The theory of optimal foraging predicts that less preferred and/or low quality foods will be used more in times of reduced availability of preferred foods (Stephens & Krebs 1986). These low-quality foods are considered fallback foods, which are not preferred in the diet but are highly consumed during periods when high-quality, preferred foods are scarce (Wrangham et al. 1998, Marshall & Wrangham 2007).

1.3.2 Fongoli's environment relative to insectivory

How does a savanna habitat affect chimpanzee insectivory, a behavior that is mainly seasonal at more forested sites? Do temperature and habitat type influence where chimpanzees eat insects? It has been suggested that chimpanzees in dry habitats are more affected by seasonality than those living in more forested habitats (Hunt & McGrew 2002). At Mt. Assirik, Senegal, seasons affect use of habitat; when temperatures rose in the dry season, vegetation coverage and water resources were thought to be more important for the chimpanzees (Baldwin et al. 1982, Tutin et al. 1983). A need for water and shaded areas was associated with thermoregulation issues in dry seasons but was not linked to food availability (Tutin et al. 1983). Fongoli has a habitat similar to Mt. Assirik, and the same hypothesis could be posited (Pruetz & Bertolani, in press). Behavioral data is collected at Fongoli to test such hypotheses, whereas at Assirik, chimpanzees were not habituated, and most data collected was based on indirect evidence. Moreover, food availability and other ecological variables were not quantified at Assirik, except on a habitat-level scale. Habitat type has been shown to correlate with certain aspects of chimpanzee diet at Fongoli (Bogart & Pruetz 2008). For example, results from my previous research indicate a selection of woodland and closed habitat types (ecotone and gallery forest) for termite fishing (Bogart & Pruetz 2008). More detailed examination of ecological variables will allow me to ascertain which factors influence this behavior within particular habitats.

At Fongoli, termites are most intensively consumed between the months of April and July, the late dry season and early wet season respectively but are consumed year-round (Bogart & Pruetz 2008, Pruetz 2006). June is considered a transitional month, when rains begin, so the intensity of termite fishing in June and July may correlate with a higher

proportion of rainfall if seasonality influences this activity. The frequency and estimated duration of termite-fishing is quantified in this study in order to more closely examine the pattern of behavior exhibited by Fongoli chimpanzees relative to chimpanzees elsewhere. Preliminary research suggests high consumption of termites in both the dry and wet seasons at Fongoli. Thus, seasonality of rainfall is not expected to influence or correlate with the consumption of insects within the Fongoli chimpanzee diet (Table 1.1).

Primates, like many animals, exploit their ranges according to the distribution of food resources (Garber 2000). Food resources occur abundantly in woodland and other open habitats at Fongoli, with more plants producing fruit in the dry season (Pruetz 2006). I use more systematic methods of behavioral observation than previous research, and I expect that the chimpanzees will feed most often in woodland habitats. I hypothesize that seasonality will affect food resource availability and use by the chimpanzees (Table 1.1). The Fongoli chimpanzees exploit fewer food species relative to most other chimpanzee populations (Pruetz 2006). The availability of fruit at Fongoli also appears to correlate positively with termite consumption by chimpanzees, whereas a negative correlation would be expected if termites were consumed in absence of a “higher quality” food, such as fruit (Bogart & Pruetz 2008). While not systematically examined, this was an unexpected outcome stemming from several sets of isolated data. This research aims to investigate this outcome more extensively. I expect that further research will demonstrate no correlation between termite fishing and ant dipping to that of low fruit abundance (Table 1.1). Given that termites are assumed to provide an important protein source for Fongoli chimpanzees, consideration of the availability of other protein sources, such as immature leaves, may prove to be an important factor influencing this behavior at Fongoli. Based on evidence from fecal analyses, it may be

posited that the Fongoli chimpanzees consume termites as a regular food source, suggesting a lack of seasonality (Bogart & Pruetz 2008).

A savanna environment is expected to be affected more by temperature and rainfall than forested habitats (Alberts et al. 2005, Altmann 1998, Baldwin 1979, Foley 1987). Feeding and foraging behaviors, such as termite fishing and ant dipping, are potentially influenced by these environmental variables. The Fongoli chimpanzees experience thermoregulatory stresses that affect their behaviors (Pruetz 2007, Pruetz & Bertolani, in press). Chimpanzees here use caves and rest more in response to increased temperature and traveling more earlier in the day, especially, when temperatures are cooler (Pruetz 2007, Pruetz & Bertolani, in press). Chimpanzees at Bossou in Guinea increase resting and terrestrial behaviors in response to increased daily temperature (Takemoto 2004). Budongo Forest chimpanzees in Uganda respond to high temperatures during mid-day by resting and social grooming more, while feeding increases during the morning and early evening when temperatures decrease (Kosheleff & Anderson, in press). Temperature and rainfall might influence activity, habitat use, and feeding and foraging behaviors of the Fongoli chimpanzee community in their hot, dry and open environment. It is expected that as temperature increases and rainfall decreases, foraging and feeding will decrease and the use of closed habitats will increase.

Insectivory is only one aspect of daily chimpanzee activity and diet. A general activity budget will provide an understanding of how prominent termite fishing and ant dipping are in relation to resting, social behaviors, and other behaviors. Habitat use was also recorded to provide a more in depth analyses of how the Fongoli chimpanzees use the mosaic savanna. The use of habitat types can then be related to temperature and rainfall. All of these

factors will provide evidence to how chimpanzees cope in a hot, dry, and mosaic habitat. Previously collected data provide support for the selective use of woodland (open canopy) and forested (closed canopy) habitat types by the chimpanzees to acquire termites in comparison with grassland (open canopy) habitat types (Bogart et al. 2005, Bogart & Pruett 2008). Thus, habitat type, or some aspect of habitat type, rather than termite mound density influences Fongoli chimpanzee termite fishing. The mosaic savanna is characterized by clumps of closed forest that the chimpanzees are expected to utilize more often during the dry season (Pruett & Bertolani, in press). Food resources are mainly distributed in woodland habitats (Pruett 2006), the use of this habitat is expected to correlate with feeding. Indirect data from previous research indicate that Fongoli chimpanzees consume insects mainly in woodland habitat (Bogart et al. 2005, Bogart & Pruett 2008). However, they also termite fish in ecotone and gallery forest habitats significantly more than would be expected based on the availability of these areas (Bogart 2005, Bogart & Pruett 2008). I use direct observational behavioral data to further reveal patterns of termite fishing and ant dipping of Fongoli chimpanzees in this study. Specifically, I expect that more in-depth analyses using behavioral data will find termite fishing occurring more frequently and for a longer duration within woodland habitat types, while ant dipping is expected to occur most frequently and for longer durations within forested habitat types (Table 1.1).

1.3.3 Benefits of insectivory

Do Fongoli chimpanzees consume more insects than conspecifics at other sites as indicated by previous findings (Bogart 2005)? If so, what ecological factors contribute to this difference? Do factors such as water content, nutritional content, the diversity of insects

available at Fongoli, or the availability of other food resources influence insectivory here? Although animal prey accounts for a low proportion of an average chimpanzee diet, fauna provide nutrients, amino acids, and proteins that cannot be acquired from plants (McGrew 1983, Sussman 1987). Termites contain many nutrients that help provide an inadequate diet for humans (Berenbaum 1995) and could therefore also provide nutrients important for growth in chimpanzees (Wrangham 1980). The dry season (November through May) at Fongoli is characterized by a significant decrease in water and certain food resources available to the chimpanzees compared to other research sites (Pruetz 2006). Thus, this type of environment may require the Fongoli chimpanzees to maximize their intake of water and other nutrients in different ways as opposed to chimpanzees at forested sites, including insect feeding.

How do chimpanzees receive ample nutrition in a savanna environment as compared to forested environments? Immature leaves provide protein for most primate species, but may be relatively scarce in a savanna habitat (McGrew 1983), particularly during the dry season. Insects are common animal prey and may provide more essential nutrients, especially protein, than other resources such as fruits and leaves (McGrew 1983). Insects are also eaten in large quantities by chimpanzees (McGrew 1983). Chimpanzees feed almost exclusively on social insects, which may give them caloric and nutritional energy when other prey are scarce (McGrew 1983). A lack of appropriate vertebrate prey in a savanna environment might be a contributing factor to high insectivory at Fongoli (Bogart & Pruetz 2008, Pruetz & Bertolani 2007). Red colobus monkeys (*Procolobus badius*) are a major prey source for chimpanzees in forested environments (Boesch 1994, Stanford 1998), but do not occur in this drier region of Senegal (Pruetz & Bertolani 2007).

1.3.4 Available insect prey

What ecological variables affect chimpanzee prey selection at Fongoli? Eggleton et al. (2002) recorded at least 133 different termite species in western Africa. If Fongoli chimpanzees are only consuming *Macrotermes*, a large fungus-eating termite, they may be exploiting only a small proportion of the known available termite species. My previous research found the Fongoli site to include at least five termite genera consisting of nine species (Bogart 2005, Bogart & Pruetz 2008). More research on the relative abundance of insect species is needed in order to understand selection by chimpanzees. My master's thesis research was the first to extensively explore such availability (Bogart et al. 2005, Bogart & Pruetz 2008). Further investigation into whether or not Fongoli chimpanzees are consuming multiple termite inhabitants at mounds, as suggested by my previous results (Bogart 2005, Bogart & Pruetz 2008), is also required. If two termite species are present, yet only one is consumed, this would suggest that the chimpanzees are selective regarding the insects they consume. Additionally, most of the available evidence for the presence of particular termite species in the diet of Fongoli chimpanzees consists of the remains of the hard mandibles and heads of *Macrotermes* soldiers in feces. The consumption of workers, immatures, and possibly other species of termites and insects is difficult to discern based on fecal macro-analysis. Micro-analysis of insect remains in feces, in conjunction with systematic behavioral observations, may yield more detailed results regarding chimpanzee diet.

In terms of termite fishing, most studies merely report the termite species included in the diet of chimpanzees (see Chapter 2). I inventory all termite species at Fongoli in order to determine availability of the species chimpanzees consume. The only comparable data comes

from Collins and McGrew (1985, 1987) for the Tanzanian sites of Mahale Bilenge, Mahale Kasoje, and Gombe.

The results of my previous research suggested that two genera and four species of termite are found in association with tools used by the Fongoli chimpanzees (Bogart et al. 2005, Bogart & Pruetz 2008). This diversity is greater than that associated with tools at any other chimpanzee site (Bogart & Pruetz 2008). However, *Macrotermes* soldiers provide the only observable evidence in chimpanzee feces. Therefore, it cannot be conclusively stated that other termites such as *Trinervitermes* are consumed by Fongoli chimpanzees. Direct evidence for chimpanzee consumption of other species of termites such as *Trinervitermes* at Fongoli has not yet been found. Several explanations could account for this. First, the Fongoli chimpanzees do not fish for *Trinervitermes*. These termites are only sharing mounds with *Macrotermes*, which are known to be eaten, as supported by observations and fecal analysis. Another explanation may be that Fongoli chimpanzees do not termite fish for *Trinervitermes* but do consume them by picking them up with their hands. *Trinervitermes* are known to forage on the surface and are also more active in the dry season (Ohiagu 1979). This species may therefore be a replacement for *Macrotermes*, which are more difficult to obtain during this time (Noirot & Darlington 2000). Finally, both *Trinervitermes* and *Macrotermes* may be consumed. Possible explanations for the lack of evidence for the consumption of *Trinervitermes* are that the heads of this genus are digestible, unlike those of *Macrotermes* soldiers, or that it is difficult to discern the smaller heads of *Trinervitermes* through macro-analyses of feces. This possibility will be examined here.

Multiple termite species inhabiting termite mounds and few direct observations of termite fishing made it difficult to determine which termite species were being consumed by

the chimpanzees during previous studies (Bogart 2005, Bogart & Pruetz 2008). Further evidence is needed in this area, and related hypotheses can now be tested through behavioral data collection on habituated chimpanzees. Since *Trinervitermes* are not consumed by any other studied chimpanzee community and previous research has very few instances of finding these termites with termite tools in previous research (Bogart & Pruetz 2008), I hypothesize that Fongoli chimpanzees only consume termites from the genus *Macrotermes* (Table 1.1).

1.3.5 Comparing Fongoli

How do Fongoli chimpanzees differ from conspecifics at other research sites in acquiring insects as a food resource? Chimpanzee populations vary in their consumption of insects. Animal prey at Kahuzi-Biega, Democratic Republic of Congo, accounts for 9% of the chimpanzee diet, with 4% being seasonally-consumed insect prey (Basabose 2002). The Gabon chimpanzees consumed ant species more than termites, while at Gombe, Tanzania, chimpanzees consume more termites than ants (Hladik 1977). Gombe chimpanzees spend up to 15% of their active time termite fishing during the rainy season, but they consume termites in all months of the year (McGrew 1983). Elsewhere in Tanzania, the Mahale B chimpanzees fish for *Macrotermes* (McGrew & Collins 1985), while the Mahale K group uses both hands and probes to acquire another termite species (Uehara 1982). At Tai, Ivory Coast and Budongo, Uganda chimpanzees consume termites without the use of tools (Boesch & Boesch 1990, Newton-Fisher 1999). Furthermore, some sites have termites, but chimpanzees are not known to consume them, such as Bossou, Guinea, Lope, Gabon, and Mahale M group, Tanzania (Matsuzawa & Yamakoshi 1996, McGrew 1994, Whiten et al. 2001). Behavioral observation will provide the data required to compare Fongoli chimpanzees to other sites.

Termite fishing and ant dipping behaviors in chimpanzees appear to vary between sites to some degree, but detailed data regarding ecological influences on such variance are lacking. McGrew and colleagues (2005) conducted a preliminary study of tool use by Fongoli chimpanzees and found that they consume driver (or army) ants (*Dorylus anomma*). Indirect evidence from ant dipping tools indicate that Fongoli chimpanzees use a two handed pull through technique to sweep the ants into their mouths as fast as possible, to avoid damage from ant bites (McGrew et al. 2005). Direct observations have confirmed this, but often the chimpanzees will use their feet sometimes to hold the tool after dipping especially when they are suspended from a tree with their hand (Pruetz, personal communication). This project explores the ant dipping behavior further in an effort to better understand any variation in such behavior between study sites, an endeavor that has only recently been undertaken on a large scale (Whiten et al. 1999).

Relatively recently, a collaborative team of chimpanzee specialists have gathered information from many long-term field sites to explore differences in behavior. Whiten and colleagues (1999, 2001) identified these behavioral variants as ‘cultural’ if a behavior is absent in one community without an ecological reason as to why, but exists in another site. Thus, if a behavior can potentially exist in a community of chimpanzees, meaning all the ecological factors to produce this behavior exist, and it is not displayed, the behavior where exhibited is labeled a ‘cultural variant’ (Whiten et al. 2003). A cultural behavior was defined by Whiten and colleagues (1999: 682) as: “one that is transmitted repeatedly through social or observational learning, to become a population-level characteristic”. Similarly, at Fongoli any observed differences from other chimpanzee populations must be considered in an ecological context.

1.3.6 Dissertation aims and major hypotheses

This project aims to examine a number of variables related to the insect foraging behavior of Fongoli chimpanzees. I investigate the environment, food availability and how food items are represented in the diet of the chimpanzees, how those foods may affect chimpanzee behavior in terms of habitat use and activity budget, and finally, how tool using behaviors assist in foraging.

Research hypotheses examine the insectivorous diet of the Fongoli chimpanzees in the context of the general diet and food availability at Fongoli. Several variables are hypothesized to influence insectivory, such as rainfall and fruit abundance. Table 1.1 is a summary of the main hypotheses tested in this dissertation research.

Table 1.1: Main research hypotheses for the Fongoli chimpanzees in Senegal.

General insectivory	Fongoli chimpanzees will spend more time consuming insects than other chimpanzee communities studied in more forested environments.
Seasonality and insectivory	Seasonality of rainfall will not influence or correlate with the consumption of insects within the Fongoli chimpanzee diet.
Seasonality and food availability	Seasonality will influence food resource availability and use by the chimpanzees.
Fruit abundance and insectivory	No correlation will exist between termite fishing and ant dipping to that of low fruit abundance.
Insectivory and habitat use	Termite fishing will occur more frequently and for a longer duration within forested and woodland habitat types compared to open habitats, while ant dipping will occur more often and for longer durations within forested habitat types.
Insect prey	Fongoli chimpanzees will consume termites from the genus <i>Macrotermes</i>

The Fongoli chimpanzee diet consists minimally of 5.4% invertebrates (Pruetz 2006). This project includes an extensive ecological and behavioral study of insect consumption by the Fongoli chimpanzees. This endeavor will provide information on the savanna chimpanzee

insectivorous diet compared to other components (fruits, leaves, and mammals). The combination of behavior and ecology will provide a thorough overview that is lacking for chimpanzee sites in general as well as adding to the savanna chimpanzee database at Fongoli. Currently, this is the only active savanna chimpanzee site where apes have been habituated. The information resulting from the proposed research is necessary for informing inferences paleoanthropologists make regarding the diet of early hominans living in a similar environment.

1.4 Dissertation implications

The results of this dissertation are applied to a referential model in order to formulate hypotheses regarding the behaviors of extinct hominans (Moore 1996). This approach entails comparing Fongoli chimpanzee diet and ecology to that of chimpanzees living in more forested sites to help determine the impact of ecological differences on these apes' behavior (discussed in Section 2.6). Such a comparison has important implications for better understanding fossil ape and early hominan ecology. Understanding how ecology plays a role in behavioral variation across chimpanzee populations can help elucidate what impacts paleo-environments may have imposed on hominans (Foley 1999, Reed 1997, Stanford 2006, Unger et al. 2006). Reconstructing behavior of early hominans requires analyses of ecology, cultural materials, and fossils found at paleontological sites. These inferences, along with research on living primates and hunter-gatherer societies frame a model for the behaviors of hominans (Unger et al. 2006). The evolution of hominans coincides with the expansion of savannas in Africa, similar to the environment at Fongoli (Bobe & Behrensmeyer 2004, Bromage & Schrenk 1995, Cerling 1992, Owen-Smith 1999, Potts 1998, Pruetz & Bertolani,

in press, Reed 1997). Accordingly, the data presented on the Fongoli chimpanzees will be used to discuss hypotheses regarding early hominans living in similar environmental conditions

This dissertation provides data on savanna chimpanzees using both ecological and behavioral methods to obtain results. The savanna mosaic habitat is considered important due to its similarities to Plio-Pleistocene environments in which early hominans dwelled (Bobe & Behrensmeyer 2004, Bromage & Schrenk 1995, Cerling 1992, Owen-Smith 1999, Potts 1998, Reed 1997). Savanna chimpanzees are useful in referencing hominan behaviors in contrast to chimpanzees living in more forested locales due to the similarity of environments between the former and hominans, specifically. At other savanna chimpanzee sites (Assirik, Senegal and Semliki, Uganda) information on diet and foraging behavior are largely based on indirect evidence, such as feeding traces or fecal analyses. At Fongoli, data on both ecology and behavior (indirect and direct methods) are provided here to offer a holistic approach. Such detail regarding the ecological context of insectivory in chimpanzees has rarely been provided, although paleoanthropological diet studies would benefit from evidence of savanna chimpanzee ecology and behavior (discussed in Chapter Two). Finally, West African chimpanzees (*Pan troglodytes verus*) are one of the most endangered chimpanzee subspecies, with about 38,000 left in the wild, a number that has dropped 50% in the last two decades (Butynski 2003, Walsh et al. 2003). Learning more about their ecology will offer support for management and conservation plans.

There are two overlying main objectives of this research. The first is to examine the insectivorous diet of the Fongoli chimpanzees and how it is related to aspects of general diet and food availability, activity, and habitat use. The second goal is to explore food availability

and the average proportion of each food in the Fongoli chimpanzee diet and relate it to monthly and yearly intake. This will provide data on the importance of insects in the diet in relation to other items. The concluding chapter compares these results to findings at other chimpanzee sites across Africa in an attempt to examine differences between savanna and more forested habitats.

1.5 Dissertation summary

Over the years at Fongoli, a number of studies have been carried out on the chimpanzee ecology and, more recently, chimpanzee behavior (Bogart & Pruetz 2008, Gašpersič & Pruetz 2008, Pruetz 2006, 2007, Pruetz & Bertolani 2007, Pruetz et al. 2008, Pruetz & Bertolani, in press, Stewart et al. 2007). The habituation of the Fongoli chimpanzee community has provided opportunities for further investigation into their insectivorous diet related to their use of other food items, habitat, and tool use. I examine how the savanna environment affects chimpanzee behavior regarding insectivory particularly.

I discuss previous research at Fongoli and at other chimpanzee sites across Africa in terms of habitat, diet, food availability, factors influencing feeding behaviors, and the insectivorous diet in Chapter Two. I also discuss human evolution models and how they have been used in conjunction with chimpanzee studies. In Chapter Three, I explain the quantitative measures I used to obtain data for this thesis, in which both ecological and behavioral methodologies are employed.

A summary of specific ecological data at Fongoli, such as temperature, relative humidity, soil temperature, rainfall, and habitat composition is presented in Chapter Four. These variables will be used for analyses relating to diet and activity and more specifically

insectivory in the following chapters. Fongoli is then compared to other sites where chimpanzees are studied in terms of how the environment influences behaviors. In Chapter Five, the results on food resource availability are discussed. These results are then examined in terms of chimpanzee use of habitat and food in Chapter Six. Also in this chapter, a general review of Fongoli chimpanzee activity patterns and habitat use is presented. Chapter Seven concentrates on the insectivorous diet and the findings of this dissertation in terms of tool use for obtaining termites and ants. Data presented in the previous chapters (four, five, and six) will all be used to understand insectivory by the chimpanzees at Fongoli in Chapter Seven. Finally, Chapter Eight discusses the main conclusions gained from this research and how they may be conceptualized in respect to chimpanzee and human evolution, specifically doing so by comparing my results to other sites across Africa in a relational model.

CHAPTER TWO

Behavioral ecology of chimpanzees

2.1 Introduction

My research examines the behavioral ecology of the Fongoli chimpanzees in southeastern Senegal specifically regarding the insectivorous diet and how this information can be utilized in models for understanding human evolution. The term ‘ecology’ was first used in the late 19th century and has come to incorporate the interactions of a living organism with its environment (Krebs 1972). Behavior is shaped by ecology, and thus the study of behavioral ecology emerged, combining the ideas of evolution, ecology, and behavior (Krebs & Davies 1993, 1997). Behavioral ecology replaced the word ‘sociobiology’, proposed in the 1970s by E.O. Wilson (Wilson 1975), which relied heavily on the idea that social behaviors are inherited and are subject to natural selection. Sociobiology thus brought in aspects of genetics and evolution to the study of behavior, but controversies arose when this was applied to human behaviors (Gould 1997). Subsequently, the term behavioral ecology was applied, as genetics is no longer considered a key variable to the concept.

Tinbergen (1963) notes that four questions can aid in the study of animal behavior: function, causation, development, and evolutionary history. Studies on animal behavior normally focus on one or several of these aspects. It is the combination of these studies, however, that provides answers as to how and why an animal behaves as it does (Krebs & Davies 1993, 1997). Methods from the field of animal behavior are used in the study of nonhuman primates. Primatology, a branch of biological (or physical) anthropology, is the study of primates and uses aspects from the fields of biology, evolutionary biology, psychology, and paleontology. Primates include prosimians, monkeys, and apes. Prosimians

are found in Asia and Africa (including Madagascar) (Hartwig 2007). Monkey species are widely distributed across the world, with New World monkeys living in Central and South America and Old World monkeys in Asia and Africa (Hartwig 2007). Apes, including lesser (gibbons and siamangs) and great apes, live in Africa and Asia (Hartwig 2007). Great apes include humans, chimpanzees, bonobos, gorillas, and orangutans, with orangutans living in Asia and with the non-human great apes living in Africa (chimpanzees, bonobos, gorillas, and orangutans). The non-human great apes (chimpanzees, bonobos, gorillas, and orangutans) have been studied in the wild for decades (DeVore 1965, Fossey & Harcourt 1977, Galdikas 1979, 1988, Goodall 1963, Kano 1982, Rodman 1977, Schaller 1963), but detailed aspects of their ecology have only recently been the focus of study (Anderson et al. 2002, Basabose 2002, Boesch et al. 2006, Conklin-Brittain et al. 2006, Hohmann et al. 2006, Itoh & Nishida 2007, Takemoto 2004, Wich et al. 2006, Yamagiwa & Basabose 2006). This chapter explores previous research conducted on chimpanzee foraging patterns, food availability, diet, insectivory and tool use, and, finally, a discussion of models of human evolution.

2.2 Foraging patterns in primates

Primate foraging patterns are impacted by differences in the nutrient content, digestibility, abundance and distribution, seasonality, and renewal rate of their foods (Garber 1987). Studies have examined the most efficient intake of energy by animals in the guise of optimal foraging theory (Pyke 1984, Stephens & Krebs 1986). This theory suggests that an animal may maximize daily energy intake (consuming more food), maximize time spent resting, or maximize daily energy gain to the daily energy lost (Pyke 1984, Stephens & Krebs

1986). The five variables integral to optimal foraging theory include diet, patch use, decision when to leave a patch, movement, and central place foraging (Pyke 1984).

Optimal foraging theory has proven problematic when applied to primates. The problems associating an optimal diet model with this taxon include that they have increased cognitive abilities, an omnivorous diet, long life histories, and are highly social (Altmann 2006, Barton & Whiten 1994, Cheney et al. 1986, Garber 1987). Many factors impact the diet of omnivorous mammals, which complicates identifying optimal foraging strategies (Garber 1987). There is no single food item or category (e.g. grasses) that provides the balanced diet a primate needs (Garber 1987). In general, primates have a long life, long gestation periods, long maturation, and longer inter-birth interval relative to many other animals, making obtaining demographic data on fitness and reproductive success difficult (Altmann 1991, 1998, 2006). There is also the question of how one accounts for heredity in wild primates (Post 1984). More efficient advances in DNA analyses have made this problem more manageable (Charpentier et al. 2007). Due to many of these factors, few studies have examined primate diets in relation to the optimal foraging model (Altmann 2006). One study on Japanese macaques (*Macaca fuscata*) found they fit the model (Agetsuma & Nakagawa 1998). However, an extensive study on baboons (*Papio cynocephalus*) found them to deviate from the optimality model (Altmann 1991, 1998).

Relatively few studies on great apes have been conceptualized in terms of the optimal foraging model. Takemoto (2003) found that the Bossou chimpanzees in Guinea searched more and fed more during times of high fruit abundance and searched for food less and rested more during times of fruit scarcity, demonstrating a poor fit to the optimal foraging model. The opposite would be expected according to the optimal foraging model. Takemoto (2003)

explains that fruit scarcity at Bossou occurs during the rainy cool season, and expending energy would be too great during this time. The chimpanzees also fed on a greater amount of leaves during times of low fruit abundance. Digestion of these leaves takes a great deal of time; hence they rest longer (Takemoto 2003). This demonstrates how difficult it is to account for all variables and assumptions of the optimal foraging diet in chimpanzees. Using this model can be misleading and a long-term study would be needed in order to account for all relevant variables.

Post (1984) advocates that optimal foraging theory is useful in hypotheses formation and testing regarding the behavioral ecology of primates, but the assumptions of this model should be made clear since the choice of food based on quality and availability can make determining optimal foraging strategy more difficult. Instead of forcing results that do not fit the optimal foraging model, a normative approach is suggested (Altmann 1998, 2006, Post 1984). With the normative approach, deviations from optimality should be viewed as potential indicators of differences in fitness and not as a part of the optimal foraging model (Altmann 2006). Finally, there is a question of whether preferred foods are always optimal foods. Preferred foods are suggested to be part of the staple diet, easy to process but hard to harvest (Marshall & Wrangham 2007). These foods are also assumed to be high quality, such as ripe fruits for chimpanzees (Wrangham et al. 1998). When preferred foods are scarce, foods of lesser quality and preference are used (Altmann et al. 1998, Conklin-Brittain et al. 1998, Wrangham et al. 1991, Wrangham et al. 1998). Foods low in quality that are exploited in times of high quality food scarcity are termed fallback foods (Altmann et al. 1998, Conklin-Brittain et al. 1998, Wrangham et al. 1991, Wrangham et al. 1993, Wrangham et al. 1998). Determining food quality entails investigating the nutritional ecology of a site.

Nutritional ecology is how an animal deals with nutritional, spatial, and temporal heterogeneity of the environment to acquire food (Milton 2006). Studies of this nature are difficult and require knowledge of the nutrient content of food items.

Studying chimpanzees in order to address foraging and feeding questions requires measuring a number of variables, from individual reproductive fitness to the quality of food resources. Since this research represents only one annual cycle, reproductive fitness, and other variables that require long-term studies, could not be measured. I therefore use the normative approach to put the results in perspective to the behavioral ecology of savanna chimpanzees. Relevant variables such as food availability, diet, activity, habitat use, and seasonality are examined in this context.

2.2.1 Food availability

Food availability and distribution have been demonstrated to influence a number of aspects of primate behavior, including grouping patterns (chimpanzee: Anderson et al. 2002, Boesch 1996, Hashimoto et al. 2003, Itoh & Nishida 2007, macaque: van Schaik & Van Noordwijk 1986), population density (guerezas, blue monkeys, and redtail monkeys: Memmides et al 2009), day range (spider monkeys: Asensio et al. 2009, golden monkey: Twinomugisha & Chapman 2008, chimpanzee: Yamagiwa & Basabose 2006)), terrestrial behaviors (chimpanzee: Takemoto 2004), social behaviors (chimpanzee: Boesch 1996, gorilla: Masi et al. 2009, macaque: Su & Birky 2007), and use of fallback foods (chimpanzee: Basabose 2002, Wrangham et al. 1991, 1998). Assessing food availability is difficult (Chapman 1988, Isbell et al. 1998, Oates 1987, Pruetz 1999, 2006, Wrangham 1980). Research on food availability and distribution previously relied on gross measures of

quantification (Boesch 1996, Chapman et al. 1994, Wrangham 1986, Yamagiwa et al. 1994). Dry seasons defined by rainfall were used to approximate fruit scarcity in many studies (Boesch 1996, Doran 1997, Wrangham 1977). However, Mitani and colleagues (2002) demonstrated that rainfall was not a reliable indicator of food availability for chimpanzees at Ngogo, Uganda. A similar finding characterizes studies of the chimpanzees at Kahuzi-Biega, Democratic Republic of Congo (Basabose 2002) as well as at Fongoli in Senegal (Pruetz 2006).

Indirect measures of food availability such as tree diameter at breast height (DBH), crown volume, tree height, and relative phenology scores are often used to infer food abundance for primates (Chapman et al. 1994). Diameter at breast height has been demonstrated as a good proxy variable for fruiting in certain tree species but not others (Chapman et al. 1992, 1994, Leighton & Leighton 1982). Some studies have used number of fruiting trees as a measure of fruit availability (Balcomb et al. 2000, Tweheyo & Babweteera 2007, Wrangham et al. 1991, 1998). In more recent studies of fruit availability for chimpanzees and bonobos, DBH is used in calculations to find basal areas of trees, along with density (Anderson et al 2000, Basabose 2002, Boesch et al 2006, Hohmann et al. 2006, Itoh & Nishida 2007, Wrangham et al 1991, Yamagiwa & Basabose 2006). For lianas, climbers, and trees with large buttresses that produce a large component of the fruit in a primate's diet, DBH generally underestimates (but overestimates trees with large buttresses) the fruit productivity and is likely an inappropriate measure (Chapman et al. 1994). This is especially prevalent at study sites where a primate species relies on a few species at any one time. Pruetz (2006) found that four foods were found in over 50% of fecal samples each month in the diet of Fongoli chimpanzees: *Adansonia digitata*, *Saba senegalensis*, *Diospyros*

mespiliformis, and *Ficus* species. *Saba senegalensis* is considered a climber, and *Adansonia digitata* is a tree with very large buttresses. Thus, using DBH at Fongoli would not be an appropriate measure to calculate fruit availability across species. Another method used by recent studies includes scoring of fruit production (Chapman et al. 1994, Furuchi et al. 2001, Hashimoto et al. 2001, Stanford & Nkurunungi 2003, Takemoto 2004, Tutin et al. 1997, Yamakoshi 1998). This research follows Takemoto (2004), who modified Chapman and colleagues' (1994) methodology. Takemoto (2004) uses basal area (the cross-sectional area of a tree) and a scoring system of zero to three to calculate the fruit availability index (percent) for each species of feeding tree, as well as overall monthly availability. These methods are explained further in Chapter Three.

The availability and distribution of other resources besides fruit is ignored in many chimpanzee studies (Balcomb et al. 2000, Hashimoto et al. 2001, Stanford & Nkurunungi 2003, Takemoto 2004, Tutin et al. 1997, Tweheyo & Babweteera 2007, Yamakoshi 1998). Although, fruit is the greatest component of chimpanzees' diet, disregarding other variables could provide misleading results. In this research, I examine the overall diet of the Fongoli chimpanzees to relate to availability of food items, particularly with regards to insectivory. In addition to fruit availability in Senegal, I calculate density of bushbabies (*Galago senegalensis*), ants, and termites, commonly exploited foods by the Fongoli chimpanzees, in estimates of food availability. While estimating food availability for omnivores such as chimpanzees is especially difficult, including more categories of food puts the plant-based diet of chimpanzees into a broader perspective.

2.3 Chimpanzee diet

Chimpanzee diets vary across research sites. I present results on chimpanzee diet geographically, according to site and subspecies of *Pan troglodytes* (Table 2.1). The insectivorous diet will be investigated further in the next section, although I examine it here as to its relative proportion in the diet. Food items consumed by chimpanzee include fruits, seeds, leaves, flowers, bark, pith or stems, nuts, termites, ants, honey and bees, vertebrate prey, and earth. Studies often lump food items that comprise a small proportion of the diet into the designation of ‘other’.

2.3.1 Eastern African chimpanzees (*Pan troglodytes schweinfurthii*)

The Gombe and Mahale chimpanzee communities in Tanzania have been studied for decades (Goodall 1963, Hladik 1977, Nishida 1968, Nishida & Kawanaka 1972, Wrangham 1977). Gombe chimpanzees are known to consume 141 different plant foods in a diet composed of fruit (68%), leaves (28%), and animals (4%) (Hladik 1977). Wrangham (1977) found the diet of the Gombe chimpanzees to contain 201 different plant parts, including fruit (43%), leaves (27%), flowers (9%), and seeds, pith, and bark (7%). Mahale chimpanzees’ diet is composed of 32% fruits, 37% leaves, 13% stem/pith, 8% flowers, 5% seeds, and 5% bark (Nishida & Uehara 1983). They consume 328 different plant food items of 198 species (Nishida & Uehara 1983). At Mahale, the chimpanzees also consume five species of birds, 12 species of mammals, and 15 genera of insects (Table 2.1) (Nishida & Uehara 1983).

The Budongo chimpanzees in Uganda consume 118 plant food items from 58 species as well as five animal species (four vertebrate and one invertebrate) (Newton-Fisher 1999). Fruit comprises most of the diet at 64.5%, while leaves and terrestrial herbaceous vegetation

make up 19.7% and 3.2%, respectively (Newton-Fisher 1999) (Table 2.1). The remainder of the diet is composed of flowers (8.8%) and animals (3.8%), including three species of monkey, a chimpanzee infant, and termites (*Cubitermes* species) (Newton-Fisher 1999).

Ficus species and the fruit of *Broussonetia papyrifera* are the most important foods (Newton-Fisher 1999, Tweheyo et al. 2004). The Budongo chimpanzees also consume honey, wasp larvae, and caterpillars (Reynolds 2005).

The Kibale (Kanyawara community), Uganda chimpanzees consume 28 species of leaves, 21 species of non-fig fruit, 14 species of terrestrial piths and leaves (TPL), and 10 species of figs (*Ficus*) (Wrangham et al. 1991). Terrestrial piths and leaves were consumed when fruit abundance was low; however, the measure of fruit abundance was more qualitative than quantitative (Wrangham et al. 1991). The Kibale chimpanzees do not eat insects, but consume four species of monkey (Wrangham et al. 1991). Ghiglieri (1984) found the diet comprised of fruit (78%), leaves (14.7%), flowers (4.2%), bark (2%), seeds (1%), and other (0.2%), but the community was largely unhabituated during his study (Table 2.1).

In Bwindi, Uganda, the Ruhija chimpanzees consume 60 plant items from more than 32 species (Stanford & Nkurunungi 2003, Stanford 2008). Fruit makes up the largest component of the diet at 64.6% (30 species), and leaves and pith comprise 27.1% (Stanford & Nkurunungi 2003) (Table 2.1). Fruits of *Ficus* species and *Myrianthus holstii* are the most important for the Bwindi chimpanzees (Stanford & Nkurunungi 2003, Stanford 2008). Animal remains make up 4.3% of the diet, including two to three different species [an antelope (*Cephalophus nigrifrons*) and a monkey (*Cercopithecus* species)] (Stanford & Nkurunungi 2003). Ants (*Dorylus* species) and bees (*Apis mellifera* and *Meliponula brocandei*) make up the remaining 4% of the diet (Stanford & Nkurunungi 2003).

Table 2.1: Proportions of chimpanzee diet across sites geographically.

	Fruit	Leaves	Seeds	Flowers	Pith	Bark	Animal ^a	Other	Plant items	Plant species	Reference	Data used ^b
Gombe, Tanzania	68	28					4		141		Hladik 1977	o
	43	27	7	9	7	7	0		201		Wrangham 1977	o
Mahale, Tanzania	32	37	5	8	13	5	0		328	198	Nishida & Uehara 1983	o
Budongo, Uganda	64.5	19.7		8.8	3.2		3.8		118	58	Newton-Fisher 1999	o
Kibale, Uganda	78	14.7	1	4.2		2	0	0.2	50		Ghiglieri 1984	o
Bwindi, Uganda	64.6	27.1					9.1		60	>32	Stanford & Nkurunungi 2003	o,f
Semliki, Uganda	39	30	15	3	9	3	0		33		Hunt & McGrew 2002	f,o
Kahuzi-Biega, DRC	40	30	3	5	17	2	0	4	137	104	Yamagiwa & Basabose 2006, Basabose 2002	o,f
Lope, Gabon	69.2	9.9	7.7	6.4	0.5		5.3	1		202	Tutin et al. 1997	o,f
	67.6	11.3	7	2.1	2.1	0.7	7.7	1.4	142		Tutin et al. 1991	o,f
	66	13	10	3	6	2	0		161		Tutin & Fernandez 1993	o
Goulougo, Republic of Congo	56	16	7	8	8	3	0	2	158	116	Morgan & Sanz 2006	f, o
Ndoki, Republic of Congo	88	3		2	5		0	3	114	108	Kuroda et al. 1996	f, o
Assirik, Senegal	57	10	10	10	3	7	0	3	60	43	McGrew et al. 1988	f, o
Bossou, Guinea	52	18	7	5	13	3	0	2	246	100	Sugiyama & Koman 1992	o
Fongoli, Senegal	62.5	16		11	3	2.5	5		60	47	Pruetz 2006	f, o

^a Includes vertebrate and invertebrate prey^b Fecal data (f), observation data (o)

Semliki, Uganda is another site considered to be savanna in habitat, but little research has been conducted there. The observed diet includes 33 different plant food items (Table 2.1), with a diet consisting of fruit (39%), leaves (30%), seeds (15%), pith (9%), flowers (3%), and bark (3%) (Hunt & McGrew 2002).

There are a total of 137 plant items from 104 species in the diet of chimpanzees (Table 2.1) at Kahuzi-Biega, Democratic Republic of Congo (Yamagiwa & Basabose 2006). The chimpanzees here also feed on honey, ants and beetles as well as *Cercopithecus* monkeys and giant forest squirrels (*Protoxerus stangeri*) (Yamagiwa & Basabose 2006). The diet of the chimpanzees was found to consist of fruits (40%), leaves (30%), pith (17%), flowers (5%), seeds (3%), bark (2%), and ‘other’ (4%) (Basabose 2002). Animal remains were found in 9% of the fecal samples, with 4% of this consisting of insects (Basabose 2002).

2.3.2 Central African chimpanzee sites (*Pan troglodytes troglodytes*)

The chimpanzees of Lope, Gabon consume 202 species of plants (Tutin et al. 1997). Their diet consists mostly of fruit at 66% (Table 2.1), followed by leaves (13%), seeds (10%), flowers (3%), pith (6%), and bark (2%) (Tutin & Fernandez 1993). Two other studies at Lope found similar results, and both will be used in the final average of the chimpanzee diet (Table 2.1; Tutin et al. 1991, 1997).

At the Goualougo Triangle research site in the Republic of Congo, chimpanzees have a diet that contains 158 different plant items from 116 species (Morgan & Sanz 2006). The diet is made up of 56% fruit, 16% leaves, 8% pith, 8% flowers, 7% seeds, 3% bark, and 2% other (Table 2.1) (Morgan & Sanz 2006).

The chimpanzees of Ndoki, also in the Republic of Congo, were reported to consume 114 plant food items from 108 species (Kuroda et al. 1996). Termites (*Macrotermes muelleri*) are also consumed here and were found in 50% of fecal samples, while driver ants (*Dorylus* species) were present in 20% of the fecal samples (Kuroda et al. 1996). From fecal remains, observations, and feeding traces the chimpanzee diet contains 88% fruit, 3% leaves, 5% pith, 2% flowers, and 3% 'other' (Table 2.1) (Kuroda et al. 1996).

2.3.3 West African chimpanzee sites (*Pan troglodytes verus*)

In Guinea, the Bossou chimpanzees consume 246 different plant items from 200 species. Only 11 times have apes here been observed to eat animal foods (termites, ants, and monkey) (Sugiyama & Koman 1987, 1992), which has been attributed to the lack of appropriate prey (Sugiyama 2004). Their diet is reliant on fruits (52%), leaves (18%), and seeds (7%) (Table 2.1), with the remainder of the diet consisting of pith (13%), flowers (5%), bark (3%) and 'other' (2%) (Sugiyama & Koman 1992).

Chimpanzees at Mount Assirik in Senegal consume 60 plant parts from 43 species (McGrew et al. 1988). Their diet consists mostly of fruit (57%), while the rest of the diet is composed of leaves (10%), seeds (10%), flowers (10%), bark (7%), pith (3%), and 'other' (including animals) (3%) (McGrew et al. 1988). The lack of animal meat in the diet is likely due to the lack of direct observations at this site (McGrew et al. 1988).

The diet of the chimpanzees in Mali has been indirectly measured in the Bafing Biosphere Reserve. Duvall (2008) found a diet consisting of 45 different food items. Through fecal analyses and comparison of plant species in Mali to that found at other research sites in Senegal, an estimated 72 species of plants are known, likely, or probable food resources to be

consumed by the Bafing chimpanzees (Duvall 2000). Due to small sample size the diet proportion has not been figured, but a list of species consumed was compiled (Duvall 2008).

Pruetz (2006) found the diet of the Fongoli chimpanzees to contain 60 plant food items of 47 species. The diet of the Fongoli chimpanzees is comprised of fruit (62.5%), leaves (16%), flowers (11%), pith (3%), bark (2.5%), and insects (5%) (Pruetz 2006).

Data from Semliki in Uganda, Lope in Gabon, and Assirik and Fongoli in Senegal are all diets based on indirect analyses, using fecal and food remains. These will be included in the analysis of general chimpanzee diet to enlarge the sample size from the central and western chimpanzee sites, which lack diet data. Also, the inclusion of these studies does not significantly vary from the results without these sites (Student's t-test on the total values, t -ratio = 1.7, df = 7, p -value = 0.13). However, these sites are excluded when the findings of this research, based on direct observation, are compared to the general chimpanzee diet in Chapter Eight.

2.3.4 Analysis of diet

I calculated a general diet for chimpanzees using 16 studies from 13 sites (Table 2.1) as discussed above (Table 2.2). Conklin-Brittain and colleagues (2001) used 11 sites and 24 studies to obtain a general diet for chimpanzees. Their calculated diet is compared to the average I calculated in Table 2.3. The current compiled dataset uses eight of the studies in Conklin-Brittain et al. (2001), but with updated information for Mahale, Bwindi, Semliki, Kahuzi-Biega, Goualougo, Assirik, Bossou, and Fongoli (see Table 2.1). The 95% confidence interval for the data I compiled from these 16 studies is listed in Table 2.3. The differences between what Conklin-Brittain and colleagues (2001) and this study found fit

within those estimated parameters (Table 2.3). Bark and miscellaneous foods, as well as animal prey and flowers are slightly out of the interval range, but these differences are small. Therefore results found here using updated data are comparable to the previous findings from Conklin-Brittain and colleagues (2001). Differences exist with the consumption of fruit and leaves between eastern and central sites (Table 2.4). Central chimpanzees eat more fruit than eastern chimpanzees, while eastern chimpanzees consume more leaves (Table 2.4). The only major difference between eastern and western chimpanzees is that the eastern chimpanzees consume more leaves (Table 2.4). Finally, central chimpanzees consume more fruit than the western chimpanzees (Table 2.4).

Table 2.2: Average chimpanzee diet composition using 13 sites and 16 studies.

	Average Chimpanzee Diet ^a	Median (%)	Min (%)	Max (%)	SD
Fruit	59.1	63.5	32	88	15.0
Leaves	19.4	17	3	37	9.4
Seeds	5.0	7	0	15	4.6
Flowers	5.3	5	0	11	3.5
Pith/stem	5.6	4.1	0	17	5.2
Bark	2.3	2	0	7	2.3
Animal [^]	2.2	0	0	9.1	3.2
Other	1.0	0.1	0	4	1.4

^asum of all studies, [^] includes invertebrates and vertebrates

Table 2.3: Average diet of chimpanzees from Conklin-Brittain and colleagues (2001) and this study's average from 13 sites.

	Chimpanzee Diet ^a	Chimpanzee Diet ^b	Lower CI (95%) ^b	Upper CI (95%) ^b
Fruit	64	59.1	51.2	67.2
Leaves	16	19.4	14.4	24.4
THV/Pith	7	5.6	2.8	8.4
Bark & Misc.	4	3,3	0.31	3.6
Animal [^]	4	2.2	0.5	3.9
Flowers	2	5.3	3.5	7.2
Seeds	3	5.0	2.8	7.8

^a The average diet from Conklin-Brittain et al. 2001, ^b The average diet from Table 2.2.

[^] includes invertebrates and vertebrates

Table 2.4: General chimpanzee diet by geographic distribution.

	Eastern chimpanzees ^a	Central chimpanzees ^b	Western chimpanzees ^c
Fruit	53.6	69.2	57.2
Leaves	26.7	10.6	14.7
Seeds	3.9	6.3	5.7
Flowers	4.7	4.3	8.7
Pith/stem	6.1	4.3	6.3
Bark	2.4	1.1	4.2
Animal [^]	2.1	2.6	1.7
Other	0.5	1.5	1.7

^a 7 sites, 8 studies, ^b 3 sites, 5 studies, ^c 3 sites, 3 studies

[^] includes invertebrates and vertebrates

Chimpanzees have been known to increase consumption of leaves and other low-quality foods during times of food scarcity (Doran 1997, Wrangham 1977, Wrangham et al. 1998). These foods are generally referred to as fallback foods (Newton-Fisher 1999, Wrangham et al. 1994, 1998). Some chimpanzees have been found to eat a wider range of foods rather than fallback foods (Wallis 1995, Doran 1997). Kibale, the Kanyawara community, chimpanzees consumed terrestrial herbaceous vegetation during times of fruit scarcity (Wrangham et al. 1991, 1993). At Kalinzu, Uganda, chimpanzees use the fruit of *Musangu leo-errerae* as a fallback food (Furuichi et al. 2001). In the Democratic Republic of Congo, the Kahuzi-Beiga chimpanzees have a higher proportion of fruiting trees during the dry season (Basabose 2002). During the rainy season when fruit availability is low, the chimpanzees take advantage of terrestrial herbaceous vegetation (Basabose 2002). The chimpanzees at Lope in Gabon also experience fruit scarcity, but it occurs during the dry season, and leaves and pith are used as a fallback food (Tutin et al. 1991).

2.4 Chimpanzee insectivory

Chimpanzees utilize a variety of different methods to forage for insects and other animals. Some methods include stealth (Garber 1987, Stanford 1998, Uehara 1997),

cooperative hunting (Boesch 2002, Stanford 1998, Uehara 1997), and tool use (Garber 1987, Hladik 1977, Nakamura & Itoh 2008, Pruetz & Bertolani 2007, Teleki 1974, 1981). These techniques reduce costs of time and energy, but the general rate of intake is low (Hladik 1977, Teleki 1974). Goodall (1964) was the first to document tool use in chimpanzees, but soon these behaviors were documented at other sites as well (Boesch & Boesch 1981, McGrew et al. 1979, Nishida & Uehara 1982, Teleki 1974). Tool use to obtain insects, such as during termite fishing and ant dipping, is a behavior that has been studied frequently across chimpanzee sites, (Fay & Carroll 1994, McGrew et al. 1979, Newton-Fisher 1999, Nishida & Uehara 1980, Sanz et al. 2004, Sugiyama and Koman 1992, Sugiyama 1995, Suzuki et al. 1995, Yamamoto et al. 2008), yet the ecological context has been rarely examined (Bogart & Pruetz 2008, Collins & McGrew 1985, 1987, Deblauwe & Janssens 2008, McBeath & McGrew 1982, Schöning et al. 2007).

Termite fishing is not found at every chimpanzee site. This behavior has been studied in east Africa at Gombe and in the Mahale Bilenze group in Tanzania (Collins & McGrew 1985, 1987). In central Africa, chimpanzees at Goulougo and Ndoki (Republic of Congo) and Dja Biosphere Reserve (Cameroon) termite fish (Deblauwe et al. 2006, Sanz et al. 2004, Suzuki et al. 1995). Finally, in West Africa the chimpanzee populations that exhibit termite fishing include Bossou in Guinea, and Mount Assirik and Fongoli in Senegal (Bogart & Pruetz 2008, McBeath & McGrew 1982, McGrew et al. 1979, Sugiyama & Koman 1987). Termites are consumed at Budongo and Kibale in Uganda and at Mahale in Tanzania but are not extracted with the aid of probes (Ghiglieri 1984, Nishida & Uehara 1980, Reynolds 2005). *Cubitermes speciosus* mounds are occasionally broken open, and the Budongo chimpanzees consume the termites with their hands and mouth (Newton-Fisher 1999,

Reynolds 2005). *Pseudacanthotermes* termites are eaten by the Mahale Kasoje group, and recently the chimpanzees have been seen to capture the winged reproductives swarming from the mounds by using wet hair on their arms (Collins & McGrew 1985, Kiyono-Fuse 2008, Nishida & Uehara 1980). For a complete list of the termite genera and species eaten at each site see Bogart & Pruetz (2008). Termites are very rarely or never consumed at Bwindi and Kalinzu in Uganda, Lope in Gabon, Taï in Ivory Coast, and Gashaka in Nigeria (Hashimoto et al. 2000, Humle 1999, Schöning et al 2007, Stanford 2008, Tutin et al. 1995).

Two types of tools can be used in chimpanzee termite fishing. The fishing probe is a flexible tool that can be inserted into a termite hole to draw out the soldiers (Figure 2.1), whereas a perforating stick is short and rigid and punctures the termite mound (Bermejo & Illera 1999, Fay & Carrol 1994, McGrew et al. 1979, Sabater Pi 1974, Sanz et al. 2004, Sugiyama 1985, Suzuki et al. 1995). Chimpanzees in only a few populations use the perforating stick, and Goualougo is the only long-term study site where this behavior is common (Sanz et al 2004, Suzuki et al. 1995, Heaton & Pickering 2006).



Figure 2.1: A flexible probe inserted into a termite mound at Fongoli.

Ant dipping for army ants (*Dorylus* species) is found at Gombe in Tanzania (McGrew 1974), Dja Biosphere Reserve in Cameroon (Deblauwe & Janssens 2008), Gashaka in Nigeria (Fowler & Sommer 2007, Schöning et al 2007), Kalinzu (Hashimoto et al. 2000) and Bwindi in Uganda (Stanford 2008), Ndakan (Fay & Carroll 1994) and Goualougo (Sanz & Morgan 2007) in the Republic of Congo, Kahuzi-Biega in Democratic Republic of Congo (Basabose 2002), Bossou in Guinea (Yamakoshi 1998), and Taï in Ivory Coast (Boesch & Boesch 1990), Assirik (McGrew et al. 1988) and Fongoli (McGrew et al. 2005) in Senegal. At Gombe, Bossou, and Taï chimpanzees also acquire the non-biting brood and workers of army ants without tools, using only their hand (McGrew 1974, Boesch & Boesch 1990). For a complete list of army ant availability and consumption across 14 sites in Africa see Schöning et al. (2008).

There are two methods used to dip for army ants. In the ‘pull-through’ method, a chimpanzee will hold the tool in one hand or foot and sweep off the ants with the other hand (McGrew 1974). This technique is found at Gombe, Fongoli, and Bossou (Boesch & Boesch 1990, McGrew 1974, McGrew et al. 2005). The second method is the ‘direct mouthing’ technique, in which the chimpanzees use their mouth to sweep the ants off the tool (also called ant-dip-single, swiping, and nibbling) (Boesch & Boesch 1990, Whiten et al. 2001). Direct mouthing is seen at Gombe, Bossou, Taï, (Boesch & Boesch 1990) and Fongoli (Pruetz, unpublished data). Weaver ants (*Oecophylla longinoda*) are consumed at Dja Biosphere Reserve in Cameroon and Lope in Gabon (Deblauwe & Janssens 2008, Tutin et al. 1995) as well as at Fongoli (Pruetz 2006). Ants of *Pachycondyla* species are eaten at Mt. Assirik in Senegal, Dja Biosphere Reserve in Cameroon, and Gashaka in Nigeria (Deblauwe & Janssens 2008, McGrew et al. 1988, Schöning et al 2007). The difference between fishing

and dipping is that the ants grab hold of the tool with their mouth and are ‘fished’ out of the nest as opposed to their crawling onto the stick in the dipping behavior. Ant fishing for carpenter ants (*Camponotus* species) has been observed at Mahale in Tanzania, Gashaka in Nigeria, and Bossou in Guinea (Nishida 1973, Nishida & Hiraiwa 1982, Schöning et al 2007, Yamamoto et al. 2008). Ant fishing for carpenter ants at Mahale, Tanzania can last for over three hours and occurs throughout the year (Nishida & Hiraiwa 1982).

2.5 Previous research on diet at Fongoli, Senegal

Pruetz (2006) used mostly indirect measures to determine the diet of the Fongoli chimpanzees. Fruits composed the majority of the diet at 62.5%, while leaves made up the second major component of the diet at 16% (Pruetz 2006). A total of 60 plant food items of 47 species were recorded, and seven species were represented in over 50% of fecal remains in a single month (Table 2.5) (Pruetz 2006). The Fongoli chimpanzees use specific techniques to consume baobab fruit (*Adansonia digitata*) (Gašperšič & Pruetz 2008). The Fongoli chimpanzees also consume mammal prey, termites, ants, and honey (Pruetz 2006). Prey species include mongoose (*Mungos mungo*), vervet monkeys (*Chlorocebus aethiops*), Patas monkeys (*Erythrocebus patas*), baboons (*Papio hamadryas papio*), and bushbuck (*Tragelaphus scriptus*) (Bogart et al. 2008, Pruetz 2006, Pruetz, unpublished data). Most notably, the Fongoli chimpanzees hunt for bushbabies (*Galago senegalensis*) with tools (Pruetz & Bertolani 2007). Termite fishing at Fongoli has been studied using indirect, ecological methods (Bogart 2005, Bogart & Pruetz 2008, McGrew et al. 2004). My previous research suggested that two genera (*Macrotermes* and *Trinervitermes*) and four species of termites are possibly eaten here (Bogart & Pruetz 2008). A correlation was observed between

termite fishing and habitat type, as chimpanzees tended to fish in woodland and closed habitat types (Bogart & Pruetz 2008). Ant dipping at Fongoli was also studied by McGrew and colleagues (2004) using indirect data. They suggest the chimpanzees at Fongoli use the ‘pull through’ method to ant dip, which has been confirmed through direct observation (personal observation; Pruetz, personal communication). Finally, activity of the Fongoli chimpanzees has been demonstrated to correlate with seasonality (Pruetz 2007, Pruetz & Bertolani, in press).

Table 2.5: Important plant foods consumed by Fongoli chimpanzees (from Pruetz 2006).

Plant genus and species	Plant Family	Parts consumed	Months consumed
<i>Adansonia digitata</i> (Baobab)	Bombacaceae	Fruit, flower, bark	All year, F = Nov-Jan, May
<i>Diospyros mespiliformis</i>	Ebenaceae	Fruit, leaves, bark	Jan- July, Oct-Dec
<i>Ficus</i> spp.	Moraceae	Fruit, leaves, bark, pith	All year
<i>Hexalobus monopetalus</i>	Annonaceae	Fruit, leaves	Sept-Oct
<i>Lannea</i> spp.	Anacardiaceae	Fruit	April-June
<i>Saba senegalensis</i>	Apocynaceae	Fruit and pith	All year (heaviest May-June)
<i>Spondias monbin</i>	Anacardiaceae	Fruit	July-Nov

2.6 Chimpanzees as a referential model

A model can have many different meanings. Here it is used to refer to an analogous pair composed of a model and a referent, where the model is used to construct a scenario about the referent’s unknown behaviors (Moore 1996). A referential model provides emphasis on the similarities between the two. Paleoanthropologists use these models to understand how extinct human ancestors behaved (Moore 1996). Fossilized bones of hominans and mammals, as well as material culture found provide few clues to hominan behavior (Moore 1996, Unger et al. 2006). Chimpanzees are often used as a referential model

as they are human's closest living relative. Therefore, behaviors or traits found in chimpanzees are used to find similarities in the last common ancestor between humans and chimpanzees (Moore 1996). This is then applied to other extinct human ancestors, or hominans. However, this can prove dangerous as chimpanzees and humans have been evolving for millions of years after the last common ancestor, thus, the use of a comparative model is used to test hypotheses concerning extinct hominan behavior (Moore 1996). Examining the similarities between chimpanzees and extinct hominans in environment, climate, morphology, food availability, diet, predation factors, and competition can provide clues as to how they lived by assessing the selective pressures most important to great ape behavior in these habitats (Foley 1999, Moore 1996, Reed 1997, Stanford 2006, Unger et al. 2006).

Savanna chimpanzees have been argued to be a better model than forested chimpanzees, in that the differences between the two habitats can provide information useful in a referential model for extinct hominans (Moore 1996). Moore (1996) postulated that the savanna woodland environment with its hot and dry climate would be different from forested sites regarding food availability, predator pressure, and competition. Moore (1996) hypothesized that the increased seasonality (wet versus dry) would affect food availability and that chimpanzees would have to travel more because important food resources are widely dispersed. More predators in savanna woodland may influence time spent in dense forest (Moore 1996). Finally, Moore (1996) suggests that primate species living in savanna woodlands would experience decreased competition. However, at Mount Assirik baboons and chimpanzees exhibit high dietary overlap (McGrew et al 1982). Moore (1996) states that if savanna chimpanzees used tools more often or in more ways this would provide support

for the hypothesized link between tool use and the savanna hypothesis (discussed in Section 2.7). This research will address some of these questions.

2.7 Human evolution

The earliest hominans lived in a variety of habitat types (Reed & Rector 2007). These range from forests, woodlands, bushlands, and grasslands. Paleoenvironmental reconstruction can provide knowledge on the foods available to hominans and speculate on what they may have eaten (Ungar 2007). Diet is an important variable that affects behavioral and ecological differences among all primates, including hominans (Fleagle 1999, Ungar 2007). Here, I discuss the research on paleoenvironments associated with hominans and what paleoanthropologists have been able to assess diet from this data and isotope data. First, the general climate during the time periods in which the earliest hominans lived is presented.

2.7.1 Paleoclimate

The African Pliocene (5-1.8 million years ago) was characterized by a relatively lush environment, lacking large deserts (O'Brien and Peters 1999). Early Pliocene environments experienced warmer climates relative to the preceding late Miocene (24-5 mya), with a decrease in polar ice activity (Kennett 1995). The Northern hemisphere glaciations occurred approximately 2.8 mya, following a high intensity of monsoons during the African summer (de Meocal and Bloemendal, 1995). After 2.8 mya, eastern and western Africa was seasonally cooler and drier, due to the increase of high latitude glacial ice cover (deMeocal and Bloemendal, 1995). Kennett (1995) explains that the last three million years have exhibited large variations during the Pliocene creating glacial-interglacial environments.

The Pleistocene (1.8 mya-10,000 years BP) was characterized by cooler conditions as a result of glaciers in higher latitudes, which in turn promoted the spread of savanna and grassland habitats in the lower latitudes (Owen-Smith 1999). East Africa had pronounced dry periods between 1.8-1.6 mya (deMeocal and Bloemendal, 1995). From C₄ evidence we know that the expansion of savanna grasslands occurred around 1.7 mya in East Africa (Cerling 1992).

2.7.2 Paleoenvironment association with hominans

Since there are no written histories from extinct hominan ancestors, we are left to interpret the fossil record to the best of our ability to understand their general behavior. To determine the climate and habitat used by hominans, methods from biogeography are used. Biogeography presents climatic evidence over the history of the Earth. In studying savanna-dwelling chimpanzees, I ultimately relate the importance of their habitat to human evolution in terms of ecology and behavior. Most importantly, the diet of the savanna chimpanzees may be more relevant in a referential model for hominan diet compared to chimpanzees living in a more forested habitat.

Africa contains many different habitats. Forests require a high mean annual rainfall and long wet seasons having tall trees making multiple canopies (Reed & Rector 2007). There are four classification of savanna and all have less mean annual rainfall than forest: woodland, bushland, shrubland, and grassland (Reed & Rector 2007). Woodland savannas had a grass-based understory with a sparser canopy than forests and can be considered open or closed based on the degree of canopy cover (Reed & Rector 2007). Bushlands have trees that reach 3-9 meters tall with few grasses, but may contain more fruit than woodland (Reed

& Rector 2007, Sept 1994). Shrublands have one to three meter tall trees and grassland has very few trees, abundant rain in certain months and is burned regularly (Reed & Rector 2007). Savannas can contain several of these microhabitats and are considered mosaic (Reed & Rector 2007). Seasonal lengths differs across Africa but is defined as wet versus dry in the amount of rainfall.

From 4.2-3 mya, several species of *Australopithecus* were living in mosaic environments composed of closed and open woodlands, bushlands, and forests (Bobe & Eck 2001, Reed 1997, Reed & Rector 2007). A few sites were more open and dry, such as Allia Bay (*A. anamensis*) and Koobi Fora (*A. afarensis*) in East Africa (Reed 1997, Reed & Rector 2007, Wynn 2000). In South Africa, Sterfontein 4 where *A. africanus* is found is also drier (Reed & Rector 2007).

Between 3.0-2.5 mya new genera appear, that of *Paranthropus* and *Homo*. During this time period hominans were living in open woodlands, bushlands, and shrublands with wetlands (Bobe & Eck 2001, Reed 1997, Reed & Rector 2007). These habitats possibly had more water available than they contain today (Reed & Rector 2007). After 2 mya, the habitats became more open, but there were two periods of extensive grasslands at 1.7 mya and 1.2 mya with subsequent returns to woodlands and bushlands (Cerling 1992 , Reed 1997)

Australopithecus, *Paranthropus*, and early *Homo* species all lived in mosaic habitats ranging from more closed (*Australopithecus*) to more open (*Paranthropus* and early *Homo*). In terms of how hominans responded to climate changes and their selection of a habitat in which to exist, three hypotheses have been postulated: the savanna hypothesis (Dart 1925), the turnover pulse hypothesis (Vrba 1992, 1995), and the variability selection hypothesis (Potts 1998).

Through the savanna hypothesis researchers attempt to explain the divergence of humans from chimpanzees as related to habitat. First proposed by Dart in 1925, this hypothesis postulated that human divergence was directly related to the spread of open savannas, while the other great apes remained among the dense forests. Recently, this hypothesis has been disputed with new evidence that open savanna habitats were not as prominent during early hominan (Australopithecine) existence and that they mainly lived in a closed habitat (Bobe & Behrensmeyer 2004, Reed 1997, Strait & Wood 1999). Reed (1997) used changes in mammal morphology of assemblages associated with hominan species in order to reconstruct paleo-habitats. It was found that gracile Australopithecines lived in more closed habitats with significant water content, while *Paranthropus* species (also known as robust Australopithecines) lived in more open areas which always included wetlands, and *Homo* existed in an even more open region with grasslands (Reed 1997). This lends further support in falsifying the traditional savanna hypothesis (Reed 1997). Open savanna habitats were not abundant until about 1.7 million years ago (mya) (Cerling 1992) and have only been associated with *Paranthropus* and early *Homo* species (Bobe & Behrensmeyer 2004, Bromage & Schrenk 1995, Reed 1997, Wesselman 1995). Bobe and Behrensmeyer (2004) suggest that instead of explaining the divergence of hominans, the savanna hypothesis could be used to explain the evolution of the genus *Homo*.

The faunal turnover hypothesis adds to the savanna hypothesis, stating that savannas were important to human evolution, but emphasizing, in addition, the pulses of faunal turnover in mammal taxa (Vrba 1992, 1995). Faunal turnover is characterized by evolution, extinction, and immigration. This hypothesis links climatic changes to that of faunal turnover. It has been demonstrated that migrations of fauna are closely associated with

climate related to the rise and fall of sea levels due to glacial events (Opdyke 1995). Two collections of micro-mammal remains at Kabwe displayed a high proportion of savanna woodland habitat species during the Early and Middle Pleistocene when *Homo* species occupied the area during interglacial periods seeking refuge from drought (Avery 2003). Avery (2003) suggested that Kabwe was located within a migration route for *Homo* species during this time, and that they migrated along rivers and lakes with tropical and subtropical habitats, rather than the rift valleys. The major dispersal events of hominans from East to South Africa and the Malawi Rift occurred between four to seven different times and all but one hominan dispersal events followed other dispersing mammals (Strait & Wood 1999). This relationship between mammals and hominans provides support for the turnover pulse hypothesis. *Homo habilis* and possibly *Paranthropus robustus* dispersed in a different direction from mammals, suggesting that these hominans possessed different anatomical or behavioral adaptations to allow for environmental fluxes (Strait & Wood 1999). This departure from a mammalian trend may lend support to a more environmental hypothesis. Further evidence for the faunal turnover hypothesis is that open savanna habitat types in Africa were not inhabited by *Paranthropus* and early *Homo* until about 1.8mya, while earlier Australopithecines lived in wooded habitats and had some morphological traits associated with an arboreal lifestyle (Bromage & Schrenk 1995).

A different hypothesis that has been presented is the variability selection hypothesis. This postulates that human emergence was brought about by the increasing variability of the climate and environment during the Plio-Pleistocene (Potts 1998). Several studies have provided evidence for this hypothesis. Bobe and Behrensmeyer (2004) examined fossil mammals from the Plio-Pleistocene in Kenya and Ethiopia dating from four to one million

years ago. They concluded that there were profound faunal changes and *Paranthropus* and *Homo* species existed during a high faunal turnover from 2.8-2.6 mya and 2.4-2.2 mya in Kenya and Ethiopia (Bobe & Behrensmeyer 2004). *Homo erectus* arrived at about 2 mya with a large increase in grassland habitat. Also, fauna occurred periodically with 100,000 year shifts that coincided with *Homo* inhabitation starting from 2.5 mya (Bobe & Behrensmeyer 2004). This last finding provides support for the variability selection hypothesis. Considering global environmental conditions during the Cenozoic, Potts (1998) explains that hominan sites demonstrate 1) large shifts of habitats, 2) a lack of agreement between environmental conditions and important adaptations to habitat, 3) extensive changes in the climatic conditions that cannot be explained solely by the seasonality hypothesis, and 4) hominans existed in diverse habitats during long periods of environmental change. All of these factors support the variability selection hypothesis (Potts 1998).

All three hypotheses may prove useful regarding our understanding of human evolution. The savanna hypothesis might be important for the explanation of *Homo* evolution. Many studies provide support of the faunal turnover hypothesis in that hominans and other mammals responded similarly to the environment. The variability selection hypothesis also receives support from different studies; hominan evolution was affected by the variability of climate changes that were presented at the time of their evolution. It cannot be said that human evolution was simple; therefore we may find various different scenarios to explain the process. Humans are a complex species, and the fossil record reveals incomplete snapshots of the past. A recent finding has demonstrated evidence for the sympatric use of habitat by both chimpanzees and *Homo ergaster*. McBrearty and Jablonski (2005) describe the first chimpanzee fossil discovered. The East African Rift Valley in

Kenya provides data indicating co-habitation between later *Homo* species and chimpanzees, extending chimpanzees' ancient boundaries further east than originally thought (McBrearty & Jablonski 2005).

The Fongoli chimpanzees live in a mosaic savanna habitat consisting of closed and open woodland, grassland, and small patches of forest (Table 2.6) (see Chapter Four). They use mostly open habitats for travel, but do not spend much time within them (Pruetz & Bertolani, in press). This may be in part to thermoregulation issues such as the reduction of direct sun exposure (Pruetz & Bertolani, in press). Fongoli provides a unique opportunity to understand the behavior of chimpanzees living in an open mosaic savanna environment. Studying the ecological context of those behaviors will provide essential evidence to be used in a referential model for hominan evolution (*sensu* Moore 1996). My research examines the insectivorous diet of the Fongoli chimpanzees. Limited research has been done on this area of the diet in hominans.

Table 2.6: Comparing defined habitat classifications to those used in this study at Fongoli, Senegal.

Habitat at Fongoli ¹	Reed & Rector's (2007) four classifications of savanna	Bobe & Eck 2001
Forest ecotone	Non-savanna ³	Forest
Gallery forest		
Tall grassland	Grassland	Grassland
Short grassland		
Woodland (open and closed)	Woodland	Woodland
Bamboo woodland	Woodland/Bushland	Woodland/Bushland
Thicket ² woodland	Bushland/Shrubland	Bushland/Shrubland

¹ Used in this research, described in Chapter Three

² Used by Pruetz & Bertolani, in press

³ Reed 1997 considered this forest

2.7.3 Evolution of human diet

The general trend in the hominan omnivorous diet is that *Australopithecus* consumed mostly fruit and leaves, *Paranthropus* consumed harder foods such as nuts, and *Homo* began to eat much more meat (Sponheimer et al. 2007, Peters 2007). *Paranthropus* species are phenotypically specialized with massive jaws for eating hard food resources (Peters & Vogel 2005, Robinson & Wilson 1998). However, they were most likely generalist but exhibited the specialization to consume challenging resources during time of food scarcity (Peters 2007, Robinson & Wilson 1998). Early *Homo* species were characterized by stone tool use, but they were also generalists that were able to process difficult foods (Peters 2007). To examine diet in hominans further, studies on isotopes are often done on teeth.

Isotope analyses can analyze stable carbon isotopes to find the C₃ and C₄ ratio. If C₃ resources were mainly consumed, forbs and trees or animals that consumed these comprised a major portion of the diet (Sponheimer et al. 2007). If C₄ resources were mainly consumed, grasses or animals that consumed grasses comprised a major portion of the diet (Sponheimer et al. 2007). Peters and Vogel (2005) used carbon isotope analyses from tooth enamel of three hominan species in South Africa to determine C₄ biomass in their diets. It was concluded that the C₄ content in their diets was most likely not from eating C₄ plants due to the lack of a significant C₄ habitat. The authors suggest animal options that may have instead been used. Peters and Vogel (2005) estimate that 25% of the diets of *Australopithecus africanus*, *Paranthropus robustus*, and *Homo ergaster* contained C₄ biomass (Peters & Vogel 2005). These authors concluded that early South African hominans were omnivores who ate various invertebrates, birds, and small to medium sized mammals. Sponheimer and colleagues (2005) confirmed this with further investigation of 14 new hominan fossils. They found that

Australopithecus and *Paranthropus* had diets composed mostly of non-C₃ foods (40% and 35% respectively) (Sponheimer et al. 2005). Intake of sedges, grasses, and animals that consume C₄ foods are suggested sources for the hominan diet (Sponheimer & Lee-Thorp 2003). Sponheimer and Lee-Thorp (2003) found that most termite species living in savanna environments in South Africa consumed C₄ in over half of ingested food. However, termites alone would not give the indicated diet of C₄ in hominans, although they could have been a contributor (Sponheimer & Lee-Thorp 2003, Sponheimer et al. 2005). Chimpanzees living in forested environments consume very little C₄ resources (Schoeninger et al. 1999). Savanna chimpanzees have been demonstrated to differ from Australopithecines in the amount of C₄ they consume (Sponheimer et al. 2006), yet they have not been compared to early *Homo* species, and these isotopic analyses neglect to measure C₄ foods that are used significantly by chimpanzees in cases where wadging occurs, rather than chewing and swallowing (i.e., bamboo feeding, Pruett, personal communication). Evidence of termite consumption stems from the bone tools found associated with *Paranthropus robustus*. These have been suggested as digging tools at termite mounds (Backwell & d'Errico 2001, 2008). Insects may have been an important dietary resource in hominan evolution, especially in open environments where other resources may have been scarce.

My research will explore the importance of insects as a food resource for savanna chimpanzees as well as their potential as a reference for the Plio-Pleistocene diet of hominans. This analysis will help to display the similarities of Fongoli to that of early hominan environments during the Pliocene and early Pleistocene, when open environments became an abundant habitat.

CHAPTER THREE

Methodology: Primate ecology and behavior

3.1 Introduction

In this chapter I describe the methodology and analyses used in this research. Methods were designed to test hypotheses discussed in Chapter One by examining both the ecology and behavior of the Fongoli chimpanzees in relation to their insectivorous diet. Due to successful habituation efforts, I was able to directly observe the Fongoli chimpanzees' behavior. This data will contribute to previously published information on the diet that was largely gained by indirect methods (Bogart & Pruetz 2008, Pruetz 2006). The savanna habitat at Fongoli provides an opportunity to examine the environment's effects on chimpanzees, so that ecological data will complement the behavioral data in providing information on the distribution and availability of food resources. Behavioral data on use of these food items will then be used in reference to these ecological variables.

3.2 Study site: Fongoli, Senegal

Research was conducted at the Fongoli Savanna Chimpanzee study site (Figure 3.3) in southeastern Senegal (12°39 N 12°13 W) from August 2006 to July 2007 (Figure 3.1). Dr. Jill D. Pruetz, Department of Anthropology, Iowa State University, initiated research at the site in 2001, and it has continued, uninterrupted, since that time. Fongoli is considered a mosaic habitat, including both open canopy (woodland, bamboo, and short and tall grassland) and closed canopy (gallery forest and ecotone forest) habitat types (Table 3.1). Cultivated and fallow fields are present seasonally. Its location in the Sudo-Guinean vegetation belt in Africa is characterized by an average rainfall of approximately 900-1100 mm per year, with a

long dry season (October-May) and a short wet (rainy) season (June-September) (Ba et al. 1997, Carter et al. 2003).



Figure 3.1: Map of Senegal and location of Fongoli (from www.faa.gov).

Table 3.1: Definitions of habitat types at Fongoli (modified from Pruetz et al. 2002).

Habitat	Classification	Definition
Bamboo Woodland	Open	Contains deciduous trees with isolated palms and a flat-leaved savanna. Understory composed of <i>Oxytenanthera abyssinica</i> (bamboo)
Forest Ecotone	Closed	Where water runoff from plateau edge produces a strip of evergreen woody vegetation. At Fongoli, <i>Cola</i> trees predominate.
Gallery Forest	Closed	Tropical semi-deciduous lowland closed forest.
Tall Grassland	Open	Savanna with isolated deciduous trees with a height of at least 2m. <i>Gardenia</i> spp. common with <40% canopy cover. Predominated by elephant grass (<i>Pennisetum purpureum</i>), reaching 2-4 meters tall.
Short Grassland-Savanna	Open	Savanna with isolated deciduous shrubs less than 3m, <i>Combretum</i> spp. common. Short grasses include species of <i>Cynodon</i> and <i>Chrysopogon aucheri</i> .
Woodland	Open and closed	Drought-deciduous lowland woodland with a canopy cover >40%. Grasses dominate understory. Considered closed (seasonally) when canopy cover is > 80%.

The Fongoli chimpanzee home range is over 63 square kilometers (Pruetz 2006). The range size estimate has increased steadily over the years, a result of identifying rarely used areas and habituation of the community. During this study the chimpanzees were followed into areas previously not included in their home range. Pruetz and colleagues (2002) found the Fongoli area to have a density of 0.09 individual chimpanzees per square kilometer based on nest surveys conducted in 2002.

The Fongoli site contains five non-human primate species: bushbaby (*Galago senegalensis*), vervet or green monkey (*Chlorocebus aethiops*), patas monkey (*Erythrocebus patas*), Guinea baboon (*Papio hamadryas papio*), and chimpanzee (*Pan troglodytes verus*). Several non-primate mammal species are known in the area as well, such as the hyena (*Crocuta crocuta*), civet (*Civettictis civetta*), leopard (*Panthera pardus*), caracal (*Caracal caracal*), golden cat (*Profelis aurata*), serval (*Leptailurus serval*), hippopotamus (*Hippopotamus amphibius*), warthog (*Phacochoerus aethiopicus*), bushbuck (*Tragelaphus scriptus*), oribi (*Ourebia ourebi*), duiker (*Cephalophus* species), Gambian sun squirrel (*Heliosciurus gambianus*), genet (*Genetta genetta*), 3-4 species of mongoose (Family Herpestidae), porcupine (*Hystrix cristata*), cane rat (*Thryonomys swinderianus*), several species of bat (Order Chiroptera) and side-striped jackal (*Canis adustus*) (personal observation, Pruetz, unpublished data).

Several human groups live sympatrically with the chimpanzees, including the Malinke, Bassari, Diahanke, Puhlar, and Bedik ethnic groups (Pruetz 2006). Chimpanzees travel through human agricultural fields, yet they are not known to raid crops at Fongoli except for the occasional beehive (Pruetz 2006). Local crops include peanuts, millet, maize, and cotton (Pruetz 2006).

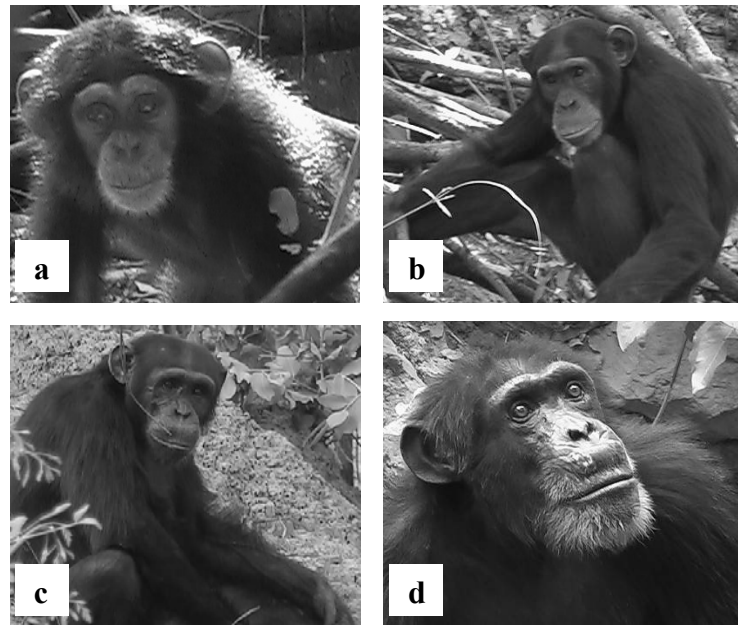


Figure 3.2: West African chimpanzees of the Fongoli community: a.) Infant female (Fanta) b.) Adolescent male (David) c.) Subadult male (Nyegi) d.) Adult male (Siberut).

3.3 Study species: West African chimpanzees (*Pan troglodytes verus*)

Studies of mitochondrial DNA have suggested that *P. t. verus* exhibit enough differences from other subspecies to be distinguished as a separate species (Morin et al. 1994). However, this is not yet a common distinction (Butynski 2003, Groves et al. 2001). West African chimpanzees typically have a dark mask around their eyes, while the rest of the face remains a lighter pink (Figure 3.2) (Stumpf 2007). Males are approximately 46.3 kilograms (kg), while females are about 41.6kg (Smith & Jungers 1997, Stumpf 2007). Wild populations are found in the countries of Senegal, Mali, Guinea-Bissau, Republic of Guinea, Sierra Leone, Liberia, Ivory Coast, Ghana, Burkina Faso, and Nigeria, while populations in Benin and Togo are now extinct (Butynski 2003). Guinea-Bissau, Sierra Leone, Liberia, Ghana, Mali, and Burkina Faso have no long-term chimpanzee study sites, but many of these countries have reserves, parks, and sanctuaries where chimpanzees reside (Brownell 2003,

Carter et al. 2003, Gippoliti et al. 2003, Hanson-Alp et al. 2003, Magnuson et al. 2003, Nisbett et al. 2003, Oates et al. 2003). Taï (Ivory Coast), Bossou (Guinea), the Nimba Mountains (Ivory Coast and Guinea), Gashaka (Nigeria), and Fongoli (Senegal) are the only active, long-term chimpanzee study sites in West Africa. Senegal is estimated to have between 100 and 400 chimpanzees (Teleki 1989, Carter et al. 2003).

3.3.1 Study subjects

The chimpanzee community at Fongoli was semi-habituated to human observers during this study, meaning observers could follow males all day and collect systematic behavioral data on them, but female chimpanzees were still wary of humans, often avoiding them. Habituation of the Fongoli chimpanzees to human observers was conducted for the first four years of Dr. Pruetz' project. Research prior to the present study used ecological methods and indirect investigation, with few direct observations (Bogart 2005, Bogart & Pruetz 2008, Pruetz et al. 2002, Pruetz 2006, Piel 2004, Socha 2006, Waller 2005). The Fongoli community size ranges from 33-36 individuals annually depending on births and deaths. The Fongoli chimpanzees range in parties or subgroups that are, on average, absolutely and relatively (to community size) larger than other communities (Pruetz & Bertolani, in press). Age classification follows Goodall (1986). Adult males are over age 16 (Figure 3.2); subadult males (late adolescence) are 13-15 years of age (Figure 3.2); adolescent (early adolescence) males are 8-12 years old; juvenile males are five to seven years old (Figure 3.2); infant males are up to five years of age (Goodall 1986). Females reach maturity (adulthood) at about 14 or 15 years of age; subadult females are 11-13 years

of age; adolescent females are eight to ten years of age; juveniles are five to seven years old; infants are up to five years of age (Figure 3.2) (Goodall 1986).

Table 3.2: Fongoli individuals at time of study.

Name	Code	Sex	Approximate age (yrs) at time of study	Male rank*	Mother
Foudouko	FO	M	Late teens >16	1	
Mamadou	MM	M	Early 20s	2	
Yopogon	YO	M	Late teens	3	
KL	KL	M	20s	4	
Diouf	DF	M	20-30	5	
Bilbo	BI	M	25-35	6	
Bandit	BN	M	30s	7	
Karamoko	KM	M	30s	8	
Siberut	SI	M	>30	9	
Lupin	LP	M	Teens	10	DA?
Ross	RS	M	Old 40s or 50s	11	
Nyegi	NY	M	Subadult ~13		
Lucille	LU	F	Older adult, likely >25, multiparous		
Daoulema	DA	F	Older adult, likely >30, multiparous		
Natasha	NA	F	Teenage, likely primiparous		
Nene	NN	F	Older adult, likely >30, multiparous		
Lingua	LI	F	Older adult, likely >25, multiparous		
Muso	MS	F	Older adult, likely >30		
Farafa	FA	F	Older adult, likely >30, multiparous		
Nickel	NI	F	11-13		NN
Tia	TI	F	11-14		
Tumbo	TM	F	11-14		
Sissy	SS	F	10-11		
Bo	BO	M	8-9		Wilema ¹
David	DV	M	8-9		FA
Luthor	LT	M	6		LU
Jumkin	JM	M	6-7		LI
Mike	MK	M	7		MU
Frito	FR	M	6		FA
Dawson	DW	M	4		DA
Lex	LX	M	2.5		LU
Jino	JI	M	2		LI
Nellie	NE	F	4-5		NN
Sonya	SN	F	1		NA
Fanta	FN	F	2		FA
Teva	TV	F	Born Apr 07		NI

¹ deceased, *at time of study

All subjects were identifiable using distinguishing marks, permanent cuts or scars, variation in coloration of skin, genital swellings size, shape and color, and missing toes or fingers. During this study, there were a total of 36 individuals in the community, including 11 adult males, seven adult females, one subadult male, four subadult females, two adolescent males, four juvenile males, three infant males, and four infant females (Table 3.2). Lupin was considered an adult male during this study due to his ascension into the male dominance hierarchy. Lupin was the 10th ranked male during most of the study but had gained rank above Bandit, ranking seventh by July. Nickel was considered an adult female during this study due to her pregnancy and birth of a female infant, even though she was thought to be younger than 13 years of age. Nyegi, a subadult male, was not seen after the seventh of June in 2007, and is now presumed to be deceased.

3.4 Ecological data collection and analyses

Temperature, rainfall, and soil characteristics were regularly monitored. Temperature was recorded daily using HOBOTM data loggers placed in shaded areas in grassland and woodland habitat types to record ambient temperatures approximately every 15 minutes. Temperature data analyzed are diurnal values, ranging from 600 hours to 1800 hours. A rain gauge was located in an open area near the Fongoli village, where rainfall (mm) was recorded daily. Soil moisture and temperature were monitored daily throughout the study in both open and closed habitat types with a pocket moisture meter as well as a hand test and thermometer.

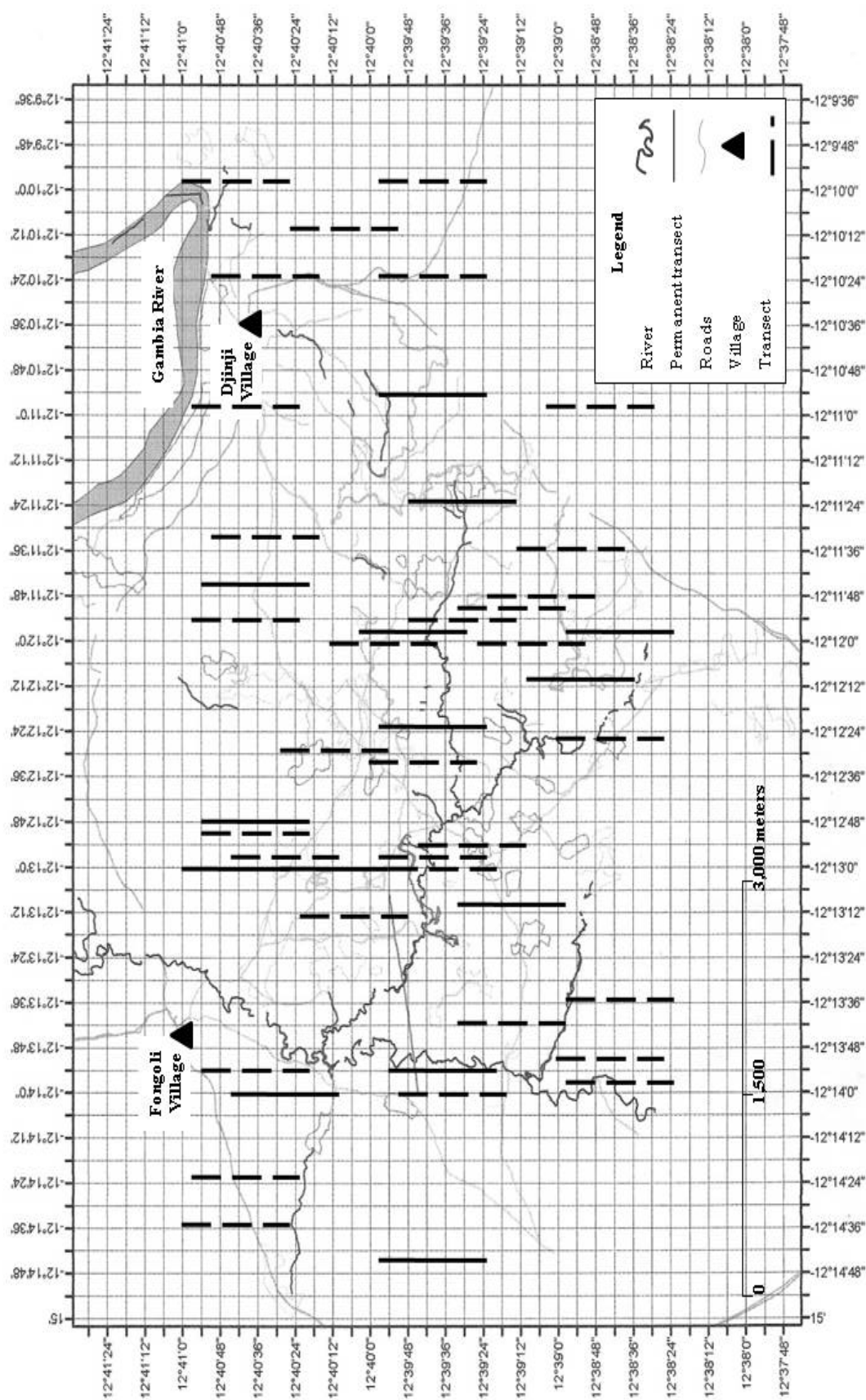


Figure 3.3: Fongoli site map with 47 transects; 16 solid lines were also used for insect density.*

* 1 square is approximately 187.5x187.5m², Map = 7x10km²

Map by Paco Bertolani, modified by S. Bogart

Throughout the study a GPS (Global Positioning System, Magellan model) unit was used to map chimpanzees' ranging, insect nests used by chimpanzees, transects, and chimpanzee nesting spots (in order to find the chimpanzees the next day). Several transect methods were applied. First, 47 transects, each 1 km in length were surveyed to assess habitat (Figure 3.3). Transects were selected using simple random sampling techniques, and all transects were oriented North to South to prevent overlap. Random sampling was determined by using the 'random-between' function in Excel to find a starting point along the latitude and longitude lines on the site map. To determine habitat type distribution the dominant habitat (greater than 50% of area) in a five meter radius at every 100 m interval along the transect (Figure 3.4a) was recorded, starting at zero meters (11 data points per transect). Thus, a total of 40,605 m² was sampled for habitat assessment in this study. Sixteen of the 47 habitat transects were also used to measure insect density (Figure 3.3). Densities of *Macrotermes* termite mounds and ant nests (*Dorylus* spp. and *Pachycondyla* spp) were recorded using intervals of 100 m along transects (10 data points). At each interval a strip transect of 20 m (total transect width of 40 m) distance to each side of the transect line (east and west) was examined for active termite mounds within 4m to each side (total 8m) of that axis (Figure 3.4b). An area of 25,600 m² was thus sampled for insect density data.

Finally, a single transect (2 km) was monitored twice a month (permanent feeding transect established by JDP in 2001, which runs east-west through the core range). A total of 205 feeding trees from 33 species were monitored along this transect (Table A4). These trees were examined for fruiting, flowering, leafing, and total coverage (crown area) percentages. A score from zero to three was given as to the amount of fruit, with three having the greatest amount of fruit. Fruits were scored on ripeness, where each species was evaluated as to the

coloration and firmness. Each species differs in coloration and these classifications are known for many species. For unfamiliar species coloration when unripe and ripe, field assistants, knowledgeable about the fruit, provided support. Ripeness was given a score of three when fruits were very ripe, two when semi-ripe, and one when the fruit was unripe (see Table A6). Trees were also measured as to basal area; minimum tree size sampled for basal area in this study was 10cm (following Basabose 2002, Tutin et al. 1997, Takemoto 2004), except for the vine species *Saba*, an important food resource for the Fongoli chimpanzees (Pruetz 2006). All *Saba* plants along the transect were monitored (N=8, Table 5.1).

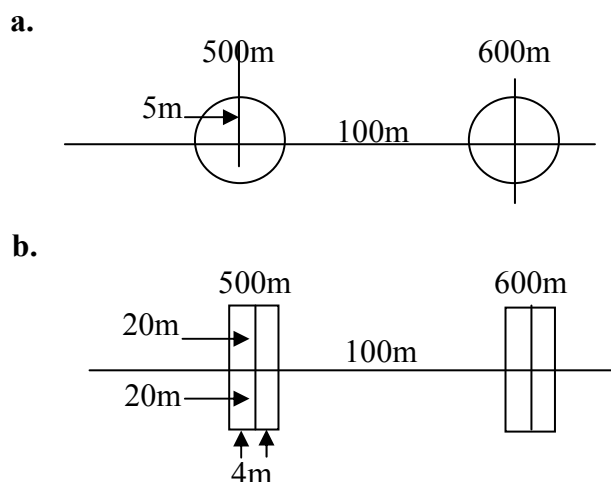


Figure 3.4: Direct interval sampling along random transects: a) habitat composition b) Insect density.

Food items were brought back to the camp and weighed on a scale in order to determine average weights per item (termites, fruits, ants, etc.). These items were then dried in the sun for several days (5-7 depending on season) in a dry box and measured for dry weight in order to find water content. Problems arose with the fruit samples sent to a lab for nutritional content. Analyzing samples from outside the United States was newly prohibited,

and I was informed the lab could not take samples while I was in the field. Therefore, nutrient content was not obtained by this study.

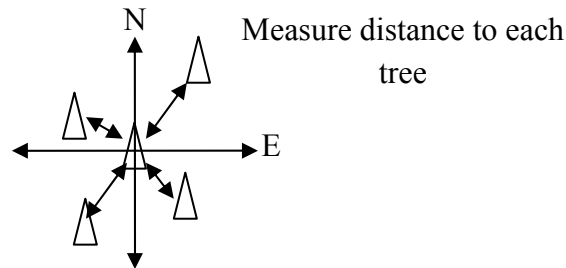


Figure 3.5: Point centered quarter method for distance sampling used to determine feeding tree densities.

Point-centered quarter sampling (Cottam & Curtis 1956) was employed to determine feeding tree densities. This sampling method has proven to provide the lowest coefficient of variance and requires fewer data points than nearest neighbor sampling (Cottam & Curtis 1956). Feeding trees were defined as a food resource according to Pruetz (2006, unpublished data). A central point (feeding tree) was used, and four quadrants were sectioned in northwest, northeast, southeast, and southwest directions (Figure 3.5). The nearest point of reference (another feeding tree) was then measured from the central point within each quadrant (Figure 3.5). Averages of the four distances provided a calculation of density. Cottam & Curtis (1956) recommend a minimum of 50 central points in order to reduce the standard error to <4.65% of the mean distance. Using stratified random sampling of the 6 generalized habitats (woodland: 18, short grassland: 39, tall grassland: 44, bamboo: 11, closed forests: 4, and field: 4) a total of 120 PCQ samples were analyzed. To determine the center point of the plots the ‘random between’ function of Excel was used to present a random output of latitude and longitude coordinates. Once a set amount of plots was

established for a particular habitat type, random coordinates were discarded if found in that habitat. The closest feeding tree to the random coordinates was chosen for the center point in PCQ sampling.

Ant nest densities were assessed using 14 plots that measured 500m². Throughout the year, seven plots were monitored in closed forested habitats and seven in open habitats. I attempted to sample half the plots in each of the seasons, wet and dry. Plot locations were chosen from randomly generated coordinates within the study site. At each location, a plot was measured to reach the 500m² around the habitat type. There were two instances in closed forests where the habitat type did not reach this area, and the plot was noted as such. A total of 3.1 square kilometers were used for ant plots. Direct counts of army ant (*Dorylus* spp.) nests were surveyed by systematically walking the plotted area and counting nests.

Termite mounds, ant nests, and feeding trees used by chimpanzees were marked when possible and mapped using a GPS. Feeding trees were assessed as to the habitat type they were in and what items were consumed from them. Marked feeding trees were only recorded when chimpanzees consumed food from them for more than 10 minutes. I attempted to mark and record as many species of plant as possible. To determine chimpanzee activity at insect mounds and nests, indirect evidence was used according to 'ethoarchaeological' methods following McGrew et al. (2003) and Bogart et al. (2005), or where direct observation of chimpanzee use continued for at least 10 minutes.

Characteristics of insect nests recorded included variables hypothesized to influence use by chimpanzees. Characteristics of the termite mounds recorded included feeding trees within 5m, percent vegetation cover, habitat, activity of the insects (based on how many new holes have been sealed), the number of tools found and, if possible, the species of the tools,

termite species, and measurements of length and height and shape of the nest. Ant nests were examined regarding the circumference of the tree at the location of the nest, nest height from the ground, the number of tools found and, if possible, the species of the tools, habitat, and nest suitability. Nest suitability follows Schöning et al. (2007); nests were categorized as to how many (estimated) ants emerge from the nest after it was hit with a stick 3 times: few (1-99), many (100-999), and enormous (>1000). Schöning and colleagues (2007) determined that the categories of 'many' and 'enormous' were suitable for ant dipping by chimpanzees. Soil was also assessed around insect nests used by the chimpanzees and scored as to whether it was dry (crumbly or hard), moist (pliable and moist to touch), or wet (when squeezed exudes water). Finally, the area near the used nest was searched for other insect nests used by the chimpanzees.

Multiple samples of termites and ants were collected. There was an attempt to collect all castes of all species (workers, immatures, reproductives, and minor and major soldiers) to provide information on insect diversity. Insects were collected using chimpanzee tool extraction techniques, an insect aspirator, or forceps and were preserved in vials of 85% ethanol. Dr. Rudolf Scheffrahn from the University of Florida identified the termite samples, and Dr. Caspar Schöning from the University of Copenhagen identified ant samples. Samples were mailed with the proper permission from the Senegalese Forestry Department and the US Government (US Fish and Wildlife form 3-177). Bees found in fecal samples were sent to Dr. Laurence Packer of York University Ontario, Canada for identification. The water content of insects was measured in the field by weighing, drying, and weighing the insects again. I attempted to obtain approximately 10 termite samples and 10 ant samples from species recorded as consumed to assess their water content.

Fresh fecal samples were examined macroscopically and microscopically to complement observed data on the chimpanzee diet. In the field, fresh chimpanzee fecal samples were collected and brought back to camp. The samples were then examined for seeds, fiber, animal matter, and leaves, with the percentages of each recorded. The samples were sieved in order to identify insects present. Any insects found were preserved in vials and sent to either Dr. Scheffrahn or Dr. Schöning for identification.

Bushbaby (*Galago senegalensis*) is a known food item for the Fongoli chimpanzees. To determine bushbaby availability, one transect (2 km) was sampled monthly in the evening (after sunset) to survey individuals using eye-shine (reflective tapetum) cues. The Fongoli chimpanzees also consume other vertebrates. Diurnal animals, such as vervet monkeys, warthogs, etc, were noted whenever they were in visual contact with the principle investigator. If a group of monkeys or other mammals were observed, the number of individuals was counted or estimated, along with age and sex class to offer an approximation of encounters. This was used to provide a species list of animals most frequently encountered at Fongoli. The use of species lists is very common, and the number of sightings improves accuracy (Sutherland 2000).

3.5 Behavioral data collection and analyses

Termite fishing by chimpanzees is defined as the insertion of a probe (bark, vine, twig, grass, leaf, etc) into a termite mound and withdrawing the tool covered in soldiers that attack the probe with their pinching mandibles (Nishida et al. 1999). The chimpanzees then consume the termites off of the tool (Nishida et al. 1999). Ant dipping is similar to termite fishing in that when a tool is inserted into an ant nest or line of ants, these insects crawl onto

the probe allowing the chimpanzee to consume them by swiping the probe through the mouth. Ant dipping is generally an arboreal (above ground) activity at many sites, while termite fishing is terrestrial (Nishida et al. 1999). Chimpanzees typically sit on a log or tree limb above an ant nest to avoid swarming, biting ants. Fongoli chimpanzees have also been observed to use their hands and feet during ant dipping and also to feed terrestrially. Direct observations of these behaviors provide data for comparison with other chimpanzee sites.

All-day follows (nest to nest) of focal subjects (adult males) were conducted to quantify daily activity and diet. Focal subjects were 10 adult males due to their better habituation and Fongoli project research protocol (females are not used as focal subjects for ethical reasons related to their susceptibility to poaching for the pet trade). Focal subjects were selected depending on who was in the party on a given day; then the subject was chosen randomly. This method was performed to provide an un-biased sample. Selection controlled for amount of time sampled per month, and data collection controlled for time of day. A total of 10 hours of observational data per male per month was attempted in order to obtain a total of 100 hours of observational data per month. Data were collected, minimally, on 20 days per month. The focal animal sampling method was combined with instantaneous recording at five-minute intervals (Table 3.3) (Altmann 1974, Martin & Bateson 1993). Data recorded during these sessions included activity, species of food eaten, part of species eaten, behavior and technique used to acquire food, and habitat type (Table 3.3, Table A1). Seed eating and fruit eating were lumped into a single category during data collection. Any behavior that was unusual or important to note between five-minute intervals was recorded *ad libitum*, e.g. meat-eating, copulating, and displaying. Data on species and part of food eaten (fruit, leaves, flowers, insects, cambium) were used in conjunction with feeding rates to produce an

average rate per minute of feeding by counting how many units (a single termite, one whole fruit, one leaf, etc) an individual consumes within a one-minute time-span. Much of this sampling was done with video recording (see below). Given the difficulty in accurately counting individual food items, these data were taken opportunistically. A total of ten samples per food item were targeted. For vertebrate prey, this measure entailed the amount of time for one individual to consume his or her portion of the meat. The individual who obtained the meat was monitored specifically. During a termite fishing bout (from start to finish), the number of tools used by the individual was also recorded. At the beginning of each data collection period the observer noted the habitat the chimpanzees occupied, identified and counted party members present, and tracked location via GPS coordinates.

Table 3.3: Example of behavioral data taken on Mamadou on February 6, 2007.

Time	Activity ^a	Food item ^b	Food species ^c	Habitat ^d
13:02	FD	fr	SB	FE
13:07	FD	fr	SB	FE
13:12	FD	fr	SB	FE
13:17	FD	fr	SB	FE
13:22	FD	fr	SB	FE
13:27	FD	fr	SB	FE
13:32	FD	fr	SB	FE
13:37	FD	fr	SB	FE
13:42	FD	fr	SB	FE
13:47	FD	fr	SB	FE
13:52	FD	fr	SB	FE
13:57	FD	fr	SB	FE
14:02	FD	fr	SB	FE
14:07	S gm	--	--	FE
14:12	S gm	--	--	FE
14:17	S gm	--	--	FE
14:22	S gm	--	--	FE
14:27	S gm	--	--	FE
14:32	R	--	--	FE
14:37	R	--	--	FE

^aActivity: FD = Feed, S gm = Social groom, R = Rest; ^bFood item: fr = fruit; ^cFood species: SB = *Saba senegalensis*; ^dHabitat: FE = Forest Ecotone

Focal animal sampling is a standard collection method used in primate behavioral observation (Altmann 1974, Dew 2003, Martin & Bateson 1993). Feeding rate is the examination of food intake per minute (Hladik 1977, Nakagawa 2009), but this method of data collection has not been extensively used in primatology due to various logistical issues of observation in dense vegetation, arboreal feeding, and habituation level of the subjects (Nakagawa 2009). I used this method when applicable during my behavioral observations of the Fongoli chimpanzees. However, problems of visibility and habituation of the Fongoli chimpanzees inhibited progress. Therefore, use of video recordings (see Section 3.5.2) was implemented in this research to further the results obtained. However, this method was also limited in collecting data sufficient for analysis (see Chapter Six).

3.5.1 Behavioral data validation

Over 963 hours of data were recorded on the 10 adult male subjects over the course of the year of this study. To assess potential variation in behavioral data from the different male subjects, frequency data were examined according to time of day and in relation to activity (across time of day) according to the 10 males (Table 3.4 and Table 3.5). Male variability in terms of total activity budget was also examined for biases in the data (Table 3.6). Additionally, individual male data were adjusted randomly to control for the amount of data taken on each male to find whether biases exist in data collection from each male (see below).

There was no significant difference between the 10 males and the distribution of data collected over the course of the day (ANOVA, F -ratio = 0.96, df = 9, 30, p -value = 0.49). Males were sampled equally across time of day (Table 3.4). However, significance exists in

terms of total data collected over the course of the day (ANOVA, F -ratio = 20.2, $df = 3, 36$, p -value < 0.0001). Data were taken mostly from 0900 hours to 2000 hours, with the morning hours having less data (16%) recorded (Table 3.4). This may have implication for the results in terms of activity budget. Pruetz and Bertolani (in press) found that activity was influenced by the time of day; the Fongoli chimpanzee fed more in the morning, while resting more often in the middle of the day. Thus, feeding in this study may be underrepresented due to lack of data in the morning hours. To find if this discrepancy exists, analyses on activity across time of day were conducted.

Table 3.4: Proportion of frequency of observations on 10 adult male focal subjects according to time of day from August 2006 to July 2007 at Fongoli (instantaneous sampling).

Time	0600-0859	0900-1159	1200-1459	1500-2000	
Bandit	20.5	30.9	24.6	24.0	100
Bilbo	16.4	34.1	29.6	19.9	100
Diouf	15.3	35.5	28.8	20.4	100
Foudouko	17.7	31.0	30.7	20.6	100
Karamoko	16.3	25.6	23.3	34.9	100
KL	16.7	30.6	28.7	24.1	100
Lupin	16.1	32.3	28.6	23.0	100
Mamadou	15.0	31.3	29.7	24.0	100
Siberut	16.6	34.0	25.2	24.2	100
Yopogon	11.7	33.6	32.6	22.1	100
Total Data	16.1	32.0	28.4	23.4	

Table 3.5: Proportion of data organized by activity across time of day using pooled data from 10 males (instantaneous focal sampling).

	0600-0859	0900-1159	1200-1459	1500-2000
Other Feed/forage	44.2	18.6	9.4	33.1
Termite Fish	5.5	4.5	4.6	15.9
Rest	25.9	48.6	64.3	33.1
Travel	13.4	5.5	2.6	9.2
Social	7.6	18.7	16.4	7.5
Other behaviors	3.3	4.2	2.6	1.2
	100	100	100	100

Data on activity budget were pooled from all males (Leger & Didrichsons 1994, Maddala 1971). There was no significant variation in activity across time of day (ANOVA, F -ratio = 0.34, df = 3, 20, p -value 0.80) (Table 3.5). When examining the activities according to time of day using matched pairs Student's t -test, no significant differences exist between any of the three-hour time slots throughout the day (df = 5): 0600-0859 hours and 0900-1159 hours t -ratio = 1.37, p -value = 0.22; 0600-0859 hours and 1200-1459 hours t -ratio = 0.78, p -value = 0.47; 0600-0859 hours and 1500-2000 hours t -ratio = 1.87, p -value = 0.12; 0900-1159 hours and 1200-1459 hours t -ratio = -0.76, p -value = 0.47; 0900-1159 hours and 1500-2000 hours t -ratio = -0.90, p -value = 0.41; 1200-1459 hours and 1500-2000 hours t -ratio = -0.37, p -value = 0.73. For example, feeding may occur proportionally more in the morning (44%) and evening (33%) hours, however significant variation between these times and the middle of the day does not exist.

Pooling the data from all 10 males may be a possible weakness of this study. Thus, individual behavioral data across males were examined for variation. Individual's activity budgets were similar between males (ANOVA, F -ratio = 0.14, df = 9, 50, p -value = 0.99) (Table 3.6). However, in examining individual activity categories, Siberut was an outlier in that he rested more than all other males (Table 3.6). If Siberut was taken out of the data set, little difference is displayed in the proportion of activity budget with and without including Siberut (Table. 3.7) and no significant difference exists between frequencies (Student's t -test on frequency, t -ratio = 1.84, df = 5, p -value = 0.12). Thus, the pooling of data for male subjects does not have an influence on data presented in this dissertation.

To control for the possibility that certain males had a preference for termite fishing (or other activity) and these individuals were consequently observed the most, a target of 10

hours of data collection per male each month was set. In examining the data on individuals (Table A7), the male with the least amount of collected data was Karamoko, while the most data was collected on K.L. (Figure 3.6). To determine if the amount of data collected affected the results, I randomly adjusted all frequencies for each male to equal the total data collected on Karamoko. Using the adjusted data (Table 3.8), the activity budget did not differ from the original data (ANOVA, F -ratio = 0.14, df = 1, 14, p -value = 0.71).

Table 3.6: Proportion of individual male activity budget at Fongoli from August 2006 through July 2007 (instantaneous sampling).

	Feed/forage	Termite fish	Rest	Travel	Social	Other	Total
Bilbo	21.3	10.7	47.4	6.6	12.4	1.7	100.0
Bandit	25.2	6.4	45.7	6.6	14.2	1.9	100.0
Diouf	23.5	7.6	42.0	8.5	15.0	3.3	100.0
Foudouko	21.6	5.2	44.1	8.8	19.0	1.4	100.0
Karamoko	25.3	4.7	42.3	7.4	16.1	4.2	100.0
KL	24.7	9.8	43.3	5.4	12.4	4.3	100.0
Lupin	27.8	11.2	38.5	6.3	13.1	3.1	100.0
Mamadou	26.4	6.4	46.2	6.9	11.3	2.7	100.0
Siberut	16.6	6.8	60.6	6.1	7.5	2.4	100.0
Yopogon	22.0	4.8	44.6	6.4	18.4	3.9	100.0
Total average of male average	23.4	7.4	45.5	6.9	13.9	2.9	

Table 3.7: Pooled proportion of daytime activity budget from 9 males and from 10 males.

	Feed/forage	Termite fish	Rest	Travel	Social	Other
Data from 9 males*	24	8	44	7	14	3
Data from 10 males	24	7	45	7	14	3

* Siberut extracted from the pooled data

Table 3.8: Original activity budget data and data adjusted for bias assessed from instantaneous focal male pooled data (N=10).

	Original activity budget (%)	Adjusted activity budget (%)	Difference
Feed/forage other	23.57	23.94	-0.37
Termite fish	7.50	8.17	-0.67
Rest	45.46	48.59	-3.13
Travel	6.83	5.01	1.82
Other Social	13.39	11.37	2.02
Other	2.77	2.47	0.30
Aggression	0.41	0.40	0.01
Drink	0.08	0.07	0.01

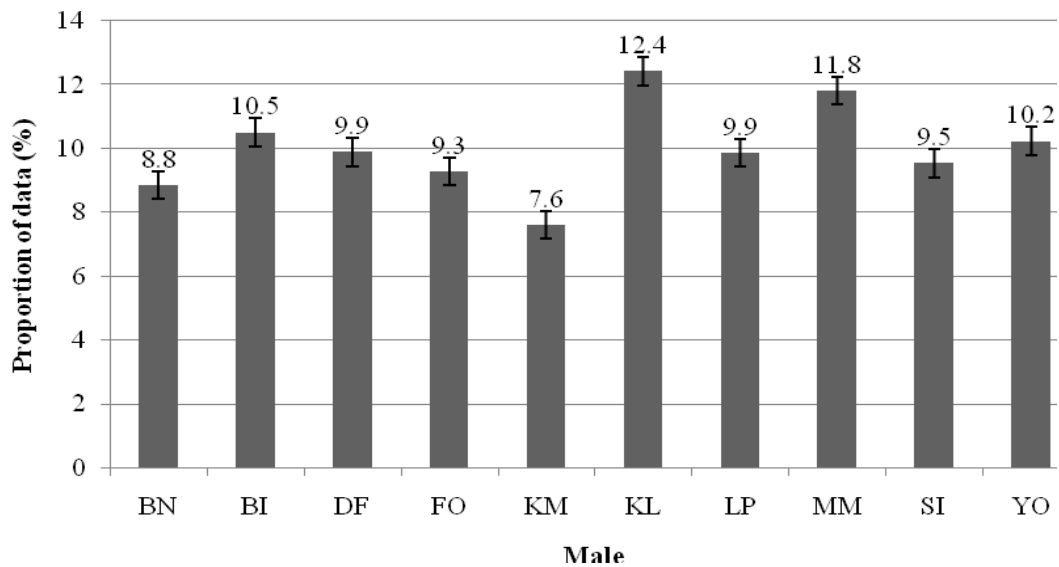


Figure 3.6: Proportion of instantaneous focal data taken from each of the ten adult males at Fongoli from August 2006 to July 2007.

Table 3.9: Original data and data adjusted for bias on monthly proportion of termite fishing (TF) assessed from instantaneous focal male data (N=10).

	Termite fishing proportion (%)	Adjusted TF proportion (%)	Difference
August	0.12	0.14	-0.02
September	0.00	0	0.00
October	0.00	0	0.00
November	0.47	0.27	0.20
December	0.00	0	0.00
January	1.06	0.96	0.10
February	3.17	1.23	1.94
March	5.87	5.6	0.27
April	24.06	22.13	1.93
May	16.78	17.49	-0.71
June	25.82	28.83	-3.01
July	22.65	23.36	-0.71

Finally, sampling error may be suggested, since termite fishing was one of the main objectives, and it could be argued that I was biased in my data collection. However many thorough steps were taken to avoid such biases. The termite fishing data obtained from 10

different males did not differ from the adjusted and original data (one-way ANOVA, f -ratio = 0.87, $df = 1, 18$, p -value = 0.36). To examine specific activity, the adjusted data on monthly termite fishing (Table 3.9) did not differ from the original (one-way ANOVA, f -ratio = 0.08, $df = 1, 22$, p -value = 0.78), and it positively correlated with the original data (Spearman's rank correlation $\rho = 0.88$, p -value < 0.001). Therefore, the differences in amount of data taken from the ten males do not significantly affect the results.

The only data that stands out in terms of potential bias in the results of this dissertation concerns those data collected across time of day. Data collected in the early morning were significantly lower than the data collected over the course of the day from 0900-2000 hours. Thus, the data might be skewed in terms of certain activities. Pruetz and Bertolani (in press) found that time of day had a significant influence on activity. Travel and feeding were conducted more often in the morning hours, while resting and grooming were conducted more often during midday (Pruetz & Bertolani, in press). Although, this research did not find such significant differences in daytime activity patterns, but the proportional trend is similar to Pruetz and Bertolani (in press). The differences between the two studies might be due to the year data were collected and the amount and method of data collected. Pruetz and Bertolani collected both focal and scan sampling data from March 2005 through March 2006, obtaining 2500 hours, more than twice as much as the data collected here. Results of this research are based only on focal animal sampling from 963 hours. Resting more during midday, when data were most often recorded in this study, would possibly skew the total proportion of resting among males, thus some behaviors might be underestimated. No significance was found between behaviors across time of day. Consequently, pooling of the data across time of day would not have an influence on the results of this study.

Additionally, individual behaviors between males did not significantly differ and pooling of data from all 10 males did not affect the overall activity budget and data found in this study.

3.5.2 Video recordings

A camcorder was used in the field to record an individual feeding, usually by a research assistant, while the primary investigator conducted focal sampling. This aided in collecting more detailed data on the techniques chimpanzees used to acquire food and allowed rate per minute analyses. Videos were analyzed in the United States. Data from these videos were used to obtain detailed descriptions of food processing, tool making techniques, feeding time, and additional behavioral data.

3.6 Analyses

Descriptive statistics were used in this study to provide basic information; for example, the proportion of sample points recorded as feeding on a specific food resource is equal to the behavior (A) frequency (or duration) divided by the total frequency (T) of all behaviors (or duration). To compare data with other sites, estimated parameters in the form of confidence intervals were used to reveal validity of the estimates. This measure allows for statistical analyses of data that cannot otherwise be conducted. Analyses were conducted using both parametric and non-parametric statistics in SAS Jump and Microsoft Excel software. A Student's *t*-test was used to test the null hypotheses using two-tailed distributions. The *p*-value was set at 0.05 to indicate significant differences between variables. Pearson's chi-squared tests were used to compare observed chimpanzee use with expected use based on availability data. Pearson's residuals were used with chi-squared tests to determine the source of significance in the data. In some cases, many variables are

examined, and multivariate statistics implemented. Certain multivariate statistics were used to find correlations between variables measured differently. Spearman's rank correlation is the non-parametric equivalent to Pearson's coefficient, a measure of asymmetry (Waite 2000). Spearman's correlation measures the relationship between variables ranking the data.

Ecological methods were used to determine food availability at Fongoli. Density of resources was measured as well as distribution. Pearson's chi-square test was used to analyze differences in the distribution of resources and densities. Multivariate statistics were used to determine if food resource availability correlated with rainfall and temperature.

In terms of food availability, the independent variable was a calculated availability index. Fruit availability data stemmed from the information acquired from the feeding transect and calculated according to a fruit availability index (FAI) following Takemoto (2004) using the scoring system (0-3) described in the methods:

$$FAI = [\sum(P_i \times F_i) / \sum(P_i \times 3)] \times 100$$

The basal area for tree (*i*) in cm² is represented by P_i and F_i is the fruit score given to tree (*i*). Other food resources were measured using proportions available or density calculated.

Diet is expressed in terms of proportion of time spent consuming each food item. The diet and foods used by the chimpanzees are examined in relation to the food availability using food item densities and FAI. The effect of seasonality on food consumption was tested using multivariate statistics to assess correlations between rainfall and proportion of use and FAI. Proportion of time spent eating insects was analyzed in conjunction with that of insect availability, fruit availability, intake rate, and water content.

Activity budget was expressed in proportion of time and correlated against rainfall and temperature. Temperature and rainfall were investigated as to whether these independent

variables have any effect on habitat use. Habitat use and preference were compared to habitat availability. Habitat preference is calculated by using Jacobs (1974) preference index (D) (Sutherland 2000).

$$D = (r - p) / (r + p - 2rp)$$

Where r was considered proportion of the use of habitat and p was the proportion of habitat in environment. If D is between -1 and 0, than the habitat was avoided, or used less often than by random chance. If D is between 0 and 1, than habitat was used more often than by random chance, or preferred. This method was used for food preferences as well. Where r was considered the proportion of fruit species i in the diet and p was the relative production of fruit i in range. This analysis incorporates the number of trees fruiting of a particular species.

When examining the insectivorous diet in further detail, specifics of ant and termite nest use were recorded, as well as details about the tools used. Analyses were conducted to assess potential associations with rainfall or temperature. Use of insect nests was examined with a chi-square test regarding the availability of insect nests and densities. Time spent termite fishing was analyzed for correlations with FAI to test the hypothesis that termites were not consumed in times of fruit scarcity.

CHAPTER FOUR

Environment at Fongoli, Senegal

4.1 Introduction

This chapter provides information on the environment at Fongoli, Senegal. Climatic variables (temperature, relative humidity, rainfall, soil temperature and moisture) and habitat composition were examined. Daily records were made for rainfall, temperature, relative humidity, soil temperature and moisture. Various types of technological equipment were used, such as remote data loggers and a pocket thermometer for air and soil temperatures, respectively, and a manual rain gauge for precipitation. Transects were used to sample habitat type distribution and abundance in this savanna mosaic environment.

4.2 Study site

Senegal is among the arid and semi-arid countries of sub-Saharan Africa (Oladipo 1980) and located between the latitudes of 12° and 17°N and longitudes of 11° and 18°W on the west coast of Africa. Neighboring countries are Mauritania, Mali, Guinea, Guinea-Bissau, and Gambia (see Figure 3.1). Fongoli is in the Sudano-Guinean zone of the southeastern part of the country, in the Kedougou Region. This region received between 800-1200 mm of rain per year in the 1960s and 500-800 mm per year in the 1990s (Tappan et al. 2004). Fongoli lies in the Shield ecoregion of Senegal, characterized by a geomorphology of erosional remnants (plateaus, hills, valleys, and terraces) and laterite soils (Tappan et al. 2004). The dominant vegetation type of this ecoregion is comprised of dense woody savannas and grasslands (vegetation type nomenclature follows Trochain 1957, Tappan et al. 2004). Forests are considered semi-dry and characterized by tree species that include *Afzelia*

africana, *Detarium microcarpum*, *Khaya senegalensis*, *Erythrophleum guineense*, with an understory of lianas and herbaceous vegetation (Carter et al. 2003). Grasslands are characterized by woody *Gardenia* species and *Combretum* species (Pruetz et al. 2002). Woody cover encompasses 10-30% of the Shield Region, and annual fires (natural and human-induced) are important for the wooded savannas to promote growth and reproduction (Figure 4.1) (Tappan et al. 2004). Between 1965 and 2000, Senegal experienced a slight decrease in shrub savannas, tree savannas, woody savannas, and forests from 78.1% to 72.2% and a slight increase in crop fields from 17% to 21% (Tappan et al. 2004). Approximately one fourth of Senegal's land is devoted to food production (Tappan et al. 2004). The estimated human population of Senegal in 2002 was 10,589,571 with a growth rate of 2.91% (Carter et al. 2003). Tappan and colleagues (2004) state that in the Shield ecoregion, mining towns and gallery forest destruction for agriculture are the areas of concern for woody vegetation decline.



Figure 4.1: Savanna fires on grassland at Fongoli: a.) wet season b.) fire c.) dry season.

4.3 Climatic data collection

Using HOBO™ data loggers, temperature and relative humidity were recorded approximately every 15 minutes. Data were collected between 0600 to 1800 hours in grassland and woodland habitat types. Data loggers from October 2006 through July 2007

failed to collect data. The average temperatures in each habitat were calculated over the course of several years to acquire a full year of data. Rainfall was measured and recorded daily with a manual rain gauge located in Fongoli village. In the first few months of this study a moisture meter was used. However, mechanical failure occurred early on in the study, and therefore the hand test was implemented instead. Soil was scored using the hand test as to whether it is dry (crumbly or hard), moist (pliable and moist to touch), or wet (when squeezed exudes water). A pocket thermometer was employed to record the daily soil temperature in open and closed habitat. This thermometer broke in December, and a new one was not obtained until January, so that soil temperature data were collected for ten months.

4.3.1 Ecological data collection

Habitat is defined as an ecological area occupied by an animal or plant species (Clements & Shelford 1939). Habitat can refer to much more than just the associated vegetation, so I use 'habitat type' to refer to vegetation organization within an area (Daubenmire 1968, Garshelis 2000). Habitat types at Fongoli were defined and described in Chapter 3 (Table 3.1). Figure 4.2 illustrates some of the habitat types described in this study based on definitions from Ellenberg & Mueller-Dombois (1967), Pruetz and colleagues (2002), Pruetz (2006), and Baldwin (1979). Habitat type distribution was assessed using transects, whose placement was selected using simple random sampling techniques determined via the random function in Microsoft Excel. This program provided coordinates for each starting point. All transects (N=47) were then walked due south to prevent overlap between transects. The dominant habitat type within a five meter radius was recorded at every 100 m interval along a 1 km transect, beginning at zero (N=11). At each sample point,

dominant habitat type, (e.g. woodland, short grassland) and understory (e.g. grasses or herbaceous vegetation typical of thicket) were recorded. For example, if the habitat type was woodland with an understory characteristic of grasses, it was labeled wooded grassland (WDgr). Over the course of the year, seasonality affected vegetation within habitat types. Fires began in December clearing grasslands and the understory of some habitats types. Grass did not begin to grow again until May when the rains began. Thus, definitions of habitat types were assessed during the beginning of the project in the wet season, August through October. During the wet season and for a portion of the dry season, some areas that were considered woodland could be deemed closed canopy woodland, which is defined as have greater than 80% canopy cover. Thus, closed versus open woodland was recorded as WD or WDc.

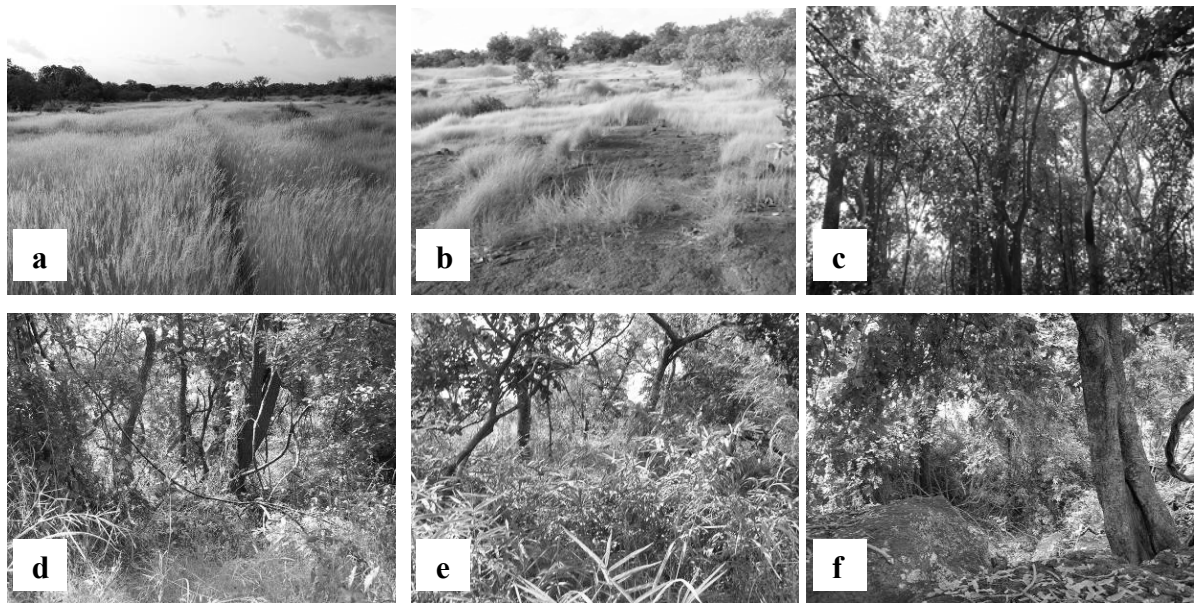


Figure 4.2: Habitat types at Fongoli: a.) tall grassland b.) short grassland c.) woodland d.) wooded grassland e.) bamboo f.) gallery forest.

4.4 Results

4.4.1 Temperature and relative humidity

Temperature and relative humidity data were analyzed using the statistical program Jump (Copyright © 2007 SAS Institute Inc.). Data analyzed were those between 0600 and 1800 hours (i.e. diurnal hours). Grassland and woodland temperatures were calculated based on data collected from June 2001 to May 2002 and from February to September 2006 (Tables A2 & A3). Relative humidity was assessed using data from February to September 2006. Data were unavailable for October through January.

The total average temperature at Fongoli was 27.5°C (15.5-45.9°C, SD = 2.81) in grassland and 29.2°C (19.4-40.1°C, SD = 2.31) in woodland. There is a significant difference between the mean monthly temperatures in these habitat types (Student's t -ratio = 4.42, df = 11, two-tailed p = 0.001), but temperatures in these habitat types positively correlated (Spearman's rank correlation ρ = 0.71, p -value = 0.009), increasing and decreasing simultaneously. Monthly averages are displayed in Figure 4.3. The total mean temperature for the site, using averages from both grassland and woodland, was 28.3°C (SD = 2.5).

In terms of average relative humidity, no significance exists between the habitat types' monthly means (Student's t -ratio = 0.86, df = 8, two-tailed p -value = 0.42; Figure 4.4). Relative humidity was highest from June through September, the rainy season (Figure 4.4). The average relative humidity at Fongoli, using grassland and woodland data from the months obtained, was 62.9% (SD = 33.9), with an average of 28.2% (SD = 10.4) in the dry season and 89.8% (SD = 6.5) in the wet season. The wet season has an average relative humidity three times that of the dry season. This does not take into account one wet season (October) and three dry season months (November-January).

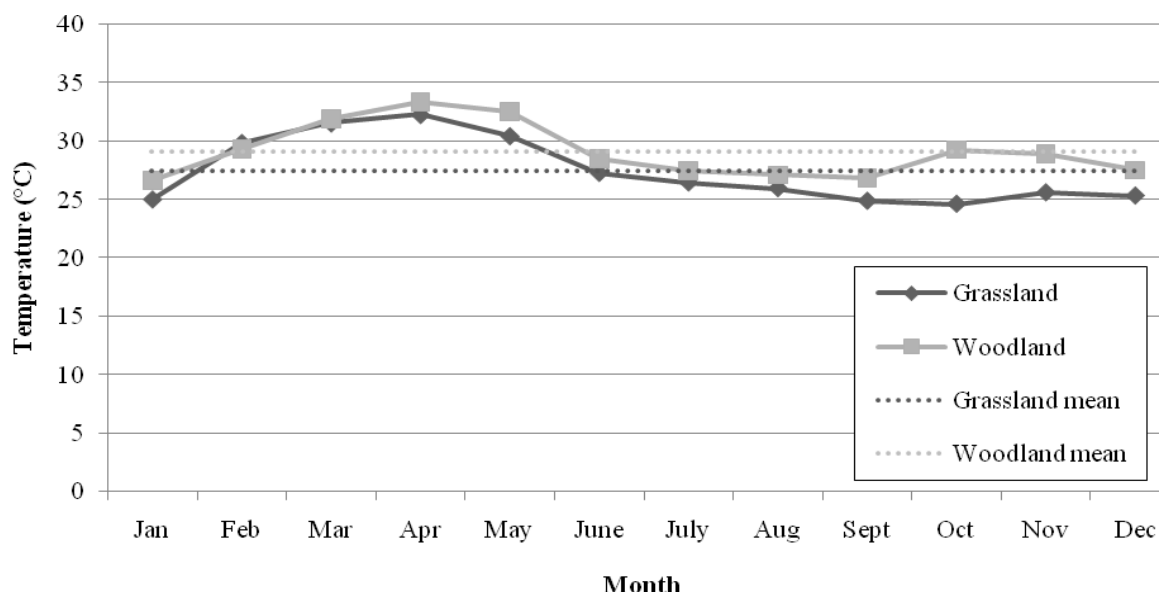


Figure 4.3: Average monthly diurnal temperatures for the habitat types grassland (dark diamond line) and woodland (light square line) at Fongoli.

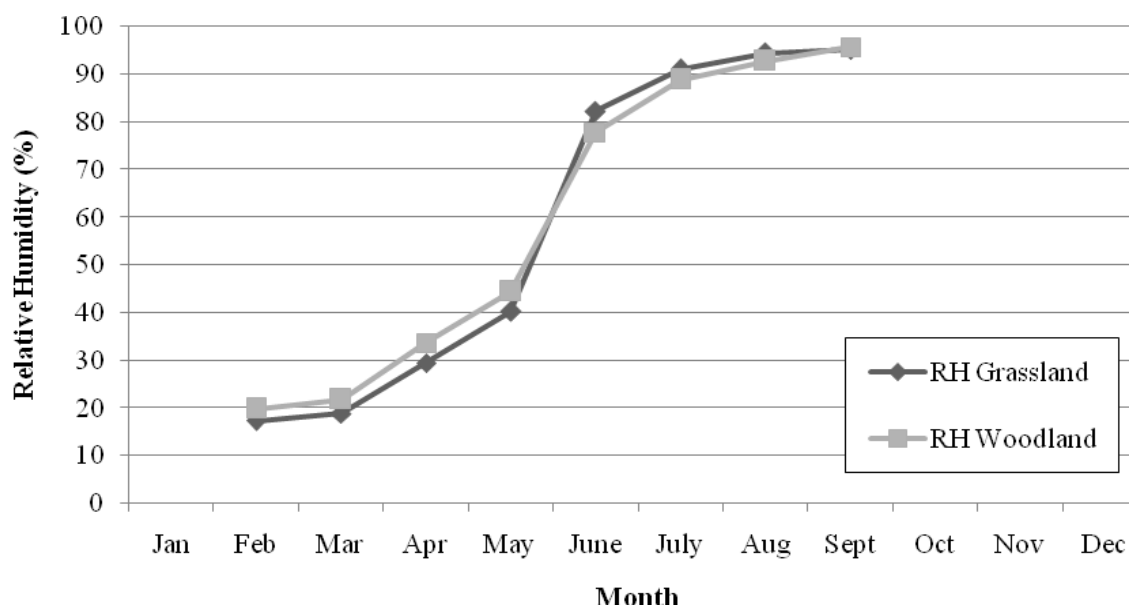


Figure 4.4: Average monthly diurnal relative humidity for grassland (dark line with diamond markers) and woodland (light line with square markers) habitat types at Fongoli.

4.4.2 Rainfall

Rainfall between August 2006 and July 2007 was 777.3 mm (range 0-246.6 mm per month). Using 60 mm to define a wet month (Moore 1992, Schoeninger et al. 1999, Stumpf 2007), the wet season duration was August through October 2006 and resumed in June through July 2007 of this study (Figure 4.5). The average monthly rainfall at Fongoli was 64.8mm, indicated in Figure 4.5 as the gray dotted line. Rainfall is positively correlated to grassland and woodland relative humidity (Spearman's rank $\rho = 0.88$, p -value = 0.004, 0.004). A wet day is defined as a day that accumulated over 0.1mm, when a trace amount of rain fell (Moron et al. 2008). This measure is to demonstrate the lack of rain in the dry season and not used in analyses. There were a total of 64 wet days (0-18) during this study (Figure 4.6). Fongoli had an average of 5.3 wet days per month from August 2006 through July 2007, indicated in Figure 4.6 as a gray dotted line. The wet season had an average of 12 wet days per month and the dry season had an average of 0.6 wet days per month.

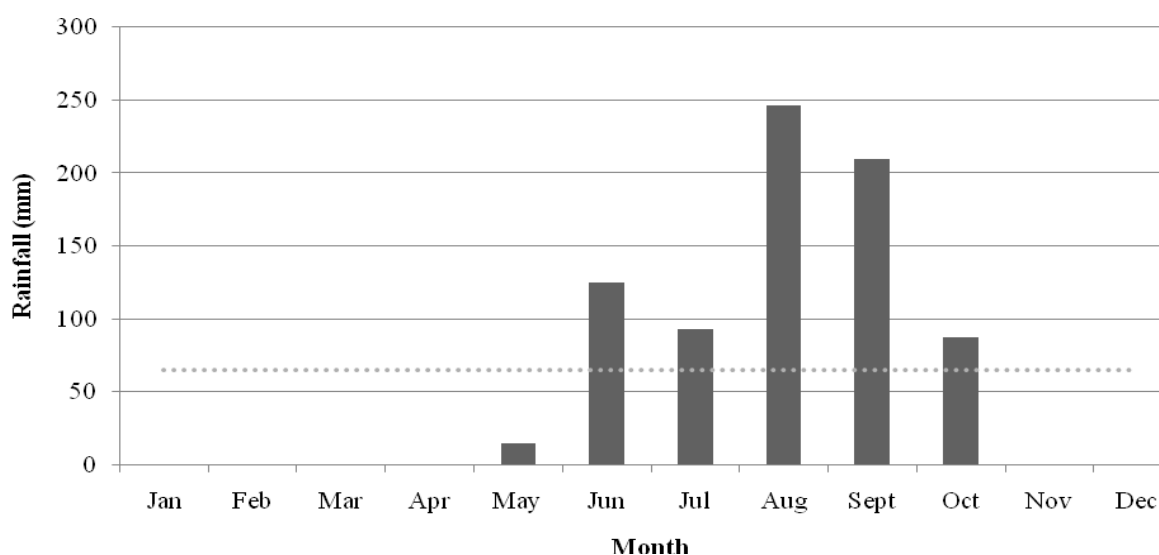


Figure 4.5: Rainfall at Fongoli from August 2006 to July 2007, annual mean represented by dotted line.

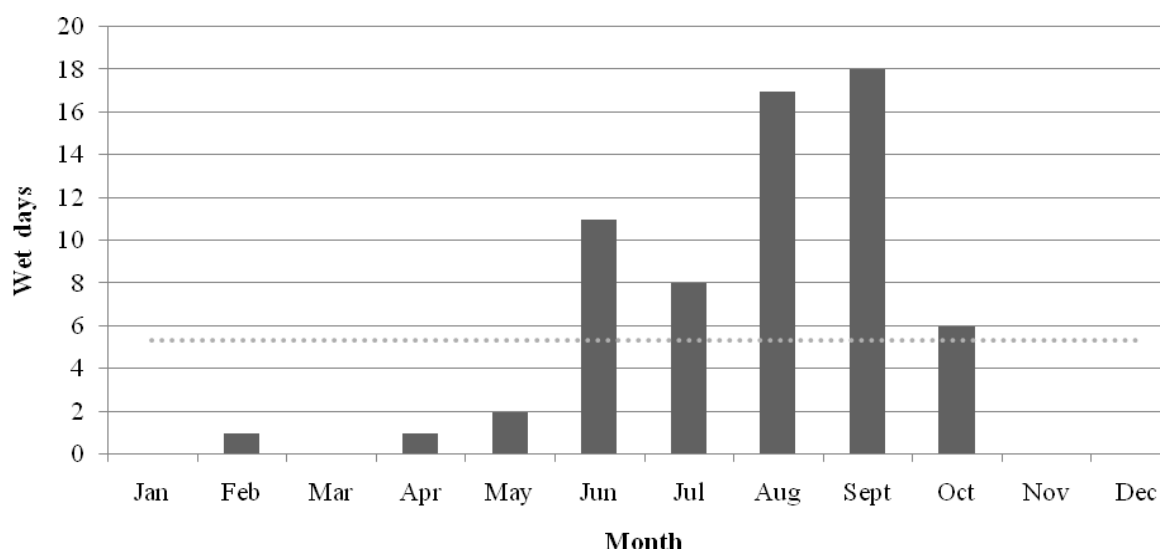


Figure 4.6: Frequency of wet days at Fongoli from August 2006 to July 2007, annual mean represented by dotted line.

4.4.3 Soil

Soil is generally dry at Fongoli (Student's t -ratio = 98.5, df = 1, two-tailed p -value = 0.007). Soil moisture was consistently dry in open and closed habitat types from August 2006 until May 2007. Only in May and June was the soil moist in both habitat types (open: seven of 213 days or 3.3%; closed seven of 209 days or 3.3%).

Soil temperature in closed habitat types averaged 26.5°C (21.5-32°C, SD = 2.2) and 30.8°C (21.9-49.7°C, SD = 7.1) in open habitat types over the year of this study (Student's t -ratio = -2.83, df = 9, two-tailed p -value = 0.02). Monthly averages of the soil temperature are displayed in Figure 4.7. Temperatures did not differ between open and closed habitat types during the months of August through November and in January (Table 4.1). The mean difference between open and closed habitat type soil temperatures between the months of February and June did show variation (Table 4.1), the largest difference reflected in April. April was the last dry season month, had no wet days (Figure 4.6) and was the hottest month,

with recorded temperatures of 32°C in grassland and 33°C in woodland. Soil temperature in open habitat types positively correlates with air temperature in grassland and woodland habitats (Spearman's rank $\rho = 0.80, 0.85, p\text{-value} = 0.005, 0.002$, respectively). However, soil temperature in closed habitats does not correlate to temperatures in either habitat type (Spearman's rank, grassland: $\rho = 0.62, p\text{-value} = 0.05$; woodland: $\rho = 0.59, p\text{-value} = 0.07$).

Table 4.1: Monthly mean soil temperature (°C) in open and closed habitat types and the mean difference from August 2006 to June 2007 at Fongoli, Senegal.

	Open habitat	Closed habitat	Mean difference
August	26.4	26.3	0.1
September	25.8	26.4	-0.6
October	26.6	26	0.6
November	25.5	25.5	0
January	23.3	23.3	0
February	31.2	25.7	5.5
March	37	26.8	10.2
April	42.9	29.9	13
May	41.8	30	11.8
June	37	28.2	8.8

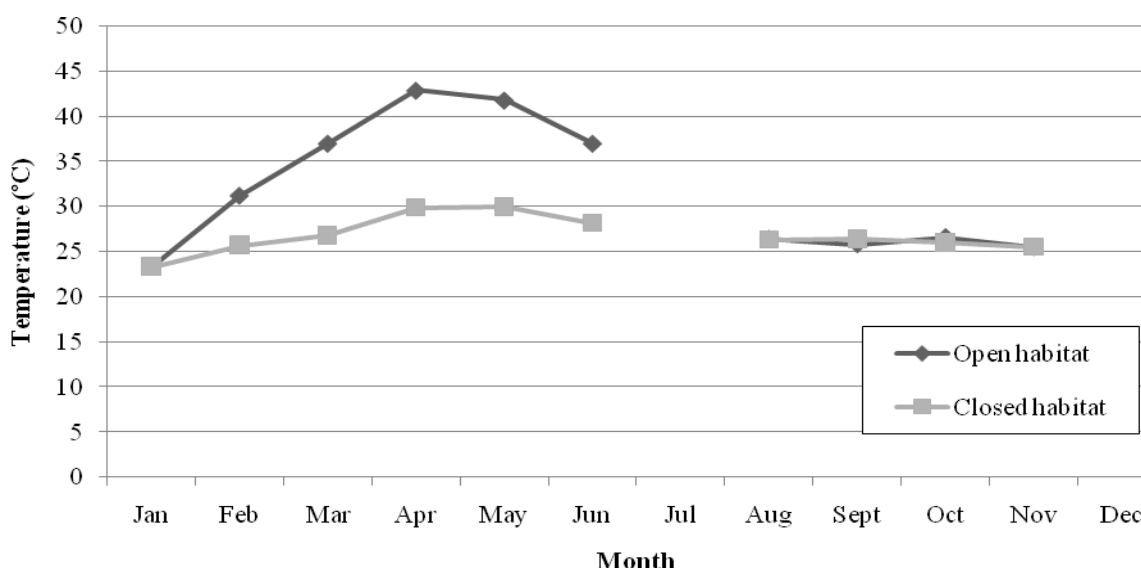


Figure 4.7: Average monthly soil temperature in closed (light grey square line) versus open habitat types (dark grey diamond line) at Fongoli from August 2006 to June 2007.

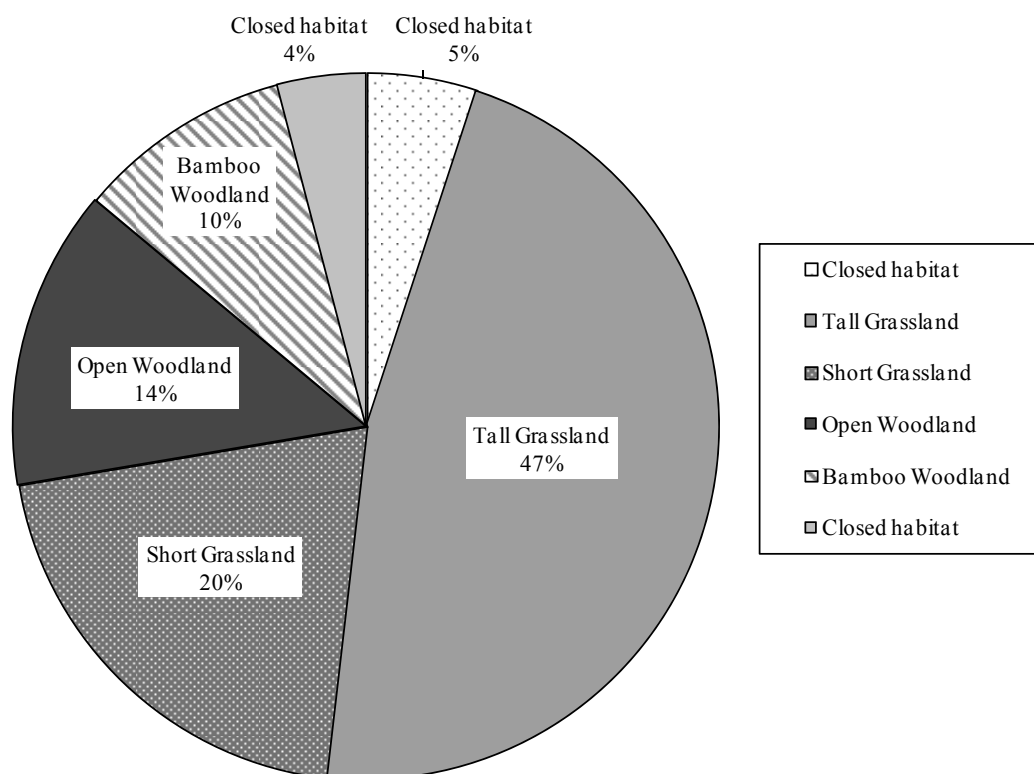


Figure 4.8 : Habitat composition based on transect data at Fongoli, Senegal.

4.4.4 Habitat composition

A total of 47 one-kilometer transects used for habitat type assessment sampled a total of 40,605 m² from 470,000m² (0.47 km²) of transects (Figure 3.3 and Table A4). The majority of the Fongoli chimpanzee home range is composed of tall and short grassland (47% and 20% respectively) (Figure 4.8). Woodland comprises 17% of the home range, and consists of open (14%) and closed (3%) habitats (Figure 4.8). Bamboo woodland composes 10% (Figure 4.8), thus all woodlands comprise a total of 27% of the Fongoli chimpanzees' home range. Human fields and villages comprise 5% of Fongoli's environment (Figure 4.8). The remaining 1% of Fongoli consists of closed habitat types (forest ecotone and gallery forests) (Figure 4.8). Closed habitat types account for only 4% of Fongoli chimpanzees'

range, while open habitat types comprise 91% of its area, with the remaining 5% composed of human disturbance.

4.5 Discussion

The chimpanzee population of Fongoli resides in the driest and hottest site where habituated chimpanzees are studied today (Table 4.2). During this study, the dry season encompassed seven months (November through May) and the wet season five months (June through October). The other savanna chimpanzee sites (Mount Assirik, Senegal and Semliki, Uganda) have a greater average rainfall and more wet days than Fongoli (Table 4.2). February through May at Fongoli contained the highest average temperatures, and April and May, with an average maxima temperature of 42.2°C and 43°C, respectively, were the hottest months. Fongoli has a greater mean maxima temperature than the other savanna sites, as well as any other chimpanzee site (Table 4.2). The only site to have comparable relative humidity measures is Bossou. Fongoli has a wider distribution of humidity as the dry season yields very low humidity when compared to Bossou (Table 4.2). There are drawbacks to comparing site data, such as the non-simultaneous measuring of climatic variables, lack of standardization, and some sites using averages over several years. Also, Mount Assirik is no longer active due to the inability of the Stirling Africa Primate Project to habituate the chimpanzees to human observers. However, a general understanding of each research site's climatic situation is necessary to confirm the conclusion that Fongoli's environment is unlike other chimpanzee sites. Many chimpanzee sites have not reported data on climatic variables, as displayed in Table 4.2. From the data obtained at 13 sites, Fongoli has lower rainfall and higher temperatures than all other sites (Table 4.2).

Table 4.2: Rainfall, temperature, and relative humidity information from chimpanzee sites.

Site	West Africa				Nigeria		Central and East Africa						
	Tai	Bossou	Mt. Assirik	Fongoli	Gashaka-Gumpti	Gombe	Mahale	Semliki	Budongo	Kibale	Kahuzi-Biega	Lope	Goulougo Triangle
Country	Ivory Coast	Guinea	Senegal	Senegal	Nigeria	Tanzania	Tanzania	Uganda	Uganda	Uganda	DRC	Gabon	Republic of Congo
Annual Mean rainfall (mm)	1829	2230	954	777	<2000	1775	1836	1206	1600	1671	1658	1536	1728 ± 47
Range of yearly rainfall	1505-2150		824-1224	--					1240-2187	1561-1859	1409-2180		
Range of monthly rainfall (mm)				0-247		0-272	1-366	34-196					
Mean rainy days per year			84	64		152	141	151	167				
Mean Temperature °C	18			28.3							20.2		
Range of Temperature °C				16-50		16-33			10-35				
Mean maxima temperature °C		26.1	35	36.7	32.2	28	27	34	28	23	26.5		26.5
Mean minima temperature °C		21	23	21.2	23.3	19	19	20	14	16	13.8		21.9
Max Relative Humidity (%)		93		96									
Min Relative Humidity (%)		74		17									

Tai: Boesch & Boesch-Achermann 2000, Hunt & McGrew 2002, Appendix, McGrew et al. 1996; Bossou: Takemoto 2004, Yamakoshi 1998; Mt. Assirik: McGrew 1992, McGrew et al. 1981, McBeath & McGrew 1982, Fongoli: this study; Gashaka-Gumpti: Hohmann et al. 2006; Clutton-Brock & Gillett 1979; Gombe: Collins & McGrew 1988, Hunt & McGrew 2002,; Mahale: Kano 1972; Semliki: Hunt & McGrew 2002; Budongo: Eggeling 1947, Reynolds 2005; Kibale: Ghiglieri 1984; Kahuzi-Biega: Yamagiwa & Basabose 2006; Lope: Tutin et al. 1991; Goulougo: Morgan & Sanz 2006

Data on soil temperature and moisture have not previously been recorded at Fongoli, nor at any other site. Fongoli's soil is consistently dry in both open and closed habitats. However, the soil temperature differed both among habitats and seasons. The end of the dry season and the beginning of the wet season (February to June) demonstrated the highest variation in soil temperatures between open and closed habitats. This coincides with peak air temperatures at Fongoli. Soil in open habitats was positively correlated to air temperature, but soil temperature in closed habitats did not correlate with air temperature and maintained a steady measure. This is one indicator that supports closed habitat types as a relief from the high temperatures in the late dry season. Closed habitat data from air temperature was not taken for an entire year and was not used in this study. Further data will provide the necessary information on air temperature.

The present study employed more vigorous methods for habitat type distribution analysis than previous research at this site. Utilizing the same methods as Pruetz (2006), habitat type structure data were recorded from 47 km of transects as opposed to her 7.5 km. Therefore, this study is a better indicator of the habitat composition at Fongoli and, accordingly, there was a difference in the percentage of woodland. Pruetz (2006) stated that the majority of Fongoli was comprised of woodland (46%) with grassland (tall and short) encompassing 36% of the chimpanzees' range. The present study demonstrates that 67% of Fongoli is comprised of grassland (tall and short) and 27% is woodland (including bamboo woodland). Pruetz (2006) had intersecting transects, with sampled data covering 0.01%, within the 63 km² range of the Fongoli chimpanzees' range. Conversely, this study's transects were randomly placed throughout the chimpanzee home range and never intersected each other; data comprised 0.06% of Fongoli. The contrast in habitat structure demonstrated

between this study and that of Pruetz (2006) is mirrored in findings from Bogart (2005). Using the same methods, I sampled eight transects (0.01%) in previous research (Bogart 2005). Results indicated that open woodland (32%) accounted for the majority of Fongoli chimpanzees' core area, with tall and short grassland each accounting for 24% of the total area sampled (48%), and another 13% was bamboo woodland (Bogart 2005, Bogart & Pruetz 2008). Closed forest encompassed four percent of the site and cultivated fields comprised the last three percent (Bogart 2005, Bogart & Pruetz 2008). The difference in habitat distribution between previous research (Bogart 2005) and the current study is again likely due to the total area surveyed. This study sampled a larger proportion of the home range (Bogart 2005, Pruetz 2006). Chapman and colleagues (1994) suggest that accuracy of data increases and sampling error decreases with a greater proportion sampled within the home range for primates with a large range that cannot be sampled at one hundred percent. The data presented here provides the most detailed description of Fongoli's habitat thus far.

Ideally, data on ecological variables should be taken over several years to account for individual yearly variation on seasonality. For this research, only the data obtained between August 2006 and July 2007 was used in drawing conclusions on rainfall and soil variables. Twenty months of data were used to calculate an average air temperature. Air temperature from closed forests did not provide a full year of data and were not used in this study to compare with grassland and woodland habitat temperatures. Only eight months (February through September) of data were used in the analyses of relative humidity. Mechanical problems with data loggers made obtaining the temperature and relative humidity during the time of this study difficult. Rainfall and temperature did not correlate (Spearman's rank correlation $s_p = -0.17$, $p\text{-value} = 0.60$). Rainfall was high only five months out of the year,

and though temperatures were higher in the dry season, temperatures actually rose in the late dry season. Therefore, these variables will not be considered as correlated and will be examined as separate variables and considered in terms of how they might influence behaviors. Data discussed in this chapter will be used in relation to data found on food availability and chimpanzee behavior in the following chapters.

CHAPTER FIVE

Foods available to the Fongoli chimpanzees

5.1 Introduction

Understanding the availability of food resources for the Fongoli chimpanzees informs our understanding of their feeding behavior in this hot, dry and open environment. I examined the availability of food resources to the Fongoli chimpanzees here to contextualize the influence of ecology on the diet of the chimpanzees discussed in subsequent chapters (Chapters Six, Seven, and Eight). Fongoli's food resource availability was also compared to other chimpanzee sites, in relation to chimpanzee behavior across populations (Chapter Eight). Several methods were employed in this study in order to measure availability for as many foods in the chimpanzee diet as possible. Strip transects, quadrat plots, transects, and point-centered quarter plots assessed the availability of chimpanzee foods at Fongoli.

In this chapter I investigate the parameters affecting food resources available to the chimpanzees as they relate to hypotheses outlined in Chapter One. Hypotheses tested include those related to the prediction that seasonality will affect the availability of foods. It was hypothesized that there will be few fruits available during the wet season at Fongoli based on previous research (Pruetz 2006). I also predicted that fruit resources would be associated with certain habitat types, particularly woodland.

5.2 Methods

To assess the proportion of plants producing food resources, a two kilometer transect was monitored twice a month for fruiting, flowering, and leafing feeding trees, shrubs, and climbers (herbaceous vines and lianas). For fruiting resources a score was given (0-3)

following Takemoto (2004). The months of August 2006, April 2007, and July 2007 were surveyed only once. August 2006, the first month of the study, was devoted to training research assistants, and the transect was not surveyed in the initial weeks. In April 2007, the chimpanzees were positioned next to the feeding transect for the first two weeks of the month, so the transect was not surveyed until the end of the month. Lastly, the study period ended before phenological data was collected a second time in July of 2007. The transect was surveyed a total of 21 times and included 205 feeding trees, shrubs, and climbers of 33 species (Table 5.1 and Table A5). The basal area of all feeding plants was calculated from the diameter at breast height (DBH), using the equation $\pi((DBH / 2)^2)$. Typically in most studies, a minimum of 10cm DBH is used (Basabose 2002, Pruetz 2006, Tutin et al. 1997, Takemoto 2004); however climbers and vines often do not grow this large at Fongoli. For particular feeding resources, i.e. *Saba* (one of the most important foods at Fongoli), a minimum DBH of 5cm was used. For large trees, such as *Adansonia digitata* (baobab), basal area is also used in conjunction with the scoring system. The number of fruiting resources per month was used to calculate the fruit availability index (FAI). The formula used for calculating monthly fruit availability index is

$$FAI = [\sum(P_i \times F_i) / \sum(P_i \times 3)] \times 100$$

Where P the basal area of fruiting trees, shrubs, and climbers of species i , and F is the fruit score of species i (Takemoto 2004, adapted from Chapman et al. 1994). Fruit availability is examined in relation to rainfall to explore possible seasonal effects, and this information will be discussed in later chapters. Some feeding plant species were only represented by one tree, shrub, or climber. The data collected from these trees is still used in analyses with the use of the scoring system to give an indicator of its availability, but samples should be considered as

underrepresented. Some important plant food resources were not represented on the feeding transect. These species were marked and recorded for fruiting, flowering, or leafing as well as habitat type and GPS location when consumed by the chimpanzees (see Table 5.3).

Table 5.1: Plant taxonomy, number of trees, average basal area (BA), and basal area per hectare for each feeding tree, shrub, and climber species compiled from permanent transect.

Genus and Species	Plant Family	Malinke name [common name]	Number of trees	Average BA	SD	BA / ha
<i>Adansonia digitata</i>	Bombacaceae	Sita [baobab]	1	11308.32	--	5654.16
<i>Baissea multiflora</i>	Apocynaceae	Banombo	2	39.30	15.5	39.30
<i>Bombax costatum</i>	Sapindaceae	Bunkungo	6	1074.03	990	3222.09
<i>Cola cordifolia</i>	Bombacaceae	Taba	10	5434.20	3798	27170.99
<i>Cordyla pinnata</i>	Sterculiaceae	Dougouta	6	424.60	320	1273.80
<i>Daniellia oliviera</i>	Papilionaceae	Santango	11	412.35	235	2267.95
<i>Diospyros mespiliformis</i>	Ebenaceae	Kukua	7	259.15	125	907.02
<i>Ficus ingens</i>	Ebenaceae	Sekho	1	11308.32	--	5654.16
<i>Gardenia erubescens</i>	Moraceae	Tankango	1	7.07	--	3.53
<i>Grewia lasiodiscus</i>	Rubiaceae	Sambe	1	28.27	--	14.14
<i>Hannoa undulata</i>	Tiliaceae	Kehko	1	706.77	--	353.39
<i>Hexalobus monopetalus</i>	Simaroubaceae	Gundje	19	151.11	51.8	1435.53
<i>Lannea acida</i>	Annonaceae	Bintinkilingo	16	264.50	96.4	2115.99
<i>Lannea microcarpa</i>	Anacardiaceae	Fekho	3	349.50	167	657.30
<i>Lannea velutina</i>	Anacardiaceae	Bembenyanya	6	162.40	59.9	487.30
<i>Oncoba spinosa</i>	Anacardiaceae	Kondongo	1	63.61	--	31.80
<i>Parkia biglobosa</i>	Flacourtiaceae	Nete	3	1633.90	2410	2450.92
<i>Piliostigma thonningii</i>	Mimosaceae	Fara	23	242.69	136	2790.96
<i>Pterocarpus erinaceus</i>	Cesalpiniaceae	Keno	58	364.20	332	10561.89
<i>Saba senegalensis</i>	Papilionaceae	Kaba	8	28.80	19	115.05
<i>Sclerocarya birrea</i>	Apocynaceae	Kenteno	1	254.44	--	127.22
<i>Spondias mombin</i>	Anacardiaceae	Minkon	1	490.81	--	245.41
<i>Sterculia setigera</i>	Anacardiaceae	Kunkusita	1	1017.75	--	508.87
<i>Tamarindus indica</i>	Sterculiaceae	Tumbingo	1	314.12	--	157.06
<i>Vitellaria paradoxa</i>	Cesalpiniaceae	Se	5	398.15	142	995.37
<i>Vitex madiensis</i>	Sapotaceae	Kutufingo	3	57.07	41.6	85.60
		Kilindingo	1	95.02	--	47.51
		Kururu	2	170.00	80.5	170.02
		Mansarinkeno	2	215.56	55	215.56
		Sunkungo	1	19.63	--	9.82
		Wonko	1	415.42	--	207.71
		Jarango	1	1017.75	--	508.87
		Nyarikoyo	1	490.81	--	245.41

Chimpanzee food resources were found in all habitat types. Assessing relative density provides an indicator of plant food resource abundance at Fongoli. To determine feeding plant resource density, point-centered quarter plots (described in Chapter Three) were used via a stratified random sampling method in the different habitat types at Fongoli (Binford 1964, Cottam & Curtis 1956). The relative densities of feeding plants were analyzed according to the availability of habitat type (Chapter Four).

Food resources used by chimpanzees were marked using a Global Positioning System (GPS: Magellan) and flagged for identification during future visits by the chimpanzees. Chimpanzees had to have fed from the tree for more than 10 minutes for the tree to be marked. This subsample was used in conjunction with transect information in Chapter Four and to find habitat type associations with various food species. Various characteristics were recorded when chimpanzees used a feeding tree, shrub, or climber. Plant food resources consumed by Fongoli chimpanzees were recorded as to habitat type and the species and parts eaten.

Water content for most food resources was measured by drying the samples (53 samples of 37 food categories, i.e. ripe fruit, unripe fruit, flower, of 28 species). To determine grams of water for each food resource, the end weight was divided by quantity of units (i.e. fruits, leaves, flowers, or insects). An attempt was made to sample all plant food species at times they were consumed by the chimpanzees. For instance, the chimpanzees eat baobab (*Adansonia digitata*) flowers as well as fruit when it is unripe and ripe. Samples of all of these stages were collected and measured. This measure was compared in relation to rate of intake and is discussed in Chapters Six and Seven.

Insect density was calculated with the use of transects as described in Chapter Three. A total of 25,600m² were sampled for *Macrotermes* species nest density and ant (*Dorylus burmeisteri* and *Pachycondyla analis*) nest density. Army ants (*D. burmeisteri*) are seasonal and more difficult to obtain via a direct count. Therefore, fourteen 500 x 500m² plots were systematically sampled. Plots were randomly sampled in both closed and open habitat types.

Bushbaby (*Galago senegalensis*) availability was measured by surveying a 2 km long strip-transect once a month at night. The reflective tapetum of the bushbabies is illuminated with the use of a flashlight, a conspicuous cue for observation. Pairs of eyes were counted when observed within 20 m of each side of the transect. Diurnal animals of relatively large body-size were recorded every time they were encountered. Animals excluded were birds, rodents, and small amphibians and reptiles.

5.3 Results

5.3.1 Feeding trees, shrubs, and climbers

Of the 33 plant species monitored along the permanent feeding transect, 22 fruited during this study (Table 5.2). All but one of the species that fruited within the year of this study are known to be consumed by the chimpanzees at Fongoli (Table 5.2). On average, 6.17 (SD = 1.03) feeding species produce fruit each month (range 4-8). The average number of plants fruiting (out of the 205 plant resources monitored) monthly was 14.5 (range 7-28, SD = 5.8). The proportion of fruiting trees, shrubs, and climbers each month are displayed in Figure 5.1. More fruiting resources were found during the dry season (65%, November through May) than during the wet season (35%). The 203 transect plant resources that fruited were examined in relation to season (i.e. number of wet months fruited/wet months), and no

significant difference was found between season and fruiting plants (Student's t -ratio = 1.68, $df = 202$, p -value = 0.10). There was also no significance among the species that fruited and the season (Student's t -ratio = -1.45, $df = 21$, p -value = 0.16). No correlation exists between rainfall and the number of individual fruiting plants (Spearman's rank correlation $\rho = -0.03$, p -value = 0.92). Fruiting is therefore not seasonal, but there is a trend for greater fruit abundance when rainfall is low, from November through May (Figure 5.1). The number of individual fruiting trees on the transect were not correlated with the average temperature at Fongoli (Spearman's rank $\rho = 0.32$, p -value = 0.31). The foods that were represented in over 50% of fecal samples by Pruetz (2006) (see Chapter Two, Table 5.2), fruited throughout the year. *Saba* and baobab fruits are the most important fruits at Fongoli and, unlike many other fruits here, consumed by the chimpanzees even when they are unripe (Pruetz 2006, this study, Chapter Six). Monthly ripeness of fruit species is displayed in Table A6. Foods categorized important by Pruetz (2006) did not fruit on the transect during this study: *Ficus* and *Spondias mombin*.

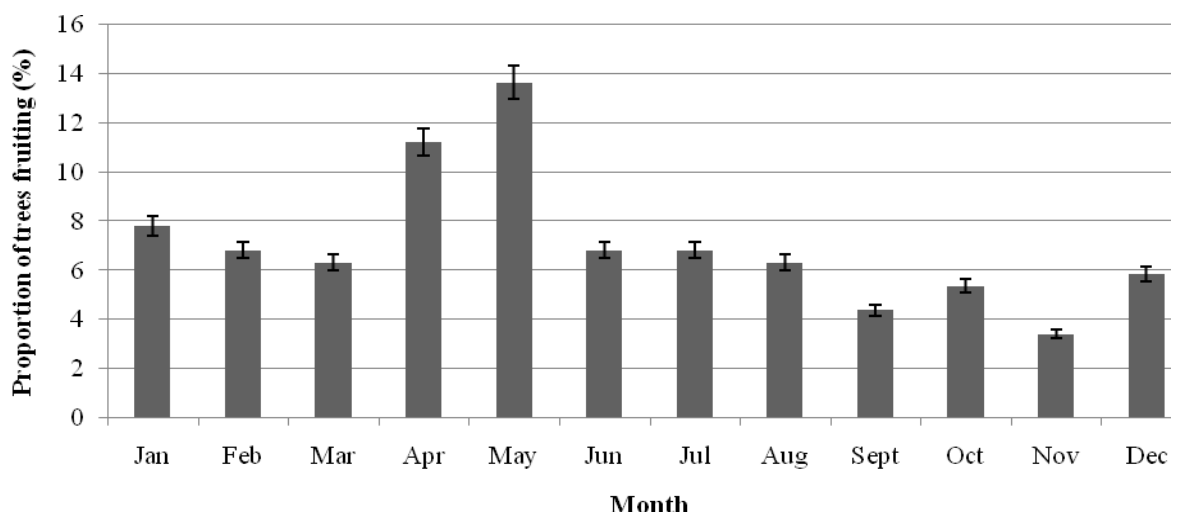


Figure 5.1: Monthly proportion of feeding trees, shrubs, and climbers in fruit on the transect between August 2006 and July 2007 at Fongoli.

Table 5.2: Monthly fruiting of plant species along the permanent transect from August 2006 through July 2007.

	Aug	Sept	Oct	Nov	Dec	Jan	Feb	Mar	Apr	May	Jun	Jul	Eaten
<i>Adansonia digitata</i> ^*			X	X	X	X	X	X	X	X			X
<i>Baissea multiflora</i>					X								
<i>Bombax costatum</i>								X					X
<i>Cola cordifolia</i>									X	X	X	X	X
<i>Cordyla pinnata</i>									X	X	X	X	X
<i>Daniellia oliviera</i>							X						X
<i>Diospyros mespiliformis</i>	X	X	X	X	X						X		X
<i>Gardenia erubescens</i>								X					X
<i>Grewia lasiodiscus</i>		X			X								X
<i>Hexalobus monopetalus</i> ^	X	X											X
<i>Lannea acida</i> ^								X	X	X			X
<i>Lannea velutina</i> ^											X	X	X
<i>Oncoba spinosa</i>	X	X		X	X	X							X
<i>Piliostigma thonningii</i> *					X	X	X		X	X			X
<i>Pterocarpus erinaceus</i>									X				X
<i>Saba senegalensis</i> ^*	X		X	X	X	X	X	X	X	X	X	X	X
<i>Sterculia setigera</i>	X	X	X	X	X	X	X						X
<i>Vitex madiensis</i>	X	X	X										X
Unknown sp 1 (tree)						X	X	X					?
Unknown sp 2						X	X						?
Unknown sp 3											X		?
Unknown sp 4 (tree)				X									?
Total species fruiting	6	6	5	6	8	7	7	6	7	6	6	4	

^ comprise >50% of fecal samples in Pruetz 2006

* highest ranked foods by this study (Chapter Six)

Data for feeding trees, shrubs, and climbers underrepresented on the transect were obtained using plant resources marked when chimpanzees were observed feeding on them (Table 5.3). A total of 116 trees from 26 species were only sampled when the chimpanzees were observed to feed from them for more than 10 minutes, some trees were revisited (N=132). Fourteen of the food species recorded were not represented on the transect. This added 33 fruiting plant resources to the list. With this added data, the average number of fruiting species per month is nine (range 5-14, SD=2.8, N=36), with an average of 17.3 (range 12-28, SD=5.03, N=207) plants fruiting each month (Figure 5.2). This data did not change the proportion of fruiting trees during the seasons (dry=63%, wet=37%). There was no correlation between rainfall and total number of individual fruiting feeding trees (Spearman's rank correlation $\rho = 0.17$, p -value = 0.60). Also, number of individual fruiting trees did not correlate with Fongoli's average temperature (Spearman's rank $\rho = -0.17$, p -value = 0.60).

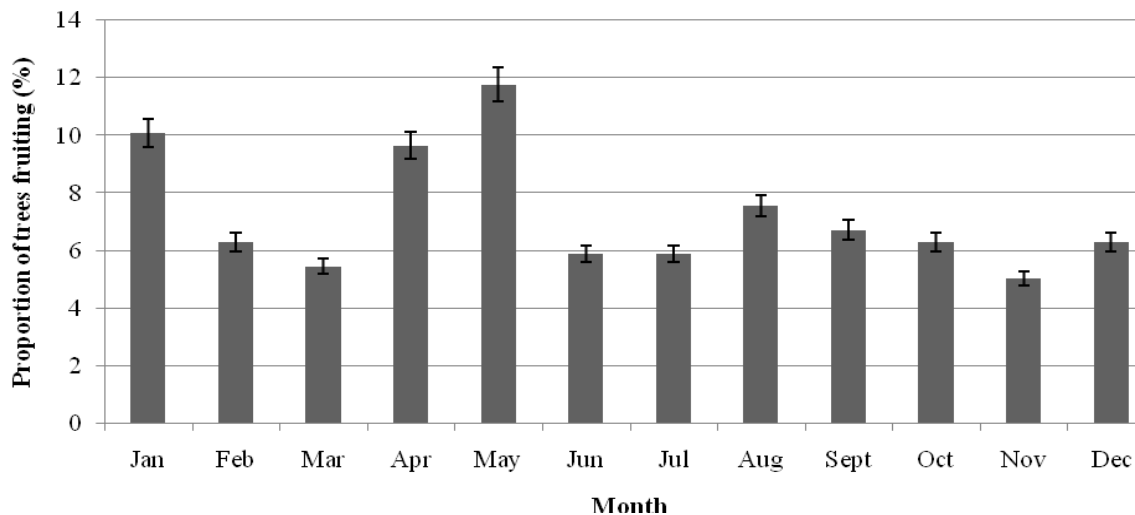


Figure 5.2: Monthly proportion of fruiting resources at Fongoli (Total) from August 2006 to July 2007.

Table 5.3: Observed chimpanzee plant feeding resources from August 2006 to July 2007.

	Number of trees	Number of records	Part eaten	Aug	Sep	Oct	Nov	Dec	Jan	Feb	Mar	Apr
<i>Adansonia digitata</i> ^*	22	24	f, l	+ X u		X u	X u, r	X r	X r	X r	X r	X r
<i>Azelia africana</i> *	9	11	f		X	X	X		X	X		
<i>Basia multiflora</i>	2	2	l	+		+						
<i>Bombax costatum</i>	7	7	f, fl						O	X	X	
<i>Ceiba pentandra</i>	1	7	f, fl					O	X			
<i>Cola cordifolia</i>	11	11	f									X
<i>Diospyros mespiliformis</i>	2	2	f						X	X		
<i>Ficus sur</i> ^*	2	2	f	X			X					
<i>Ficus abutilifolia</i> ^*	1	1	f				X					
<i>Ficus ingens</i> ^*	1	1	f						X			
<i>Ficus sycomorus</i> ^*	4	4	f				X u	X r				
<i>Ficus umbellate</i> ^*	6	8	f	X	X			X	X			
<i>Gardenia erubescens</i>	1	1	f							X		
<i>Hannoa undulata</i>	1	1	f							X		
<i>Hexalobus monopetalus</i> ^	1	1	f	X								
<i>Landolphia heudelotti</i>	1	1	f								X	
<i>Lannea acida</i> ^	5	5	f									X
<i>Lannea microcarpa</i> ^	1	1	f									X
<i>Parkia biglobosa</i>	1	1	f									X
<i>Piliostigma thonningii</i> *	7	7	f								X	X
<i>Pterocarpus erinaceus</i>	7	7	l, fl, b		+ B				O		+	+
<i>Saba senegalensis</i> ^*	8	8	f							X	X	X
<i>Spondias mombin</i>	7	11	f	X	X	X						
<i>Strychnos spinosa</i>	1	1	f						X			
<i>Tamarindus indica</i>	6	6	f					X	X			
<i>Zizyphus mauritania</i>	1	1	f							X		
	116	132										

Part eaten: f- fruit, l- leaf, fl- flower, b- bark

X = fruiting (u-unripe, r-ripe), O = flower, + = leaf, B = bark. (no data for May-July)

^ comprise >50% of fecal samples in Pruett 2006

* highest ranked foods by this study (Chapter Six)

Using the fruiting score of food resources available each month on the permanent transect, an index of fruit availability is obtained (FAI following Takemoto 2004). The availability of baobab, *Saba*, and *Sterculia* is greatest, while *Daniellia* and *Gardenia erubescens* were relatively rare (Figure 5.3). The monthly average fruit availability for all fruiting species, obtained from averaging FAI across species, is displayed in Figure 5.4. Average fruit availability was greatest from November through May, which is the dry season in Senegal. During the dry season, 74% of all fruits were available to the Fongoli chimpanzees.

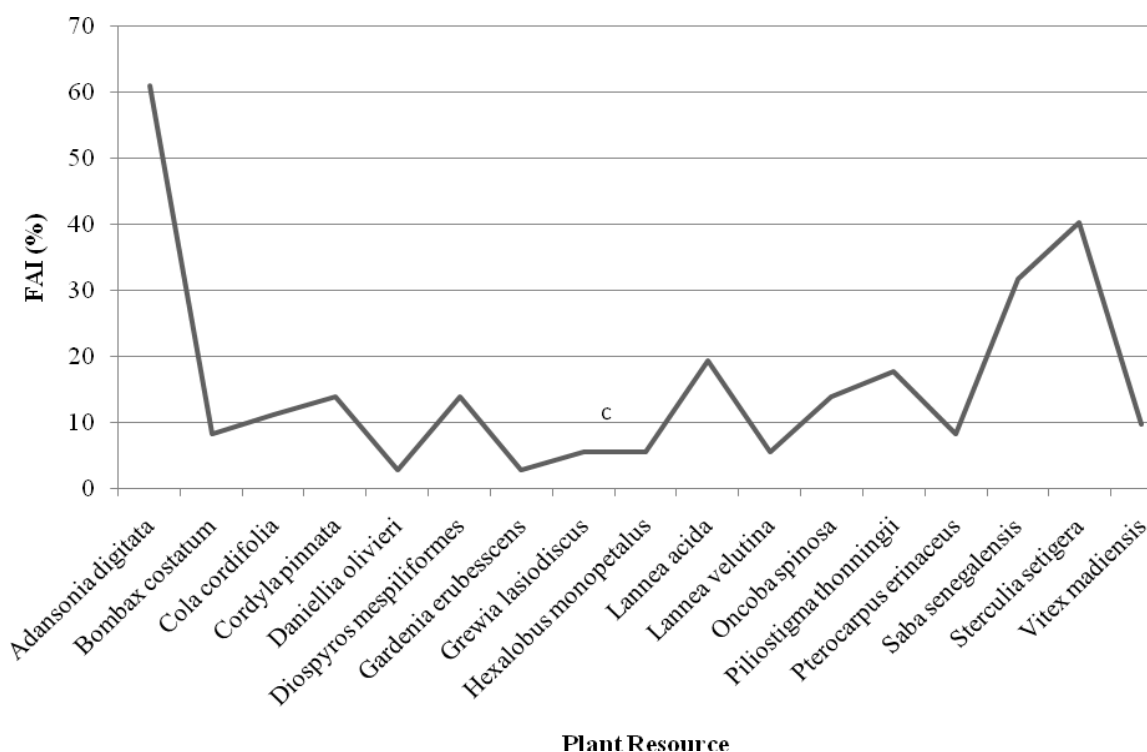


Figure 5.3: Fruit availability index (FAI) for each of the known fruiting species on the transect at Fongoli from August 2006 to July 2007.

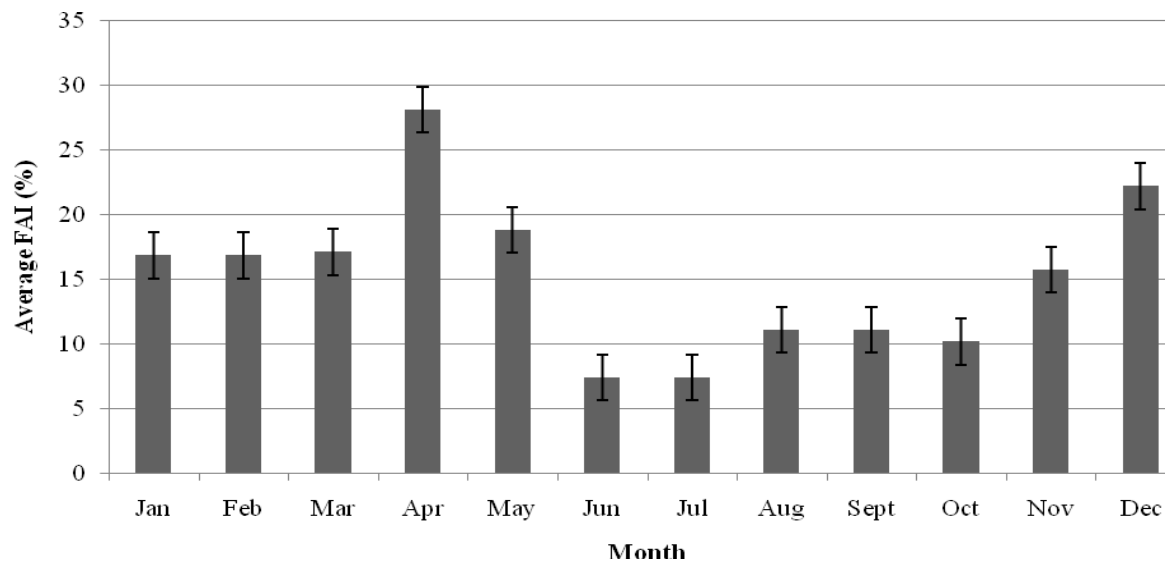


Figure 5.4: Monthly average of fruit availability index for all analyzed species from August 2006 to July 2007.

Fruit availability was lower in the wet season (Figure 5.5). A relationship exists between availability of fruit and monthly rainfall. The average monthly fruit availability index for all species combined was negatively correlated with rainfall (Spearman's $\rho = -0.65$, p -value = 0.02). Four species of fruit that were considered in the top ranked foods by Pruettz (2006) or this study and were measured along the feeding transect were examined in relation to rainfall. Baobab had a strong negative correlation with rainfall (Spearman's rank correlation $\rho = -0.89$, p -value < 0.0001), fruiting more in the dry months (Figure 5.5). There was also a negative correlation between rainfall and *Piliostigma thonningii* (Spearman's rank correlation $\rho = -0.38$, p -value = 0.23) and *Saba* and rainfall (Spearman's rank correlation $\rho = -0.50$, p -value = 0.09), but neither were significant. The only fruit production positively correlated with the wet season is *Hexalobus monopetalus* (Spearman's rank correlation $\rho = 0.66$, p -value = 0.02). Associations can be seen in Figure 5.5. Fruit availability of all foods analyzed was not correlated with average temperatures at Fongoli. (Spearman's rank $\rho =$

0.37, p -value = 0.23). Five of the species analyzed were among the top ten fruit species in the diet (Chapter Six): *Adansonia digitata*, *Bombax costatum*, *Gardenia erubescens*, *Piliostigma thonningii*, *Saba senegalensis*. The average fruit availability of these five fruits combined positively correlated the average temperature (Spearman's rank ρ = 0.63, p -value = 0.03).

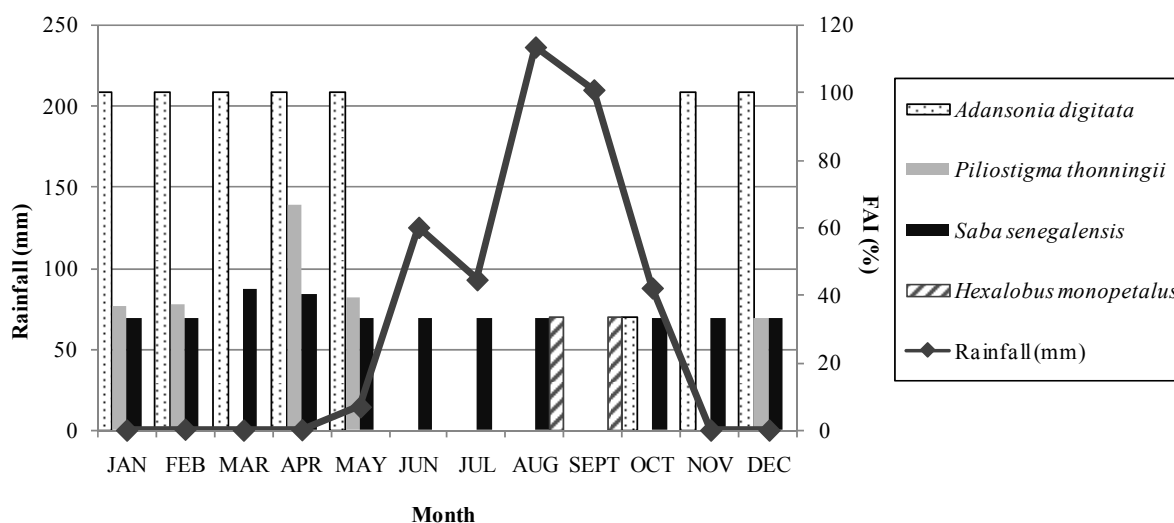


Figure 5.5: Monthly rainfall and fruit availability index for four fruit species from August 2006 to July 2007.

A total of 23 (including four unidentified) species flowered during the time of this study. Of those species that flowered, six (26%) are known as food resources for the chimpanzees (this study, Pruetz 2006). On average, 18 plants flowered (3-36, SD = 12.8) from all 23 species. A monthly average of 1.4 (range 0-4, SD=1.2) consumed plant species flowered during this study (Table 5.4). Number of individual flowering plants did not correlate with rainfall (Spearman's rank correlation ρ = -0.15, p -value = 0.63). However, number of individual flowering plants is positively correlated with grassland and woodland temperatures (Spearman's rank correlation ρ = 0.86, 0.74, p -value = 0.0003, 0.007).

Table 5.4: Monthly numbers of individual flowering plants for each species known to be consumed by chimpanzees at Fongoli.

	Aug	Sept	Oct	Nov	Dec	Jan	Feb	Mar	Apr	May	Jun	Jul
<i>Adansonia digitata</i>	1	1	0	0	0	0	0	0	0	0	1	0
<i>Bombax costatum</i>	0	0	0	0	2	9	3	0	0	0	0	0
<i>Ceiba pentandra</i>	0	0	0	0	1	0	0	0	0	0	0	0
<i>Daniellia oliviera</i>	0	0	0	0	0	4	3	0	0	0	0	0
<i>Parkia biglobosa</i>	0	0	0	0	0	0	1	1	0	0	0	0
<i>Pterocarpus erinaceus</i>	0	0	0	0	0	4	3	3	1	1	1	0
Total	1	1	0	0	3	17	10	4	1	1	2	0

All 33 species of plants along the transect contained leaves at some point during the year. The proportion of the 205 trees along the permanent transect that contained leaves is displayed in Figure 5.6 (dark bars). In examining the number of months each species contained leaves in each season, there is significantly less resources that contained leaves in the dry season (Student's *t*-test, *t*-ratio = 2.72, *df* = 32, two-tailed *p*-value = 0.01). Number of leafing resources of all species did not correlate with temperature (Spearman's rank correlation $\rho = -0.45$, *p*-value = 0.14), or rainfall (Spearman's rank correlation $\rho = 0.38$, *p*-value = 0.23). Of the 33 species, six (18%) are known to be consumed by the Fongoli chimpanzees: *Baissea multiflora*, *Bombax costatum*, *Diospyros mespiliformis*, *Ficus ingens*, *Hexalobus monopetalus*, and *Pterocarpus erinaceus*. The proportion of the plants with leaves is represented in Figure 5.6 by the light bars. There was no significant difference between leafing resources during months in the dry season and those in the wet season (Student's *t*-test, *t*-ratio = 0.05, *df* = 5, two-tailed *p*-value = 0.96). However, illustrated in Figure 5.6 there is a dip in the proportion of leafing resources during the hottest months from February to March. There is a negative correlation between number of trees of consumed leaf species to temperature (Spearman's rank correlation $\rho = -0.58$, *p*-value = 0.04), but not to rainfall

(Spearman's rank correlation $\rho = 0.27$, p -value = 0.39). Therefore, as temperatures increase leaves that the chimpanzees consume become scarce.

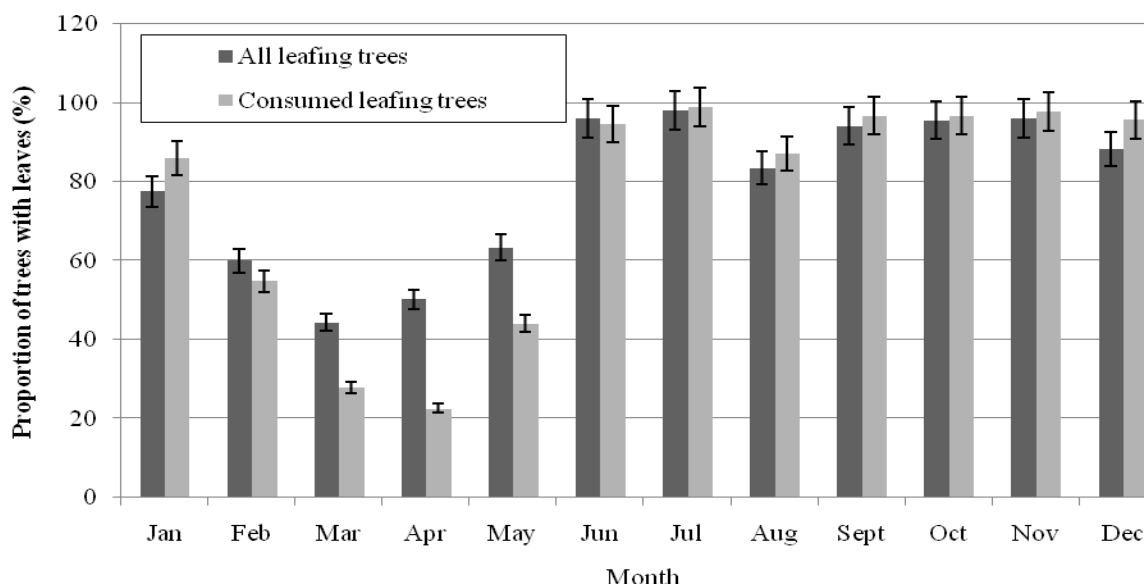


Figure 5.6: Monthly proportion of leafing trees from August 2006 to July 2007 at Fongoli.

The densities of feeding plants per hectare among the different types of habitat at Fongoli are displayed in Table 5.5. A total of 120 (48 in wet and 72 in dry season) food PCQ plots were used to estimate feeding tree density. Stratified random sampling was done based on the proportion of each habitat type in the Fongoli chimpanzees' range. Therefore, individual habitat type samples were small and not sufficient to result in the small standard error of <4.65% with 50 points indicated by Cottam and Curtis (1956). Fongoli is characterized by an estimated density of 30 feeding trees per hectare (Table 5.5). The density of feeding plants was greater in gallery forest (closed habitat) and in woodland than all other habitat types (Table 5.5). Using the proportion of habitat estimated from transect sampling (Chapter Four), the area each habitat constitutes was calculated for Fongoli's 63 km² and listed in Table 5.5. The total number of feeding plants at Fongoli in each habitat was then

calculated (Table 5.5). The density of feeding trees was greatest in gallery forest. However, since this habitat type only comprises approximately 0.76 ha at Fongoli, there were fewer gallery forest feeding resources than any other habitat type excluding field (Table 5.5). The greatest numbers of feeding resources were in woodland and grassland habitats (Table 5.5).

Table 5.5: Results of PCQ plots to sample feeding trees at Fongoli in relation to habitat composition (Chapter 4) to find total number of plant resources in each habitat.

	Mean distance (m) ¹	Sample size (PCQ plots)	Trees per ha	Fongoli's area (ha) ³	Total number of feeding trees
Field	62.9	4	2.5	2.65	6.62
Short Grassland	22.8	39	19.2	12.92	247.97
Bamboo woodland	19.7	11	25.8	6.24	160.91
Tall Grassland	14.8	44	45.7	29.48	1347.42
Woodland	8.4	18	141.7	10.5	1482.2
Closed Forest	8.15	4	150.6	0.756	113.85
Entire range total	18.29	120 ²	29.9	6300	188370

¹distance between stems >10cm DBH (vines >5cm), ²Total sample size (N), ³the composition of habitat obtained in Chapter 4 multiplied by Fongoli's total area (6300ha)

Subjects consumed plant foods from 26 different species, on 116 different plants (Table 5.2). Trees were sometimes visited more than once, providing a total of 132 samples. This is only a sub-sample of feeding resources used by chimpanzees, used to supplement transect data and identify habitat types where these feeding species are found. A total of 57% of plant food resources (N=75) were found in open woodland habitat (bamboo woodland included) (Figure 5.7). Twenty-nine percent of plant foods (N=39) were found in tall grassland, while 14% (N=18) were in closed habitat (Figure 5.7). Regarding major feeding species, *Adansonia digitata* (baobab) was most often found in woodland (50%, N=12/24) and in grassland (42%, N=10/24) habitats. Approximately 82% of *Cola cordifolia* (N=9/11) was found in gallery forest. Woodland habitat contained 75% (N=6/8) of *Saba senegalensis*

records and 100% (N=11) of *Spondias mombin*. In grassland habitat types, baobab (26%, N=10) and *Ceiba pentandra* (18%, N=7) plants were the most frequent food resources.

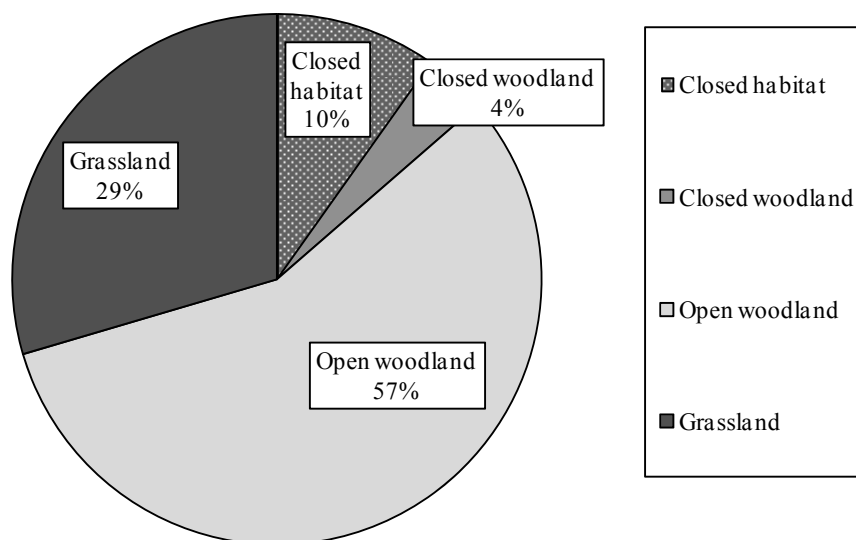


Figure 5.7: Observed plant resource distribution from chimpanzee behavioral data among habitat types at Fongoli.

Water content of various food resources, listed in Table 5.6, will be used in relation to rate of food intake in Chapters Six and Seven to estimate the amount of water an individual might get from a particular food resource. Fruits are examined with seeds in tact within the pulp of the fruit. Unit is defined as one fruit, one leaf, one termite, one flower, or one stem for pith (Table 5.6). Unripe baobab fruit contained the most grams per unit of water; however ripe fruit dried out to only 12.03 grams per unit, a difference of 136 grams. This difference is greater than all other fruit analyzed between unripe and ripe fruit. There was little difference between ripe and unripe *Saba* (Table 5.6). *Cola cordifolia* decreased in water content by almost half from unripe to ripe fruit. A final note is that *Piliostigma thonningii* also dropped over half of its water content from ripe to unripe fruit. Some foods were difficult to count, and number of sampled units was unknown (Table 5.6)

Table 5.6: Grams of water per unit for various food resources at Fongoli.

Food Organism	Part	Number of parts weighed	Grams per unit
Plant species			
<i>Adansonia digitata</i>	Unripe Fruit	4	150.55
<i>Adansonia digitata</i>	Ripe Fruit	6	12.03
<i>Allophylus africanus</i>	Fruit	250	0.135
<i>Bombax costatum</i>	Flowers	10	4.39
<i>Bombax costatum</i>	Leaves	40	0.372
<i>Ceiba pentandra</i>	Fruit	7	53.5
<i>Cola cordifolia</i>	Unripe Fruit	2	41.63
<i>Cola cordifolia</i>	Ripe Fruit	4	27.84
<i>Cordyla pinnata</i>	Fruit	9	18.87
<i>Diospyros mespiliformis</i>	Fruit	25	3.5
<i>Ficus ingens</i>	Fruit	133	0.8215
<i>Ficus sur</i>	Fruit	29	7.04
<i>Ficus sycomorus</i>	Fruit	15	9.31
<i>Ficus umbellata</i>	Fruit	18	0.692
<i>Gardenia erubescens</i>	Fruit	13	5.95
<i>Grewia lasiodiscus</i>	Fruit	20	0.144
<i>Hannoa undulata</i>	Fruit	5	0.748
<i>Hexalobus monopetalus</i>	Fruit	9	5.38
<i>Landolphia heudelotti</i>	Unripe Fruit	11	9.96
<i>Lannea acida</i>	Fruit	82	0.279
<i>Lannea microcarpa</i>	Fruit	139	0.241
<i>Oncoba spinosa</i>	Fruit	8	9.49
<i>Piliostigma thonningii</i>	Ripe Fruit	2	17.03
<i>Piliostigma thonningii</i>	Unripe Fruit	7	6.3
<i>Pterocarpus erinaceus</i>	Flowers	Not per unit	14.04
<i>Pterocarpus erinaceus</i>	Leaves	188	0.194
<i>Saba senegalensis</i>	Ripe Fruit	1	73.37
<i>Saba senegalensis</i>	Unripe Fruit	9	59.72
<i>Saba senegalensis</i>	Pith	10	0.431
<i>Sclerocarya birrea</i>	Fruit	6	8.79
<i>Spondias mombin</i>	Fruit	8	5.02
<i>Strychnos spinosa</i>	Fruit	5	29.35
<i>Tamarindus indica</i>	Fruit	12	10.28
<i>Vitex madiensis</i>	Fruit	36	1.96
<i>Zizyphus mauritania</i>	Fruit	70	0.097
<i>Zizyphus mucronata</i>	Fruit	28	0.186
Animal species			
<i>Pachycodyla analis</i>	Ants	Not per unit	0.25
<i>Dorylus (Anomma) burmeisteri</i>	Ants	Not per unit	0.24
<i>Macrotermes</i> sp.	Termites	328	0.03

5.3.2 Insects

Ten strip transects (Sutherland 2000, Greenwood & Robinson 2006) of 40 x 8m² were used to count insect nests along each of the 16 insect/habitat transects (7 in wet season, 9 in dry season) at each 100 meter interval as explained in detail in Chapter Three (Figure 3.4). Termite mounds comprised 76% of all encounters along transects, while ant nests comprised 23%. Monthly counts of termite mounds were significantly higher than ant nests (Student's $t = -3.23$, $df = 11$, two-tailed $p = 0.008$), and *Macrotermes* had a nest density of 23.6 per hectare (0.00236/m²). Termite mounds used by chimpanzees were found more often in the dry season than the wet season (Student's $t = -2.09$, $df = 69$, two-tailed $p = 0.04$). Therefore, termite mounds had a higher density during the dry season with 29.5/ha (70% of the termites found) than during the wet season with 16.1/ha (30% of the termites found). Seasonal difference in visibility may have been a factor in the data recorded. Ant nests of either army ants (*Dorylus* spp.) or *P. analis* had a density of seven nests per hectare (0.0007m²). Ant nests were found at proportionally the same density during the wet and dry seasons (50/50%), with a slightly higher density in the wet season at 8.04/ha as opposed to the dry season with 6.25/ha. Presence of ant nests and termite mounds were not statistically correlated with rainfall (Spearman's correlation $\rho = -0.04$, -0.53 , p -value = 0.91, 0.08, respectively).

A total of 3.1 km² were assessed for army ant density (1.34 km² in closed habitats and 1.75 km² in open habitat types). Fourteen plots were assessed throughout the year, eight times in the wet season (1.59 km²) and six times in the dry season (1.5 km²). Army ant nests were found in closed habitats (68%) more often than in open habitats (32%) (N=60). All army ant nests were found in the wet season (100%). There were 0.19 army ant nests per

hectare at Fongoli, with 0.31/ha in closed habitat types and 0.11/ha in open habitat types. However, since army ants are highly seasonal and only found in the wet season a better measure of their density would be to use the wet season data, suggesting a density of 0.38 army ant nests per hectare at Fongoli during the wet season.

5.3.3 Vertebrates

The night transect was surveyed once a month for bushbabies (N=57), and a total of 960,000m² (0.96 km²) were sampled. On average, 4.75 bushbabies were seen each month (Figure 5.8), for a relative density of bushbabies at Fongoli of 59 per square kilometer (0.594/ha) (80,000 m² or 0.08 km² sampled each month). They were found most often in the dry season (67%), with the highest density in January (125/km²). Dry season (November through May) density (67.9/ km²) was higher than the wet season density (47.5/ km²) (dry season: 0.56 km² sampled; wet season: 0.40 km² sampled).

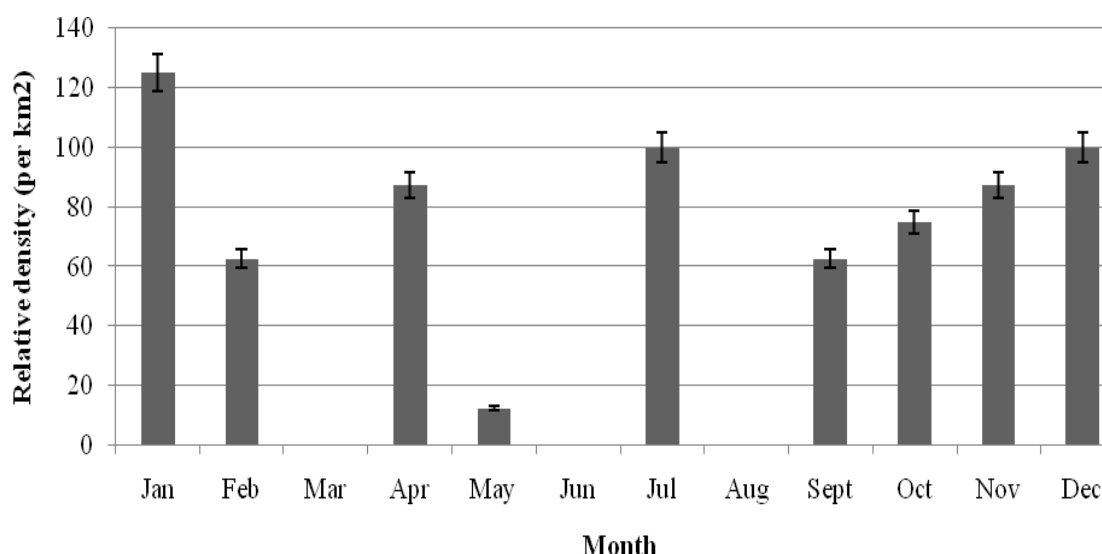


Figure 5.8: Monthly relative density (per km²) of bushbabies at Fongoli from August 2006 to July 2007.

Table 5.7: Vertebrates recorded at Fongoli from August 2006 to July 2007.

Animal	Genus and species (if known)	Months encountered ¹	Total individuals (encounters)	Proportion of individuals (encounters)	Habitats ²
Baboons	<i>Papio hamadryas papio</i>	Jan, Mar, May	498 (12)	64% (14.1%)	GR, WD, FE, GF, FL
Bushbaby	<i>Galago senegalensis</i>	Oct ^w , Jan, Mar	7 (4)	0.9% (4.7%)	WD, PL
Bushbuck	<i>Tragelaphus scriptus</i>	Mar Apr, Jun ^w	14 (11)	1.8% (13%)	GR, WD, FE, PL
Civet	<i>Civettictis civetta</i>	Mar	1 (1)	0.1% (1.2%)	PL
Genet	<i>Genetta genetta</i>	Aug ^w , Jan	2 (2)	0.3% (2.4%)	GF
Mongoose	<i>Mungos mungo</i> & <i>Herpestes ichneumon</i>	Aug ^w , Sept ^w , Nov, Jan, Mar, Apr, May	93 (13)	12% (15.3%)	GR, WD, PL, GF
Monitor lizard	<i>Varanus</i> sp.	Nov	1 (1)	0.1% (1.2%)	GF
Patas monkey	<i>Erythrocebus patas</i>	Aug ^w , Oct ^w , Nov, Jun ^w	37 (7)	5.7% (8.2%)	WD, GR, PL
Porcupine	<i>Hystrix cristata</i>	Aug ^w , Sept ^w	3 (2)	0.4% (2.4%)	GF
Striped jackal	<i>Canis adustus</i>	May	1 (1)	0.1% (1.2%)	WD
Vervet monkey	<i>Chlorocebus aethiops</i>	Aug – Oct ^w , Nov-May, Jun ^w	109 (25)	14% (29.4%)	WD, GR, GF, FE, FL, BAM
Warthog	<i>Phacochoerus aethiopicus</i>	Nov, Dec, Apr, May, Jun ^w	15 (6)	2% (7.1%)	WD, GR, PL, BAM

¹Wet month = ^w, ²Habitat: tall grassland (GR), woodland (WD), forest ecotone (FE), gallery forest (GF), field (FL), short grassland (PL), bamboo woodland (BAM).

A total of 85 encounters with vertebrates were recorded over the year of this study, and these data should be considered conservative underestimates. Out of the 12 different animals, one was a reptile (monitor lizard) and the rest were mammals (Table 5.7). The three mammalian vertebrates most frequently encountered were baboons (14.1%), vervet monkeys (29.4%), and two mongoose species (15.3%) (Table 5.7).

5.4 Discussion

A total of 35 plant food resources consumed by the chimpanzees fruited during this study, with an average of nine species fruiting each month. Proportionally more plant resources fruit during the dry season (63%) than the wet season (37%). The proportion of feeding trees per month in this study resembles previous reports (Pruetz 2006), in that the late dry season contained the most fruiting trees. However, no seasonality existed in the amount

of fruiting plant resources found at Fongoli during this study. Pruetz (2006) found that the Fongoli chimpanzees were not limited by ripe fleshy fruits. However, fruiting resources were scored even when fruit was unripe, but noted as such (Pruetz 2006, this study). A calculated fruit availability index (FAI) was used to assess fruit abundance. This measure is considered more relevant than number of fruiting plants in relation to chimpanzee feeding behavior because it examines the amount of fruit in each tree, not just presence of fruit (Boesch 1996). The average FAI negatively correlated with rainfall demonstrates that food availability was seasonal. Baobab and *Saba senegalensis* were the most important fruits in the Fongoli chimpanzee diet (also found by Pruetz 2006) and these species were also the most abundant. Baobab was abundantly available during the dry season based on fruit availability index and rainfall data. Only one of the top ranked fruits (Pruetz 2006 and Chapter Six) examined for availability positively correlated with rainfall (*Hexalobus monopetalus*). Five of the top ten ranked foods were most abundant when temperatures were the highest in the dry season. This analysis demonstrated that fruit was more abundant in the dry season. The availability of fruit is discussed in terms of the feeding behaviors of the Fongoli chimpanzees in Chapter Six.

Flowers consumed by chimpanzees were plentiful in January and February. *Bombax costatum* and *Pterocarpus erinaceus* flowers were the most accessible at Fongoli. Flowering plants did not correlate with rainfall but positively correlated with temperature. Thus, as temperature increased at Fongoli, chimpanzees can find more flowers to consume. I examine the diet of the Fongoli chimpanzees in Chapter Six, showing that flower abundance is related to flower consumption.

Leaves are less abundant in the dry season and the leaf species consumed by the Fongoli chimpanzees were more abundant with lower temperatures. *Baissea multiflora*,

Bombax costatum, *Diospyros mespiliformis*, *Hexalobus monopetalus*, and *Pterocarpus erinaceus* were the most abundant leaf resources in the wet season, with over 90% of these trees surveyed containing leaves. In the dry season, *Diospyros mespiliformis* and *Ficus ingens* were the most abundant leaf species, with over 90% of the trees surveyed contained leaves.

Plant food resources have a relative density of 30 plants per hectare at Fongoli. Density of plants consumed was highest in woodland and gallery forest habitat types. However, analyses of density and the proportion of each habitat type at Fongoli reveals that food resources are most abundant in woodland (1446.19 plants) and tall grassland (1347.42 plants) habitat types. Woodland only comprises a small proportion (14% not including bamboo woodland) of Fongoli's area, but this habitat type contains the most resources. Tall grassland does not have a large density in plant resources but is a large proportion of Fongoli's composition. This habitat type contains a majority of plant resource for the Fongoli chimpanzees, but based on qualitative assessment resources are more widely scattered here than in woodland habitats. Most plant food resources (71%) used by the chimpanzees were in open woodland and tall grassland habitat types at Fongoli. The two most frequently consumed fruits, *Adansonia digitata* (baobab) and *Saba senegalensis*, were found most often in woodland habitats.

Food resources were assessed for water content. Unripe fruit of baobab (150.55g/fruit) and both ripe (73.37g/fruit) and unripe (59.72g/fruit) *Saba* fruit contained the most water per unit of all foods. Baobab and *Cola cordifolia* fruits contained more water when unripe. A significant decrease of grams per unit of water in ripe fruit may explain the use of unripe fruits by the chimpanzees, which will be explored in the following chapters. Water content of

insects did not contain many grams of water per unit (one termite or ant) (Table 5.6). These data are examined further in terms of feeding rate by the chimpanzees in Chapter Seven.

Termites were significantly more abundant than ants at Fongoli (Student's $t = -3.23$, $df = 11$, two-tailed $p = 0.008$). *Macrotermes* were available throughout the year (23.6/ha), with slight seasonal effects, and were somewhat more abundant during the dry season. However, visibility of termite mounds in the wet season may have been a cause of the lower density. Data on availability of insects was compared to use by the chimpanzees in Chapter Seven.

The higher density of army ants from transect methods as opposed to ant plots may be explained by the fact that army ants were found in the dry season (50% in wet, 50% in dry) using transect methods, whereas, no army ant nests were observed in ant plots during the dry season. This may be a sampling error. It is possible that ant nests were more difficult to sample with the ant plots. Ants are more active during the wet season (Schöning et al. 2007). Therefore, finding ant nests was more difficult when they retreat further into the ground during the dry season. The transects sampled a smaller search area, and this method may be more suitable than systematically searching a large ant plot in the dry season. Transect data were used for analyses in the following chapters as this method seems to be more reliable (research not conducted on these methods).

The nocturnal bushbaby is common at Fongoli, with estimated density of 59 per square kilometer. Bushbabies were found more frequently during the dry season. However, viability (leaf and tall grass obstruction) during the wet season may have been a factor in bushbaby counts. Further research will be able to confirm this finding. Encounter rate and density could not be compared with the other vertebrate data, because no defined time or area

was searched in regards to the latter. A more intensive study would accomplish this by walking transects. Consequently, data presented by this study suggest that baboons, vervet monkeys, and mongoose species are the most common diurnal animals at Fongoli.

This chapter presented the relative availability of most of the food resources in the Fongoli chimpanzee diet. Plant resources and termite mounds had the highest relative densities. Excluding ants and leaves, all food resources analyzed for density were found to be more abundant in the dry season. These data are important in relation to chimpanzee use of food items. Data are used in the subsequent chapters in context with chimpanzee selection of food items.

CHAPTER SIX

Feeding behavior of the Fongoli chimpanzees

6.1 Introduction

In this chapter the feeding behaviors of the Fongoli chimpanzees are examined in light of ecological factors that might influence those behaviors. The savanna habitat at Fongoli likely affects the behaviors of the chimpanzees in various ways. In order to examine its effects, chimpanzee activity and habitat type use are examined with respect to diet. In previous research at Fongoli, diet has been suggested as being affected by the environment (Pruetz 2006). Many wild chimpanzee studies concentrate on their feeding behaviors only. My research examined the use of plant foods, termites, and ants by the chimpanzees in an ecological context, employing a number of different methods. Given our lack of data on chimpanzees living in a savanna habitat, multiple measures provide not only new data, but also a comparative sample that others may replicate.

Fongoli is a mosaic savanna comprised of many different habitat types (see Chapter 3). The abundance of these habitat types is predicted to effect how the chimpanzees use them. The habitat use and activity budget of the chimpanzees were examined here in detail to further understand the feeding ecology of these apes in a savanna environment. ‘Habitat use’ is how an animal uses the physical or biological components within an area (Hall et al.1997). Data on temperature, rainfall, habitat composition, and food availability from Chapters Four and Five are used to examine the behavioral data in this chapter in an ecological context. Several related hypotheses presented in Chapter One are examined here. First, data collected from known feeding trees and data on food items indicated by undigested material in fecal samples are examined. Behavioral data are provided in terms of activity budget, habitat use,

and diet, as well as feeding rates obtained from video. A correlation between habitat use and activity was predicted; feeding and foraging were expected to occur most often in grassland and woodland habitat types because resources are most abundant in these habitat types, while social and resting behaviors were estimated to occur more often in closed habitats to escape heat and be near water (Bogart & Pruetz 2008, Pruetz & Bertolani, in press). Data on diet composition, in general, were examined to further examine insectivory in relation to other food items. Chapter Seven will elaborate on the findings of insectivory. Finally, the data presented in this chapter are analyzed in terms of ecological data from Chapters Four and Five. These analyses are used to investigate whether seasonality and/or temperature have any effect on the diet and, subsequently, the chimpanzees' activity or habitat use. Food availability data from Chapter Five is used to test hypotheses regarding whether the chimpanzees use food resources in relation to seasonality and these food's availability. Food availability was presented in Chapter Five and use of habitat was expected to correlate.

6.2 Methods

6.2.1 Fecal remains

Fresh fecal remains were collected and examined regarding the percentage of seeds, fiber, leaves, flowers, parasites, insects, and animal matter. Fecal analyses were primarily used to find insects consumed and to complement the plant based diet found from behavioral data. Therefore sample size was small. From the fecal remains, insects were removed and collected for identification. Termites were identified by Dr. Rudolf Scheffrahn from the University of Florida, and ants were identified by Dr. Caspar Schöning from the University

of Copenhagen. Seeds were identified with the aid of knowledgeable field assistants as well as a reference collection.

6.2.2 Behavior

Adult male chimpanzees were followed all day if possible to obtain behavioral data via focal animal instantaneous (five-minute interval) sampling. Males were selected from a random order. When one male was observed one day, the next male in the list was selected the next day, if he was in the party. If that male was not in the party, the next male on the list would become the focal subject. Once a male reached a maximum of twelve hours for the month he was no longer sampled until the next month unless the remaining male subjects were not available for observation. Instantaneous recording at five-minute intervals was used to quantify the behavior of the focal subject (Altmann 1974, Martin & Bateson 1993). Variables recorded were the habitat, activity, the food species and part eaten if feeding or foraging (Table A1), and food acquisition behavior, including tool use. This research lumps seed eating with fruit eating, not separating the two for analyses. Coordinates were taken with the use of a GPS whenever the party moved greater than 100m throughout the day. During the first month of study, I familiarized myself with all group members, research protocol, habitat types, and the Fongoli landscape and range. Therefore, little systematic behavioral data were collected for analyses in August 2006 (Table A7). Data were pooled for all males to provide a general activity budget, habitat use, and proportion of time spent feeding on food items for the overall Fongoli community. This data does not represent females or other age classes, so representation of the data and conclusions should be considered for this discrepancy.

Video recording was conducted when possible in order to estimate the feeding rate (item per minute) of as many resources as possible. Videos were analyzed in the United States, and the number of units (fruit, insect, leaf) per minute was recorded to provide information on feeding rates.

Analyses conducted on habitat preference and fruit preference use Jacob's preference index: $D = (r - p) / (r + p - 2rp)$. Multivariate statistics were used to correlate several variables using nonparametric statistics. Spearman's rank correlation coefficient was used to apply a ranking order to numerous variables in order to determine the strength of a correlation between two data sets.

6.3 Results: Fecal diet

Fresh feces were collected when possible for dietary analyses, and 144 samples (79 in dry season, 64 in wet season) were examined. The composition of fecal samples is displayed according to month in Table 6.1. Fecal analysis demonstrates a high proportion fruit and seeds (represented by seeds) (74%) and fiber (22%) in the diet. The remaining 3.5% of the sample was composed of insects, flowers, whole leaves and grass, and bark. Forty-one fecal samples (28.4% of fecal samples) contained termites. Twenty of these independent samples were identified as *Macrotermes subhyalinus* (Table A8). Ant remains were found in eight fecal samples (5.6% of samples), and seven were sent for identification. Four of these samples were weaver ants (*Oecophylla longinoda*), and three were army ants (*Dorylus burmeisteri*) (Table A7). Bees were found in five fecal samples (3.5% of samples) and identified as honey bees (*Apis mellifera*) by Dr. Laurence Packer of York University Ontario, Canada.

Table 6.1: Fecal analyses according to month (proportion of the volume of fecal remains) from August 2006 to July 2007 at Fongoli.

	Aug	Sept	Oct	Nov	Dec	Jan	Feb	Mar	Apr	May	Jun
Fiber	33.7	9.1	4.17	29.5	9.3	30.5	29.4	47.5	26.1	14.2	13.5
Seeds	60.4	90.8	94	61.3	89.3	66.5	63	43.8	73	85.7	82.16
Termites	0.06	0	0.17	0.6	0.22	1.05	0.2	0	0.65	0	3.54
Ants	0.12	0.06	0	0.17	1.13	0	0	0	0	0	0.02
Flowers	0.94	0	0	0	0.13	0	7.5	0	2.22	0	0.6
Whole leaves	2.12	0	0	4.3	0	0	0	0	0	0	0
Whole grass	1.9	0	1.67	4	0	2.11	0	0	0	0	0.2
Bark	0.06	0	0	0	0	0	0	0	0	0	0
Bees	0	0	0	0.25	0.03	0.05	0	0	0	0.16	0
Parasites	0.12	0	0	0	0	0	0	0	0	0	0
Number of samples	17	16	6	15	16	19	10	4	13	2	25

6.4 Results: Behavior

6.4.1 Activity and habitat use

I recorded a total of 963 hours and 20 minutes of behavioral data on ten adult male subjects (Table A7). The majority of the daily activity budget of Fongoli chimpanzees was spent resting, which accounted for 45% of their time (Figure 6.1). Feeding and foraging comprised 32% of their time, with 8% of that time spent termite fishing. Social behavior accounted for 14% of their active time, while 7% of their active time was spent traveling. Some examples of behaviors placed in ‘other’ include self-groom, self-play, drink, and make nest. Resting comprised the highest proportion of time in all months except two: November and January (Figure 6.2). During November and January the Fongoli chimpanzees spent the majority of their time feeding and foraging (Figure 6.2). Termite fishing can make up to 19.5% of the chimpanzees’ active time during the late dry season months (Figure 6.2).

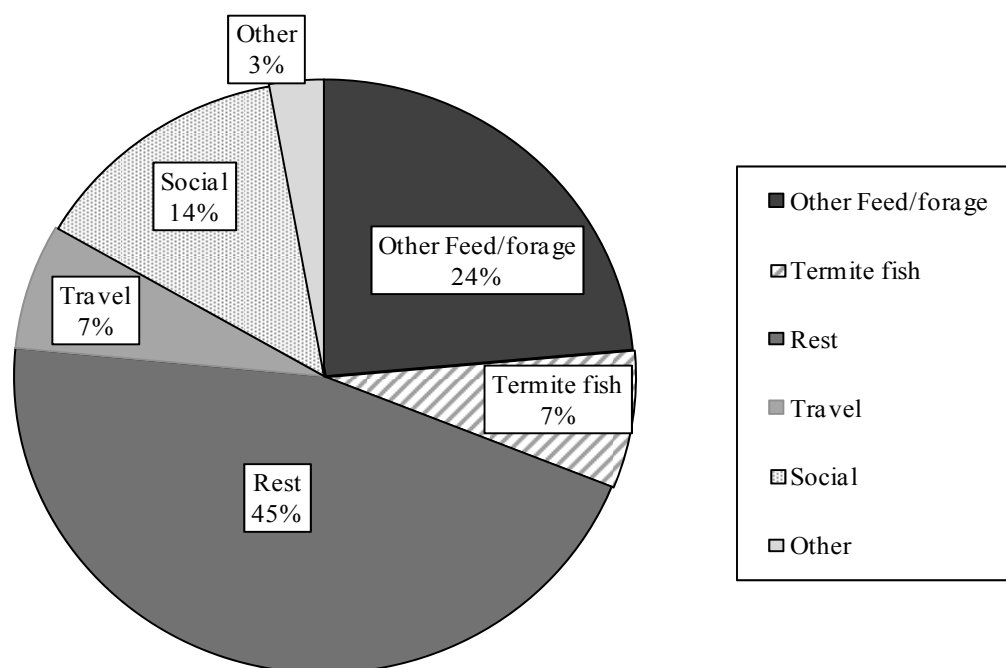


Figure 6.1: Activity budget of Fongoli chimpanzees (proportion of frequency from instantaneous sampling of 10 adult males from August 2006 to July 2007).

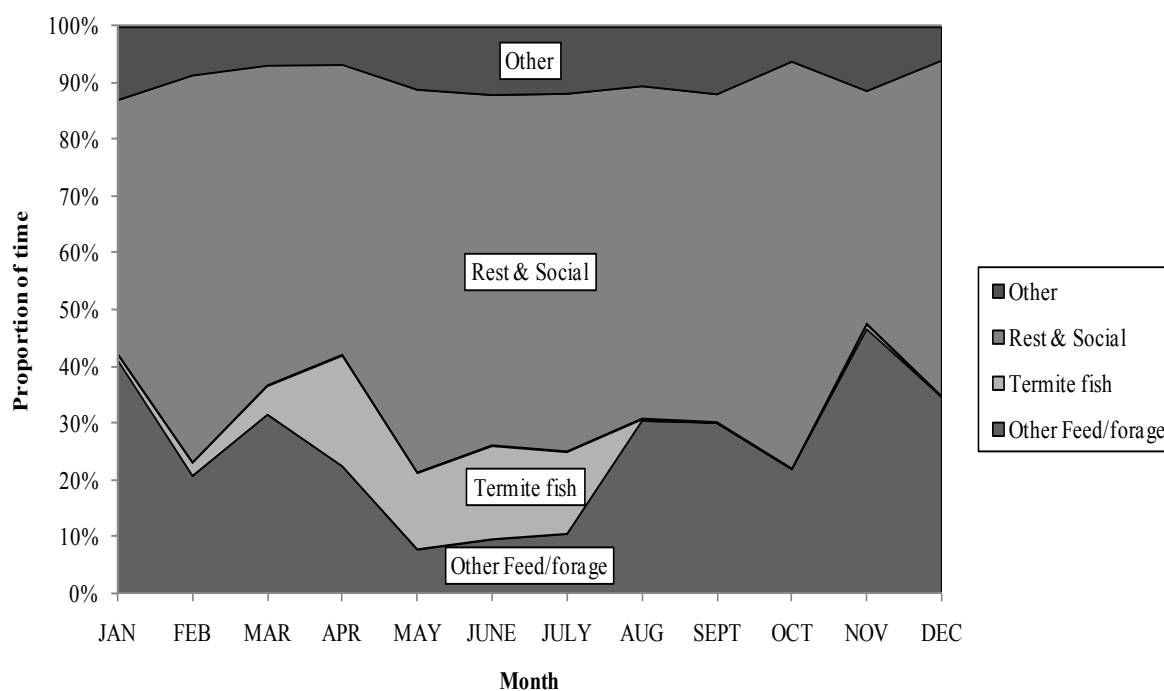


Figure 6.2: Monthly proportion of Fongoli chimpanzee activity from August 2006 to July 2007 based on data from instantaneous focal sampling.

Most of the chimpanzees' active time was spent in woodland or closed habitat types (81%) versus other open habitats (19%). When chimpanzees were in open woodland, their time was spent primarily resting (43%) and feeding and foraging (including termite fishing) (32%) (Figure 6.3). Resting was also the principal activity in closed habitat types (60%). The dominant activity in bamboo and grassland habitats was foraging and feeding (Figure 6.3). Traveling was the most prevalent activity when the chimpanzees were in fields. A more specific examination of the behaviors revealed that feeding and foraging occurred more in open woodland (54.6%) and grassland (21.3%) habitats, while termite fishing occurred most often in open woodland (59.2%) and closed habitat types (22%) (Figure 6.4). The chimpanzees rested predominantly in open woodland (50.4%) and closed habitat types (44.8%) as well. Traveling was also largely in open woodland (61.1%) and, to a lesser degree, grassland habitats (20.3%). Social behaviors were observed mainly in open woodland (52%) and closed habitats (30.3%).

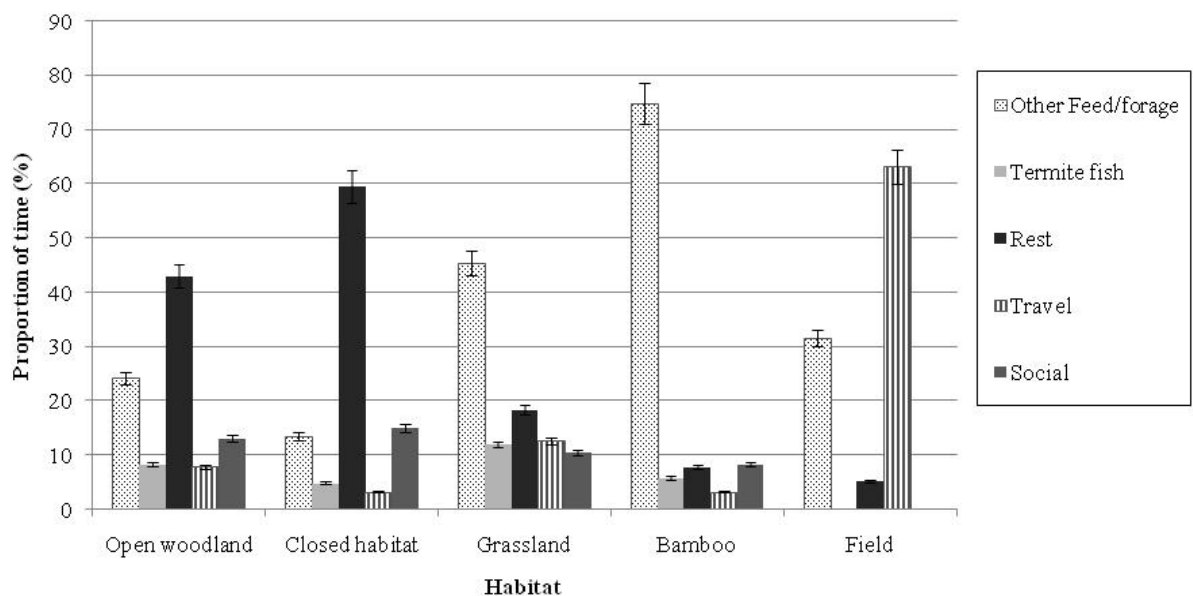


Figure 6.3: Proportion of time spent doing a particular activity when Fongoli chimpanzee individuals were within each habitat type (data based on instantaneous focal sampling).

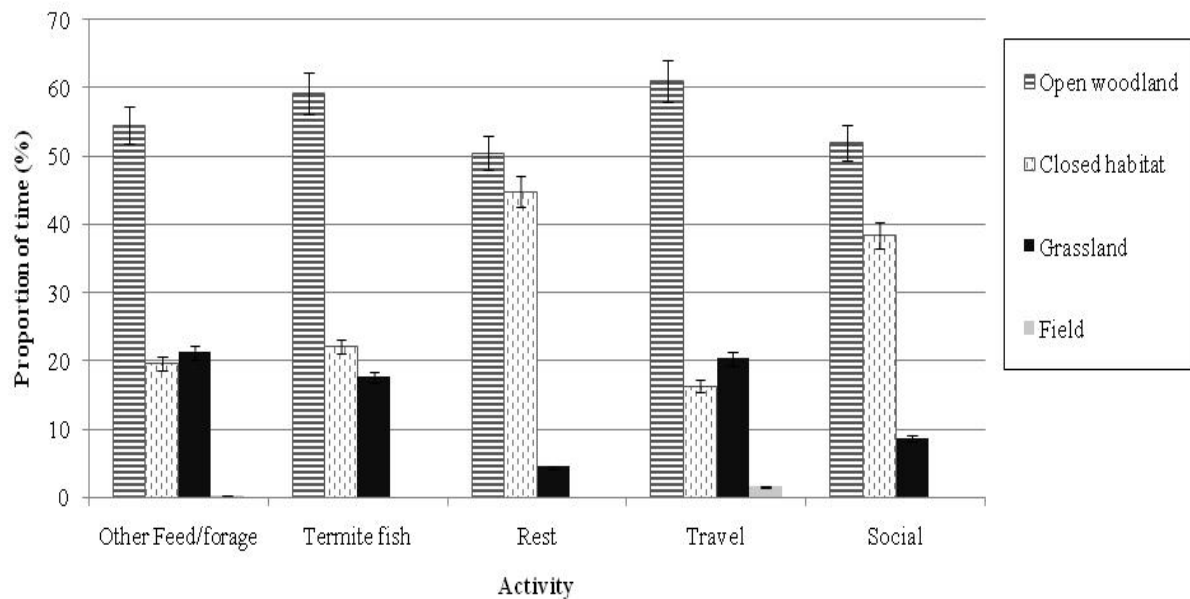


Figure 6.4: Proportion of Fongoli chimpanzee time spent in each habitat type when performing a particular activity (data based on instantaneous focal sampling).

The Fongoli chimpanzees did not change their activity budget according to season (Figure 6.5). There was no significant difference in the overall proportion of behaviors between the wet and dry seasons (Student's paired t -ratio = 0.02, $df = 4$, p -value = 0.98).

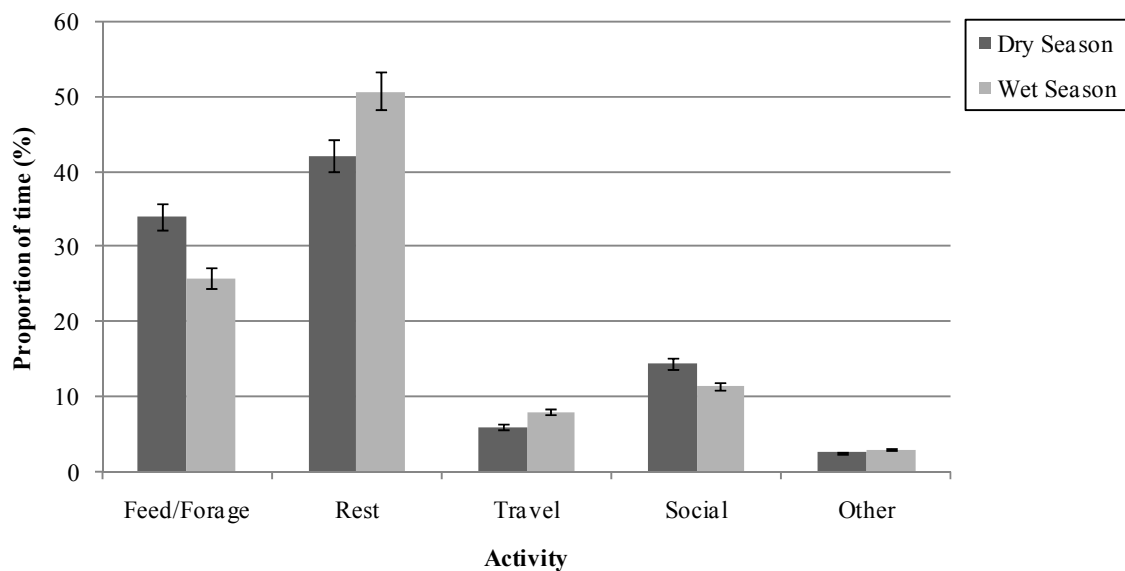


Figure 6.5: Seasonal proportion of chimpanzee behaviors (based on instantaneous focal sampling).

6.4.2 Feeding budget

The Fongoli chimpanzees were observed to consume a total of 56 plant foods items during this study, including individual species of figs (*Ficus*). Forty-eight species were identifiable (Table 6.2). In the Table 6.2, THV is terrestrial herbaceous vegetation and grass is leaves of the grass that were eaten. In addition to these plant foods, termites, ants, honey, dirt, seeds from feces, and a vervet monkey were also consumed by focal subjects. The top ten consumed plant foods composed 74.6% of the plant diet (see Table 6.2). The top five foods comprised 59.1% of the plant diet. These foods included fruits of *Saba senegalensis*, *Adansonia digitata*, *Azizelia africana*, *Ficus* species, and *Piliostigma thonningii* (Table 6.2).

Table 6.2: Identified plant foods observed to be consumed by chimpanzees at Fongoli.

Proportion of plant diet	Part ¹	Genus and Species	Proportion of plant diet	Part ¹	Genus and Species
18.20	fr	<i>Saba senegalensis</i>	0.73	fr	<i>Daniellia oliviera</i>
17.35	fr	<i>Adansonia digitata</i>	0.66	fr	<i>Diospyros mespiliformis</i>
9.98	fr	<i>Azizelia africana</i>	0.54	fr	<i>Lannea microcarpa</i>
8.10	fr	<i>Ficus sp.</i>	0.50	fr	<i>Allophylus africanus</i>
5.47	fr	<i>Piliostigma thonningii</i>	0.46	fr	<i>Hannoa undulata</i>
3.51	fr	<i>Spondias mombin</i>	0.39	fr	<i>Landolphia heudelotti</i>
3.12	fr	<i>Strychnos spinosa</i>	0.27	l	<i>Ficus sp.</i>
3.08	fr	<i>Tamarindus indica</i>	0.23	l	<i>Saba senegalensis</i>
2.93	b	<i>Pterocarpus erinaceus</i>	0.19	fl	<i>Adansonia digitata</i>
2.89	fl	<i>Ceiba pentandra</i>	0.19	p	<i>Saba senegalensis</i>
2.85	fl	<i>Pterocarpus erinaceus</i>	0.15	fr	<i>Cissus populnea</i>
2.62	l	<i>Baissea multiflora</i>	0.15	fr	<i>Zizyphus mauritania</i>
2.35	fr	<i>Bombax costatum</i>	0.15	fr	<i>Elaeis spp.</i>
2.27	fr	<i>Gardenia erubescens</i>	0.15	l	<i>Bombax costatum</i>
1.62	l	<i>Pterocarpus erinaceus</i>	0.15	l	<i>Hymenocardia acida</i>
1.50	fr	<i>Ceiba pentandra</i>	0.15	p	<i>Cissus populnea</i>
1.43	fr	<i>Cola cordifolia</i>	0.12	fl	<i>Hymenocardia acida</i>
1.27	fr	<i>Parkia biglobosa</i>	0.12	l	<i>Ficus umbellata</i>
1.16	p	<i>Oxytenanthera abyssinica</i>	0.077	fr	<i>Vitex madiensis</i>
1.00	fr	<i>Cordyla pinnata</i>	0.039	l	THV
0.96	fl	<i>Bombax costatum</i>	0.04	p	Grass
0.85	fr	<i>Lannea acida</i>			

¹Part: fruit (fr), leaves (l), flower (fl), bark (b), pith (p)

Fruit (including seeds) was the prominent food resource for the chimpanzees, including 32 species (Table 6.2) and 61.3% of the overall diet (Figure 6.6). Termites were the second most important food resource in terms of food time budget for the Fongoli chimpanzees, forming 24.1% of the observed diet (Figure 6.6). The remaining portion of the diet consisted of flowers (5.1%, 5 species), leaves (4.41%, 11 species), bark (2.15%, 1 species), and pith (1.22%, 5 species). Bark and pith are presented together as 'other plant' in Figure 6.6. Dirt and feces (seeds) are labeled as 'other' in Figure 6.6 and comprise 1.18% of the diet. The final 0.54% of the diet, 'other animal', included ants, meat, and honey (Figure 6.6). Bark only made up 2.15% of the total time spent on diet but was mainly consumed in the month of August (Figure 6.7). In fact, bark of the tree *Pterocarpus erinaceus* was the main food consumed in August (65.8% of the diet), with fruit accounting for only 27% of the time spent feeding during that month (Figure 6.7). Fruit comprised the majority of feeding budget from September through March (Figure 6.7). During April, fruit and termites were nearly equal in the feeding budget, but from May through July termites surpassed fruit in the diet (Figure 6.7). The Fongoli chimpanzees can spend up to 63% of their monthly feeding budget on termites (June: Figure 6.7). Flowers were mostly consumed from December through February, while leaves were eaten throughout the year (Figure 6.7). Feces (seeds) and dirt (not shown) were mainly consumed in the month of December, while ants and vertebrates were only consumed in June and July.

Seasonality had an effect on the food resources included in the diet (one-way ANOVA, $F\text{-ratio} = 3.06$, $df = 9$, $10 p = 0.04$). Fruit was a large portion of the dry season diet (69.7%) but comprised less than half (42.4%) of the wet season diet (Figure 6.8). Termites comprised a larger portion of the diet during the wet season (37.2%) than the dry season

(18%). Leaves and bark were consumed largely in the wet season (9.8% and 6.8%, respectively), while flowers were generally consumed in the dry season (7.2% of the diet) (Figure 6.8).

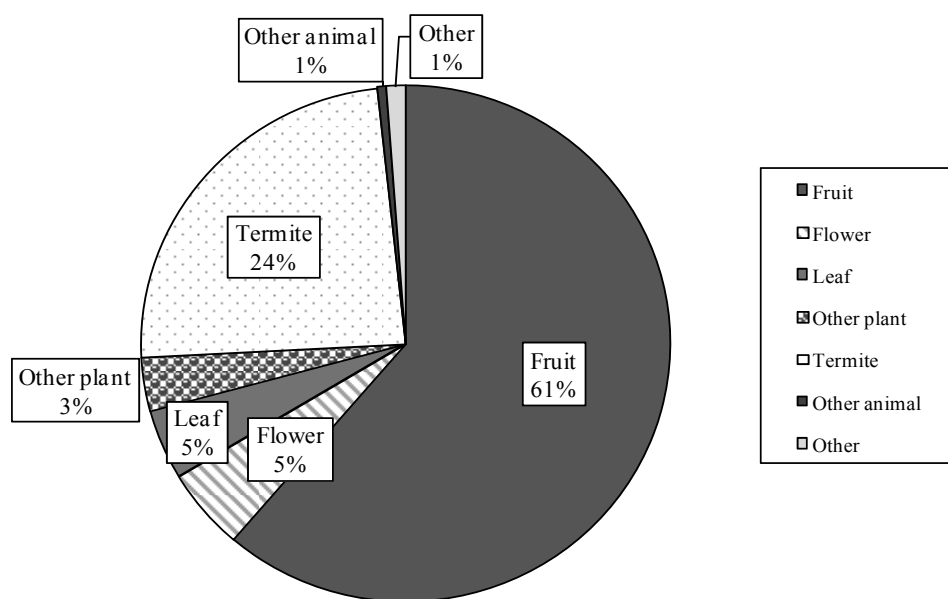


Figure 6.6: Proportion of time spent feeding on particular food items by Fongoli chimpanzees from August 2006 to July 2007 (instantaneous data focal males).

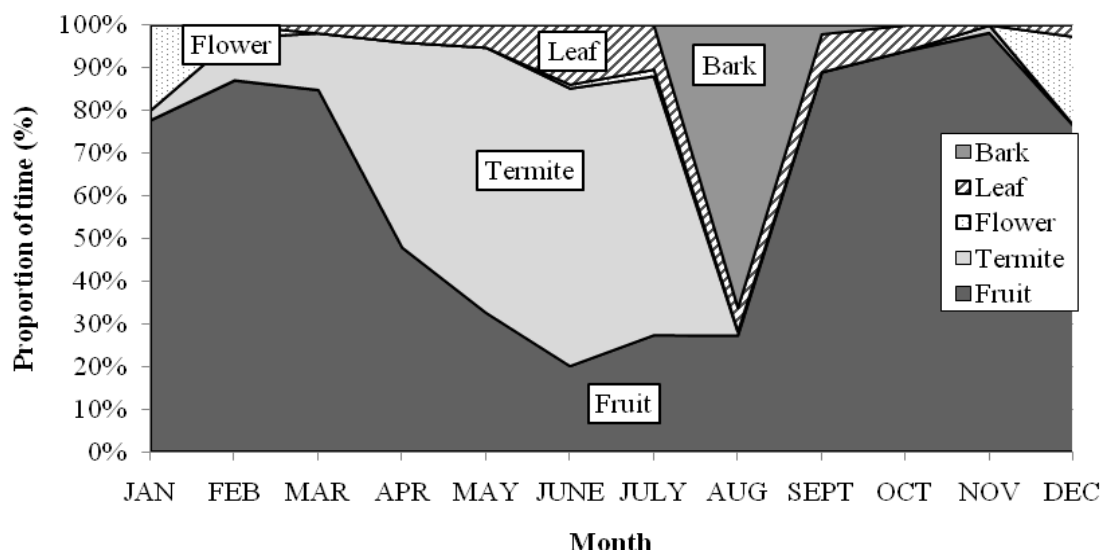


Figure 6.7: Monthly proportion of time spent feeding on the top five food items by Fongoli chimpanzees from August 2006 to July 2007 (based on instantaneous focal male subjects).

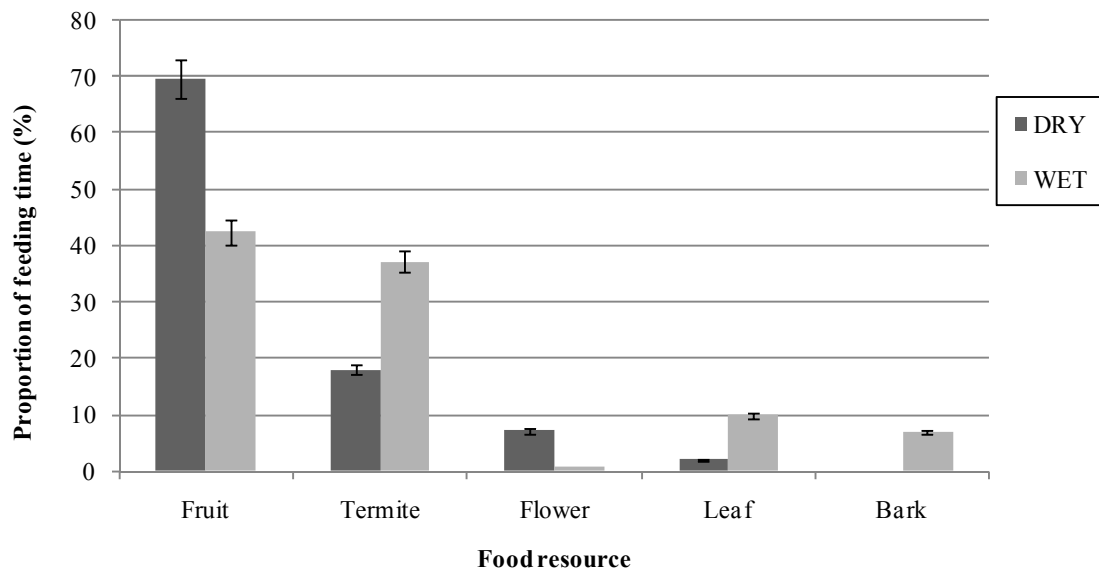


Figure 6.8: Proportion of time (with percentage error bars) Fongoli chimpanzees spent feeding on top five food resources according to season.

The monthly proportion of feeding time did not correlate with rainfall (Spearman's rank correlation $\rho = -0.17$, p -value = 0.58). The top ranked food items are listed in Table 6.3. The number of plant species and parts consumed in each season was similar, with an average of 10 species and 11.3 parts in the dry season and 9.8 species and 11.4 parts during wet months. The food resource that accounted for the highest proportion each month was typically over 50%, except from December to April, which was likely a factor of the greater number of plant species consumed. Fruits were the top ranked item during most months, with the exceptions being May through August. The diet in August was dominated by the bark of *Pterocarpus erinaceus* (66%), in a month not led by frugivory. The months of May through July were dominated by termites of *Macrotermes* species. *Ficus* fruits are important in the diet during the transitional period of the late wet season (August and September) and early dry season (November) (Table 6.3). Baobab fruit (*Adansonia digitata*) (Figure 6.9a) was among the top food species eaten during three months, with the greatest proportion in

November when it is unripe (Table A6). *Saba senegalensis* fruit (Figure 6.9b) was among the top ranked foods during six months of the year and accounted for the highest percentage of the plant-based diet in five of those months.

Table 6.3. Monthly feeding budget of the Fongoli chimpanzees from August 2006 to July 2007 (based on instantaneous focal male data).

	Number of plant species	Number of plant parts	Number of other items	Top ranked foods	Part ¹	Proportion of monthly diet
Aug	7	8	1	<i>Pterocarpus erinaceus</i> <i>Ficus</i> spp.	b f	66 19
Sept	6	8		<i>Spondias mombin</i> <i>Ficus</i> spp.	f f	50 30
Oct	9	9		<i>Azizelia africana</i> <i>Adansonia digitata</i> <i>Spondias mombin</i>	f f f	55 21 11
Nov	8	8	2	<i>Adansonia digitata</i> <i>Ficus</i> spp.	f f	71 19
Dec	11	13	3	<i>Adansonia digitata</i> <i>Ceiba pentandra</i> <i>Tamarindus indica</i>	f fl f	43 16 13
Jan	12	13	1	<i>Azizelia africana</i> <i>Pterocarpus erinaceus</i> <i>Strychnos spinosa</i>	f fl f	30 14 12
Feb	13	14	1	<i>Saba senegalensis</i> <i>Strychnos spinosa</i> <i>Gardenia erubescens</i> <i>Macrotermes</i> spp.	f f f a	36 11 11 10
Mar	11	11	1	<i>Saba senegalensis</i> <i>Piliostigma thonningii</i> <i>Macrotermes</i> spp.	f f a	48 13 13
Apr	7	9	2	<i>Macrotermes</i> spp. <i>Piliostigma thonningii</i> <i>Saba senegalensis</i>	a f f	47 22 15
May	9	11	1	<i>Macrotermes</i> spp. <i>Saba senegalensis</i> <i>Parkia biglobosa</i>	a f f	63 14 11
Jun	13	18	2	<i>Macrotermes</i> spp. <i>Saba senegalensis</i> <i>Baissea multiflora</i>	a f l	63 13 9
Jul	14	14	3	<i>Macrotermes</i> spp. <i>Saba senegalensis</i> <i>Baissea multiflora</i> <i>Cola cordifolia</i>	a f l f	57 11 6 6

¹Part: fruit (f), leaves (l), flower (fl), bark (b), animal (a), pith (p)

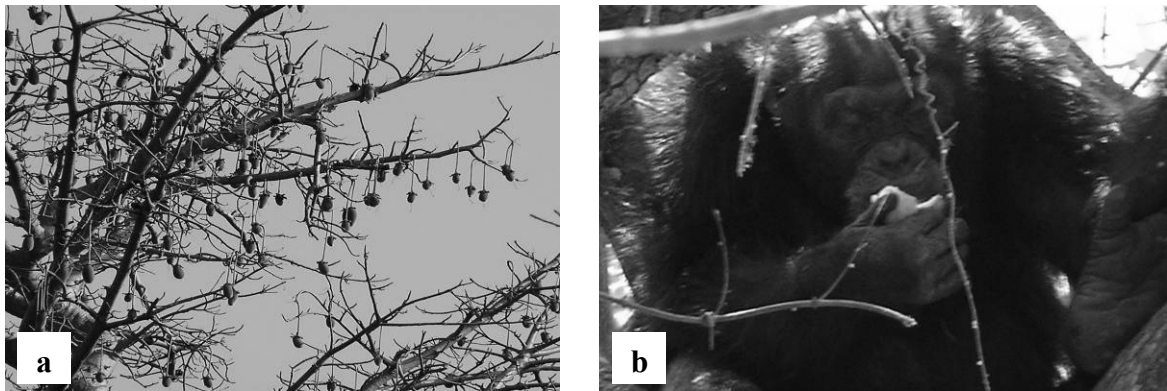


Figure 6.9: Fruits at Fongoli a.) Baobab (*Adansonia digitata*) fruit, b.) Mamadou eats *Saba* fruit.

6.4.3 Feeding rates

A total of 56 feeding observations were recorded to analyze counts of individual food parts consumed (Table 6.4). One unit is equal to one fruit, one leaf, one termite, and so on. Many samples were too small to examine species patterns. Samples discussed here include ripe baobab, unripe *Cola*, ripe *Saba*, and *Macrotermes* species (Table 6.4).

Table 6.4: Feeding rates of several food resources at Fongoli.

	Class	Number of units	Unit per min	Number of observations	Minimum units/min	Maximum units/min	SD of units/min
<i>Adansonia digitata</i> *	ripe	6	5	6	0.35	15	5.8
<i>Adansonia digitata</i>	unripe	2	0.15	1			
<i>Azelia africana</i>	ripe	2	25	2	20	30	7.1
<i>Bombax costatum</i>	flowers	11	13.5	2	12	15	2.1
<i>Cola cordifolia</i> *	unripe	6	1.76	6	0.78	2.5	0.56
<i>Ficus sycomorus</i>	ripe	9	195	2	150	240	63.6
<i>Oxytenanthera abyssinica</i>	pith	2	1.3	2	0.73	1.9	0.81
<i>Piliostigma thonningii</i>	ripe	4	0.48	3	0.21	0.95	0.41
<i>Saba senegalensis</i> *	ripe	53	3.1	11	1.62	6.67	1.5
<i>Saba senegalensis</i>	unripe	2	0.15	1			
	Season						
<i>Macrotermes</i> spp.	Dry	208	7.13	19	2.3	17.3	4.01
<i>Macrotermes</i> spp.	Wet	33	32.5	1			
<i>Macrotermes</i> spp.**	All-year	241	8.4	20	2.3	32.5	6.9

*Discussed in Section 6.8 Discussion, ** discussed in Chapter Seven

6.5 Analyses

6.5.1 Chimpanzee habitat use and habitat availability

The chimpanzees selectively use specific habitats, using certain closed and open habitats more than would be expected given their availability (Pearson's standardized $\chi^2 = 100.27$, $df = 8$, $p\text{-value} < 0.0001$). Tall and short grassland were used significantly less often than would be expected (Table 6.5). Conversely, open woodland and gallery forest were each utilized more often than expected (Table 6.5). All other habitat types were used according to their representative proportion in the chimpanzee's range.

The Fongoli chimpanzees exhibit habitat preference. Using Jacob's Preference Index $D = (r - p) / (r + p - 2rp)$, if D is between -1 and 0, then the habitat type was avoided. If D is between 0 and 1, there is a preferential use of that habitat type. The habitat types of open woodland, gallery forest, and forest ecotone were all used preferentially (Table 6.5), while the habitats of grassland (short and tall), bamboo, and field were avoided relative to their composition at Fongoli (Table 6.5). When woodland and closed habitat types were examined in opposition to other open habitat types, there was a preference for woodland and closed habitats and an avoidance of other open habitats.

Resting and feeding behaviors were the main daily activities of Fongoli chimpanzees (see Figure 6.2), encompassing 77% of their time. These activities occur most often in open woodland and closed habitat types (see Figure 6.5). Results indicate a correlation between activity and habitat use.

Table 6.5: Proportion of chimpanzee habitat use, habitat availability at Fongoli, and preference index (D).

	Proportion of use	Proportion of habitat	Jacobs Preference Index (D)
Open Woodland	53.9	13.7	0.76
Closed Woodland	5.46	2.9	0.31
Gallery Forest	15.87	0.2	0.98
Forest Ecotone	11.87	1	0.86
Tall Grassland	8.7	46.8	-0.81
Short Grassland	2.68	20.5	-0.81
Bamboo	1.36	9.9	-0.77
Field	0.16	5	-0.91

6.5.2 Habitat use, rainfall, and temperature

The Fongoli chimpanzees used open woodland (54%) more than any other habitat, followed by closed habitats (gallery forest, ecotone forest, and closed woodland) (33%) (Table 6.5). The use of specific habitat types was correlated with rainfall. During times of little to no rainfall, closed habitats were used more often (Spearman's rank correlation $\rho = -0.63$, p -value = 0.03). Open woodland was used more often during times of more rainfall (Spearman's rank correlation $\rho = 0.73$, p -value = 0.007). Average temperatures did not correlate with use of any particular habitat type (condensed categories: bamboo woodland, field, closed habitat, grassland, open woodland).

6.5.3 Activity, rainfall, and temperature

Activity other than feeding and foraging does not correlate with rainfall. There is a negative correlation between feeding and rainfall (Spearman's rank correlation $\rho = -0.80$, p -value = 0.002). As rainfall increases, the active time spent feeding decreases. The data on fruit diet and seasonality also support this conclusion (see Figure 6.11).

The only behaviors found to correlate with temperature were termite fishing and social behaviors. Chimpanzees termite fished more often with an increase of average

temperature at Fongoli (Spearman's rank correlation $\rho = 0.70$, p -value = 0.01). Social behaviors also increased with higher temperatures (Spearman's rank correlation $\rho = 0.66$, p -value = 0.02). Interestingly, resting did not correlate with average temperatures at Fongoli (Spearman's rank correlation $\rho = 0.22$, p -value = 0.50).

6.5.4 Habitat types used for feeding

Both activity analyses and habitat analyses indicated a preference of open woodland and grassland habitat types during feeding and foraging. Regarding feeding trees, shrubs, and climbers, 57% were in woodland and 29% were in grassland (Figure 6.1). These habitat types together hold 86% of the plant feeding resources. The baobab tree (*Adansonia digitata*) was the most abundant feeding tree species found in both open woodland (16%) and grassland (26%) habitat types and was one of the top five ranked foods (see Table 6.2). Use of habitat for feeding did not correlate with availability of plant food resources (Spearman's rank correlation $\rho = 0.77$, p -value = 0.07) (Table 6.6). Thus, food items in each habitat type were used in accordance with their availability as displayed in Table 6.5.

Table 6.6: Feeding tree availability and proportion of use by Fongoli chimpanzees according to habitat type.

	Total number of feeding trees	Proportion of use for feeding
Field	6.62	0.22
Short grassland	247.97	1.67
Bamboo	160.92	4.30
Tall grassland	1347.42	19.61
Open woodland	1446.19	57.10
Closed habitat	113.85	17.09

6.5.5 Observed diet and food availability

Of the top ten fruit species consumed by the chimpanzees (Table 6.2), five were analyzed regarding availability in Chapter 5 (Table 6.7). The top two foods in the diet of the chimpanzees, *Adansonia digitata* and *Saba senegalensis*, were among the most abundant chimpanzee fruits at Fongoli (see Chapter 5). There was a positive correlation between the proportion of certain fruits in the diet and the fruit availability index of those fruits (Spearman's rank correlation $\rho = 0.90$, p -value = 0.04). This indicates that consumption of a fruit species increased as its availability increased (Figure 6.10).

Table 6.7: Fruit proportion of use by Fongoli chimpanzees and index of availability used for analyses.

	Rank among fruits in the diet	Proportion of fruit diet	FAI %
<i>Saba senegalensis</i>	1	21.78	31.81
<i>Adansonia digitata</i>	2	20.77	61.11
<i>Piliostigma thonningii</i>	5	6.55	17.72
<i>Bombax costatum</i>	9	2.81	8.33
<i>Gardenia erubescens</i>	10	2.72	2.78

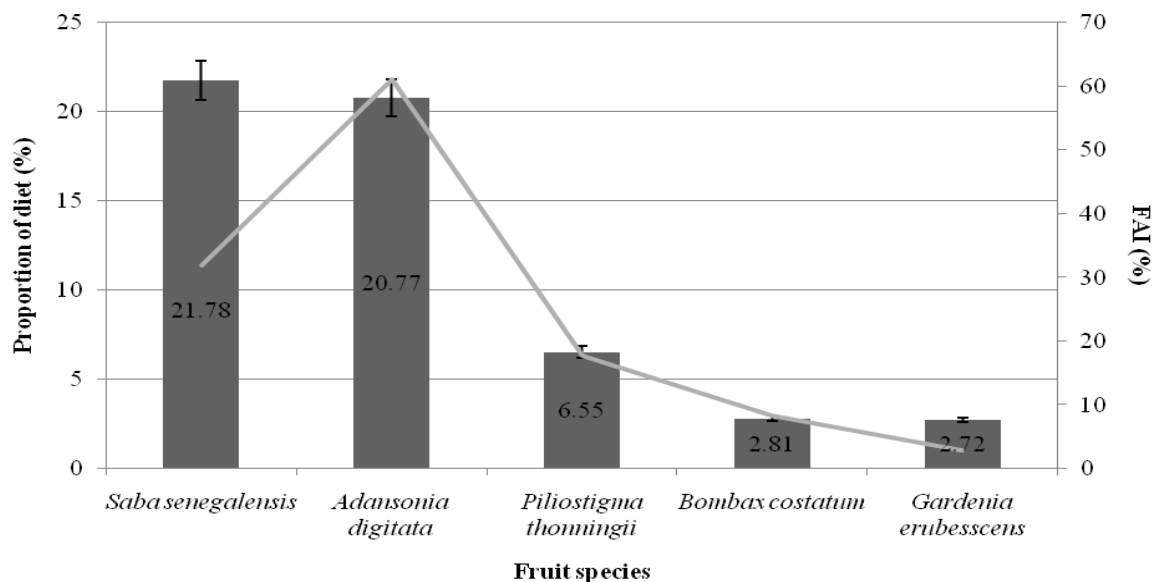


Figure 6.10: Fruit availability index (line) and proportion of feeding budget (bars) of five fruits from August 2006 to July 1007 at Fongoli.

Of 23 species that flowered during this study the Fongoli chimpanzees consumed six. The monthly consumption of flowers did not correlate to the frequency of individual flowering plants of the six species (Spearman's rank correlation $\rho = -0.49$, p -value = 0.10). However, consumption of flowers was positively correlated with total flowering plants of all 23 species (Spearman's rank correlation $\rho = 0.66$, p -value = 0.02).

Proportion of time spent feeding on leaves did not correlated with proportion of all species leafing at Fongoli (Spearman's rank correlation $\rho = 0.49$, p -value = 0.10). Consumption of leaves also did not correlated with the proportion of consumed species leafing (Spearman's rank correlation $\rho = 0.33$, p -value = 0.30). This is likely a factor of the low proportion of use across months. Leaves are not consumed relative to abundance.

Food items in the diet of the Fongoli chimpanzees were used in proportion to their availability (Figure 6.11). Density in Figure 6.11 represents abundance. Termites and plant foods were not used more than expected in terms of abundance. Density was unknown for other vertebrates and other food items such as bees.

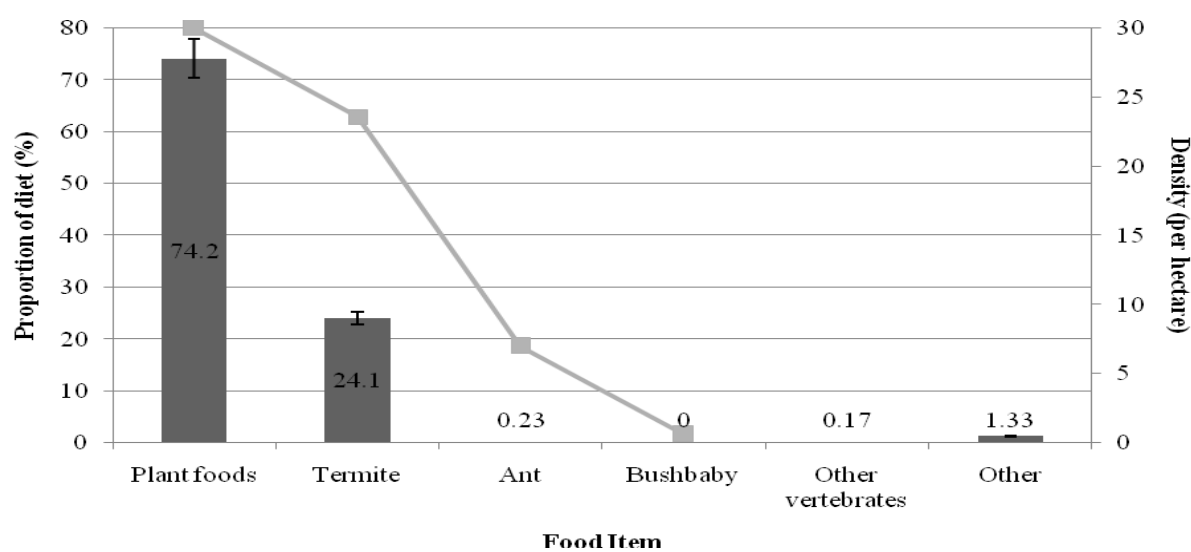


Figure 6.11: Density (line) per hectare and proportion of feeding (bar) of food items.

6.5.6 Diet, rainfall, and temperature

Both *Adansonia digitata* and *Saba senegalensis* produced fruit mainly in the dry season (Chapter 5). These two fruits composed 36% of the plant-based diet. The monthly fruit availability of baobab (*Adansonia digitata*) and *Saba* were negatively correlated with rainfall, but *Saba* was not significant (Spearman's rank correlation $\rho = -0.89$ and -0.51 , p -value = <0.0001 and 0.09 , respectively) (Table 6.8). However, the proportion of *Saba* in the diet was positively correlated with average temperatures (Spearman's rank correlation $\rho = 0.77$, p -value = 0.004), while baobab was not correlated with temperature (Spearman's rank correlation $\rho = -0.17$, p -value = 0.60). Examining baobab fruit, there was a positive correlation between monthly fruit availability (FAI) and the proportion of time spent feeding on baobab (Spearman's rank correlation $\rho = 0.64$, p -value = 0.03). There was also a positive correlation between *Saba* monthly availability (FAI) and the time spent feeding on it during this study (Spearman's rank correlation 0.67 , p -value = 0.02) The chimpanzees ate these fruits in proportion to their availability. A diet composed largely of fruits in the dry season (69.7%) was congruent with the availability of these top fruit species.

Table 6.8: Monthly rainfall, temperature, proportion of time spent feeding on baobab and *Saba*, and fruit availability index of these species used in analysis.

	Rainfall (mm)	Average temperature °C	Proportion of baobab in diet	Baobab FAI (%)	Proportion of <i>Saba</i> in diet	<i>Saba</i> FAI (%)
August	236.4	26.57	0.0	0	3.6	33.3
September	210	25.90	0.0	0	0.0	0
October	87.7	26.96	21.4	33.3	0.0	33.3
November	0	27.27	70.5	100	0.0	33.3
December	0	26.45	43.0	100	0.2	33.3
January	0	25.84	8.2	100	1.0	33.3
February	0.5	29.63	0.4	100	35.5	33.3
March	0	31.77	2.6	100	48.3	41.7
April	0.2	32.85	0.0	100	14.5	40
May	14.4	31.53	0.9	100	14.3	33.3
June	125.1	27.93	0.0	0	13.1	33.3
July	92.8	26.98	0.0	0	10.7	33.3

The monthly proportions of consumption of each food item were analyzed in relation to rainfall and average temperature at Fongoli. Monthly termite consumption was the only food resource found to associate with average temperature. Monthly consumption of termites positively correlated with temperature (Spearman's rank correlation $\rho = 0.67$, p -value = 0.02). Leaf and bark (cambium) consumption correlated with rainfall. Monthly leaf consumption positively correlated with rainfall (Spearman's rank correlation $\rho = 0.81$, p -value = 0.001). Cambium consumption also positively correlated with rainfall (Spearman's rank correlation $\rho = 0.66$, p -value = 0.02).

6.6 Preferred fruits

Preferred foods are selected disproportionately to their relative abundance (Leighton 1993, Manly et al. 2002, Marshall & Wrangham 2007). The Fongoli chimpanzees do not demonstrate a high preference for most fruits in the diet. I used Jacobs Preference Index (D) to compare the proportion of consumed fruits and the proportion of fruiting trees of those species (Table 6.9). If D is between -1 and 0, then the fruit was avoided. If D is between 0 and 1, there is a preferential use of that fruit. Only the fruit of *Strychnos spinosa* was strongly preferred, with D greater than 0.5. Fruits of *Ceiba pentandra*, *Saba senegalensis*, *Parkia biglobosa*, *Gardenia erubescens*, and *Azizelia africana* displayed some preference (above 0). *Cola cordifolia*, *Lannea acida*, and *Vitex madiensis* were used less than their availability offered at Fongoli.

Table 6.9: Jacobs preference index using proportion of fruiting trees.

	Proportion (%) of fruit diet	Proportion (%) of fruiting trees	Jacobs Preference Index (D)
<i>Adansonia digitata</i>	0.2077	0.1563	0.17
<i>Azzeria africana</i>	0.1195	0.0625	0.34
<i>Bombax costatum</i>	0.0281	0.0250	0.06
<i>Ceiba pentandra</i>	0.0180	0.0063	0.49
<i>Cola cordifolia</i>	0.0171	0.1188	-0.77
<i>Cordyla pinnata</i>	0.0120	0.0063	0.32
<i>Daniellia oliviera</i>	0.0088	0.0063	0.17
<i>Diospyros mespiliformis</i>	0.0078	0.0250	-0.53
<i>Ficus</i> spp.	0.0969	0.0938	0.02
<i>Gardenia erubescens</i>	0.0272	0.0125	0.38
<i>Hannoa undulata</i>	0.0055	0.0063	-0.06
<i>Landolphia heudelotti</i>	0.0046	0.0063	-0.15
<i>Lannea acida</i>	0.0102	0.0813	-0.79
<i>Lannea microcarpa</i>	0.0065	0.0063	0.02
<i>Parkia biglobosa</i>	0.0152	0.0063	0.42
<i>Piliostigma thonningii</i>	0.0655	0.0938	-0.19
<i>Saba senegalensis</i>	0.2178	0.0938	0.46
<i>Spondias mombin</i>	0.0420	0.0438	-0.02
<i>Strychnos spinosa</i>	0.0374	0.0063	0.72
<i>Tamarindus indica</i>	0.0369	0.0375	-0.01
<i>Vitex madiensis</i>	0.0009	0.0125	-0.86
<i>Zizyphus mauritania</i>	0.0023	0.0063	-0.46

6.7 Comparing the fecal and behavioral data on diet

A number of chimpanzee studies have used fecal analyses to determine diet, especially when subjects were not habituated to human observers (Basabose 2002, Deblauwe & Janssens 2008, Duvall 2008, McGrew et al. 1988, Pruetz 2006, Yamagiwa & Basabose 2006). Previous research at Fongoli combined analyses of fecal remains and opportunistic observation of feeding ($N=144$) to report diet composition (Pruetz 2006). Due to increased habituation to human observers, this study used both methods. However, fecal remains were only used for an informative matter on species of insects and plants consumed. Some of the food items observed to be consumed by the Fongoli chimpanzees were not present in the

fecal remains, such as feces (seeds) and dirt (since the fecal remains were washed and sieved). No meat was found in fecal remains during this study, but observed meat-eating is discussed in Chapter Seven. Cambium was difficult to identify in fecal remains as well. There were significant differences between the observed feeding budget and the diet as measured via fecal remains (One-way ANOVA, $F\text{-ratio} = 15.8$, $df = 8, 9$, $p = 0.0002$). This significance is illustrated in Table 6.12. Fruit, ants, meat, and the category of other were within the estimated parameters (Table 6.12). Flowers, bark, and bees/honey from fecal data were within the parameters of the observed diet. However, these food items within the observed diet were outside of the estimated intervals from the fecal diet (Table 6.12). Leaves and termites observed to be consumed were outside of the estimated intervals (confidence interval of 95%) of the fecal diet, and vice versa as there was no overlap in the parameters between the two methods (Table 6.12).

Table 6.10: Composition of food items as indicated by fecal remains and observed data from August 2006 to July 2007 at Fongoli.

	Fecal diet data			Observed diet data		
	Proportion of diet	Lower CI (95%)	Upper CI (95%)	Proportion of diet	Lower CI (95%)	Upper CI (95%)
Fiber/Leaves	23.37	14.4	33.5	5.63	2.7	8.6
Seeds/Fruit	74.45	62.8	84.3	61.3	43.3	80.8
Termites	0.93	0	1.3	24.1	4.2	38.6
Ants	0.17	0	0.36	0.23	0	0.5
Flowers	1.03	0	2.5	5.1	0	8.4
Bark	0.01	0	0.1	2.15	0	17.7
Bees/Honey	0.05	0	0.02	0.14	0	0.3
Meat	0	--	--	0.17	0	0.5
Other	0	--	--	1.18	0	2.5

Termites did not comprise a large percentage of volume in the fecal remains, as they were small, even when present in the hundreds. Thus, using fecal remains to determine the

abundance of termites and possibly other insects in the diet of chimpanzees appears to be unreliable. However, fecal remains indicated insect consumption during months where the chimpanzees were not observed to consume them. Insects (termites and ants) were consumed in all months of the year except March and May according to fecal analyses (see Table 6.1). Behavioral data indicated termite consumption during these months; therefore, both fecal and behavioral data indicated a diet that contains insects throughout the year. This information is discussed further in Chapter Seven. In terms of fiber/leaves, a source of error may be in focal observations.

6.8 Discussion

The Fongoli chimpanzees spend most of their feeding budget on fruit and termites. The observed diet in this study differs slightly from previous research. Pruetz (2006), based on 144 feeding observations, noted the diet as comprised of fruit (62.5%), leaves (16%), flowers (11%), invertebrates (5%), pith (3%), and bark (2.5%). Fruit and bark are comparable to the data found in this study. However, I found termites to be the second most prominent food resource (24.1%). Flowers were the third ranked component of the diet at 5.1%, and leaves were fourth with 4.41%. The differences in diet were most likely a result of observational limitations in the earlier study. This project identified 39 plant species and 51 plant items consumed by the chimpanzees from both observational and fecal data (Table 6.13). When cross-referencing this list of food resources with that of Pruetz (2006), three species and 15 parts were added. In addition, two species of vertebrate and one species of ant were added (Table 6.14).

Table 6.11: Cross reference of plant resources consumed in this study to that of Pruetz (2006).

Genus and Species	Bogart 2009		Pruetz 2006	
	Parts eaten ²	Criteria ¹	Parts eaten ²	Criteria ¹
<i>Acacia ehrenbergiana</i>			b	R
<i>Adansonia digitata</i>	f, fl	O, F	uf, rf, fl, b	O, F, R
<i>Azizelia africana</i>	f	O	f	F
<i>Allophylus africanus</i>	f	O, F	f	F
<i>Andropogon chevalieri</i>			l±	F
<i>Asparagus</i> spp.			p	R
<i>Baissea multiflora</i>	l	O	l	O
<i>Bombax costatum</i>	fl, f, l	O, F	fl, uf	O
<i>Borassus aethiopum</i>			p	R
<i>Ceiba pentandra</i>	fl, f	O	fl	O
<i>Cissus populnea</i>	f, p	O, F	f	F
<i>Cissus rufescens</i>			f	F
<i>Cola cordifolia</i>	f	O	f	F, R
<i>Cordyla pinnata</i>	f	O	f	F, R
<i>Daniellia oliviera</i>	f	O	f, fl	O
<i>Diospyros mespiliformis</i>	f	O, F	f, l, b	O, F, R
<i>Elaeis</i> spp.	f	O	p	R
<i>Ficus</i> spp.	f, l	O, F	uf, rf	F
<i>Ficus abutilifolia</i>	f	O		
<i>Ficus asperifolia</i>	l±	F	l±	F
<i>Ficus ingens</i>	f	O	uf, l	O
<i>Ficus sur</i>	f	O	p	R
<i>Ficus sycomorus</i>	f	O	b	O, R
<i>Ficus trichopoda</i>			l	O
<i>Ficus umbellata</i>	f, l	O, F		
<i>Gardenia erubescens</i>	f	O	f	F, R
<i>Grewia lasiodiscus</i>	f	F	f	F
<i>Hannoa undulata</i>	f	O, F	f	F
<i>Hexalobus monopetalus</i>	f	F	f, l	O, F, R
<i>Hymenocardia acida</i>	fl, l	O	fl	O
<i>Landolphia heudelotti</i>	f	O	f	O, F, R
<i>Lannea acida</i>	f	O, F	f	F
<i>Lannea microcarpa</i>	f	O, F	f	O, F
<i>Nauclea latifolia</i>			p	R

Table 6.11: Continued

<i>Oncoba spinosa</i>	f	F	f	F
<i>Oxytenanthera abyssinica</i>	p	O		
<i>Parinari excelsum</i>			f	F
<i>Parkia biglobosa</i>	f	O, F	f, fl	F, R
<i>Piliostigma thonningii</i>	f	O, F	uf, rf	F
<i>Pterocarpus erinaceus</i>	b, fl, l	O, F	b, f, fl	O, F, R
<i>Saba senegalensis</i>	f, p	O	uf, rf, p	O, F, R
<i>Sclerocarya birrea</i>			f	F
<i>Spondias mombin</i>	f	O, F	uf, rf	O, F
<i>Sterculia setigera</i>			f	F
<i>Strychnos spinosa</i>	f	O, F	f	F, R
<i>Tamarindus indica</i>	f	O, F	f	F
<i>Vitellaria paradoxa</i>			f	F
<i>Vitex madiensis</i>	f	O, F	f	F
<i>Zizyphus mauritania</i>	f	O, F	f	F
<i>Zizyphus mucronata</i>	f	F		

¹ Observed (O), fecal remains (F), feeding traces (R)

² fruit (f: uf - unripe, rf - ripe), pith (p), leaves (l), whole leaves probably eaten for medicinal purposes (l±), flowers (fl), bark (b), animal (a)

Table 6.12: Cross reference of animal foods in the Fongoli diet.

Genus and Species	Bogart 2009		Pruetz 2006	
	Parts eaten ²	Criteria ¹	Parts eaten ²	Criteria ¹
Unknown vertebrate			a	F
<i>Cercopithecus aethiops sabeus</i>	a	O	a	O, F, R
<i>Mungos mungos</i>	a	O		
<i>Tragelaphus scriptus</i>	a	O		
<i>Galago</i> spp.	a	O	a	F
<i>Oecophylla longinoda</i>	a	F	a	O, R
<i>Dorylus</i> spp.	a	O, F	a	O, R
<i>Pachycondyla analis</i>	a	O		
<i>Macrotermes</i> spp.	a	O, F	a	F, R
<i>Apis mellifera</i>	a	O, F	a	O, F, R

¹ Observed (O), fecal remains (F), feeding traces (R)

² Animal (a)

Fecal analyses indicate a diet mostly composed of fruit and leaves. This finding conflicts with the observed diet slightly, in that termites were the second most frequently

consumed food item of the Fongoli chimpanzee diet. The presence of insects may be underrepresented in the fecal remains because of their small proportional volume relative to other items in a sample. Using the proportion of samples is a better indicator of insects in the diet. For example, termites were found in 28.4% of the samples, ants in 5.6% of the samples, and bees in 3.5% of the samples. Bees are usually whole when they appear in feces and are likely inadvertently ingested by the chimpanzees when they eat honey. Additionally, the use of fecal data and observational data combined demonstrate a diet that contains insects throughout the year (see Chapter Seven for further investigation). Previous research (Pruetz 2006) found termites in 11.8% of the total fecal samples collected ($n = 894$). However, I did not concentrate on obtaining fecal samples for this research as behavioral data was the primary objective. Therefore, my fecal analysis is based on a small sample size and not a total representation of the diet.

The Fongoli chimpanzees displayed some preferences in terms of fruit resources. *Strychnos spinosa*, *Ceiba pentandra*, *Saba senegalensis*, *Parkia biglobosa*, *Gardenia erubescens*, and *Azizelia africana* were preferred, and all were among the monthly top ranked consumed foods (Table 6.2). Seasonal availability of fruit did affect the diet, as fruits were consumed more in the dry season, when they were more abundant. Results on the monthly plant food diet and the analyses of fruit availability indicated that when fruits were not as abundant in the wet season, the chimpanzees consumed leaves and bark as well as termites more frequently. The consumption of leaves is not dependant on availability. However, availability for vertebrates other than bushbabies is based on opportunistic encounters with potential prey species.

Water content and food processing may affect the Fongoli chimpanzee diet. Some fruits offer needed water content during the dry season. Unripe fruit of *Cola cordifolia* was in the top ten ranked foods of those measured according to water content (Chapter Five), and was consumed largely in the late dry season. *Saba senegalensis* was the fruit that was consumed the most at Fongoli. Both unripe and ripe *Saba senegalensis* fruit was consumed and provided many grams of water (Chapter Five). Ripe *Saba* provides the most grams of water per feeding minute (Table 6.15). *Saba* is ripe during the wet season, so water content may not have been a factor. Feeding rate on unripe *Saba* is limited, but this fruit could have importance in water intake. Ripe baobab (*Adansonia digitata*) fruits contain less water than *Cola* or *Saba* but when combined with feeding rates they offer some source of water. These fruits are consumed throughout the dry season.

Table 6.13: Food consumption rate per minute (RPM) and water content of three fruits consumed at Fongoli.

	Sample size of rpm (N)	Fruit condition	RPM	Water (gm/unit)	Water per minute (grams)
<i>Adansonia digitata</i>	6	ripe	5	12.03	60.15
<i>Cola cordifolia</i>	6	unripe	1.76	41.63	73.27
<i>Saba senegalensis</i>	11	ripe	3.1	73.37	227.45

The Fongoli chimpanzees spent most of the day resting (45%) and feeding or foraging (32%). In November and January more time was spent foraging and feeding than resting. Baobab was extensively consumed in November by the chimpanzees when it was unripe (Table A6). This may explain the increased time spent feeding for November. In January, food availability was relatively similar to other months. Chimpanzees fed on the fruit of *Azizelia africana*, the highest ranked food, at 30% during this month. However, data on feeding rate was not available for this fruit. This fruit is characterized by a very hard

outer shell, so that processing time is hypothesized to be long. Therefore, increased time spent feeding and foraging in January may also have been a product of food processing. Food items influenced the activity of the chimpanzees during November and January.

Activity as well as fruit availability determines habitat use at Fongoli. Open woodland and grassland habitat types contain the top plant food items in the diet, and these habitats were used most for feeding and foraging. Furthermore, the chimpanzees rest most often in closed habitats and open woodland (46.3% and 42.4% respectively). Closed habitat types and open woodland are used preferentially. Fongoli's environment influences habitat use as well. Rainfall, rather than temperature, impacted habitat use, as closed habitats were used more as rainfall decreased. It could be speculated that the use of closed habitat types for resting is a predator vigilance strategy, but few predators of chimpanzees live in Fongoli's range.

Data presented here suggest a diet composed mostly of fruits and termites, which differs greatly from all other chimpanzee communities studied in Africa (discussed in Chapter Eight). Diet was influenced by food availability and demonstrates seasonal differences. The activity of the Fongoli chimpanzees differs from other sites (discussed in Chapter Eight), and is related to habitat use at Fongoli. The Fongoli chimpanzees exploit both closed forests and woodland habitats for resting and social behaviors and exploit woodland and grassland for feeding and foraging. Chapter Seven will provide further investigation of the insectivorous diet at Fongoli, proven to be an important resource for chimpanzees here.

CHAPTER SEVEN

The animal diet of the Fongoli chimpanzees

7.1 Introduction

The results of this study indicate that insects are a main component of the chimpanzee diet at Fongoli (Chapter 6). Here, I examine the insectivorous diet in further detail and relate it to the findings in the last chapter. Data were obtained through ecological measures and behavioral observation. Specific characteristics of insect nests, further investigation of insects in the diet, and examination of the tools used to obtain insects are the primary foci of this chapter. Hypotheses explained in Chapter One that were examined here deal with the insectivorous behavior of the Fongoli chimpanzees. I hypothesized that seasonality or rainfall would not affect insect consumption. To test this hypothesis, I examined chimpanzee termite fishing and ant dipping in conjunction with temperature and rainfall. Termite fishing was expected to occur in woodland and forest habitats based on previous results based on indirect data (Bogart 2005), while ant dipping was proposed to occur in forested habitats (Schöning et al. 2007, 2008). Analyzing habitat use during these activities tests this hypothesis. I also present data on the availability of insects and their use, which was expected to be proportional. The hypothesis that insect foraging does not correlate with low fruit availability was also tested. Finally, the Fongoli chimpanzees were hypothesized to consume termites from only one genus (*Macrotermes*), as other termites found at Fongoli are rarely consumed by chimpanzees at other research sites. Data presented in this chapter will be compared to other chimpanzee sites in Chapter Eight.

7.1.1 Termites, ants, and bees, oh my!

Tool use by chimpanzees has been observed across the entirety of where they have been studied in Africa (Fay & Carroll 1994, Goodall 1963, McBeath & McGrew 1982, McGrew & Collins 1985, Suzuki et al. 1995). Foraging for food is one of the main daily objectives for chimpanzees (Kibale: Ghiglieri 1984, Wrangham et al. 1991; Budongo: Fawcett 2000, Newton-Fisher 1999, Tweheyo et al. 2003; Tai: Boesch & Boesch-Achermann 2000; Gombe: Goodall 1986, Teleki 1981), and they employ the use of tools to obtain foods that they otherwise would not be able to attain (McGrew 1992). Chimpanzees habitually consume eusocial insects such as Hymenoptera (ants, wasps, and bees) and Isoptera (termites) with the use of tools (Collins & McGrew 1985, Fay & Carroll 1994, Humle & Matsuzawa 2001, McBeath & McGrew 1982, McGrew et al. 1979, McGrew 1983, Nishida & Uehara 1980, Sanz et al. 2004, Suzuki et al. 1995). Termite fishing and ant dipping involve the insertion of a modified probe made of an organic material (twig, grass, vine) into an insect nest to attain insects on the tool for consumption (Nishida et al. 1999). A chimpanzee generally ant dips while above the ground or nest. As the ants swarm the area and bite, the tool is used so that the ants climb onto the probe (Nishida et al. 1999). Chimpanzee termite fishing is terrestrial, with an individual usually seated or standing alongside the ground nests (i.e. mounds) of termites. The termites attack the tool that is inserted into holes of nests, holding on with their pincers as they are pulled out on the tool (Nishida et al. 1999).

Across Africa, termites are a diverse taxon. Eggleton et al. (2002), for example, recorded 133 different species in only two countries. Chimpanzees are known to consume termites of the genera *Macrotermes* and *Pseudocanthotermes* and to ignore other genera that are found in their respective ranges (Bogart 2005, Collins & McGrew 1985, 1987, McGrew

1983). My previous research identified a total of six termite genera with over nine species at Fongoli, but *Pseudocanthotermes* was not among them (Bogart 2005, Bogart & Pruetz 2008). Of those six genera, only two (*Macrotermes* & *Trinervitermes*) were found in association with termite mounds used by chimpanzees (Bogart & Pruetz 2008). *Trinervitermes* are not consumed by chimpanzees at any other research site. *Macrotermes* are consumed by the Fongoli chimpanzees and are also consumed at most other African sites (Bogart 2005, Bogart & Pruetz 2008). These termites have a large head (Figure 7.1a), with no distinguishing taste, but are somewhat ‘juicy’ (personal observation). One *Macrotermes* mound may house up to two million termites (Harris 1956, Luscher 1955), with a density of 400 termites per m⁻² (Jones 1990). These insects cultivate cellulose-producing Basidiomycete (*Termitomyces* species) in fungus gardens within the mounds (Pearce 1981, Jones 1990). *Macrotermes* species are affected by seasonal climate changes, forcing them to descend deeper (sometimes greater than 40 meters) into their mounds during the dry season to escape the sun and heat (Lepage et al. 1974). *Macrotermes* in Guinea have been found to construct their mounds differently according to temperature and habitat type (Korb & Linsenmair 1998). Air circulation passages are constructed to maintain a temperature between 25-30 degrees Celsius and humidity of 94±4% (Darlington 1984, 1985, Vogal 1978).

My previous research on termite ecology at Fongoli also indicated another genus of termite was possibly consumed by the chimpanzees, but this was never confirmed via direct observation (Bogart, 2005). The grass-harvesting *Trinervitermes* species is more active in the dry season, foraging on the surface of the ground (Ohiagu, 1979). These termites are fairly small and taste like dirt (personal observation).

Previous research confirmed that the Fongoli chimpanzees consume weaver ants (*Oecophylla longinoda*), an army ant (*Dorylus*) species and honeybees (*Apis mellifera*) (Pruetz 2006). No survey has been conducted at Fongoli to explore the diversity of ant or bee species. Weaver ants are large, arboreal, and aggressive (Wilson 1975). Army ants (*Dorylus* (*Anomma*) *burmeisteri*) are very large (Figure 7.1b) and have the largest colonies of any social insect, as many as 20 million workers (Wilson 1975). These ants typically attack and prey on termites and other arthropods (Wilson 1975).

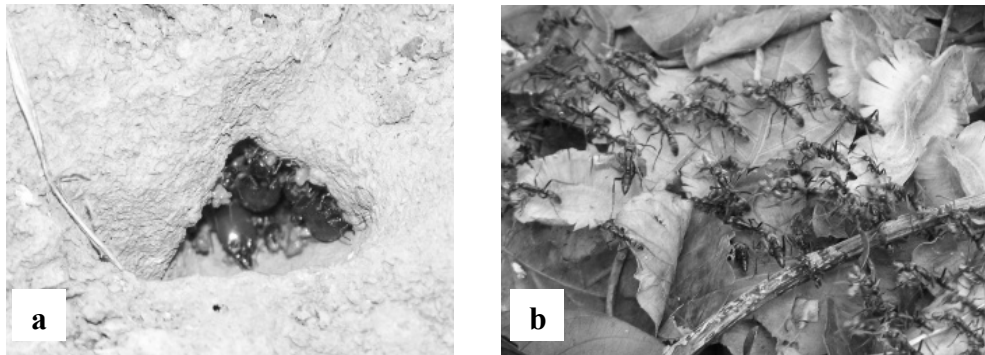


Figure 7.1: Insects at Fongoli: a) *Macrotermes* spp heads coming out of nest hole, b) army ants. (Pictures taken by Sally Macdonald).

The Fongoli chimpanzees are known to consume stinging honeybees, as a consequence of raiding their hives for honey (Pruetz 2006). Honeybees live in colonies of tens of thousands and construct hives (Wilson 1975). I examined the insects (ants and termites) available at Fongoli for the chimpanzees, using several ecological methods to obtain data on the insect distribution and the chimpanzee use of insects as a food resource.

7.2 Methods

All termite mounds used by the chimpanzees in my presence were recorded as to the habitat, percent vegetation cover, feeding plant resources within five meters, soil moisture

(dry, moist, or wet), and length, height, and shape of the nest. Nest shape followed Bogart (2005). Activity of termites was based on the amount of new holes sealed on the mound (distinguished by soil consistency) and was scored from zero to three, where zero is the equivalent of no activity (abandoned) and three is a mound of high activity. Insect samples were taken from most termite mounds and sent to Dr. Rudolf Scheffrahn from the University of Florida for identification. Tools were collected from each mound. Tool length was measured, and the species of plant was recorded, if known.

Ant nests observed to be used by the chimpanzees were recorded as to the habitat, percent vegetation cover, feeding plant resources within five meters, soil moisture, and circumference of the tree at the location of the nest. Activity of the ants was assessed using an estimate of individuals reacting to disturbance: few (1-99), many (100-999), and enormous (>1000) following Schöning et al. (2007). Samples were collected and sent to Dr. Caspar Schöning from the University of Copenhagen for identification. Used tools were collected, length was measured, and the species of plant was noted.

Behavioral methods are explained in detail in Chapters Three and Six. When insect eating was observed, I noted every instance a new tool was obtained by the chimpanzee focal subject.

7.3 Results

7.3.1 Termites in the diet

As discussed in Chapter Six, termites made up 24.1% of the total diet from focal observations (see Figure 6.8) and were consumed more often from April through July. Termite fishing accounts for 8% of the chimpanzees' active time annually (Chapter Six), and

composes a larger portion of their total activity during the wet season (10% of time) than the dry season (6% of time). All focal subjects, ten males, were observed termite fishing during this study (Table 7.1). Termites became a prominent food resource in April (late dry season), with this emphasis lasting through July (wet season) (see Figure 6.4). Termite fishing, as an activity, was primarily during the late dry season, in April and May (42.4%), and during the early wet season, in June and July (46.6%) (Figure 7.2). Fecal remains reveal termites are consumed in August, October through February, April and June (see Table 7.4), providing evidence for termite fishing during months when it was not observed due to poor visibility conditions, i.e. tall elephant grass, in October and December. Therefore, termites are consumed all year long (see Table 7.4).

Table 7.1: Termite fishing data taken from 10 adult males at Fongoli from August 2006 through July 2007 (organized by proportion of total frequency data).

Male	Total number of termite fishing bouts	Proportion of frequency of termite fishing data (%)	Total time termite fished (minutes)
KL	20	16.84	620
Lupin	15	14.96	595
Bandit	21	12.49	435
Diouf	18	10.25	380
Mamadou	17	10.25	370
Bilbo	13	9.07	315
Siberut	15	8.72	320
Yopogon	16	6.36	200
Foudouko	9	6.24	235
Karamoko	7	4.83	170

A bout is a temporal cluster of a behavior repeated in succession several times (Martin & Bateson 1993). Bout length was an estimate based on the instantaneous data. For instance, a male termite fished for 10 of the five-minute intervals, the bout estimate is 45 minutes. The estimated average time a focal male termite fished during a single bout was 12 minutes (range = 0-180 minutes, SD = 13). The monthly averages of termite fishing bout

durations (estimated) are displayed in Figure 7.3. April holds the highest average duration at 37 minutes (0-180 minutes). The average bout duration during the wet season was approximately 10 minutes (total time 1700 minutes), while the average duration of termite fishing bouts during the dry season was about 13 minutes (total time 1940 minutes).

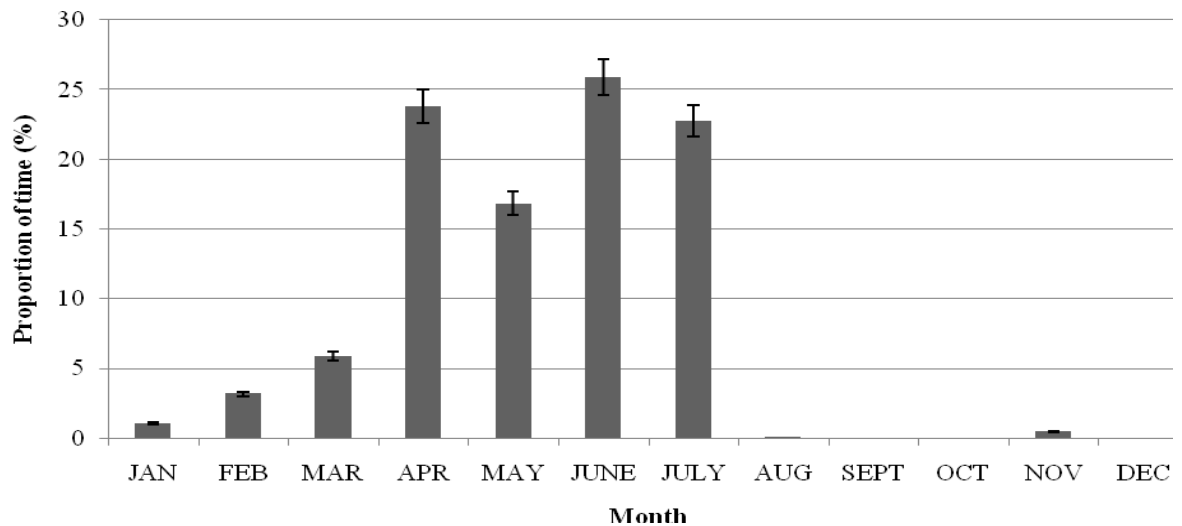


Figure 7.2: Monthly proportion of total time spent termite fishing by 10 adult male chimpanzees at Fongoli from August 2006 to July 2007.

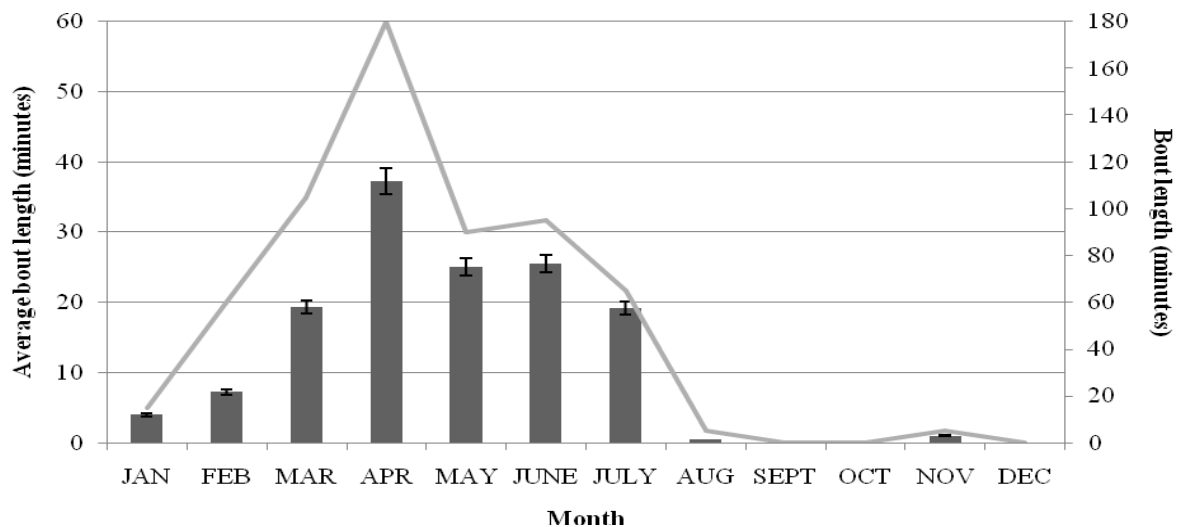


Figure 7.3: Monthly average bout duration (bar) and maximum bout length (line on secondary axis) of termite fishing adult male chimpanzees at Fongoli from August 2006 to July 2007.

The average feeding rate of termite intake is 8.4 per minute (range 2.3-32.5 termite per minute, $N=20$, $SD = 6.9$) (see Chapter Six). Therefore, an average bout of 31 minutes would provide a chimpanzee with 259 termites. Combining this with the data on water content, an average bout of termite fishing would provide 7.8 grams of water (Table 7.2). However, out of the 20 observations used to measure intake, only one was collected during the wet season. This observation had the highest rate of intake at 32.5 termites per minute (Table 7.3). The average rate of intake for the dry season is 7.13 termites per minute (range 2.3-17.33 termites per minute) (Table 7.3).

Table 7.2: Rate of intake, water content, and average duration of a bout for termite eating to calculate the average amount of water intake from a bout of termite fishing.

	Rate per minute	Water per unit (grams)	Total grams per minute	Average duration (minutes)	Average water intake (grams)
Termites	8.4	0.03	0.25	30.8	7.76

Table 7.3: Seasonal variation of total time termite fishing, average bout length, and rate of intake of termites.

	Wet	Sample size	Dry	Sample size
Total time (minutes)	510	90	1022	61
Average bout length (minutes)	11.78	90	24.28	61
Rate of intake (per minute)	32.5	1	7.13	19

7.3.2 Other insects in the diet

In Chapter Six, I showed that insects are consumed throughout the year at Fongoli, based on both fecal and behavioral data. Table 7.2 displays the animal diet of the Fongoli chimpanzees. Ants were only observed to be eaten by the chimpanzees from June to August but were found in fecal remains in August, September, November, December, and June (Table 7.4). There was a total of three genera of ants consumed: *Oecophylla longinoda*, *Dorylus (Anomma) burmeisteri*, *Pachycondyla analis*. Weaver ants (*Oecophylla longinoda*)

were found in fecal samples (57%), and chimpanzees were seen eating these ants during focal follows in June and July. Army ants (*Dorylus burmeisteri*), also known as driver ants, were found in fecal remains (43%) and were observed to be eaten as well. Chimpanzees were also seen to eat *Pachycondyla analis* were ants.

Honeybees (*Apis mellifera*) were found in five fecal samples (3.5% of samples) during November through January and in May. The presence of bees was assumed to be a result of honey consumption, as only one or two whole bees were found in each fecal sample. Chimpanzees were observed eating honey in April and July. Observations were generally brief due to honeybee attacks after a chimpanzee raids a hive. Several instances were observed in which a chimpanzee hastily grabbed a honeycomb and ran. This instigated the bees to attack anyone in close proximity, often the observer, and observations could not be recorded accurately. Thus, data are underrepresented in terms of honey/bee consumption.

Table 7.4: Monthly observed (O) and fecal (X) data of animal matter in the diet.

	Aug	Sept	Oct	Nov	Dec	Jan	Feb	Mar	Apr	May	Jun	Jul
Termite	O, X		X	O, X	X	O, X	O, X	O	O, X	O	O, X	O
Ant	X, O	X		X	X						O, X	O
Honey/Bee				X	X	X			O	X		O
Meat	O											O

7.3.3 Vertebrate Diet

Three observations of non-bushbaby meat eating were recorded during this study. The first was of a sub-adult female, Tia, eating a banded mongoose (*Mungos mungo*) (Bogart et al. 2008). This instance lasted two hours, but was not recorded during focal sampling because subjects were exclusively adult males. The second observation was in July when an adult

male, Siberut, consumed a vervet, or green, monkey (*Chlorocebus aethiops*). The duration of this observation was approximately 25 minutes. In June, a bushbuck (*Tragelaphus scriptus*) was obtained and consumed by many individual male and female chimpanzees. The duration is unknown and this data was again not included in focal observations.

Twelve observations of bushbaby (*Galago senegalensis*) hunting were observed from June 2007 through August 2007 (June: 8, July: 2, August: 2) (Pruetz, unpublished data). These data were not included in focal data, as most were exhibited by females and adolescents. Of these 12 hunting attempts, two were successful (one in July by a subadult female and one in August). The hunting and obtaining of a bushbaby by Fodoukou (adult male subject) was observed in August.

7.3.4 Ant nests

Chimpanzees used a total of ten ant nests during this study. Of the ten, two were identified as army ants (20%), and five were *Pachycondyla analis* (50%) (Table 7.5). All ant nests were recorded in the wet season. All ant nests were in woodland habitats, with 60% in open and 20% in closed woodland. The soil conditions of ant nests were recorded as dry in 50% of all observations. Thirty percent of nests were considered moist, and none were wet. This may have had some effect on ant activity, but little is written on African ants. It appears that the moist nests were used in the middle of the wet season. The average vegetation cover was 70% (median 70%), with a range of 65-95%. The average circumference of the trees where the nests were located was 113.6cm (median 75cm), with a range of 15-350 cm. None of the nests were considered 'enormous' in terms of ant population (following Schöning et al. 2007). Seventy percent of nests had an estimated population of 'few' (1-99) and 10% 'many'

(100-999). Four samples of ants (*Dorylus* and *Pachycodyla* species) were measured for water content, but the number of ants was not known. The average water content of ant samples was 0.25g (0.23-1.87g, SD = 0.81). These individuals were measured for an average length of 1.6cm (0.53-2.1cm, SD = 0.66).

Table 7.5: Characteristics of ant nests used by focal male subjects from August 2006 through July 2007 at Fongoli.

Nest number	Date	Habitat	Soil ¹	Percent vegetation cover	Tree circumference (cm)	Ant classification	Nest suitability ²
100	8/16/06	Woodland	D	80	350	<i>Dorylus burmeisteri</i>	M
101	8/17/06	Closed woodland	M	95	45	no ants recovered	F
102	8/25/06	Woodland	M	40	30	<i>Pachycondyla analis</i>	F
103	6/13/07	Closed woodland	D	65	180	<i>Pachycodyla analis</i>	F
104	7/6/07	Woodland	M	--	--	<i>Pachycodyla analis</i>	F
105	6/22/07	Woodland	D	65	15	no ants recovered	F
106	6/22/07	Woodland	D	70	75	<i>Pachycodyla analis</i>	F
107	6/22/07	--	--	--	--	<i>Dorylus burmeisteri</i>	--
108	6/26/07	--	--	--	--	no ants recovered	--
109	6/28/07	Woodland	D	75	100	<i>Pachycodyla analis</i>	F

¹ Soil: moist (M), dry (D) ² Nest suitability: few (F), many (M), enormous (E)

7.3.5 Termite mounds

During this study, 64 termite mounds were marked and recorded where chimpanzees termite fished for over 10 minutes during a single bout. Two mounds were revisited on another day, providing a total of 66 samples. Mounds were used more during the dry season (65%) than the wet season (35%). However, when controlling for season length, use was not significantly different than the expected values ($\chi^2 = 0.59$, $df = 1$, p -value = 0.06). Woodland comprised the majority of the habitat type that chimpanzees use to termite fish (80%) (Figure 7.4). Fished termite mounds were found in closed forests in 23% of the sample (Figure 7.4).

A total of 89% of the mounds were classified with dry soil and 11% of moist soil. The average vegetation coverage was 51.2% (median = 55%), with a range of 0-90%. Termite mounds used by the chimpanzees had an average width of 338.2cm (median 340cm, range 30-550cm) and height of 121.8cm (median 100cm, range 8-400cm). Most mounds were classified as convex in shape (97%) and the other 3% as castle. Convex mounds are semicircular in shape, whereas, castle shaped mounds are large with stalagmite structures. The average scored (0-3) termite activity is 1.98 (median = 2, range 1-3). Termite samples were collected from 27 of the mounds. All termite mounds contained *Macrotermes subhyalinus* except two; one was *Trinervitermes trinervius* and another *Microtermes* species. Six samples containing 328 termites were measured to obtain a water content of 0.03g/termite (0.02-0.06g/unit, $SD = 0.03$). The total average length of *Macrotermes* was 1.12cm (0.09-2.15cm, $N=11$, $SD = 0.84$).

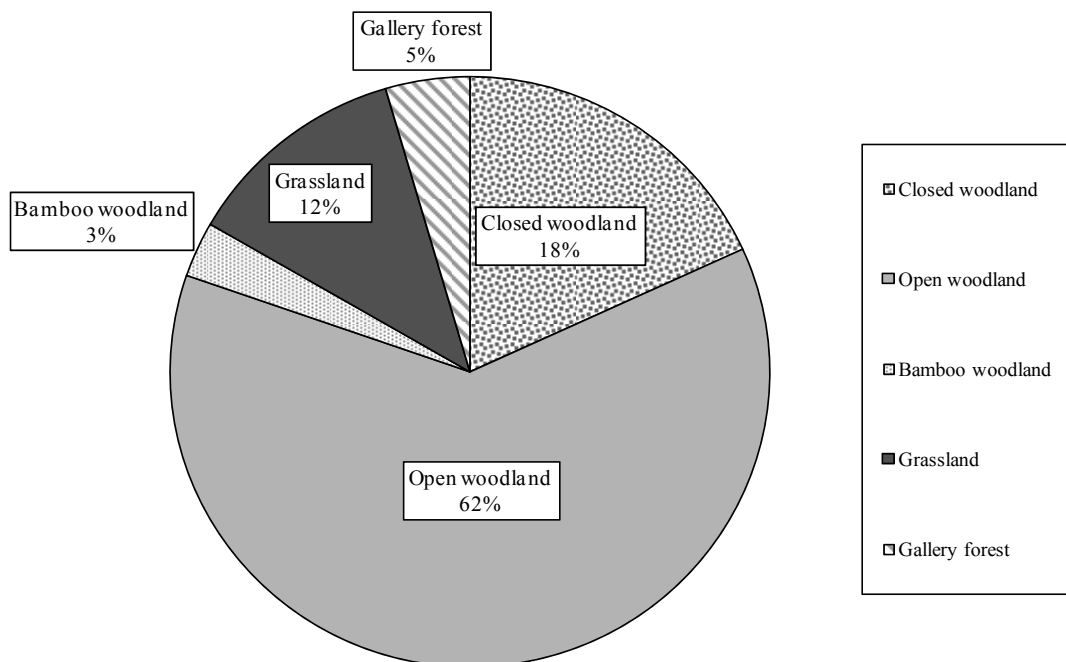


Figure 7.4: Termite mounds used by focal male chimpanzees from August 2006 through July 2007 and their distribution among habitat types.

7.3.6 Tools

There were a total of nine tools found at ant nests used by the chimpanzees at Fongoli. The average length is 38.9cm (median 38.4cm, $SD = 9.9$) with a range of 25.7-60cm. *Hexalobus monopetalus* (67%) was the main species used to make the tools ($n = 6$). *Saba senegalensis* (22%) and *Vitex madiensis* (11%) were the other materials used.

A total of 470 tools were collected from termite mounds. The average number of tools at a mound was 9.4 (1-48). The average length of the tools was 29.9cm (median 27.5cm, $SD = 12$), with a range from 9.2-96.5cm. There was no significant difference in tool lengths between seasons (Student t -test, $df = 149$, p -value = 0.07) (Table 7.6). Accounting for season length, an average of 45.7 tools were found during the dry months and 30 tools per wet month. Tools were made from twigs, vines, and grass. Of the grass-made tools, four were found during February and March (dry season). Tools were mostly made from *Saba senegalensis* (51%), *Grewia lasiodiscus* (16%), *Daniellia oliviera* (9%), and *Hexalobus monopetalus* (9%).

Table 7.6: Characteristics of termite fishing tools used by Fongoli chimpanzees from August 2006 through July 2007 during the wet and dry seasons.

	Dry season tools	Wet season tools
N = total tools	320	150
Mean (cm)	28.9	31.9
Maximum (cm)	95.5	96.5
Minimum (cm)	9.2	12.2

7.4 Analyses

7.4.1 Insect foraging, rainfall, and temperature

Rainfall did not correlate with termite fishing in frequency (Spearman's rank correlation $\rho = 0.01$, p -value = 0.97) or average bout duration (Spearman's rank correlation $\rho = -0.09$, p -value = 0.79). The Fongoli chimpanzees exhibit no seasonal preference for termite fishing. Rainfall positively correlated with ant nests recorded as used by chimpanzees (Spearman's rank correlation $\rho = 0.65$, p -value = 0.02) but not with frequency of ant dipping (Spearman's rank correlation $\rho = 0.40$, p -value = 0.20).

Table 7.7: Monthly proportion of termite fishing, rainfall, average soil temperature, and average air temperature.

	Proportion of termite fishing (%)	Rainfall (mm)	Average soil temperature (°C)	Average air temperature (°C)
August	0.12	236.4	26.4	26.6
September	0.00	210	26.1	25.9
October	0.00	87.7	26.3	27.0
November	0.47	0	25.5	27.3
December	0.00	0	---	26.5
January	1.06	0	23.3	25.8
February	3.17	0.5	28.5	29.6
March	5.87	0	31.9	31.8
April	24.06	0.2	36.4	32.9
May	16.78	14.4	35.9	31.5
June	25.82	125.1	32.6	27.9
July	22.65	92.8	---	27.0

Average soil temperature (Table 7.7) positively correlated to frequency of termite fishing (Spearman's rank correlation $\rho = 0.77$, p -value = 0.01). Frequency of termite fishing also positively correlated with air temperature (Spearman's rank correlation $\rho = 0.70$, p -value = 0.01). Average air temperature positively correlated with the proportion of time spent on termites in the diet (Spearman's rank correlation $\rho = 0.67$, p -value = 0.02) (Table 7.7), as

well as with average bout length of termite fishing (Spearman's rank correlation $\rho = 0.79$, p -value = 0.002). Ant dipping did not correlate with average soil and air temperatures (Spearman's rank correlation $\rho = -0.51$, 0.07, p -value = 0.09, 0.82, respectively). However, number of used ant nests recorded did negatively correlate with average soil temperature (Spearman's rank correlation $\rho = -0.59$, p -value = 0.04).

7.4.2 Chimpanzee use of insect nests and insect nest availability

Chimpanzees displayed a selective use of habitat type for termite fishing ($\chi^2 = 92.03$, $df = 6$, p -value < .0001). Using Pearson's residuals, the selective use of open woodland habitat for termite fishing is greater than what is expected regarding the availability of this habitat (Table 7.8). There exists a strong avoidance of grassland for termite fishing relative to the availability of this habitat (Table 7.8). Termite mounds were used more often in the dry season than the wet season (Table 7.9). The chimpanzees displayed a clear preference for closed habitat types and open woodland and avoidance of all other habitat types for termite fishing (Table 7.8; Jacobs preference index: -1-0 = avoidance, 0-1 = preference). Use was proportionate to the availability of termite mounds, represented by density (Table 7.9).

Table 7.8: Proportion of termite mounds used by focal male chimpanzees from August 2006 through July 2007 in relation to availability of habitat types to provide a preference index.

	Proportion of used termite mounds (N)	Proportion of habitat	Jacobs preference index (D)
Closed woodland	18.2% (12)	2.9%	0.76
Open woodland	62.12% (41)	13.7%	0.82
Bamboo	3.03% (2)	9.9%	-1.00
Grassland	12.12% (8)	67.3%	-0.87
Closed forest	4.54% (3)	1.2%	0.97
Field	0	5%	-1.00

Table 7.9: Seasonal use of termite mounds by focal male chimpanzees from August 2006 through July 2007 and density of termite mounds.

	Used termite mounds	Density of termite mounds (per ha)
Dry season	43 (65%)	29.5
Wet season	23 (35%)	16.1

Ant nests were used only in the wet season (Table 7.10). This is expected in terms of the availability of ants, using density data obtained from insect transects and ant plots (see Chapter Five). Army ants were recorded using plots only during the wet season.

Table 7.10: Ant nest use by male chimpanzees and density per hectare during this study.

	Used ant nests	Density of ants nests (per ha)
Wet	10	8.04
Dry	0	6.25

7.4.3 Termite fishing in relation to fruit availability

The average monthly fruit availability index (FAI) for all fruits monitored on the feeding transect positively correlated to the monthly average FAI of five of the top ten fruits analyzed in Chapter Six (Pairwise correlation $r = 0.78$, p -value = 0.003). This suggests that using the five foods for analyses provides a relative indicator of all fruit availability. Also, the top ten ranked fruits comprised the majority of the fruit-based diet (88%), with the five fruits used for fruit availability index encompassing 62% of top ranked fruits. Here, I address whether termite fishing is correlated with fruit availability (Figure 7.5). There was no correlation using Spearman's rank comparing average bout length of termite fishing and fruit availability (Spearman's $\rho = 0.49$, p -value = 0.11) (Figure 7.5). Additionally, there was no correlation between the total time chimpanzees termite fished each month and the availability of fruit (Spearman's $\rho = 0.32$, p -value = 0.31). The proportion of time spent (using frequency

data) termite fishing each month was not correlated to fruit availability (Spearman's rank correlation $\rho = 0.47$, p -value = 0.17). This revealed that termite fishing was not reliant on fruit availability (Figure 7.5).

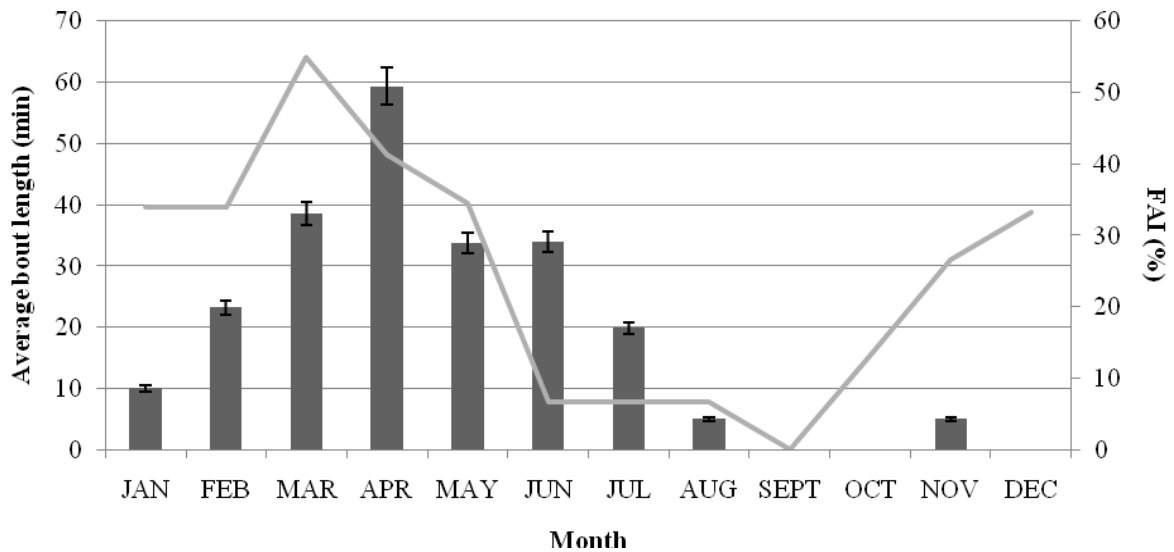


Figure 7.5: Average fruit availability (FAI%) for five top ranking fruits (line and secondary axis) and average termite fishing bout length by focal male chimpanzees (bar) from August 2006 through July 2007.

7.4.4 Termite fishing in relation to leaf availability

The amount of leafing trees was examined for its influence on termite fishing. The number of consumed tree species leafing did not correlate with the proportion of feeding time spent on termites (Spearman's $\rho = -0.38$, p -value = 0.22), as well as with the frequency of termite fishing conducted as an activity (Spearman's $\rho = -0.41$, p -value = 0.19) (Table 7.11). Average bout length negatively correlated with the number of consumed leafing trees species (Spearman's $\rho = -0.59$, p -value = 0.05), but did not correlate with leaf consumption by focal male chimpanzees (Spearman's $\rho = 0.10$, p -value = 0.77) (Table 7.11).

Table 7.11: Leaf availability and consumption in relation to termite consumption and termite fishing from August 2006 through July 2007.

	Proportion of tree species leafing (%)	Leaf proportion of feeding budget (%)	Termite proportion of feeding budget (%)	Average bout length of termite fishing (minutes)	Proportion of termite fishing (%)
January	86.0	0.0	2.2	4.0	1.1
February	54.8	0.0	9.8	7.3	3.2
March	28.0	1.8	13.0	19.3	5.9
April	22.6	3.9	46.6	37.2	23.8
May	44.1	5.2	62.2	25.0	16.8
June	94.6	13.4	62.7	25.5	25.9
July	98.9	9.8	57.3	19.2	22.7
August	87.1	5.4	0.9	0.5	0.1
September	96.8	9.0	0.0	0.0	0.0
October	96.8	6.0	0.0	0.0	0.0
November	97.8	0.0	1.7	1.0	0.5
December	95.7	0.2	0.0	0.0	0.0

7.5 Discussion: Are insects important?

From the data presented here, I conclude that termites are an integral element of the Fongoli chimpanzee diet. The only month of the year when termites were not consumed by Fongoli chimpanzees was September. This may be due to the relatively sparse behavioral data collected in September (Table A7), because Pruett (2006) did find evidence of termites in the diet during this month in a previous study. Thus, I can reliably state that termites are eaten year-round at Fongoli. The Fongoli chimpanzees can spend up to 19% of their active daily budget on termite fishing in the late dry season, and termites can make up more than half of their feeding budget in the late dry season (May = 62.2%) and early wet season (June = 62.7%) (see Chapter Six). Termites are proportionally high in the Fongoli chimpanzee diet relative to that of other chimpanzees (discussed in Chapter Eight) and are consumed proportionally more in relation to other food items during the wet season. However, data on

termite fishing is distributed equally over the seasons and is not correlated to rainfall or to fruit scarcity. Thus, termite fishing is not a seasonal behavior and it is not a result of low fruit availability. Feeding and foraging, including termite fishing, comprises 34% of the chimpanzees' active time in the dry season and drops to 26% during the wet season. This difference of 8% appears to be the result of an increase in resting, which rose from 42% in the dry season to 51% in the wet season. The chimpanzees exhibited a longer average termite fishing bout length in the dry season than the wet season. The increased bout length may be a result of termite activity. It may take longer to obtain termites in the dry season due to their descent further underground as a result of high temperatures (Lepage et al. 1974). However, at Fongoli, data indicated that termite fishing increased as soil and air temperature increased. This increase may be due to the fact that termites are harder to obtain and thus spending more time termite fishing was needed to obtain enough termites to complement the diet. Therefore, temperature, rather than rainfall, plays a role in bout length and frequency of termite fishing. From this data I suggest that termites are not seasonally preferred in terms of rainfall, since the majority of termite fishing occurs over four months, April through July, that span both late dry and early rainy seasons. Additionally, the Fongoli chimpanzees prefer closed and open woodland habitats for termite fishing, providing support for the stated hypothesis and concurring with my previous research (Bogart 2005). Termite mound characteristics also duplicate findings regarding *Macrotermes* species found in my previous research (Bogart 2005).

Termite fishing tools recorded in the present study match those found in my previous research (Bogart 2005). The average length of a termite fishing tool at Fongoli is 29.9 cm, which is very similar to previous findings of 29.5 cm (Bogart 2005). On average, 9.4 tools

can be found at a mound, and the dominant material used to make the tool was *Saba senegalensis*, which also coincides with previous research (Bogart 2005). Previous research indicated that *Saba senegalensis* was generally found within 1.1m from a termite mound (Bogart 2005).

Chimpanzees were only observed to eat ants in the wet season during this study, but fecal analyses suggest consumption during November and December (dry season) as well. Three species were consumed: *Oecophylla longinoda* (weaver ant), *Dorylus* (*Anomma*) *burmeisteri* (army ant), and *Pachycondyla analis*. Army ants were also found in the dry season fecal samples. Pruetz (2006) found army ants in fecal remains and feeding traces in the dry season as well, in December and from February to April. She also found weaver ants were eaten in February and May (Pruetz 2006). However, this is likely due to sampling error in this study as the previous study contained a larger fecal sample. Density data indicate army ants are rare in the dry season (zero/ha using ant plots, 6.25/ha using transect data). Use of ants in the diet correlated with their availability at Fongoli. Ants were always consumed in woodland habitats. Nest suitability was mostly scored as “few”, with one nest scored as “many”. Schöning and colleagues (2007) determined that the categories of ‘many’ and ‘enormous’ were suitable for ant dipping by chimpanzees. Are ant nests at Fongoli “unsuitable” for the chimpanzees? This may be one reason the chimpanzees do not consume ants very often in relation to termite consumption, or it may be that the chimpanzees eat so many of the ants from a nest, that by the time it was sampled, few ants were left. Further research into nest suitability at unused ant nests should be employed in the future. Tools used to ant dip had an average length of 38.9cm and were most commonly made of *Hexalobus monopetalus*.

Honeybees (*Apis mellifera*) were typically consumed during the dry season in this study, with one observation in July (wet season). This is similar to previous findings. Pruetz (2006) found honeybees consumed from February through June (observation and feeding traces). Research is needed as to the activity of the bees and availability at Fongoli.

Honeybees are perennial and have large colonies (Wilson 1975). Thus, bees and honey should be available all year long, but may not be from the same source (i.e. flower species' seasonality) and may have a different taste (Pruetz, personal communication). As explained before, observations of honey eating is usually interrupted due to bee attack, providing underrepresented data on this behavior. Several human individuals with agricultural fields around Fongoli's range harvest bees and their honey and they have complained that the chimpanzees raid their hives (personal observation). This is likely another reason for the limited observations, as chimpanzees are harder to follow and watch when they are close to human villages or fields (personal observation). However, this behavior is also costly and may be represented correctly in the study.

One species of termite, three species of ants, and one species of bee comprise the insect diet at Fongoli. Other animal diet in this study was not systematically observed except for one case of bushbaby feeding and one of vervet monkey feeding. Data presented in this chapter and in Chapters Five and Six will be reviewed and compared to findings at other chimpanzee research sites in the next chapter. Implications of this study will also be discussed in the concluding chapter.

CHAPTER EIGHT

Conclusions: Savanna chimpanzees

8.1 Introduction

The Fongoli chimpanzees spend most of their feeding time budget on fruit (61%) and termites (24%), and can spend more than half their monthly feeding time on termites (62%). Insectivory at Fongoli is a prominent activity that can last up to three hours in a single bout. A number of variables were examined to investigate the behavioral ecology of savanna chimpanzees as it relates specifically to their insectivory at the Fongoli, Senegal research site. This dissertation provides the first research to extensively study the behaviors of the Fongoli chimpanzee in regards to their insectivorous diet. Research conducted previously at Fongoli indicated chimpanzees termite fish throughout the year (Pruetz 2006, Bogart & Pruetz 2008). This differs from many other chimpanzee sites (McGrew 1983, McGrew et al. 1979, McGrew & Collins 1985). I hypothesized that the environment of this hot, dry site was a variable influencing this behavior. Published data is limited on savanna chimpanzee behavior and ecology (McGrew et al. 1979, McGrew & Hunt 2002, Moore 1996, Pruetz 2006, 2007, Pruetz & Bertolani 2007). Lack of habituation in the past has prevented detailed data on chimpanzee behavior. Objectives examined here included assessing availability and use of food resources in the diet of the chimpanzees with a focus on the inclusion of insects in the diet and in the context of chimpanzee habitat use and activity budget. Tool use in extractive foraging was also investigated. The savanna environment at Fongoli was assessed as to its impact on the variables considered in this study. This research revealed a number of correlations between the environment and chimpanzee behaviors, including significant

differences between the diet of the Fongoli chimpanzees and chimpanzees living in more forested environments.

8.2 Summary of results

The environment at Fongoli has significant effects on the behavior of the chimpanzees living here. Fongoli is dominated by grassland habitat types (68%) and can be characterized as a savanna, with open habitats comprising 91% of the chimpanzees' home range. Closed forest habitat types (4%) were associated with resting and social behaviors and were used more during times of little to no rainfall. Conversely, woodland and grassland habitat types were important for feeding and foraging, including termite fishing. These habitats had the highest proportion of plant feeding resources (84%), lending support to the prediction that fruit would be widely distributed in woodland habitats. Results here demonstrate that habitat use is correlated with activity and, in terms of feeding, reflect food availability. These data provide evidence in favor of the prediction that states that time spent feeding would be in woodland habitats where food resources were expected to be denser. The Fongoli chimpanzees spent most of their active day resting (45%), followed by foraging and feeding (32%). Time spent feeding and foraging is greater in the dry season, negatively correlating with rainfall. High temperatures were correlated with increased termite fishing and social behaviors. This data indicate that Fongoli chimpanzees feed and forage more when fruit abundance is high and rested more with fruit scarcity. This correlates with what was found at Bossou, Guinea (Takemoto 2003). These behaviors are indicators for deviations from the optimal foraging model. During the dry season, the Fongoli chimpanzees spend most of their feeding time on fruits, termites, and flowers. During the wet season, termites,

bark, fruit, leaves, ants, and other animal prey are the food items that Fongoli chimpanzees spend most of their daytime feeding on.

Fruit comprised the majority (61.3%) of the Fongoli chimpanzees' time spent feeding in this study, thus frugivory is foremost similar to what has been observed in chimpanzees elsewhere (Basabose 2002, Ghiglieri 1984, Hladik 1977, Hunt & McGrew 2002, Kuroda et al. 1996, McGrew et al. 1988, Morgan & Sanz 2006, Newton-Fisher 1999, Nishida & Uehara 1983, Stanford & Nkurunungi 2003, Sugiyama & Koman 1992, Tutin & Fernandez 1993, Tutin et al. 1991, 1997, Wrangham 1977, Yamagiwa & Basabose 2006). Fruit resource availability was negatively correlated with rainfall, with fruit scarcity during the wet season. This seasonality in fruit availability does affect diet composition, with the chimpanzees consuming fruits significantly more in the dry season. This supports the hypothesis that seasonality has an effect on the availability and use of food resources in this environment. Chimpanzees use foods in proportion to their availability. Fruits of *Adansonia digitata* (baobab) and *Saba senegalensis* were important foods for the chimpanzees and were available during the dry season at Fongoli. A total of 39 plant species and 51 plant parts were consumed during this study. Three species and 15 plant parts were not recorded in the previous study by Pruetz (2006). Two new species of vertebrate and one new species of ant were added to the initial report on the Fongoli chimpanzee diet (see Table 6.13).

The second major component of the Fongoli chimpanzee diet is termites (24.1%). Data presented in this research does not support that leaves would be the second major component in the feeding budget in the diet similar to what has been observed in early studies at Fongoli (Pruetz 2006) and other chimpanzee communities (Section 8.5). The chimpanzees consume *Macrotermes subhyalinus*, as demonstrated from observations and

fecal analyses, and this offered support for the hypothesis stated in Chapter One that only *Macrotermes* termites would be consumed at Fongoli. Termite mounds of *Macrotermes* were abundant at Fongoli, with a density of 23.6 mounds per hectare. The dry season (29.5/ha) was found to contain a higher density than the wet season (16.1/ha), but this may have been a factor of decreased visibility during the wet season. Termite fishing occurs all year long and did not correlate with rainfall in terms of frequency, thus supporting the hypothesis that seasonality will not affect termite fishing. In addition, termite consumption is not correlated with low fruit abundance, supporting the hypothesis that fruit scarcity will not affect termite fishing. However, the chimpanzees at Fongoli spend more time and longer bouts termite fishing during the dry season, correlating with high temperatures. Most termite feeding and foraging occurs during the transitional period between the late dry season and the early wet season, from April to July, and in open woodland habitats. This stage of the annual cycle was associated with more variation between open and closed habitat soil temperatures (see Chapter Five). These soil temperatures were positively correlated to termite fishing frequency (Chapter Seven). The higher proportion and longer bouts of termite fishing in the hot, dry season may be related to termite ecology. Temperature does affect *Macrotermes* density among habitat types and mound architecture (Korb & Linsenmair 1998), and their mounds have an impact on the chemistry of the ecosystem (Jones 1990). Termites usually delve deeper underground to escape the heat in dry seasons (Lepage et al. 1974). Further investigation of termite behavior at Fongoli would be needed to test this hypothesis.

Fongoli chimpanzees consumed several ant species: *Oecophylla longinoda* (weaver ant), *Dorylus (Anomma) burmeisteri* (army ant), and *Pachycondyla analis*. Ants were represented in less than 1% of the diet but consumed through much of the year (fecal and

observational data). Army ant density was highest in the wet season, and Fongoli chimpanzees were observed to consume them more at this time. This does not support the hypothesis that seasonality will not affect ant dipping. Availability may impact the use of ants in the Fongoli diet. The fact that termites are found at significantly higher densities than ants at Fongoli may also be a contributing factor. The consumption of honeybees (*Apis mellifera*) is a by-product of beehive raiding. It was difficult to observe honey consumption, but this occurred during the dry season (fecal remains and observation).

8.3 Benefits of insectivory

The high intake of termites in the Fongoli chimpanzee diet likely has various nutritional effects. Insects have more protein and phosphorus content than plant foods as revealed in analyses by Hladik (1977), Conklin-Brittain and colleagues (1998), and Deblauwe & Janssens (2008). Chimpanzees at the Dja Biosphere Reserve in Cameroon consume twice as many insects per day than gorillas at this site and selected termites specifically for certain nutrients (Deblauwe & Janssens 2008). *Macrotermes* species eaten by the Dja chimpanzees provided significant protein intake per day as well as the daily requirements of manganese (Deblauwe & Janssens 2008). Moreover, *Macrotermes* have high levels of iron and zinc (Deblauwe & Janssens 2008), vitamin B₁₂ levels (Wakayama et al. 1984), and lipids (52.8%) (Deblauwe & Janssens 2008). Also, *Macrotermes* likely provide essential amino acids in the chimpanzee diet (Hladik 1977).

Many human cultures consume social insects (DeFoliart 1999, McGrew 2001). According to studies of entomophagy (the consumption of insects) in humans, insects provide more calories (i.e. energy), essential nutrients, and protein than beef, chicken, or fish

(Berenbaum 1995). Many of the nutrients found in termites are used by African people who are malnourished (Berenbaum 1995). Two sources of protein for primates are insects and leaves, which each contain more than 20% protein in dry weight (Hladik 1977). Both monkeys and apes consume leaves for protein (Conklin-Brittain et al. 1998). Leaves are generally the second major component of the chimpanzee diet (Conklin-Brittain et al. 2001). This research found that leaves were more abundant in the wet season and were consumed more often during this time of year. Whereas, time spent feeding on termites was not correlated with rainfall but consumed heavily from April to May, the late dry season and early wet season. The dry season at Fongoli does not offer many leaves for consumption, thus, termites and other prey most likely provide protein for the chimpanzees.

Animal prey is often lumped with both vertebrate and invertebrate animals in the diet of the chimpanzee. However, when dissociated, insects make up most of the proportion (Pruetz 2006, Stanford & Nkurunungi 2003, Tutin et al. 1991). Thus, insects in the diet of chimpanzees provide specific nutrients that are important in growth and maintenance of health (Wrangham 1980). Leaf abundance is minimal during the dry season at Fongoli and the chimpanzees can obtain their protein from termites and other prey. Nutrition may be a driving factor for the high proportion of termites in the Fongoli diet and should be examined in future research. It may be speculated that the high temperatures at Fongoli may affect certain nutrients. Further research should investigate these measures.

8.4 Fallback foods?

A fallback food is a low-quality food that is highly consumed during times of food scarcity (Newton-Fisher 1999, Wrangham 1977, Wrangham et al. 1994, 1998). Fallback

foods (FBFs) are associated with tool use and more extensive food processing, while preferred foods are easy to process but require more harvesting, as they are more widely distributed (Marshall & Wrangham 2007). Marshall and Wrangham (2007) suggest two types of FBFs, staple and filler. Staple FBFs are always in the diet and may compose a large proportion of diet seasonally, while filler FBFs are never a large proportion of the diet and cannot sustain an individual when no other resources are eaten. Tool use has been linked to periods of low fruit availability, and chimpanzees use tools to obtain these high-quality fallback foods (Yamagiwa 2004). However, I propose that tool use for extracting termites at Fongoli does not adhere to this pattern. Rather, leaves and bark/cambium may be the fallback foods at Fongoli.

When fruit availability was low in the wet season at Fongoli, data on the monthly plant food diet revealed that the chimpanzees consume leaves and bark/cambium. The cambium of the tree *Pterocarpus erinaceus* appears to be a staple FBF, because it made up 65.8% of the diet in the month of August; however it is not always included in the diet (Figure 8.1). The consumption of bark is not correlated with monthly fruit availability (Spearman's rank correlation $\rho = -0.26$, $p\text{-value} = 0.42$), nor is it correlated with the monthly fruit consumption (Spearman's rank correlation $\rho = -0.04$, $p\text{-value} = 0.90$). Bark/cambium eating may be medicinal (Krief et al. 2006), but further investigation is needed to confirm this. Mature and immature leaves were available all year long based on transect data, but were more abundant in the wet season. Leaves in the diet did not correlate with fruit availability (Spearman's rank correlation $\rho = -0.23$, $p\text{-value} = 0.48$). There was a negative correlation of leaf-eating with fruit consumption (Spearman's rank correlation $\rho = -0.59$, $p\text{-value} = 0.04$), suggesting leaves are eaten when fruits are not consumed (Figure 8.1). Since

leaves are more abundant in the dry season, when fruit abundance is low, leaves may be a fallback food. I propose leaves as a filler FBF. A total of 23 plant species flowered (70%) during this study, and six species (26%) are known food resources for the Fongoli chimpanzees. Flowers were consumed by the chimpanzees during several months of the year (Figure 8.1). Flower feeding did not correlate with fruit availability (Spearman's rank correlation $\rho = 0.03$, p -value = 0.93), and did not correlate with monthly consumption of fruits (Spearman's rank correlation $\rho = -0.23$, p -value = 0.46). Termites were abundant at Fongoli and are not consumed in relation to fruit availability (Chapter Seven); also, the monthly consumption of termites and fruit did not correlate (Spearman's rank correlation $\rho = -0.22$, p -value = 0.48). Termites are consumed all year long. Thus, this research indicates that flowers and termites are not fallback foods at Fongoli.

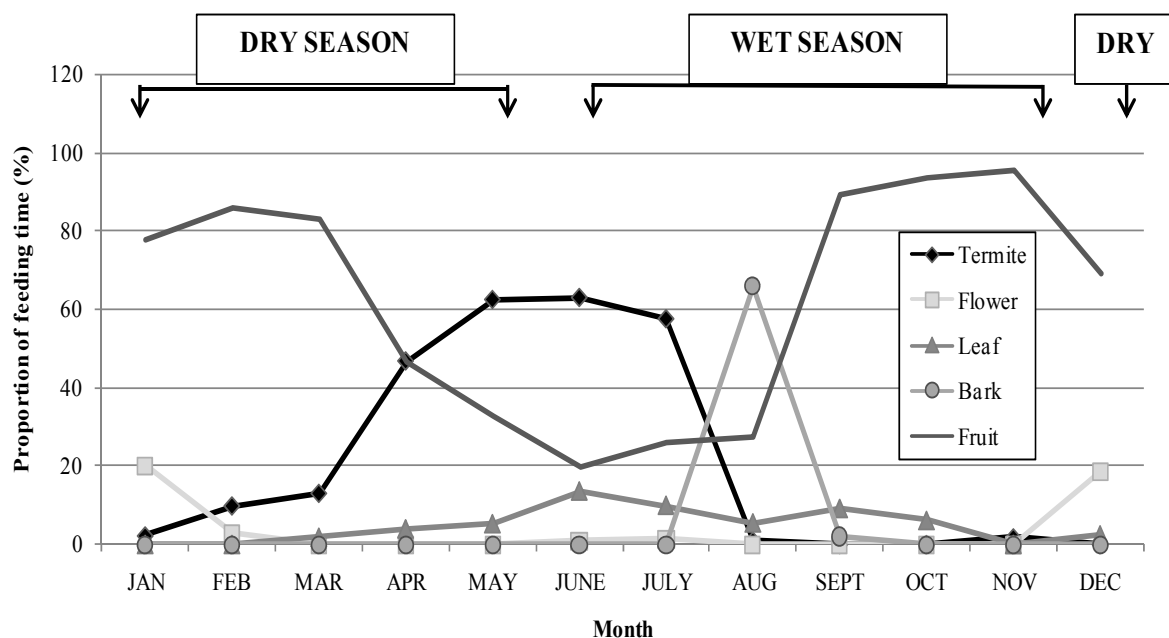


Figure 8.1: Seasonal proportion of feeding budget spent on fruit, termites, flowers, leaves, and bark by the Fongoli chimpanzees (data based on focal male instantaneous sampling) from August 2006 through July 2007.

8.5 How does Fongoli compare to other sites?

Fongoli is the hottest and driest long-term chimpanzee research site in Africa where these apes have been habituated to observer presence (see Chapter Four). This study provides results similar to previous findings on activity (Pruetz & Bertolani, in press). Fongoli chimpanzees rest (45%) more than any other community of chimpanzees, and forage and feed (32%) less (Boesch & Boesch-Achermann 2000, Fawcett 2000, Ghiglieri 1984, Goodall 1986, Teleki 1981, Huffman 1990, Tweheyo et al. 2003). However, the Fongoli diet, time spent feeding, as measured during this study was found to differ from previous research at Fongoli and chimpanzees found at other sites. Tools for extraction of insects also differed compared to results from other chimpanzee sites.

8.5.1 Diet

Fruit is the major component of the Fongoli chimpanzee diet, which coincides with other studies of chimpanzees (Basabose 2002, Ghiglieri 1984, Hladik 1977, Hunt & McGrew 2002, Kuroda et al. 1996, McGrew et al. 1988, Morgan & Sanz 2006, Newton-Fisher 1999, Nishida & Uehara 1983, Stanford & Nkurunungi 2003, Sugiyama & Koman 1992, Tutin & Fernandez 1993, Tutin et al. 1991, 1997, Wrangham 1977, Yamagiwa & Basabose 2006). However, termites are consumed to a greater degree by the Fongoli chimpanzees than chimpanzees at any other site. Comparing the general diet of the chimpanzee, obtained from 7 sites and 8 studies (excluding studies on non-habituated chimpanzees: Semliki, Lope, Goualougo, Ndoki, Assirik, and Fongoli) in Chapter Two, to that of the Fongoli chimpanzees a difference emerges (Table 8.1). Interval estimates of the Fongoli diet (95% confidence interval) provide parameters to examine this difference between the general chimpanzee diet

with that at Fongoli. Seeds are included in fruit consumption at Fongoli. The general diet of chimpanzees contains proportions of leaves, pith, and termites outside of the Fongoli parameters (Table 8.1). The Fongoli chimpanzees spend more time consuming termites and less time on leaves and pith than previously found at other chimpanzee sites.

Table 8.1: General diet of the chimpanzee (7 sites, 8 studies) compared to the Fongoli chimpanzee diet.

	General diet ¹ (%)	Fongoli Diet ² (%)	Fongoli diet Lower CI (95%)	Fongoli diet Upper CI (95%)
Fruit	55.1	61.3	43.2	80.8
Leaves	25.1	4.41	2	7.5
Seeds	2.9	0	0	0
Flowers	5.0	5.1	-1	8.3
Pith/stem	6.6	1.22	0.41	1.8
Bark	2.4	2.15	-6.4	17.7
Termites	2.1	24.1	4.2	38.5
Animal (other than termites)		0.4	-0.14	1.03
Other	0.77	1.32	-0.61	2.6

¹ Averaged from: Basabose 2002, Ghiglieri 1984, Hladik 1977, Newton-Fisher 1999, Nishida & Uehara 1983, Stanford & Nkurunungi 2003, Sugiyama & Koman 1992, Wrangham 1977

² This study

The seasonal fruit availability found at Fongoli is similar to some sites, such as Bossou, Guinea (Takemoto 2004, Yamakoshi 1998), Kahuzi-Biega, Democratic Republic of Congo (Basabose 2002), Ngogo, Uganda (Potts 2004), and Bwindi, Uganda (Nkurunungi 2005, Stanford 2008). The sites of Budongo (Tweheyo & Babweteera 2007) and Kalinzu (Hashimoto et al. 2001), Uganda, and Lope, Gabon (Tutin et al. 1997) have the opposite pattern, with greater fruit available in the wet season. Kibale, in Uganda, displays two peaks of fruiting throughout the year (Wrangham et al. 1998). The diet composition in terms of plant parts and species consumed at Fongoli is considered narrow in relation to most other research sites (Table 8.2). Data presented here is only a portion of the Fongoli diet found;

species and parts consumed are constantly being added (Pruetz, unpublished data). For example this study identified a few more species and parts than previously published work (Pruetz 2006).

Table 8.2: Number of plant parts and species consumed at chimpanzee sites.

Site	Number of plant parts eaten	Number of plant species eaten	Reference
Gombe, Tanzania	141		Hladik 1977
	201		Wrangham 1977
Mahale, Tanzania	328	198	Nishida & Uehara 1983
Budongo, Uganda	118	58	Newton-Fisher 1999
Kibale, Uganda	50		Ghiglieri 1984
Bwindi, Uganda	60	>32	Stanford & Nkurunungi 2003
Semliki, Uganda	33		Hunt & McGrew 2002
Kahuzi-Biega, DRC	137	104	Yamagiwa & Basabose 2006, Basabose 2002
Lope, Gabon		202	Tutin et al. 1997
	142		Tutin et al. 1991
	161		Tutin & Fernandez 1993
Goualougo, Republic of Congo	158	116	Morgan & Sanz 2006
Ndoki, Republic of Congo	114	108	Kuroda et al. 1996
Assirik, Senegal	60	43	McGrew et al. 1988
Bossou, Guinea	246	100	Sugiyama & Koman 1992
Fongoli, Senegal	51	39	This study

Chimpanzees expend 8% of their total active time termite fishing over the year at Fongoli. During the transitional seasons, April through June, the Fongoli chimpanzees spent up to 19% of their activity budget termite fishing. This is comparable to the Gombe female chimpanzees, who can use up to 15% of their wet season active time termite fishing (McGrew et al. 1979, McGrew 1983). Data suggest a sex difference at Gombe, with females termite fishing more than males (McGrew 1979, McGrew 1992), but for other sites, such as Goualougo Triangle, no sex-bias was found (Sanz et al. 2004). Sexual differences could not be examined at Fongoli due to protocol, as all data stem from male focal subjects. Termites are eaten throughout the year at only a few other chimpanzee sites: Okorobiko at Rio Muni

(McGrew et al. 1979), Ndoki forest in the Congo (Suzuki et al., 1995), and Goualougo Triangle in DRC (Sanz et al. 2004). Seasonality of termite fishing occurs during the initial months of the wet season at other sites such as Mt. Assirik, Senegal (McGrew et al., 1979) and Mahale, Tanzania (McGrew & Collins, 1985), and even though Gombe chimpanzees consume termites all year, they exhibit a peak during the wet season as well (McGrew et al., 1979).

Why do the Fongoli chimpanzees consume more termites than chimpanzees at other sites? There may be several reasons for this. It may be that appropriate vertebrate prey is low at Fongoli, and the abundance of termites here provides an opportunity for the chimpanzees to obtain the necessary nutrients and amino acids (Berenbaum 1995, Bogart & Pruetz 2008, McGrew 1983, Pruetz & Bertolani 2007, Sussman 1987, Wrangham 1980). A typical prey species for chimpanzees is the red colobus monkey (*Piliocolobus badius*) (Boesch 1994, Stanford 1998), which are not found in Fongoli's dry savanna habitat. The Fongoli chimpanzees are known to eat other vertebrates, such as bushbabies, but the density of bushbabies is well below that of termite mounds (0.594/ha and 23.6 mounds/ha, respectively) and one *Macrotermes* termite mound can contain two million termites (Harris 1956, Luscher 1955). Bushbabies seem to be consumed seasonally (Pruetz & Bertolani 2007, Pruetz, unpublished data), whereas, termites are consumed all year, with a high intake from April to July. Data on other vertebrate density of appropriate prey species is the next step of analysis. Termite fishing increases with higher temperatures. It may be that the Fongoli chimpanzees are limited by high heat in terms of the stresses associated with hunting. Termite fishing is a stationary activity, which most likely requires little energy expenditure, thus providing the chimpanzees with their required nutrients. Leaf, another source of protein, availability is low

at Fongoli during the dry season. Termites would provide protein to the chimpanzees when leaves are lacking.

Seasonality in ant dipping behaviors was observed at Fongoli with this behavior exhibited during the wet season, but fecal analysis suggests ant eating during the dry season as well. It may be that ants are opportunistically consumed at Fongoli. The species typically eaten were more abundant in the wet season and this was when they were eaten the most. Seasonality was observed at the other chimpanzee site in Senegal, Assirik, with wet season ant dipping as well (Baldwin 1979, McGrew 1992). Army ants (*Dorylus* spp.) and weaver ants (*Oecophylla longinoda*) are consumed at many chimpanzee sites (McGrew 1992, Schöning et al. 2008). However, *Pachycondyla analis* (formally *Megaponera foetens*) has only been reported as consumed by the chimpanzees of Mt. Assirik in Senegal, Dja Biosphere Reserve in Cameroon, and Gashaka in Nigeria (Deblauwe & Janssens 2008, McGrew et al. 1988, Schöning et al. 2007).

Honeybees (*Apis mellifera*) are reported in the diet of most chimpanzee communities, such as Assirik in Senegal (Baldwin 1979), Gombe and Mahale in Tanzania (McGrew 1979, 1983, Tutin et al. 1995), Kahuzi-Biega in DRC (Basabose 2002), Goualougo in Republic of Congo (Sanz & Morgan 2007), Ndakan in Central African Republic (Fay & Carroll 1994), and Gashaka in Nigeria (Fowler & Sommer 2007). Other species of bees (stingless bees, such as sweat bees) are also eaten at some other sites, for example, Bossou in Guinea, Lope in Gabon, and Mahale in Tanzania (McGrew 1983, Sugiyama & Koman 1987, Tutin et al. 1995).

8.5.2 Tools

Fongoli termite fishing tools had a mean length of 29.9 (SD=12) cm, with a lower confidence level (95%) of 28.8 cm and an upper confidence level of 31 cm. Tools for termite extraction at Gombe fall within the parameters of Fongoli tools analyzed (Table 8.3). However, Fongoli tool are shorter than all other sites, although some sites have a small sample size compared to this study. Also, tool length did not differ from my previous research at Fongoli (29.9 versus 29.5 cm) (Bogart 2005). Perforating sticks, or puncturing sticks, were not found during this study, but one was described in my previous research (Bogart 2005). The Fongoli chimpanzees do not use this type of tool very often. Only Ndoki and Goualougo in Republic of Congo have reported regular use of perforating sticks, with means of 52.7 cm (24-93 cm, N=66) and 47cm (5-91 cm, N=19), respectively (Suzuki et al. 1995 Sanz et al. 2004).

Table 8.3: Flexible probe lengths for termite extraction across chimpanzee sites.

Site	Tool length mean (cm)	Range (cm)	Total number of tools	Source
Fongoli, Senegal	29.9	9.2-96.5	470	This study
Mt. Assirik, Senegal	32.5	13-71	173	McGrew et al., 1979
Gombe, Tanzania	30.7	7-100	145	McGrew et al., 1979
Mahale, Tanzania	37.7	12-84	290	McGrew & Collins, 1985
Okorobiko, Equatorial Guinea	49.7	27-65	46	McGrew et al., 1979
Ndoki, Republic of Congo	50.8	27-71	42	Suzuki et al., 1995
Goualougo Triangle, Republic of Congo	43.1	11-104	852	Sanz et al. 2004, Sanz & Morgan 2007
Dja Biosphere, Cameroon Reserve	55.6	33-125	45	Deblauwe et al. 2006

The ant dipping tools had a mean length of 38.9 cm (SD=9.9), with a lower confidence level (95%) of 31.3 cm and an upper confidence level of 46.5 cm. No other site's

tools fit within these parameters (Table 8.4). However, this is most likely a product of small sample size from this study. Tai's ant dipping tools were shorter than Fongoli's tools and contained a larger sample size. The Gashaka tools are reported to be longer in the dry season to obtain the ants when they retreat further underground (Fowler & Sommer 2007).

Typically, sites that contain more aggressive ants known to have a stinging bite, such as army ants (*Dorylus* species), have longer tools (Schöning et al. 2008). Fongoli chimpanzees use tools to consume two hostile ant species that give a painful bite (*Dorylus* spp. and *Pachycondyla analis*). Their tools are expected to be long, but this study did not offer evidence for this. However, sample size is a probable source of error.

Table 8.4: Ant tool lengths across chimpanzee sites.

Site	Tool length mean (cm)	Range (cm)	Total number of tools	Source
Fongoli, Senegal	38.9	25.7-60	9	This study
Fongoli, Senegal	79	42-152	24	McGrew et al. 2005
Mt. Assirik, Senegal	72		48	McGrew et al. 2003
Gombe, Tanzania	66, 63	15-113,--	13, 30	McGrew 1974
Bossou, Guinea	53.7	23-154	189	Humle & Matsuzawa 2002
Tai, Ivory Coast	23.9	11-58	28	Boesch & Boesch 1990
Kalinzu, Uganda	79	60-90	14	Hashimoto et al. 2000
Goualougo Triangle, Republic of Congo	63.6 95.8		Herb (n=206) Twig (n=61)	Sanz & Morgan 2007
Gashaka, Nigeria	Dip: 83.8 Fish: 19.5	28-160 5-44	72 38	Fowler & Sommer 2007
Lope, Gabon	55.7	18-89	28	Tutin et al. 1995

8.6 Paleoanthropology: Models of human evolution

Paleoanthropologists are limited as to what they can state about hominan behavior based on evidence from fossilized bones, artifacts, and studies of paleo-ecology. Using chimpanzees as a referential model in discussing hominan behavior will provide testable hypotheses for paleoanthropologists (Moore 1996). Variables, such as environmental

influences on behavior, provide evidence that can be tested for the paleoclimate of hominans. Several models have been postulated for hominan evolution in relation to environment: the savanna hypothesis, the turnover pulse hypothesis, and the variability selection hypothesis. Chimpanzees are often used in conjunction with these models. The savanna and faunal turnover hypotheses state that human evolution was congruent with the expansion of savannas in Africa (Dart 1925, Vrba 1992, 1995) and the variability selection hypothesis describes environmental changes correlating with human evolution (Potts 1998). Hominans lived on mosaic habitats with *Australopithecus* inhabiting more closed habitats and *Paranthropus* and early *Homo* species living in more open habitats (Bobe & Eck 2001, Reed 1997, Reed & Rector 2007). Diet analysis using carbon isotopes and material culture has found that *Australopithecus* and *Paranthropus* may have consumed some proportion of termites (Backwell & d'Errico 2001, 2008, Peters & Vogel 2005, Sponheimer et al. 2005, Sponheimer & Lee-Thorp 2003). Hominans most likely used tools before evidence of stone tools appears in the fossil record at about 2.6 mya (Beck 1980, McGrew 1992, Sigaut 1993). Tools used by hominans before the evolution of stone tools would have been similar to nonhuman primate tools used for food procurement and made of organic materials, which would not survive in the archaeological record (Teaford et al. 2002). Early hominans may have used similar methods of extracting invertebrates, cracking nuts, and other food related tool use like those that have been observed in non-human apes today (Foley & Lahr 2003, Joulain 1996, Panger et al. 2002). In fact *Australopithecus* may have had the manipulative capabilities for tool making around 3.2 mya (Panger et al. 2002).

Chimpanzees are the closest living relatives to humans (Cheng et al. 2005, Groves 2001) and studying their behaviors can provide testable hypotheses for paleoanthropologists.

Behaviors found for chimpanzees can be similar to those of human ancestors if environmental conditions were comparable to what we find in chimpanzees (Unger et al. 2006). Savanna chimpanzees offer this type of relationship to human evolution as it relates to the emergence of *Homo*. How the ecology influences behaviors in chimpanzees can reveal patterns that can then be tested in terms of the ecology in paleo-environments (Foley 1999, Reed 1997, Stanford 2006, Unger et al. 2006). Savanna chimpanzees have not been extensively studied, but have been hypothesized as a good referential candidate (Moore 1996, Pruetz & Bertolani, in press). Fongoli chimpanzees live in a mosaic savanna, similar to extinct hominans (Bobe & Eck 2001, Bobe & Behrensmeyer 2004, Reed 1997, Reed & Rector 2007, Strait & Wood 1999). The savanna environment is hypothesized to affect many different aspects of chimpanzees and hominans living there (Moore 1996). Thus, the Fongoli chimpanzees can provide a referential model (Moore 1996) for human evolution in a savanna environment. Moore (1996) suggested that savanna environments were food stressed. However, this research provides evidence to the contrary. Food resources are abundant in woodland and grassland habitat types at Fongoli. Thus, savanna environments are not depauperate in terms of food and would likely provide similarities to hominans in a mosaic savanna.

Termites are an important component of the Fongoli chimpanzee diet. Moore (1996) states that if savanna chimpanzees used tools more often than forested chimpanzees, that the hypothesis that a correlation between the environment and tools use exists would be supported. The Fongoli chimpanzees termite fish more than any other chimpanzee community studied. Additionally, the Fongoli chimpanzees also use tools for bushbaby hunting (Pruetz & Bertolani 2007). These findings lend support for Moore's hypothesis.

Several aspects of the Fongoli chimpanzee ecology correlate with the high degree of termite consumption. Fongoli chimpanzees termite fish more as temperatures increase. However, rainfall and fruit scarcity have no effect of termite fishing. The low diversity of prey species available at Fongoli may be a contributing factor. Fongoli has a high density of *Macrotermes* mounds, which are readily available in woodland habitats. Other invertebrates, such as ants, are not very common at Fongoli. Bushbabies have a lower individual density than invertebrates surveyed. Other vertebrates are expected to be comparable or lower to bushbaby density. Olive baboons (*Papio Anubis*) in Ivory Coast's Comoe National Park are found to be 1.2 baboons/km² (Kunz & Linsenmair 2008). Kunz and Linsenmair (2008) state that baboons in West Africa might be more versatile in group size. Density studies at Fongoli will be able to provide further data on the topic. Leaves provide another source of protein but have low availability during the dry season. *Macrotermes* termites are an abundant source of protein at Fongoli that is readily available when other sources of meat or leaves are low. Fongoli's termite density is much higher than what has been found at sites where these data have been collected. In Tanzania, Mahale has 0.1 *Macrotermes* mounds per hectare and Gombe has 5.6 mounds per hectare (Collins & McGrew 1985). Mount Assirik, the other site in Senegal that is no longer active, had 0.43 termite mounds per hectare, with the greatest density in the woodland habitat type (0.83/ha) (McBeath & McGrew 1982). If environmental factors such as these were prominent in hominan savannas, hypotheses may be posited from the findings in this study. Did Plio-Pleistocene hominans also have a high intake of insects? Termites have been suggested as a resource for hominans, such as *Paranthropus* (Backwell & d'Errico 2001, 2008, Sponheimer & Lee-Thorp 2003, Sponheimer et al. 2005).

The insectivorous diets of chimpanzees and hominans have been largely ignored in general. Regarding the faunivorous diet of chimpanzees, mammalian prey has especially been a focal topic of discussion amongst anthropologists (Milton 1999, 2003, Mitani & Watts 2001, Stanford & Bunn 2001, Ungar & Teaford 2002). Meat eating is of interest to anthropologists because it is associated with hunting and sharing of food (Stanford & Bunn 2001, Mitani & Watts 2001). These behaviors are examined in relation to the prevalence of hunting in human evolution. The emergence of *Homo* is said to coincide with increased hunting and the appearance stone tools (Milton 1999, 2003, Stanford & Bunn 2001). Most references to hominan behavior therefore focus on meat-eating, especially in conjunction with the aid of stone tools, and ignore any possibility that insects may have played a more important role in the diets of hominans (see Ungar & Teaford 2002). However, chimpanzees consume more insects on average than they do mammals (McGrew 1983). Isotopic analyses carried out on *Paranthropus (Australopithecus) robustus* demonstrate that they exploited open habitats for food, such as woodland and grassland (Sponheimer & Lee-Thorp 1999). Thus, consumption of grasses and animals that consume grasses were likely a component of the diet (Peters & Vogel 2005, Sponheimer & Lee-Thorp 2003, Sponheimer et al. 2005). *Paranthropus robustus* in South Africa has been associated with bone tools that have similar microware patterns to those found on experimental termite foraging tools (Backwell & d'Errico 2001, 2008). Similar to chimpanzees today, hominans during the Plio-Pleistocene may have been more reliant on consuming insects than they were on large vertebrates.

Some believe that a significant change in hominan diet occurred between *Australopithecus* and *Homo*, with the latter having a dramatic increase in meat procurement (Milton 1999, 2003). It has been suggested that this change in diet correlated with an increase

in brain size, a change in gut formation and a modification in dentition (Milton 2003). Foraging may have an important role in the evolution of cognition (Cheney et al. 1986, Milton 1981, Parker & Gibson 1977). Human evolution demonstrates a reliance on technology, skilled behaviors, and social skills over the course of 2.5 million years (Milton 2003). It does not seem like a massive step from termite foraging tools to hunting with tools, and the latter have been recorded for chimpanzees at Fongoli (Pruetz & Bertolani 2007) and Mahale (Huffman & Kalunde 1993, Nakamura & Itoh 2008). Perishable tools may have assisted early hominans in food processing and procurement, allowing a variable diet (Teaford et al., 2002). Early hominan diets, before the occurrence of stone tools, have been largely ignored (Ungar & Teaford 2002, Ungar 2007). I suspect early hominans exploited termites and other insects, but how often they spent feeding on invertebrates can only be speculated from studies of appropriate animal models, such as chimpanzees and hunter-gatherer societies. The Fongoli chimpanzees' reliance on termites may be used as a referential model of hominans living in a similar habitat. Prior to the acquisition of stone tools, foraging for termites would provide a viable resource for Plio-Pleistocene hominans. It may have been more of a shift from insectivory in early hominans (pre-Homo) to higher procurement of vertebrate prey in Homo species with advanced tool use and larger brains.

8.7 A role in conservation

Two major threats to chimpanzees are habitat loss and hunting for bushmeat, pet trade, traditional medicinal purposes, or medical research (Hill 2002, Kromos 2003). At Fongoli, the major threat is habitat loss (burning of forests for fields) and competition for food resources with humans (Pruetz 2006, Pruetz et al. 2008). Many other animals have been

eradicated from the area. There are no lions or buffaloes (Pruetz et al. 2008). Fongoli's environment has a small amount of closed habitat for the chimpanzees to escape the heat (Pruetz & Bertolani, in press), and thus protecting what is there is important. Fongoli chimpanzees rely on grassland and woodland habitat types for most food resources (fruit and termites) and closed forests for resting and social behaviors. The Fongoli chimpanzees display a preference for woodland and closed habitats (Chapter Six). Conserving these habitats is essential for the Fongoli chimpanzees and presumably for chimpanzees in Senegal, in general, as well as those inhabiting similar habitat types in the Manding Plateau. Conservation of feeding trees is associated with the long-term survival of chimpanzees (Tweheyo & Babweteera 2007). People rely on cultivated fields in this area, typically adjacent to water resources that the chimpanzees frequent (personal observation). My research indicates avoidance of agricultural fields by the Fongoli chimpanzees, at least seasonally (Chapter Six). In addition, there has been additional disturbance in the past several years, with shepherds from the northern deserts coming to Fongoli during Senegal's dry season. These shepherds have been cutting many trees in grassland and woodland habitats to feed their sheep (personal observation). If this type of destruction continues, food resources will be severely depleted at Fongoli. I propose a cultural study on field use and shepherd disturbance for future research, which is already underway (Pruetz, personal communication). This type of research can have positive secondary effects with the surrounding peoples, possibly aiding in relations and providing ideas for facilitating better situations between chimpanzees and humans.

8.8 Concluding remarks

The use of tools to obtain termites is a behavior that expends much of the Fongoli chimpanzees' time and effort. Chimpanzee feeding and foraging occurred more often in the dry season and termite fishing in particular increased as temperatures increased at Fongoli. Fruit abundance is also higher in the dry hot season; thus, termites are not a fallback food when the chimpanzees' main source of food is scarce. The Fongoli chimpanzees spend more time obtaining termites as a food resource than any other chimpanzee community studied thus far. This food resource provides protein and essential minerals and nutrients that cannot be obtained from a solely frugivorous diet (Deblauwe & Janssens 2008, McGrew 1983, Sussman 1987, Wakayama et al. 1984). In addition, minimal leaf abundance may also be a contributing factor to the year-long consumption of termites at Fongoli. This research provides the first detailed research on the importance of insectivory in the savanna chimpanzees' diet at Fongoli based on direct observation. It is not unwarranted to posit that hominans could have employed this behavior to obtain insects as well, given similar ecological conditions. Given that chimpanzees are prolific tool users with organic materials, hominans most likely used these tools as well before the evolution of stone tools at 2.5 mya. Evidence for these behaviors does not fossilize. This could have potentially led to tool use for hunting in hominans, which has also been observed in the Fongoli chimpanzee community (Pruetz & Bertolani 2007). Chimpanzees have been evolving as long as humans, but they can serve as a reference for interpreting human evolution. The Fongoli chimpanzees especially, provide information on behavioral adaptations to a savanna environment, which has been associated with the type of environment *Paranthropus* and *Homo* species inhabited (Bobe & Behrensmeyer 2004, Bromage & Schrenk 1995, Reed 1997, Wesselman 1995). This research

provides testable hypotheses such as examining certain environmental factors affecting insect consumption similar to those found here that can be applied to hominan sites. This study's findings have established that the environment at Fongoli is a contributing influence on the diet and activity of the chimpanzees, and most importantly to their insectivory. Fongoli chimpanzees have demonstrated a variety of unique behaviors, from cave use, hunting with tools, and wading in pools of water (Pruetz 2001, 2007, Pruetz & Bertolani 2008, in press). The findings of this research add to these exceptional behaviors in that no other chimpanzee community has been found to consume termites to the degree seen at Fongoli.

APPENDIX

Table A1: Codes for data collection.

Activity	Code	Food Item/Part	Code	Habitat	Code
Feeding	FD	Fruit	Fr	Woodland with indicator (c-closed, o-open, gr- grassland, th-thicket, etc.)	WD
Foraging	FG	Leaves	Lv	Gallery forest	GF
Drinking	DR	Flower	Fl	Forest ecotone	FE
Traveling	TR	Shoot or Pith	Sh/Pi	Field	FL
Social (sx-sex, pl-play, gm-groom)	S	Bark	Bk	River	RIV
Aggression – to m/f and age class, or human (di- display, c-contact)	AG	Termite	T	Tall grassland	GR
Rest/Inactive	R	Ant	A	Short grassland (formally Plateau)	PL
Other behavior (spl-self play, sgm- self groom, nest-build nest)	OT	Vertebrate	V	Bamboo	BAM
Termite fishing	TF	Invertebrate (other than ant and termite)	Inv	Mountain	MNT
Vocalize (ph-pant hoot, b-bark, etc)	V	Dirt	DT		
Out of Sight	OOS				

Table A2: Grassland temperatures and analyses.

	Aug	Sept	Oct	Nov	Dec	Jan	Feb	Mar	Apr	May	June	July
Mean (°C)	26.0	24.9	24.6	25.6	25.4	25.0	29.9	31.6	32.3	30.5	27.3	26.5
Maxima (°C)	31.3	31.0	30.3	32.6	30.6	28.5	43.3	44.0	44.7	45.9	37.5	33.7
Minima (°C)	22.0	21.2	21.2	21.5	22.6	20.3	18.1	19.1	23.2	15.5	22.0	21.5
Median (°C)	25.8	24.5	24.5	25.1	25.0	25.4	28.1	28.4	30.5	29.4	26.5	25.9
Sample	2288	1433	1447	1397	1446	1449	2024	2242	2169	2241	2166	2242
Standard deviation	2.07	2.12	1.84	2.52	2.08	1.79	6.11	6.30	6.68	7.28	3.25	2.27
Confidence interval (95%)	0.08	0.11	0.09	0.13	0.11	0.09	0.27	0.26	0.28	0.30	0.14	0.09

Table A3: Woodland Temperatures and analyses.

	Aug	Sept	Oct	Nov	Dec	Jan	Feb	Mar	Apr	May	June	July
Mean (°C)	27.1	26.9	29.3	28.9	27.6	26.7	29.4	32.0	33.4	32.6	28.6	27.5
Maxima (°C)	32.3	31.5	34.0	38.8	34.0	38.3	38.6	39.2	39.7	40.1	35.0	32.3
Minima (°C)	22.0	21.8	24.8	23.2	21.3	22.1	19.4	21.8	24.3	23.8	23.1	21.5
Median (°C)	27.1	26.7	29.1	28.7	27.1	26.0	29.8	32.1	33.6	32.8	28.4	27.5
Sample	3007	2173	1488	1440	1519	1519	2717	3007	2910	2412	2314	3007
Standard deviation	2.04	2.08	2.07	2.54	3.05	2.57	4.13	3.68	3.06	3.55	2.36	2.01
Confidence interval (95%)	0.07	0.09	0.11	0.13	0.15	0.13	0.16	0.13	0.11	0.14	0.10	0.07

Table A4: Habitat¹ transect data.

Transect	Meters along transect										
	0	100	200	300	400	500	600	700	800	900	1000
1A	PS	PS	PS	GR	GR	WD	WD	GR	WD	WD	WD
1	BM	BM	PS	PS	GR	PS	GR	PS	GR	PS	GR
2A	PS	WD	BM	WD	GR	GR	GR	GR	GR	GR	WD
2	GR	GR	GR	GR	BM	GR	PS	PS	BM	PS	PS
3	GR	GR	GR	WDc	GR	GR	GR	GR	GR	WDc	WD
3A	GR	WD	GR	GR	GR	WD	GR	GR	GR	GR	GR
4A	WD	BM	BM	BM	BM	PS	PS	PS	PS	BM	GR
4	GR	GR	GR	PS	PS	FE	GR	PS	FE	FE	GR
5	WD	FL	FL	GR	GR	GR	GR	GR	GR	PS	FE
5A	WD	PS	PS	GR	GR	GR	GR	GR	GR	FL	FL
6	PS	PS	GR	GR	BM	FL	FL	FL	GR	GR	GR
6A	GR	PS	GR	GR	GR	WD	GR	PS	GR	GR	GR
7	GR	GR	GR	FE	WD	WD	GR	GR	GR	GR	GR
7A	GR	GR	GR	GR	GR	GR	PS	GR	GR	GR	GR
7	WD	WD	WD	WDc	WD	PS	WD	WD	WD	PS	PS
8	PS	PS	PS	PS	GR	GR	PS	PS	PS	GR	GR
8A	GR	GR	PS	WD	PS	PS	PS	WD	GR	PS	PS
9A	GR	GR	GR	GR	GR	GR	BM	BM	BM	PS	PS
9	WD	GR	WD	WD	GR	GR	GR	GR	GR	GR	GR
10	GR	GR	GR	GR	WD	BM	WD	PS	BM	BM	BM
10A	GR	GR	WDc	GF	GR	GR	PS	PS	GR	GR	FL
11A	GR	GR	GR	GR	GR	GR	FL	GR	GR	GR	WD
11	GR	FL	GR	GR	GR	BM	PS	PS	PS	BM	PS
12	GR	GR	GR	GR	PS	WD	GR	PS	GR	GR	GR
12A	WD	GR	WD	WD	GR	GR	GR	GR	GR	GR	WD
13	BM	BM	GR	GR	GR	GR	BM	BM	GR	BM	GR
13A	VIL	VIL	VIL	VIL	WDc	WDc	WDc	WDc	WDc	FL	FL
14	FL	FL	FL	GR	GR	GR	GR	GR	BM	BM	WD
14A	PS	PS	PS	PS	WD	WD	WD	WDc	PS	PS	PS
15A	WDc	GR	WDc	PS	PS	PS	PS	PS	WD	WD	WD
15	PT	PS	PS	PS	PS	PS	PS	PS	PS	GR	PS
16A	GR	GR	FL	FL	BM	GR	GR	GR	FL	GR	BM
17A	WD	WD	WD	WD	WD	PS	PS	GR	PS	GR	GR
18A	WD	WD	WD	WD	GR	GR	BM	WD	BM	GR	WD
19A	GR	GR	GR	WD	WD	WD	GR	GR	GR	WD	GR
20A	GR	GR	PS	PS	PS	FL	FL	GR	GR	GR	GR
21A	PS	BM	WD	PS	GR	WD	GR	PS	PS	GR	PS
22A	GR	GR	GR	GR	GR	GR	GR	GR	FL	GR	GR
23A	FL	GR	BM	BM	BM	WD	GR	PS	PS	BM	GR
24A	BM	GR	GR	GR	PS	GR	GR	GR	GR	GR	GR
25A	PS	BM	PS	GR	GR	GR	BM	GR	BM	GR	GR
26A	GR	GR	GR	BM	GR	GR	GR	BM	GR	GR	GR
27A	WD	WD	WD	PS	GR	WDc	WD	WD	GR	GR	WD
28A	BM	PS	BM	BM	BM	BM	PS	PS	BM	PS	WD

Table A4. (Continued)

29A	GR	WD	GR	GR	GR	WD	GR	PS	PS	PS	GR
30A	GR	GR	GR	WDc	GR	PS	PS	PS	PS	WD	PS
31A	BM	BM	GR	GR	GR	GR	GR	BM	GR	GR	GR

[†]Habitat: bamboo (BM), forest ecotone (FE), field (FL), gallery forest (GF), tall grassland (GR), short grassland (PS), human village (VIL), closed woodland (WDc), open woodland (WD).

Table A5: Transect trees and basal areas.

Tree Number	Malinke name	Genus and Species	BA (cm ²)	Height (m)
219	Sita	<i>Adansonia digitata</i>	11308.32	10
431	Banombo	<i>Baissea multiflora</i>	28.27	
420L	Banombo	<i>Baissea multiflora</i>	50.26	
12	Bunkungo	<i>Bombax costatum</i>	490.81	9.2
13	Bunkungo	<i>Bombax costatum</i>	530.86	10
208	Bunkungo	<i>Bombax costatum</i>	1661.69	14.4
285	Bunkungo	<i>Bombax costatum</i>	226.95	3.5
341	Bunkungo	<i>Bombax costatum</i>	706.77	8.8
377	Bunkungo	<i>Bombax costatum</i>	2827.08	13.9
40	Taba	<i>Cola cordifolia</i>	1075.08	
41	Taba	<i>Cola cordifolia</i>	9502.13	
42	Taba	<i>Cola cordifolia</i>	11308.32	
43	Taba	<i>Cola cordifolia</i>	5673.79	
44	Taba	<i>Cola cordifolia</i>	6360.93	
45	Taba	<i>Cola cordifolia</i>	7853.00	
46	Taba	<i>Cola cordifolia</i>	754.67	
225	Taba	<i>Cola cordifolia</i>	1133.97	15.6
434	Taba	<i>Cola cordifolia</i>	7853.00	
483	Taba	<i>Cola cordifolia</i>	2827.08	
19	Dougouta	<i>Cordyla pinnata</i>	176.69	7.8
69	Dougouta	<i>Cordyla pinnata</i>	415.42	8
279	Dougouta	<i>Cordyla pinnata</i>	490.81	9.8
289	Dougouta	<i>Cordyla pinnata</i>	1017.75	12
338	Dougouta	<i>Cordyla pinnata</i>	314.12	9.5
361	Dougouta	<i>Cordyla pinnata</i>	132.72	11.3
207	Santango	<i>Daniellia oliviera</i>	754.67	8.9
212	Santango	<i>Daniellia oliviera</i>	380.09	11.7
223	Santango	<i>Daniellia oliviera</i>	201.04	9.1
286	Santango	<i>Daniellia oliviera</i>	113.08	7.9
288	Santango	<i>Daniellia oliviera</i>	132.72	6.2
295	Santango	<i>Daniellia oliviera</i>	754.67	11.9
298	Santango	<i>Daniellia oliviera</i>	706.77	6.7
342	Santango	<i>Daniellia oliviera</i>	380.09	12
346	Santango	<i>Daniellia oliviera</i>	346.32	11.1
371	Santango	<i>Daniellia oliviera</i>	452.33	9
443	Santango	<i>Daniellia oliviera</i>	314.12	13
238	Kukua	<i>Diospyros mespiliformis</i>	132.72	8.3
246	Kukua	<i>Diospyros mespiliformis</i>	254.44	12.8

Table A5. (Continued)

247	Kukua	<i>Diospyros mespiliformis</i>	254.44	11.8
275	Kukua	<i>Diospyros mespiliformis</i>	254.44	4.4
385	Kukua	<i>Diospyros mespiliformis</i>	490.81	10.1
389	Kukua	<i>Diospyros mespiliformis</i>	314.12	13.7
474	Kukua	<i>Diospyros mespiliformis</i>	113.08	10.1
236	Sekho	<i>Ficus ingens</i>	11308.32	17.7
32	Tankango	<i>Gardenia erubescens</i>	7.07	1.5
grewia	Sambe	<i>Grewia lasiodiscus</i>	28.27	
417	Kehko	<i>Hannoa undulata</i>	706.77	6.2
22	Gundje	<i>Hexalobus monopetalus</i>	201.04	8.3
26	Gundje	<i>Hexalobus monopetalus</i>	176.69	8.3
27	Gundje	<i>Hexalobus monopetalus</i>	153.92	6.2
31	Gundje	<i>Hexalobus monopetalus</i>	132.72	5.1
33	Gundje	<i>Hexalobus monopetalus</i>	95.02	5.9
58	Gundje	<i>Hexalobus monopetalus</i>	201.04	5.9
66	Gundje	<i>Hexalobus monopetalus</i>	63.61	7.6
71	Gundje	<i>Hexalobus monopetalus</i>	113.08	7
168	Gundje	<i>Hexalobus monopetalus</i>	132.72	
214	Gundje	<i>Hexalobus monopetalus</i>	113.08	3.6
218	Gundje	<i>Hexalobus monopetalus</i>	113.08	5.2
245	Gundje	<i>Hexalobus monopetalus</i>	113.08	7.1
257	Gundje	<i>Hexalobus monopetalus</i>	153.92	7.3
296	Gundje	<i>Hexalobus monopetalus</i>	226.95	4.3
299	Gundje	<i>Hexalobus monopetalus</i>	283.49	7.1
358	Gundje	<i>Hexalobus monopetalus</i>	153.92	7.2
399	Gundje	<i>Hexalobus monopetalus</i>	176.69	
404	Gundje	<i>Hexalobus monopetalus</i>	113.08	5
484	Gundje	<i>Hexalobus monopetalus</i>	153.92	6.1
28	Bintinkilingo	<i>Lannea acida</i>	153.92	
55	Bintinkilingo	<i>Lannea acida</i>	226.95	8.8
62	Bintinkilingo	<i>Lannea acida</i>	95.02	
63	Bintinkilingo	<i>Lannea acida</i>	254.44	11.6
65	Bintinkilingo	<i>Lannea acida</i>	226.95	8.5
107	Bintinkilingo	<i>Lannea acida</i>	226.95	6.1
211	Bintinkilingo	<i>Lannea acida</i>	452.33	12
241	Bintinkilingo	<i>Lannea acida</i>	226.95	9.3
273	Bintinkilingo	<i>Lannea acida</i>	452.33	12.4
297	Bintinkilingo	<i>Lannea acida</i>	254.44	
318	Bintinkilingo	<i>Lannea acida</i>	201.04	9.5
359	Bintinkilingo	<i>Lannea acida</i>	346.32	7.3
370	Bintinkilingo	<i>Lannea acida</i>	283.49	9.1
425	Bintinkilingo	<i>Lannea acida</i>	346.32	6.1
466	Bintinkilingo	<i>Lannea acida</i>	283.49	9.9
475	Bintinkilingo	<i>Lannea acida</i>	201.04	7.2
216	Fekho	<i>Lannea microcarpa</i>	615.68	13.7
221	Fekho	<i>Lannea microcarpa</i>	415.42	5.3

Table A5. (Continued)

231	Fekho	<i>Lannea microcarpa</i>	283.49	8.3
57	Bembenyanya	<i>Lannea velutina</i>	176.69	5
84	Bembenyanya	<i>Lannea velutina</i>	132.72	5.5
362	Bembenyanya	<i>Lannea velutina</i>	226.95	8
397	Bembenyanya	<i>Lannea velutina</i>	226.95	5.3
467	Bembenyanya	<i>Lannea velutina</i>	78.53	8.4
469	Bembenyanya	<i>Lannea velutina</i>	132.72	7.3
Oncoba	Kondongo	<i>Oncoba spinosa</i>	63.61	
226	Nete	<i>Parkia biglobosa</i>	283.49	9.4
228	Nete	<i>Parkia biglobosa</i>	201.04	10.2
458/272	Nete	<i>Parkia biglobosa</i>	4417.31	14.3
17	Fara	<i>Piliostigma thonningii</i>	314.12	9.4
59	Fara	<i>Piliostigma thonningii</i>	201.04	11.3
67	Fara	<i>Piliostigma thonningii</i>	176.69	5.8
97	Fara	<i>Piliostigma thonningii</i>	380.09	4.6
203	Fara	<i>Piliostigma thonningii</i>	314.12	5.6
242	Fara	<i>Piliostigma thonningii</i>	63.61	6.2
243	Fara	<i>Piliostigma thonningii</i>	78.53	8.5
253	Fara	<i>Piliostigma thonningii</i>	176.69	8.1
256	Fara	<i>Piliostigma thonningii</i>	132.72	5.6
271	Fara	<i>Piliostigma thonningii</i>	132.72	6.3
294	Fara	<i>Piliostigma thonningii</i>	95.02	7.5
306	Fara	<i>Piliostigma thonningii</i>	95.02	9.4
319	Fara	<i>Piliostigma thonningii</i>	283.49	6.7
332	Fara	<i>Piliostigma thonningii</i>	452.33	12.1
333	Fara	<i>Piliostigma thonningii</i>	201.04	6.5
335	Fara	<i>Piliostigma thonningii</i>	660.44	11.8
360	Fara	<i>Piliostigma thonningii</i>	283.49	7.1
365	Fara	<i>Piliostigma thonningii</i>	201.04	
369	Fara	<i>Piliostigma thonningii</i>	201.04	6
379	Fara	<i>Piliostigma thonningii</i>	314.12	8.4
382	Fara	<i>Piliostigma thonningii</i>	283.49	
400	Fara	<i>Piliostigma thonningii</i>	226.95	11.5
422	Fara	<i>Piliostigma thonningii</i>	314.12	7.2
5	Keno	<i>Pterocarpus erinaceus</i>	132.72	7.5
10	Keno	<i>Pterocarpus erinaceus</i>	176.69	10.2
11	Keno	<i>Pterocarpus erinaceus</i>	153.92	7.2
23	Keno	<i>Pterocarpus erinaceus</i>	176.69	9.4
30	Keno	<i>Pterocarpus erinaceus</i>	132.72	
34	Keno	<i>Pterocarpus erinaceus</i>	201.04	10.3
35	Keno	<i>Pterocarpus erinaceus</i>	176.69	6.7
36	Keno	<i>Pterocarpus erinaceus</i>	95.02	5.9
47	Keno	<i>Pterocarpus erinaceus</i>	226.95	9.1
48	Keno	<i>Pterocarpus erinaceus</i>	95.02	8.4
49	Keno	<i>Pterocarpus erinaceus</i>	153.92	9.2
50	Keno	<i>Pterocarpus erinaceus</i>	314.12	7

Table A5. (Continued)

51	Keno	<i>Pterocarpus erinaceus</i>	2205.91	6.3
52	Keno	<i>Pterocarpus erinaceus</i>	254.44	15
53	Keno	<i>Pterocarpus erinaceus</i>	283.49	8.5
57	Keno	<i>Pterocarpus erinaceus</i>	804.15	10.1
59	Keno	<i>Pterocarpus erinaceus</i>	804.15	6.1
64	Keno	<i>Pterocarpus erinaceus</i>	314.12	5.6
65	Keno	<i>Pterocarpus erinaceus</i>	113.08	9.4
74	Keno	<i>Pterocarpus erinaceus</i>	153.92	3.7
81	Keno	<i>Pterocarpus erinaceus</i>	176.69	7.8
89	Keno	<i>Pterocarpus erinaceus</i>	176.69	12.3
94	Keno	<i>Pterocarpus erinaceus</i>	132.72	11.3
95	Keno	<i>Pterocarpus erinaceus</i>	254.44	6.4
96	Keno	<i>Pterocarpus erinaceus</i>	153.92	6.2
100	Keno	<i>Pterocarpus erinaceus</i>	283.49	9.8
106	Keno	<i>Pterocarpus erinaceus</i>	490.81	14.9
201	Keno	<i>Pterocarpus erinaceus</i>	254.44	11.8
202	Keno	<i>Pterocarpus erinaceus</i>	176.69	7.1
209	Keno	<i>Pterocarpus erinaceus</i>	283.49	7
213	Keno	<i>Pterocarpus erinaceus</i>	113.08	6.4
215	Keno	<i>Pterocarpus erinaceus</i>	201.04	6.5
220	Keno	<i>Pterocarpus erinaceus</i>	132.72	6
244	Keno	<i>Pterocarpus erinaceus</i>	415.42	12.6
248	Keno	<i>Pterocarpus erinaceus</i>	283.49	9.4
249	Keno	<i>Pterocarpus erinaceus</i>	283.49	12.5
250	Keno	<i>Pterocarpus erinaceus</i>	490.81	8.6
251	Keno	<i>Pterocarpus erinaceus</i>	95.02	7.2
252	Keno	<i>Pterocarpus erinaceus</i>	132.72	10.1
277	Keno	<i>Pterocarpus erinaceus</i>	153.92	9.8
278	Keno	<i>Pterocarpus erinaceus</i>	346.32	14.5
293	Keno	<i>Pterocarpus erinaceus</i>	346.32	8.1
294	Keno	<i>Pterocarpus erinaceus</i>	314.12	11.5
324	Keno	<i>Pterocarpus erinaceus</i>	346.32	14
331	Keno	<i>Pterocarpus erinaceus</i>	530.86	10.7
339	Keno	<i>Pterocarpus erinaceus</i>	804.15	12.9
340	Keno	<i>Pterocarpus erinaceus</i>	706.77	13.4
344	Keno	<i>Pterocarpus erinaceus</i>	961.99	14.7
345	Keno	<i>Pterocarpus erinaceus</i>	346.32	12.2
368	Keno	<i>Pterocarpus erinaceus</i>	660.44	9
372	Keno	<i>Pterocarpus erinaceus</i>	346.32	7.5
374	Keno	<i>Pterocarpus erinaceus</i>	415.42	6.4
390	Keno	<i>Pterocarpus erinaceus</i>	754.67	10.5
395	Keno	<i>Pterocarpus erinaceus</i>	415.42	8.9
430	Keno	<i>Pterocarpus erinaceus</i>	706.77	11.2
464	Keno	<i>Pterocarpus erinaceus</i>	804.15	10.2
465	Keno	<i>Pterocarpus erinaceus</i>	380.09	10.3
471	Keno	<i>Pterocarpus erinaceus</i>	283.49	12.7

Table A5. (Continued)

14	Caba	<i>Saba senegalensis</i>	12.56	
24	Caba	<i>Saba senegalensis</i>	19.63	7.5
72	Caba	<i>Saba senegalensis</i>	28.27	
77	Caba	<i>Saba senegalensis</i>	63.61	
78	Caba	<i>Saba senegalensis</i>	38.48	
227	Caba	<i>Saba senegalensis</i>	28.27	
423	Caba	<i>Saba senegalensis</i>	38.48	
Caba	Caba	<i>Saba senegalensis</i>	0.79	
279	Kenteno	<i>Sclerocarya birrea</i>	254.44	12.2
235	Minkon	<i>Spondias mombin</i>	490.81	13.1
351	Kunkusita	<i>Sterculia setigera</i>	1017.75	12.7
452	Tumbingo	<i>Tamarindus indica</i>	314.12	
112	Se	<i>Vitellaria paradoxa</i>	201.04	6.1
320	Se	<i>Vitellaria paradoxa</i>	490.81	10.4
322	Se	<i>Vitellaria paradoxa</i>	572.48	10.2
337	Se	<i>Vitellaria paradoxa</i>	346.32	8.4
357	Se	<i>Vitellaria paradoxa</i>	380.09	6.2
37	Kutufingo	<i>Vitex madiensis</i>	12.56	3.6
58	Kutufingo	<i>Vitex madiensis</i>	95.02	6.3
97	Kutufingo	<i>Vitex madiensis</i>	63.61	6.9
239	Kuroru		113.08	8.9
240	Kuroru		226.95	6.7
274	Mansarinkeno		176.69	10.3
283	Sunkungo		19.63	3
286	Kilindingo		95.02	
349	Wonko		415.42	8.6
366	Jarango		1017.75	13.3
388	Nyarikoyo		490.81	12.5
393	Mansarinkeno		254.44	7.6

Table A6: Fruit ripeness (ur = unripe, sr = semi-ripe, r = ripe).

	Aug	Sept	Oct	Nov	Dec	Jan	Feb	Mar	Apr	May	Jun	Jul
<i>Adansonia digitata</i>	ur		ur	ur	r	r	r	r	r	r		
<i>Baissea multiflora</i>					ur							
<i>Bombax costatum</i>							ur	ur				
<i>Cola cordifolia</i>									ur	ur	sr	r
<i>Cordyla pinnata</i>									ur	ur	r	r
<i>Daniellia oliviera</i>							r					
<i>Diospyros mespiliformis</i>	ur	ur	ur	ur	sr	r	r				ur	
<i>Ficus sycomorus</i>				ur	r							

Table A6. (Continued)

	Aug	Sept	Oct	Nov	Dec	Jan	Feb	Mar	Apr	May	Jun	Jul
<i>Gardenia erubescens</i>							ur	ur				
<i>Grewia lasiodiscus</i>		ur			ur							
<i>Hexalobus monopetalus</i>	ur	ur										
<i>Lannea acida</i>								ur	ur	ur		
<i>Lannea velutina</i>											ur	ur
<i>Oncoba spinosa</i>	ur	ur		ur	sr	sr						
<i>Piliostigma thonningii</i>					ur	sr	r	r	r	r		
<i>Pterocarpus erinaceus</i>									ur			
<i>Saba senegalensis</i>	ur		ur	ur	ur	ur	sr	sr	sr	sr	r	r
<i>Spondias mombin</i>	ur	r	r									
<i>Sterculia setigera</i>	ur	ur	ur	ur	r	r	r					
<i>Vitex madiensis</i>	ur	ur	ur									

Table A7: Total observation time (hours.minutes).

	Aug	Sept	Oct	Nov	Dec	Jan	Feb	Mar	Apr	May	Jun	Jul	Total
FO	02.10	02.30	00.10	03.05	11.20	08.35	10.40	12.25	03.15	12.00	10.55	10.55	88.00
MM	05.05	03.25	09.45	05.20	14.00	09.55	11.45	07.40	12.10	10.30	14.40	11.45	116.00
YO	02.55	03.35	05.15	03.00	08.55	10.05	10.05	12.25	09.10	10.40	11.15	12.00	99.20
KL	10.05	11.15	12.50	08.05	08.55	07.00	15.00	07.15	09.20	10.00	09.20	12.45	121.50
DF	04.05	04.20	08.00	04.30	09.25	09.15	10.30	11.55	03.35	05.40	10.50	11.50	93.55
BL	01.00	02.00	12.20	06.00	10.10	03.30	08.25	12.20	10.50	06.00	11.30	17.30	101.35
BN	00.50	01.35	07.10	00.35	11.10	05.35	08.05	05.20	06.15	12.30	14.10	11.40	84.55
KM	00.50	02.30	01.00	05.40	11.30	06.40	06.35	01.35	05.55	04.35	14.25	09.15	70.30
SI	02.25	04.40	03.05	01.05	12.00	08.25	10.00	09.10	11.00	10.35	10.25	09.55	92.45
LP	00.00	03.40	03.05	02.30	12.10	09.15	11.00	09.00	12.40	05.35	14.15	11.20	94.30
	29.25	39.30	62.40	39.50	109.35	78.15	102.05	89.05	84.10	88.05	121.45	118.55	963.20

Table A8: Fecal sample insects identified.

Sample	Genus	Species	Comments
FS 13	<i>Macrotermes</i>	<i>subhyalinus</i>	
FS 40	<i>Macrotermes</i>	<i>subhyalinus</i>	
FS 41	<i>Macrotermes</i>	<i>subhyalinus</i>	
FS 42	<i>Macrotermes</i>	<i>subhyalinus</i>	
FS 50	<i>Macrotermes</i>	<i>subhyalinus</i>	
FS 51	<i>Macrotermes</i>	<i>subhyalinus</i>	
FS 52	<i>Macrotermes</i>	<i>subhyalinus</i>	
FS 53	<i>Macrotermes</i>	<i>subhyalinus</i>	
FS 54	<i>Macrotermes</i>	<i>subhyalinus</i>	

Table A8. (Continued)

FS 68	<i>Macrotermes</i>	<i>subhyalinus</i>	
FS 69	<i>Macrotermes</i>	<i>subhyalinus</i>	
FS 70	<i>Macrotermes</i>	<i>subhyalinus</i>	
FS 71	<i>Macrotermes</i>	<i>subhyalinus</i>	w/ a few <i>Cubitermes</i> mandibles
FS 72	<i>Macrotermes</i>	<i>subhyalinus</i>	
FS 74	<i>Macrotermes</i>	<i>subhyalinus</i>	
FS 76	<i>Macrotermes</i>	<i>subhyalinus</i>	
FS 112	<i>Macrotermes</i>	<i>subhyalinus</i>	
FS 113	<i>Macrotermes</i>	<i>subhyalinus</i>	
FS 114	<i>Macrotermes</i>	<i>subhyalinus</i>	
FS 115	<i>Macrotermes</i>	<i>subhyalinus</i>	
FS 29	<i>Oecophylla</i>	<i>longinoda</i>	Weaver ant
FS 7	<i>Oecophylla</i>	<i>longinoda</i>	Weaver ant
FS 7	<i>Oecophylla</i>	<i>longinoda</i>	Weaver ant
FS 12	<i>Oecophylla</i>	<i>longinoda</i>	Weaver ant
FS 44	<i>Dorylus (Anomma)</i>	<i>burmeisteri</i>	Army ant
FS 41	<i>Dorylus (Anomma)</i>	<i>burmeisteri</i>	Army ant
FS 70	<i>Dorylus (Anomma)</i>	<i>burmeisteri</i>	Army ant

LIST OF REFERENCES

Referencing follows CBE Style Manual , 6th edition, Cambridge University Press and American Journal of Physical Anthropology

- Alberts SC, Altmann J, Hollister-Smith JA, Mututua RS, Sayialel SN, Muruthi PM, Warutere JK. 2005. Seasonality and long term change in a savannah environment. In: Brockman DK, van Schaik CP, editors. Seasonality in Primates. New York: Cambridge University Press. p.157-196.
- Agetsuma N, Nakagawa N. 1998. Effects of habitat differences on feeding behaviors of Japanese monkeys: comparison between Yakushima and Kinkazan. *Primates* 39:275-289.
- Altmann, J. 1974. Observational study of behavior: sampling methods. *Behaviour*, 49, 227-265.
- Altmann SA. 1991. Diets of yearling female primates (*Papio cynocephalus*) predict lifetime fitness. *Proc. Natl. Acad. Sci. USA* 88:420-423.
- Altmann SA. 1998. Foraging for Survival: Yearling Baboons in Africa. Chicago, Illinois: University of Chicago Press.
- Altmann SA. 2006. Primate foraging adaptations: two research strategies. In: Hohmann G, Robbins MM, Boesch C, editors. Feeding Ecology in Apes and Other Primates. Cambridge and New York: Cambridge University Press. p. 243-262.
- Anderson DP, Nordheim EV, Boesch C, Moermond TC. 2002. Factors influencing fission–fusion grouping in chimpanzees in the Taï National Park, Côte d’Ivoire. In: Boesch C, Hohmann G, Marchant LF, editors. Behavioural Diversity in Chimpanzees and Bonobos. Cambridge: Cambridge University Press. p. 90–101.
- Arnhem E, Dupain J, Vercauteren Drubbel R, Devos C, Vercauteren M. 2008. Selective logging, habitat quality and home range use by sympatric gorillas and chimpanzees: a case study from an active logging concession in southeast Cameroon. *Folia Primatologica* 79:1-14.
- Asensio N, Korstjens AH, Aureli F. 2009. Fissioning minimizes ranging costs in spider monkeys: a multiple-level approach. *Behavioral Ecology and Sociobiology* 63:649-659.
- Avery DM. 2003. Early and Middle Pleistocene environments and hominid biogeography; micromammalian evidence from Kabwe, Twin Rivers and Mumbwa Caves in central Zambia. *Palaeogeography, Palaeoclimatology, Palaeoecology* 189:55-69.

- Ba AT, Sambou B, Ervik F, Goudiaby A, Camara C, Diallo D. 1997. Vegetation et flore: Parc Transfrontalier du Niokolo Badiar. Niokolo Badiar, Union Européenne-Niokolo Badiar.
- Backwell LR, d'Errico F. 2001. Evidence of termite foraging by Swartkrans early hominids. *Proceedings of the National Academy of Sciences of the United States of America* 98: 1358-1363.
- Backwell LR, d'Errico F. 2008. Early hominid bone tools from Drimolen, South Africa. *Journal of Archaeological Science* 35:2880-2894.
- Balcomb SR, Chapman CA, Wrangham RW. 2000. Relationship between chimpanzees (*Pan troglodytes*) density and large, fleshy-fruit tree density: conservation implications. *American Journal of Primatology* 51:197-203.
- Baldwin PJ. 1979. The Natural History of the Chimpanzee (*Pan troglodytes verus*), at Mt. Assirik, Senegal [Dissertation]. Scotland, United Kingdom: University of Stirling
- Baldwin PJ, Sabater-Pi J, McGrew WC, Tutin CEG. 1982. Comparisons of nests made by different populations of chimpanzees (*Pan troglodytes*). *Primates* 22:367-385
- Barton RA, Whiten A. 1994. Reducing complex diets to simple rules: food selection by olive baboons. *Behavioral Ecology and Sociobiology* 35:283-293.
- Basabose AK. 2002. Diet composition of chimpanzees inhabiting the montane forest of Kahuzi, Democratic Republic of Congo. *American Journal of Primatology* 58:1-21.
- Beck BB. 1980. Animal Tool Behavior: The Use and Manufacture of Tools by Animals. New York: Garland Publishing. 231p.
- Berenbaum MR. 1995. Bugs in the System: Insects and Their Impact on Human Affairs. Reading, Massachusetts: Addison-Wesley Publishing Company.
- Bermejo M, Illera J. 1999. Tool-set for termite-fishing and honey extraction by wild chimpanzees in the Lossi Forest, Congo. *Primates* 40:619-627.
- Binford LR. 1964. A consideration of archaeological research design. *American Antiquity* 29:425-441.
- Bobe R, Behrensmeyer AK. 2004. The expansion of grassland ecosystems in Africa in relation to mammalian evolution and the origin of the genus *Homo*. *Palaeogeography, Palaeoclimatology, Palaeoecology* 207:399-420.
- Bobe R, Eck GG. 2001. Responses of African bovids to Pliocene climatic change. *Paleobiology Suppl.* 27:1-47.

- Boesch C. 1991. The Effects of Leopard Predation on Grouping Patterns in Forest Chimpanzees. *Behaviour* 117:220-242.
- Boesch C. 1994. Chimpanzees and red colobus monkeys: a predatory-prey system. *Animal Behaviour* 47:1135-1148.
- Boesch C. 1996. Social grouping in Taï chimpanzees. In: McGrew WC, Marchant LF, Nishida T, editors, *Great Ape Societies*. Cambridge: Cambridge University Press. p. 101–113.
- Boesch C. 2002. Cooperative hunting roles among Taï chimpanzees. *Human Nature* 13:27-46
- Boesch C, Boesch H. 1981. Sex differences in the use of natural hammers by wild chimpanzees: A preliminary report. *Journal of Human Evolution*. 10: 585-593.
- Boesch C, Boesch H. 1990. Tool use and tool making in wild chimpanzees. *Folia Primatologica* 54:1-15.
- Boesch C, Boesch-Achermann H. 2000. *The Chimpanzees of the Taï Forest: Behavioural Ecology and Evolution*. Oxford, England: Oxford University Press, pp. 316.
- Boesch C, Marchesi P, Marchesi N, Fruth B, Joulian F. 1994. Is nut cracking in wild chimpanzees a cultural behaviour? *Journal of Human Evolution* 26:325-338.
- Boesch C, Goné Bi Z, Anderson D, Stahl D. 2006. Food choice in Taï chimpanzees: Are cultural differences present? In: Hohmann G, Robbins M, Boesch C, editors, *Feeding Ecology in Apes and Other Primates*. Cambridge: Cambridge University Press. p. 365-399.
- Bogart SL. 2005. Insectivory, termite diversity, and tool use of the Fongoli chimpanzees (*Pan troglodytes verus*), Senegal, West Africa [Thesis]. Iowa State University, Iowa.
- Bogart SL, Pruetz JD. 2008. Ecological context of chimpanzee (*Pan troglodytes verus*) termite fishing at Fongoli, Senegal. *Journal of American Primatology* 70:605-612.
- Bogart SL, Pruetz JD, McGrew WC. 2005. Termite de jour: termite fishing by West African chimpanzees (*Pan troglodytes verus*) at Fongoli, Senegal. *American Journal of Physical Anthropology Supplement* 40: 75.
- Bogart SL, Pruetz JD. 2008. Ecological context of chimpanzee (*Pan troglodytes verus*) termite fishing at Fongoli, Senegal. *Journal of American Primatology* 70:605-612.
- Bromage TG, Schrenk F. 1995. Biogeographic and climate basis for a narrative of early hominid evolution. *Journal of Human Evolution* 28:109-114.

- Brownell A. 2003. Burkina Faso. In Kromos R, Boesch C, Bakarr MI, Butynski TM, editors, West African Chimpanzees: Status Survey and Conservation Plan. Gland, Switzerland and Cambridge, UK: Union for Conservation of Nature and Natural Resources. p 121-122
- Butynski TM. 2003. The robust chimpanzee (*Pan troglodytes*): taxonomy, distribution, abundance and conservation status. In Kromos R, Boesch C, Bakarr MI, Butynski TM, editors, West African Chimpanzees: Status Survey and Conservation Plan. Gland, Switzerland and Cambridge, UK: Union for Conservation of Nature and Natural Resources. p 5-12.
- Carter J, Ndiaye S, Pruetz JD, McGrew WC. 2003. Senegal. In: Kormos R, Boesch C, Bakarr MI, Butynski TM, editors. West African Chimpanzees: Status Survey and Conservation Action Plan. IUCN/SSC Primate Specialist Group, p. 31-39.
- Cerling TE. 1992. Development of grasslands and savannas in East Africa during the Neogene. *Palaeogeography, Palaeoclimatology, Palaeoecology* 97:241-247.
- Chapman CA. 1988. Patterns of foraging and range use by three species of neotropical primates. *Primates* 29:177-194.
- Chapman CA, Chapman LJ. 2000. Interdemic variation in mixed-species association patterns: common diurnal primates of Kibale National Park, Uganda. *Behavioral Ecology and Sociobiology* 47:129-139.
- Chapman CA, Chapman LJ, Wrangham RW, Hunt K, Gebo D, Gardner L. 1992. Estimation of fruit abundance of tropical trees. *Biotropica* 24:527-531.
- Chapman CA, Wrangham RW, Chapman LJ. 1994. Indices of habitat-wide fruit abundance in tropical forests. *Biotropica* 26:160-171.
- Chapman CA, Wrangham RW, Chapman LJ. 1995. Ecological constraints on group size: an analysis of spider monkey and chimpanzee subgroups. *Behavioral Ecology and Sociobiology* 36:59-70.
- Charpentier MJE, Widdig A, Alberts SC. 2007. Inbreeding depression in non-human primates: a historical review of methods used and empirical data. *American Journal of Primatology* 69:1370-1386.
- Chen FC, Lee WH. 2001. Genomic divergences between humans and other hominoids and the effective population size of the common ancestor of humans and chimpanzees. *American journal of human Genetics* 68:444-456.

- Cheney D, Seyfarth R, Smuts B. 1986. Social relationships and social cognition in nonhuman primates. *Science* 234:1361-1366.
- Cheng Z, Ventura M, She X, Khaitovich P, Graves T, Osoegawa K, Church D, DeJong P, Wilson RK, Paabo S, Rocchi M, Eichler EE. 2005. A genome-wide comparison of recent chimpanzee and human segmental duplications. *Nature* 437:88-93.
- Chepstow-Lusty A, Winfield M, Wallis J, Collins A. 2006. The importance of local tree resources around Gombe National Park, Western Tanzania: implications chimpanzees. *Ambio* 35:124-129.
- Clements FE, Shelford VE. 1939. *Bio-Ecology* New York: Wiley.
- Collins DA, McGrew WC. 1985. Chimpanzees' (*Pan troglodytes*) choice of prey among termites (Macrotermitinae) in western Tanzania. *Primates* 26:375-389.
- Collins DA, McGrew WC. 1987. Termite fauna related to differences in tool-use between groups of chimpanzees (*Pan troglodytes*). *Primates* 28: 457-471.
- Conklin-Brittain N, Wrangham RW, Hunt KD. 1998. Dietary response of chimpanzees and cercopithecines to seasonal variation in fruit abundance: II. Nutrients. *International Journal of Primatology* 19:971-987.
- Conklin-Brittain N, Knott CD, Wrangham RW. 2001. The feeding ecology of great apes. In: Brookfield Zoo, editor. *The Apes: Challenges for the 21st Century*. Brookfield, IL: Chicago Zoological Society. p. 167-174.
- Conklin-Brittain NL, Knott CD, Wrangham RW. 2006. Energy intake by wild chimpanzees and orangutans: methodological considerations and a preliminary comparison. In: Boesch C, Hohmann G, Robbins MM, editors. *Feeding Ecology in Apes and Other Primates*. Cambridge: Cambridge University Press. p. 445-471.
- Cottam G, Curtis JT. 1956. The use of distance measures in phytosociological sampling. *Ecology* 37:451-461.
- Darlington JPEC. 1984. Two types of mound built by the termite *Macrotermes subhyalinus* in Kenya. *Insect Science Applications* 5:481-492.
- Darlington JPEC. 1985. The structure of mature mounds of the termite *Macrotermes michaelseni* in Kenya. *Insect Science Applications* 6:149-156.
- Dart RA. 1925. *Australopithecus africanus*: the man-ape of South Africa. *Nature* 115:195-199.

- Daubenmire R. 1968. *Plant Communities: A Textbook of Plant Synecology*. New York: Harper and Row.
- Deblauwe I, Guislain P, Dupain J, Van Elsacker L. 2006. Use of a tool-set by Pan troglodytes troglodytes to obtain termites (*Macrotermes*) in the periphery of the Dja Biosphere Reserve, Southeast Cameroon. *American Journal of Primatology* 68:1191–1196.
- Deblauwe I, Janssens GPJ. 2008. New insights into insect prey choice by chimpanzees and gorillas in southeast Cameroon: the role of nutritional value. *American Journal of Physical Anthropology* 135:42-55.
- DeFoliart GR. 1999. Insects as food: why the western attitude is important. *Annual Review of Entomology* 44:21-50.
- DeVore I, editor. 1965. *Primate Behavior: Field Studies of Monkeys and Apes*. New York: Holt, Rinehart and Winston.
- Dew LJ. 2003. Feeding ecology and seed dispersal. In: Setchell JM, Curtis DJ, editors. *Field and Laboratory Methods in Primatology*. Cambridge: Cambridge University Press. p.174-183.
- Doran D. 1997. Influence of seasonality on activity patterns, feeding behaviour, ranging, and grouping patterns in Tai chimpanzees. *International Journal of Primatology* 18:183–206.
- Duval CS. 2000. Important habitat for chimpanzees in Mali. *African Study Monographs* 21:173-203.
- Duvall CS. 2008. Chimpanzee diet in the Bafing area, Mali. *African Journal of Ecology* 46:679-683.
- Eggleton P, Bignell DE, Hauser S, Dibog L, Norgrove L, Madong B. 2002. Termite diversity across an anthropogenic disturbance gradient in the humid forest zone of West Africa. *Agriculture, Ecosystems and Environment* 90:189-202.
- Ellenberg H., Mueller-Dombois D. 1967. Tentative physiognomic-ecological classification of plant formations of the Earth. *Ber. Geobot. Inst. ETH Stiftg. Ruebel, Zuerich* 37:21-55.
- Fawcett KA. 2000. Female relationships and food availability in a forest community of chimpanzees. [Dissertation]. University of Edinburgh.
- Fay JM, Carroll RW. 1994. Chimpanzee tool use for honey and termite extraction in Central Africa. *American Journal of Primatology* 34:309-317.

- Federal Aviation Administration http://www.faa.gov/airports_airtraffic/air_traffic/publications/ifim/country_list/index.cfm?countryCode=sg. Updated: 11:11 am ET August 30, 2007.
- Fleagle JG. 1999. Primate Adaptations and Evolution. 2nd edition. New York: Academic Press.
- Foley, R. 1987. Another Unique Species: Patterns in Human Evolutionary Ecology. New York: Wiley.
- Foley R. 1999. Evolutionary geography of Pliocene African hominids. African Biogeography, Climate Change, & Human Evolution - Human Evolution Series:328-348
- Fossey D, Harcourt AH. 1977. Feeding ecology of free-ranging Mountain gorilla (*Gorilla gorilla beringei*). In: Clutton-Brock TH, editor. Primate Ecology: Studies of feeding and ranging behaviour in lemurs, monkeys and apes. London, New York: Academic Press p. 415-447.
- Fowler A, Sommer V. 2007. Substance technology of Nigerian chimpanzees. International Journal of Primatology 28:997-1023.
- Furuchi T, Hashimoto C, Tashiro Y. 2001. Fruit availability and habitat use by chimpanzees in the Kalinzu Forest, Uganda: examination of fallback foods. International Journal of Primatology 22:929-945.
- Gagneux P, Willis C, Gerloff U, Tautz D, Morin PA, Boesch C, Fruth B, Hohmann G, Ryder OA, Woodruff DS. 1999. Mitochondrial sequences show diverse evolutionary histories of African hominoids. Proceedings of the National Academy of Science, USA 96:5077-5082.
- Galat G, Galat-Luong A, Nizinski G. 2008. Our cousins chimpanzees and baboons face global warming by digging wells to filtrate drinking water. 13th IWRA World Water Congress IUCN.
- Galdikas BMF 1979. Orangutan adaptation at Tanjung Puting Reserve: Mating and ecology. In: Hamburg DA, McCown ER, Editors. Perspective on Human Evolution, vol. 5: The Great Apes. Menlo Park, California: Benjamin/Cummings Publishing Co. p. 195-233.
- Galdikas BMF. 1988. Orangutan diet, range, and activity at Tanjung Puting, Central Borneo. International Journal of Primatology 9:1-35
- Garber PA. 1987. Foraging strategies among living primates. Annual Review of Anthropology 16:339-364.

- Garber 2000 The ecology of group movement: evidence for the use of spatial, temporal, and social information in some primate foragers. In: Boinski S, Garber PA, editors. *On the Move: How and Why Animals Travel in Groups*. Chicago, IL: University of Chicago Press. p.261-298.
- Garshelis DL.2000. Delusions in habitat evaluation: measuring use, selection, and importance. In: Boitani L, Fuller TK, editors. *Research Techniques in Animal Ecology: Controversies and Consequences*. New York, New York: Columbia University. p. 111-164.
- Gašpersič M, Pruetz JD. 2008. Savanna chimpanzees (*Pan troglodytes verus*) and baobab fruits (*Adansonia digitata*): Investigation of percussive technology among three chimpanzee communities in southeastern Senegal. *Folia Primatologica* 79:332-333.
- Ghiglieri MP. 1984. *The Chimpanzees of Kibale Forest: A Field Study of Ecology and Social Structure*. New York: Columbia University Press, 226p.
- Gipoliti S, Embalo DS, Sousa C. 2003. Guinea-Bissau. In Kromos R, Boesch C, Bakarr MI, Butynski TM, editors, *West African Chimpanzees: Status Survey and Conservation Plan*. Gland, Switzerland and Cambridge, UK: Union for Conservation of Nature and Natural Resources, p. 55-62.
- Goldberg TL, Ruvolo M. 1997. Molecular phylogenetics and historical biogeography of east African chimpanzees. *Biological Journal of the Linnean Society* 61:301-324.
- Gonder MK, Oates JF, Disotell TR, Forstner MRJ, Morales JC, Melnick DJ. 1997. A new West African chimpanzee subspecies. *Nature* 388:337.
- Goodall J. 1963. Feeding behaviour of wild chimpanzees. *Symposia of the Zoological Society of London* 10:39-48
- Goodall J. 1964. Tool-using and aimed throwing in a community of free-living chimpanzees. *Nature* 201:1264-1266.
- Goodall J. 1986. *The chimpanzees of Gombe: patterns of behavior*. Cambridge, Massachusetts: Harvard University Press, 673p.
- Gould SJ. 1997. Darwinian Fundamentalism. *The New York Review of Books* 44:June 12, 1997.
- Greenwood JJD, Robinson RA. 2006. Principles of sampling. In: Sutherland WJ, editor, *Ecological Census Techniques*. New York: Cambridge University Press. p. 11-86.
- Groves C. 2001. *Primate taxonomy*. Washington DC: Smithsonian Institution Press.

- Groves C. 2005. *Mammal Species of the World* (3rd edition). Wilson DE, Reeder DM, editors Johns Hopkins University Press.
- Hanson-Alp R, Bakarr MI, Lebbie A, Bangura KI. 2003. Sierra Leone. In Kromos R, Boesch C, Bakarr MI, Butynski TM, editors, *West African Chimpanzees: Status Survey and Conservation Plan*. Gland, Switzerland and Cambridge, UK: Union for Conservation of Nature and Natural Resources. p. 77-88.
- Harris WV. 1956. Termite mound-building. *Insectes Sociaux* 3:261-268.
- Hartwig W. 2007. Primate Evolution. In: Campbell CJ, Fuentes A, Mackinnon KC, Panger M, Bearder SK, editors. *Primates in Perspective*. New York: Oxford University Press. p. 11-22.
- Hashimoto C, Furuichi T, Tashiro Y. 2000. Ant dipping and meat eating by wild chimpanzees in the Kalinzu Forest, Uganda. *Primates* 41:103–108.
- Hashimoto C, Furuichi T, Tashiro Y. 2001. What factors affect the size of chimpanzee parties in the Kalinzu Forest, Uganda? Examination of fruit abundance and number of estrous females. *International Journal of Primatology* 22:947–959.
- Hashimoto C, Suzuki S, Takenoshita Y, Yamagiwa J, Basabose AK, Furuichi T. 2003. How fruit abundance affects the chimpanzee party size: a comparison between four study sites. *Primates* 44:77-81.
- Heaton JL, Pickering TR. 2006. Archaeological analysis does not support intentionality in the production of brushed ends on chimpanzee termiting tools. *International Journal of Primatology* 27:1619-1633.
- Hill CM. 2002. Primate conservation and local communities- ethical issues and debates. *American Anthropologist* 104:1184-1194.
- Hladik CM. 1977. Chimpanzees of Gabon and chimpanzees of Gombe: some comparative data on the diet. In: Clutton-Brock TH, editor. *Primate Ecology: Studies of feeding and ranging behaviour in lemurs, monkeys and apes*. London, New York: Academic Press. p. 481-501.
- Hohmann G, Fowler A, Sommer V, Ortmann S. 2006. Frugivory and gregariousness of Salonga bonobos and Gashaka chimpanzees: the influence of abundance and nutritional quality of fruit. In: Boesch C, Hohmann G, Robbins MM, editors. *Feeding Ecology in Apes and Other Primates*. Cambridge: Cambridge University Press. p. 123-160.

- Huffman MA. 1990. Some socio-behavioral manifestations of old-age in chimpanzees. In: Nishida T, editor. *The Chimpanzees of the Mahale Mountains: Sexual and Life History Strategies*. Tokyo: University of Tokyo Press. p. 237-255.
- Huffman MA, Kalunde MA 1993. Tool-assisted predation on a squirrel by a female chimpanzee in the Mahale Mountains, Tanzania. *Primates* 34:93–98.
- Humle T. 1999. New record of fishing for termites (*Macrotermes*) by the chimpanzees of Bossou (*Pan troglodytes verus*), Guinea. *Pan Africa News* 6:3-4.
- Humle T, Matsuzawa T. 2001. Behavioral diversity among the wild chimpanzee populations of Bossou and neighboring areas, Guinea and Cote d'Ivoire, West Africa. *Folia Primatologica* 72:57-68.
- Hunt KD, McGrew WC. 2002. Chimpanzees in the dry habitats of Assirik, Senegal and Semliki Wildlife Reserve, Uganda. In: Boesch C, Hohmann G, Marchant LF, editors. *Behavioural Diversity in Chimpanzees and Bonobos*. Cambridge: Cambridge University Press. p. 35-51.
- Isbell LA, Young TP. 1996. The evolution of bipedalism in hominans and reduced group size in chimpanzees: alternative responses to decreasing resource availability. *Journal of Human Evolution* 30:389-397.
- Isbell LA, Pruett JD, Lewis M, Young TP. 1998. Locomotor activity differences between sympatric patas monkeys (*Erythrocebus patas*) and vervet monkeys (*Cercopithecus aethiops*): Implications for the evolution of long hindlimb length in Homo. *American Journal of Physical Anthropology* 105:199-207.
- Itoh N, Nishida T. 2007. Chimpanzee grouping patterns and food availability in Mahale Mountains National Park, Tanzania. *Primates* 48:87-96.
- Jacobs J. 1974. Quantitative measurement of food selection. *Oecologia* 14:413-417.
- Jones JA. 1990. Termites, Soil Fertility and Carbon Cycling in Dry Tropical Africa: A Hypothesis. *Journal of Tropical Ecology* 6:291-305.
- Joulain F. 1996. Comparing chimpanzee and early hominid techniques: some contributions to cultural and cognitive questions. In: Mellars PA, Gibson KR, editors. *Modeling the Early Human Mind*. Cambridge: Cambridge University Press p. 173-188.
- Kano T. 1982. The social group of pygmy chimpanzees (*Pan paniscus*) of Wamba, Zaire. *Primates* 23:171-188.

- Kennett JP. 1995. A review of polar climatic evolution during the Neogene, based on the marine sediment record. In: Vrba ES, Denton GH, Partridge TC, Burckle LH, editors. *Paleoclimate and Evolution, with Emphasis on Human Origins*, New Haven: Yale University Press p. 49-64.
- Kiyono-Fuse M. 2008. Use of wet hair to capture swarming termites by a chimpanzee in Mahale, Tanzania. *Pan African News* 15:4.
- Korb J, Linsenmair KE. 1998. The effects of temperature on the architecture and distribution of *Macrotermes bellicosus* (Isoptera, Macrotermitinae) mounds in different habitats of a West African Guinea savanna. *Insectes Sociaux* 45:51-65.
- Kosheleff VP, Anderson CNK. In press. Temperature's influence on the activity budget, terrestriality, and sun exposure of chimpanzees in the Budongo Forest, Uganda. *American Journal of Physical Anthropology*
- Krebs JR, Davies NB. 1993. *An Introduction to Behavioural Ecology*, 3rd edition. Blackwell Publishing. 420 p.
- Krebs JR, Davies NB. 1997. *Behavioural Ecology: An Evolutionary Approach*, 4th edition. Blackwell Publishing. 456 p.
- Krief S, Huffman MA, Venet T, Hladik CM, Grellier P, Loiseau PM, Wrangham RW. 2006. Bioactive Properties of Plant Species Ingested by Chimpanzees (*Pan troglodytes schweinfurthii*) in the Kibale National Park, Uganda. *American Journal of Primatology* 68:51-71.
- Kormos R. 2003. Urgent action needed for West African chimpanzees. *Oryx* 37:16-17.
- Kunz BK, Linsenmair K.E. 2008. The disregarded west: diet and behavioural ecology of olive baboons in the Ivory Coast. *Folia Primatologica* 79:31-51
- Kuroda S, Nishihara T, Suzuki S, Oko RA. 1996. Sympatric chimpanzees and gorillas in the Ndoki Forest, Congo. In: McGrew WC, Marchant LF, Nishida T, editors. *Great Ape Societies*. Cambridge, MA: Cambridge University Press. p. 71-81.
- Leger DW, Didrichsons IA. 1994. An assessment of data pooling and some alternatives. *Animal Behavior* 48:823-832.
- Leighton M, Leighton DR. 1982. The relationship of size of feeding aggregate to size of food patch: howler monkeys (*Alouatta palliata*) feeding in *Trichilia cipo* fruit trees on Barro Colorado Island. *Biotropica* 14:81-90.

- Lepage M, Morel G, Resplendino C. 1974. Discovery of termite galleries extending deep underground to water level in North Senegal. *Comptes rendus Hebdomadaires des Seances de L'Academie des Sciences (serie d)* 278:1855-1858.
- Luscher M. 1955. Air circulation in *Macrotermes* mounds. *Acta Tropica* 12:289-307.
- Maddala GS. 1971. The use of variance components models in pooling cross section and time series data. *Econometrica* 39:341-358.
- Magnuson L, Adu-Nsiah M, Kpelle D. 2003. Ghana. In Kromos R, Boesch C, Bakarr MI, Butynski TM, editors, *West African Chimpanzees: Status Survey and Conservation Plan*. Gland, Switzerland and Cambridge, UK: Union for Conservation of Nature and Natural Resources. p. 111-116.
- Mammides C, Cords M, Peters MK. 2009. Effects of habitat disturbance and food supply on population densities of three primate species in the Kakamega Forest, Kenya. *African Journal of Ecology* 47:87-96.
- Marshall AJ, Wrangham RW. 2007. Evolutionary consequences of fallback foods. *International Journal of Primatology* 28:1219-1235.
- Martin P, Bateson P. 1993. *Measuring Behaviour. An Introductory Guide*. Cambridge, Massachusetts: Cambridge University Press.
- Masi S, Cipolletta C, Robbins MM. 2009. Western-lowland gorillas (*Gorilla gorilla gorilla*) change their activity patterns in response to frugivory. *American Journal of Primatology* 71:91-100.
- Matsumoto-Oda A, Kasagula MB. 2000. Preliminary study of feeding competition between baboons and chimpanzees in the Mahale Mountains National Park, Tanzania. *African Study Monographs* 21:147-157.
- Matsuzawa T, Yamakoshi G. 1996. Comparison of chimpanzee material culture between Bossou and Nimba, West Africa. In: Russon AE, Bard KA, Parker ST, editors. *Reaching Into Thought: The Minds of the Great Apes*. Cambridge, MA: Cambridge University Press. p. 211-232.
- McBeath NM, McGrew WC. 1982. Tools used by wild chimpanzees to obtain termites at Mt. Assirik, Senegal: the influence of habitat. *Journal of Human Evolution* 11:65-72.
- McBrearty S, Jablonski NG. 2005. First Fossil Chimpanzee. *Nature* 437: 105-107.
- McGrew WC. 1974. Tool use by wild chimpanzees in feeding upon driver ants. *Journal of Human Evolution* 3:501-508.

- McGrew WC. 1979. Evolutionary implications of sex differences in chimpanzee predation and tool use. In: Hamburg DA, McCown ER, editors. *The Great Apes*. Menlo Park, California: Benjamin/Cummings. p. 440-463.
- McGrew WC. 1983. Animal foods in the diets of wild chimpanzees (*Pan troglodytes*): why cross-cultural variation? *Journal of Ethology* 1:46-61.
- McGrew WC. 1992. *Chimpanzee Material Culture: Implications for Human Evolution*. Cambridge: Cambridge University Press.
- McGrew WC. 1994. Tools compared: the material of culture. In: Wrangham RW, McGrew WC, de Waal FBM, Heltne PG, editors. *Chimpanzee cultures*. Cambridge, Massachusetts: Harvard University Press. p. 25-39.
- McGrew WC. 2001. The other faunivory: primate insectivory and early human diet. In: Stanford CB, Bunn HT, editors. *Meat-Eating and Human Evolution*. Oxford: Oxford University Press. p 160-178.
- McGrew WC, Collins DA. 1985. Tool use by wild chimpanzees (*Pan troglodytes*) to obtain termites (*Macrotermes herus*) in the Mahale Mountains, Tanzania. *American Journal of Primatology* 9:47-62.
- McGrew WC, Tutin CEG, Baldwin PJ. 1979. Chimpanzees, tools, and termites: cross cultural comparisons of Senegal, Tanzania, and Rio Muni. *Man* 14:185-214.
- McGrew WC, Baldwin PJ, Tutin CEG. 1981. Chimpanzees in a hot, dry and open habitat: Mt. Assirik, Senegal, West Africa. *Journal of Human Evolution* 10:227-244.
- McGrew WC, Baldwin PJ, Tutin CEG. 1988. Diet of wild chimpanzees (*Pan troglodytes verus*) at Mt. Assirik, Senegal: I. Composition. *American Journal of Primatology* 16:213-226.
- McGrew WC, Baldwin PJ, Marchant LF, Pruett JD, Scott SE, Tutin CEG. 2003. Ethoarchaeology and elementary technology of unhabituated wild chimpanzees as Assirik, Senegal, West Africa. *PaleoAnthropology* 1:1-20.
- McGrew WC, Johnson-Fulton S, Pruett JD. 2004. Elementary technology of the wild chimpanzees of Fongoli, Senegal. *American Journal of Physical Anthropology Suppl* 38:146.
- McGrew WC, Pruett JD, Fulton BJ. 2005. Chimpanzees use tools to harvest social insects at Fongoli, Senegal. *Folia Primatologica* 871:1-5.

- deMeocal PB, Bloemendal J. 1995. Plio-Pleistocene climatic variability in subtropical Africa and the Paleoenvironment of hominid evolution: A combined data-model approach. In: Vrba ES, Denton GH, Partridge TC, Burckle LH, editors. *Paleoclimate and Evolution, with Emphasis on Human Origins*, New Haven: Yale University Press p. 262-288.
- Milton K. 1981. Food choice and digestive strategies of two sympatric primate species. *American Naturalist* 117: 496-505.
- Milton K. 1999. A hypothesis to explain the role of meat-eating in human evolution. *Evolutionary Anthropology* 8:11-21.
- Milton K. 2003. Micronutrient intakes of wild primates: are humans different? *Comparative Biochemistry and Physiology - Part A* 136:47-59.
- Milton K. 2006. Introduction to analyzing nutritional ecology: picking up the pace: nutritional ecology as an essential research tool in primatology. In: Boesch C, Hohmann G, Robbins MM, editors. *Feeding Ecology in Apes and Other Primates*. Cambridge: Cambridge University Press. p. 381-396.
- Mitani JC, Watts DP. 1999. Demographic influences on the hunting behavior of chimpanzees. *American Journal of Physical Anthropology* 109:171-182.
- Mitani JC, Watts DP. 2001. Why do chimpanzees hunt and share meat? *Animal Behaviour* 61:915-924.
- Mitani JC, Watts DP, Muller MN. 2002. Recent developments in the study of wild chimpanzee behavior. *Evolutionary Anthropology* 11:9-25.
- Moore J. 1996. Savanna chimpanzees, referential models and the last common ancestor. In: McGrew WC, Marchant LF, Nishida T, editors. *Great Ape Societies*. Cambridge: Cambridge University Press. p 275-292.
- Morgan D, Sanz C. 2003. Naïve encounters with chimpanzees in the Goualougo Triangle, Republic of Congo. *International Journal of Primatology* 24:369-381.
- Morgan D, Sanz C. 2006. Chimpanzee feeding ecology and comparisons with sympatric gorillas in the Goualougo Triangle, Republic of Congo. In: Boesch C, Hohmann G, Robbins MM, editors. *Feeding Ecology in Apes and Other Primates*. Cambridge: Cambridge University Press. p. 97-122.
- Morin PA, Moore JJ, Chakraborty R, Jin L, Goodall J, Woodruff DS. 1994. Kin selection, social structure, gene flow, and the evolution of chimpanzees. *Science* 265:1193-1201.

- Moron V, Robertson AW, Ward RM, Ndiaye O. 2008. Weather Types and Rainfall over Senegal. Part I: Observational Analysis. *Journal of Climate* 21:266-287.
- Nakagawa N. 2009. Feeding rate as valuable information in primate feeding ecology. *Primates* 50:131-141.
- Nakamura M, Itoh N. 2008. Hunting with tools by Mahale chimpanzees. *Pan Africa News* 15:3-6.
- Newton-Fisher NE. 1999. Termite eating and food sharing by male chimpanzees in the Budongo Forest, Uganda. *African Journal of Ecology* 37:369-371.
- Nisbett RA, Peal AL, Hoyt RA, Cater J. 2003. Liberia. In Kromos R, Boesch C, Bakarr MI, Butynski TM, editors, *West African Chimpanzees: Status Survey and Conservation Plan*. Gland, Switzerland and Cambridge, UK: Union for Conservation of Nature and Natural Resources, p. 89-98.
- Nishida T. 1968. The social group of wild chimpanzees in the Mahale Mountains. *Primates* 9:167-224.
- Nishida T 1973. The ant-gathering behaviour by the use of tools among wild chimpanzees of the Mahale Mountains. *Journal of Human Evolution* 2:357-370.
- Nishida T. 1990. *The chimpanzees of the Mahale Mountains*. Tokyo: University of Tokyo Press.
- Nishida T, Hiraiwa M. 1982. Natural history of a tool-using behavior by wild chimpanzees in feeding upon wood-boring ants. *Journal of Human Evolution* 11:73-99.
- Nishida T, Kawanaka K. 1972. Inter-unit-group relationships among wild chimpanzees of the Mahale Mountains. *Kyoto University African Studies* 7:131-169.
- Nishida T, Uehara S. 1980. Chimpanzees, tools, and termites: another example from Tanzania. *Current Anthropology* 21:671-672
- Nishida T, Uehara S. 1983. Natural diet of chimpanzees (*Pan troglodytes schweinfurthii*): long-term record from the Mahale Mountains, Tanzania. *African Study Monographs* 3:109-130.
- Nishida T, Kano T, Goodall J, McGrew WC, Nakamura M. 1999. Ethogram and ethnography of Mahale chimpanzees. *Anthropological Science* 107:141-188.

- Nkurunungi JB. 2005. The availability and distribution of fruit and non-fruit plant resources in Bwindi: their influence on gorilla habitat use and food choice [Dissertation]. Makerere University.
- Noirot C, Darrlington JPEC. 2000. Termite nests: architecture, regulation and defense. In: Abe T, Bignell DE, Higashi M, editors. *Termites: Evolution, Sociality, Symbioses, Ecology*, Dordrecht, Boston, London: Kluwer Academic Publishers. p. 121-140.
- Oates JF. 1987. Food distribution and foraging behaviour. In: Smuts BB, Cheney DL, Seyfarth RM, Wrangham RW, Struhsaker TT, editors. *Primate Societies*. Chicago: University of Chicago Press. p.197-209.
- Oates J, Gadsby L, Jenkins P, Gonder K, Bocian C, Adeleke A. 2003. Nigeria. In Kromos R, Boesch C, Bakarr MI, Butynski TM, editors, *West African Chimpanzees: Status Survey and Conservation Plan*. Gland, Switzerland and Cambridge, UK: Union for Conservation of Nature and Natural Resources. p. 123-132.
- Oates JF, Tutin CEG, Humle T, Wilson ML, Baillie JEM., Balmforth Z, Blom A, Boesch C, Cox D, Davenport T, Dunn A, Dupain J, Duvall C, Ellis CM, Farmer KH, Gatti S, Greengrass E, Hart J, Herbinger I, Hicks C, Hunt KD, Kamenya S, Maisels F, Mitani JC, Moore J, Morgan BJ, Morgan DB, Nakamura M, Nixon S, Plumptre AJ, Reynolds V, Stokes EJ, Walsh PD. 2008. *Pan troglodytes*. In: IUCN 2008. 2008 IUCN Red List of Threatened Species. <www.iucnredlist.org>. Downloaded on 03 March 2009.
- Oates JF, Groves CP, Jenkins PD. 2009. The type locality of *Pan troglodytes vellerosus* (Gray, 1862), and implications for the nomenclature of West African chimpanzees. *Primates* 50:78-80.
- O'Brien EM, Peters CR. 1999. Landforms, climate, ecogeographic mosaics, and the potential for hominid diversity in Pliocene Africa. In: Bromage TG & Schrank F, editors. *African Biogeography, Climate Change, & Human Evolution*, Oxford: Oxford University Press p.115-137
- Ohiagu CE. 1979. A Quantitative study of seasonal foraging by grass harvesting termite, *Trinervitermes geminatus* (Wasmann), (Isoptera, Nasutitermitinae) in southern Guinea Savanna, Mokwa, Nigeria. *Oecologia* 40:179-188.
- Oladipo EO. 1980. An analysis of heat and water balances in West Africa. *Geographical Review* 70:194-209.
- Opdyke ND. 1995. Mammalian migration and climate over the last seven million years. In: Vrba ES, Denton GH, Partridge TC, Burckle LH, editors. *Paleoclimate and Evolution, with Emphasis on Human Origins*. New Haven: Yale University Press. pp. 109-114.

- Owen-Smith N. 1999. Ecological links between African savanna environments, climate change, and early hominid evolution. In: Bromage TG & Schrank F, editors. African Biogeography, Climate Change, & Human Evolution. Oxford: Oxford University Press. p.138-149.
- Panger MA, Brooks AS, Richmond BG, Wood B. 2002. Older than the Oldowan? Rethinking the emergence of hominin tool use. *Evolutionary Anthropology* 11:235-245.
- Parker ST, Gibson KR. 1977. Object manipulation, tool use and sensorimotor intelligence as feeding adaptations in cebus monkeys and great apes. *Journal of Human Evolution* 6: 623-641.
- Peters CR. 2007. Theoretical and actualistic ecobotanical perspectives on early hominin diets and paleoecology. In: Ungar PS, editor. *Evolution of the Human Diet*. Oxford: Oxford University Press. p. 233-261.
- Peters CR, Vogel JC. 2005. Africa's wild C₄ plant foods and possible early hominid diets. *Journal of Human Evolution* 48:219-236.
- Pearce GD. 1981. Zambian mushrooms – customs and folklore. *Transactions of the British Mycological Society* 139-142.
- Piel AK. 2004. Scarce resources and party size in a community of savanna chimpanzees in southeastern Senegal [Thesis]. Iowa State University.
- Post DG. 1984. Is optimization the optimal approach to primate foraging? In: Rodman PS, Cant JGH, editors. *Adaptations for Foraging in Nonhuman Primates: Contributions on an Organismal Biology of Prosimians, Monkeys, and Apes*. New York: Columbia University Press. p. 280-303.
- Potts K. 2004. The response of the Ngogo chimpanzee (*Pan troglodytes*) community to a period of ripe fruit scarcity. *American Journal of Physical Anthropology Supp.* 38:162.
- Potts R. 1998. Environmental hypotheses of Hominin evolution. *Yearbook of Physical Anthropology* 41:93-136.
- Pruetz JD. 1999. Socioecology of adult female vervet *Cercopithecus aethiops* and patas monkeys *Erythrocebus patas* in Kenya: Food availability, feeding competition, and dominance relationships [Dissertation]. University of Illinois at Urbana-Champaign, Illinois
- Pruetz JD. 2001. Use of caves by savanna chimpanzees (*Pan troglodytes verus*) in the Tomboronkoto region of Senegal. *Pan African News* 8:26–28

- Pruetz JD. 2006. Feeding ecology of savanna chimpanzees (*Pan troglodytes verus*) at Fongoli, Senegal. In: Boesch C, Hohmann G, Robbins MM, editors. Feeding Ecology in Apes and Other Primates. Cambridge: Cambridge University Press. p. 161-182.
- Pruetz JD. 2007. Evidence of cave use by savanna chimpanzees (*Pan troglodytes verus*) at Fongoli, Senegal: implications for thermoregulatory behavior. *Primates* 48:316-319.
- Pruetz JD, Bertolani P. 2007. Savanna chimpanzees, *Pan troglodytes verus*, hunt with tools. *Current Biology* 17:1-6.
- Pruetz JD, Bertolani P. in press. Chimpanzee (*Pan troglodytes verus*) behavioral responses to stresses associated with living in a savanna-mosaic environment: Implications for hominin adaptations to open habitats.
- Pruetz JD, Marchant LF, Arno J, McGrew WC. 2002. Survey of savanna chimpanzees (*Pan troglodytes verus*) in southeastern Senegal. *American Journal of Primatology* 58:35-43.
- Pruetz JD, Fulton SJ, Marchant LF, McGrew WC, Schiel M, Waller M. 2008. Arboreal nesting as anti-predator adaptations by savanna chimpanzees (*Pan troglodytes verus*) in southeastern Senegal. *American Journal of Primatology* 70:393-401.
- Pusey AE. 1979. Inter-community transfer of chimpanzees in Gombe National Park. In: Hamburg DA, McCown ER, editors. The Great Apes. Menlo Park, CA: Benjamin/Cummings. P. 465-479.
- Pyke GH. 1984. Optimal foraging theory: a critical review. *Ann. Rev. Ecol. Syst.* 15:523-575.
- Reed KE. 1997. Early hominid evolution and ecological change through the African Plio-Pleistocene. *Journal of Human Evolution* 32:289-322.
- Reed KE, Rector AL. 2007. African Pliocene paleoecology: hominin habitats, resources, and diets. In: Ungar PS, editor. *Evolution of the Human Diet*. Oxford: Oxford University Press. p. 262-288.
- Remis MJ. 1997. Western Lowland gorilla (*Gorilla gorilla gorilla*) as seasonal frugivores: use of variable resources. *American Journal of Primatology* 43:87-109.
- Reynolds V. 1992. Chimpanzees in the Budongo Forest, 1962-1992. *Journal of Zoology* 228:695-699.
- Reynolds V. 2005. *The Chimpanzees of the Budongo Forest. Ecology, Behaviour and Conservation*. Oxford: Oxford University Press.

- Robinson BW, Wilson DS. 1998. Optimal foraging, specialization, and a solution to Liam's paradox. *American Naturalist* 151:223-235.
- Rodman PS. 1977. Feeding behaviour of orang-utans of the Kutai Nature Reserve, east Kalimantan. In: Clutton-Brock TH, editor. *Primate Ecology: Studies of feeding and ranging behaviour in lemurs, monkeys and apes*. London, New York: Academic Press. p. 384-413.
- Russak SM, McGrew WC. 2008. Chimpanzees as fauna: comparisons of sympatric large mammals across long-term study sites. *American Journal of Primatology* 70:402-409.
- Ruvolo M. 1997. Molecular phylogeny of the Hominoids: Inferences from multiple independent DNA sequence data sets. *Molecular Biology and Evolution* 14:248-265.
- Sabater Pi J. 1974. An elementary industry of the chimpanzees in the Okorobiko Mountains, Rio Muni (Republic of Equatorial Guinea), West Africa. *Primates* 15:351-364.
- Sanz CM, Morgan D. 2007. Chimpanzee tool technology in the Goualougo Triangle, Republic of Congo. *Journal of Human Evolution* 52:420-433.
- Sanz C, Morgan D, Gulick S. 2004. New insights into chimpanzees, tools, and termites from the Congo Basin. *American Naturalist* 164:567-581.
- Schaller GB. 1963. *The Mountain Gorilla: Ecology and Behavior*. Chicago: University of Chicago Press.
- Schoeninger MJ, Moore J, Sept JM. 1999. Subsistence strategies of two savanna chimpanzee populations: the stable isotope evidence. *American Journal of Primatology* 49:297-314.
- Schöning C, Ellis D, Fowler A, Sommer V. 2007. Army ant prey availability and consumption by chimpanzees (*Pan troglodytes vellerosus*) at Gashaka (Nigeria). *Journal of Zoology* 271:125-133.
- Schöning C, Humle T, Möbius Y, McGrew WC. 2008. The nature of culture: technological variation in chimpanzee predation on army ants revisited. *Journal of Human Evolution* 55:48-59.
- Sept JM. 1994. Beyond bones – archaeological sites, early hominid subsistence, and the costs and benefits of exploiting wild plant foods in east African riverine landscapes. *Journal of Human Evolution* 27:295-320.
- Sigaut F. 1993. How can we analyse and describe technical actions. In: Berthelet A, Chavaillon J, editors. *The Use of Tools by Human and Non-Human Primates*. Oxford: Claredon Press. p. 381-397.

- Smith RJ, Jungers WL. 1997. Body mass in comparative primatology. *Journal of Human Evolution* 32:523–559.
- Socha AJ. 2006. Habitat use and nesting ecology of savanna chimpanzees (*Pan troglodytes verus*) in southeastern Senegal [Thesis]. Iowa State University.
- Sommer V, Adanu J, Faucher I, Fowler A. 2004. Nigerian chimpanzees (*Pan troglodytes vellerosus*) at Gashaka: two years of habituation efforts. *Folia Primatologica* 75:295-316.
- Sponheimer M, Lee-Thorp JA. 1999. Isotopic evidence for the diet of an early hominid, *Australopithecus africanus*. *Science* 283:368-370.
- Sponheimer M, Lee-Thorp JA. 2003. Differential resource utilization by extant great apes and australopithecines: towards solving the C₄ conundrum. *Comparative Biochemistry and Physiology Part A* 136:27-34.
- Sponheimer M, Lee-Thorp J, de Ruiter D, Codron D, Codron J, Baugh AT, Thackeray F. 2005. Hominins, sedges, and termites: new carbon isotope data from the Sterkfontein valley and Kruger National Park. *Journal of Human Evolution* 48:301-312.
- Sponheimer M, Loudon JE, Codron D, Howells ME, Pruett JD, Codron J, de Ruiter DJ, Lee-Thorp JA. 2006. Do “savanna” chimpanzees consume C₄ resources? *Journal of Human Evolution* 51:128-133.
- Sponheimer M, Lee-Thorp J, de Ruiter D. 2007. Icarus, isotopes, and Australopith diets. In: Ungar PS, editor. *Evolution of the Human Diet*. Oxford: Oxford University Press. p. 132-149.
- Stanford CB. 1998. *Chimpanzee and Red Colobus: The Ecology of Predator and Prey*. Cambridge, Massachusetts: Harvard University Press.
- Stanford CB. 2006. The behavioral ecology of sympatric African apes: implications for understanding fossil hominid ecology. *Primates* 47:91–101.
- Stanford C. 2008. *Apes of the Impenetrable Forest: Behavioral Ecology of Sympatric Chimpanzees and Gorillas*. Upper Saddle River, New Jersey: Pearson Education Inc.
- Stanford CB, Bunn HT. 2001. *Meat-Eating and Human Evolution*. Oxford: Oxford University Press.
- Stanford CB, Nkurunungi JB. 2003. Behavioral ecology of sympatric chimpanzees and gorillas in Bwindi Impenetrable National Park, Uganda: diet. *International Journal of Primatology* 24:901-918.

- Stanford CB, Wallis J, Mpongo E, Goodall J. 1994. Hunting decisions in wild chimpanzees. *Behaviour* 131:1-18.
- Stephens DW, Krebs JR. 1986. *Foraging Theory*. Princeton: Princeton University Press.
- Stewart F, Pruetz JD, Hansell MH. 2007. Do chimpanzees build comfortable nests? *American Journal of Primatology* 69:930-939.
- Strait DS, Wood BA. 1999. Early hominid biogeography. *Proceedings of the National Academy of Science, USA* 96:9196-9200.
- Stumpf R. 2007. Chimpanzees and bonobos. In: Campbell CJ, Fuentes A, Mackinnon KC, Panger M, Bearder SK, editors. *Primates in Perspective*. New York: Oxford University Press, p. 321-344.
- Su HH, Birky WA. 2007. Within-group female-female agonistic interactions in Taiwanese macaques (*Macaca cyclopis*). *American Journal of Primatology* 69:199-211.
- Sugiyama Y. 1989. Population dynamics of chimpanzees at Bossou, Guinea. In: Heltne PG, Marquardt LG, editors. *Understanding Chimpanzees*. Cambridge, MA: Harvard University Press. p. 134-145.
- Sugiyama Y. 1995. Tool-use for catching ants by chimpanzees at Bossou and Monts Nimba, West Africa. *Primates* 36:193-205.
- Sugiyama Y. 2004. Demographic parameters and life history of chimpanzees at Bossou, Guinea. *American Journal of Physical Anthropology* 124:154-165.
- Sugiyama Y, Koman J. 1987. A preliminary list of chimpanzees' alimentation at Bossou Guinea. *Primates* 28:133-147.
- Sugiyama Y, Koman J. 1992. The flora of Bossou: its utilization by chimpanzees and humans. *African Study Monographs* 13:127-169.
- Sussman RW. 1987. Species-specific dietary patterns in primates and human dietary adaptations. In: Kinzey WG editor. *The Evolution of Human Behavior: Primate Models*. Albany: State University of New York Press. p. 143-156.
- Sutherland WJ. 2000. *The Conservation Handbook: Research, Management and Policy*. United Kingdom: Blackwell Science, 278p.
- Suzuki S, Kuroda S, Nishihara T. 1995. Tool-set for termite-fishing by chimpanzees in the Ndoki Forest, Congo. *Behaviour* 132:219-235.

- Takemoto H. 2000. The seasonal change in feeding behavior of chimpanzees caused by the seasonal change of food availability. *Reichorui Kenkyu* [Primate Res.] 16:280.
- Takemoto H. 2003. Phytochemical determination for leaf food choice by wild chimpanzees in Guinea, Bossou. *Journal of Chemical Ecology* 29:2551-2573.
- Takemoto H. 2004. Seasonal change in territoriality of chimpanzees in relation to microclimate in the tropical forest. *American Journal of Physical Anthropology* 124:81-92.
- Tappan GG, Sall M, Wood EC, Cushing M. 2004. Ecoregions and land cover trends in Senegal. *Journal of Arid Environments* 59:427-462.
- Teaford MF, Ungar PS. 2000. Diet and the evolution of the earliest human ancestors. *Proceedings of the National Academy of Science* 97:13506-13511.
- Teaford MF, Ungar PS, Grine FE. 2002. Paleontological evidence for the diets of African Plio-Pleistocene hominins with special reference to early *Homo*. In: Ungar PS, Teaford MF, editors. *Human Diet: Its Origin and Evolution*. Westport, Connecticut, London: Bergin & Garvey. p. 143-166.
- Teleki G. 1974. Chimpanzee subsistence technology: materials and skills. *Journal of Human Evolution* 3:575-594.
- Teleki G. 1981. The omnivorous diet and eclectic feeding habits of chimpanzees in Gombe National Park, Tanzania. In: Harding RSO, Teleki G, editors, *Omnivorous Primates: Gathering and Hunting in Human Evolution* New York: Columbia University Press. p. 303-343.
- Teleki G. 1989 Population status of wild chimpanzees (*Pan troglodytes*) and threats to survival. In: Heltne PG, Marquardt LA, editors, *Understanding Chimpanzees*. Cambridge, MA: Harvard University Press. p. 312-353.
- Tinbergen N. 1963. On Aims and Methods in Ethology. *Zeitschrift für Tierpsychologie* 20: 410-433.
- Trochain J. 1957. (French) Accord interafricain sur la definition des types de vegetation de l'Afrique tropicale. *Bulletin de l'Institut d'Otudes Centrafricaines* 55-93.
- Tutin CEG, Fernandez M. 1993. Composition of the diet of chimpanzees and comparisons with that of sympatric gorillas in the Lope Reserve, Gabon. *American Journal of Primatology* 30:195-211.

- Tutin CEG, McGrew WC, Baldwin PJ. 1983. Social organization of savanna-dwelling chimpanzees, *Pan troglodytes verus*, at Mt. Assirik, Senegal. *Primates* 24:154-173.
- Tutin C, Fernandes M, Rogers M, Williamson E, McGrew W. 1991. Foraging profiles of sympatric lowland gorillas and chimpanzees in the Lope, Gabon. *Philosophical Transactions of the Royal Society, London B* 334:179-186.
- Tutin CEG, Ham R, Wrogemann D. (1995). Tool-use by chimpanzees (*Pan t. troglodytes*) in the Lope Reserve, Gabon. *Primates* 36:181–192.
- Tutin CEG, Ham RM, White LJT, Harrison MJS. 1997 The primate community of the Lope Reserve. Gabon: diets, responses to fruit scarcity, and effects on biomass. *American Journal of Primatology* 42:1-24.
- Tweheyo M, Babweteera F. 2007. Production, seasonality and management of chimpanzee food trees in Budongo Forest, Uganda. *African Journal of Ecology* 45:535-544.
- Tweheyo M, Lye AK, Weladji RB. 2003. Chimpanzee diet and habitat selection in the Budongo forest reserve, Uganda. *Forest Ecology and Management* 188:267-278.
- Tweheyo M, Lye KA, Weladji RB. 2004. Chimpanzee diet and habitat selection in the Budongo Forest Reserve, Uganda. *Forest Ecology and Management* 188:267-278.
- Twinomugisha D, Chapman CA. 2008. Golden monkey ranging in relation to special and temporal variation in food availability. *African Journal of Ecology* 46:585-593.
- Uehara S. 1982. Seasonal changes in the techniques employed by wild chimpanzees in the Mahale Mountains, Tanzania, to feed on termites (*Psuedocanthotermes spiniger*). *Folia Primatologica* 37:44-76
- Uehara, S. 1997. Predation on mammals by the chimpanzee (*Pan troglodytes*): an ecological review. *Primates* 38: 193-214.
- Ungar PS. 2007. Limits to knowledge on the evolution of hominin diet. In: Ungar PS, editor. *Evolution of the Human Diet*. Oxford: Oxford University Press. p. 395-407.
- Ungar PS, Teaford MF. 2002. *Human Diet: Its Origin and Evolution*, Westport, Connecticut, London: Bergin & Garvey.
- Unger PS, Grine FE, Teaford MF. 2006. Diet in early Homo: a review of the evidence and a new model of adaptive versatility. *Annual Review Anthropology* 35:209–28.

- van Schaik CP, van Noordwijk MA. 1986. The hidden costs of sociality intra-group variation in feeding strategies in Sumatran long-tailed macaques (*Macaca fascicularis*). Behaviour 99:296-315.
- van Schaik CP, Fox EA, Sitompul AF. 1996. Manufacture and use of tools in wild Sumatran orangutans. Naturwissenschaften 83:1432-1904.
- Vogel S. 1978. Organisms that capture currents. Scientific American 239:108-117.
- Vrba ES. 1992. Mammals as a key to evolutionary theory. Journal of Mammalogy 73(1):1-28.
- Vrba ES. 1995. The fossil record of African antelopes (Mammalia, Bovidae) in relation to human evolution and paleoclimate. In: Vrba ES, Denton GH, Partridge TC, Burckle LH, editors. Paleoclimate and Evolution, with Emphasis on Human Origins. New Haven: Yale University Press. pp. 385-424.
- Waite S. 2000. Statistical Ecology in Practice: A guide to analyzing environmental and ecological field data. England: Pearson Education Ltd. 414p.
- Wakayama EJ, Dillwith JW, Howard RW, Blomquist GJ. 1984. Vitamin B12 levels in selected insects. Insect Biochemistry 14:175-179.
- Waller MT. 2005. Competition between chimpanzees and humans over fruit of *Saba senegalensis* in southeastern Senegal [Thesis]. Iowa State University.
- Wallis J. 1995. Seasonal influence on reproduction in chimpanzees of Gombe National Park. International Journal of Primatology 16:435-51.
- Walsh P, Abernethy K, Bermejo M, Beyers R, de Wachter P, Ella Akou M, Huijbregts B, Idiata Mambounga D, Kamdem Toham A, Kilbourn AM, Lahm S, Latour S, Maisels F, Mbina C, Mihindou Y, Ndong Obiang S, Ntsame Effa E, Starsky MP, Telfer P, Thibault M, Tutin CEG, White LJT, Wilkie D. 2003. Catastrophic ape decline in western equatorial Africa. Nature 422:1-3.
- Wesselman HB. 1995. Of mice and almost-men: regional paleoecology and human evolution in the Turkana basin. In: Vrba ES, Denton GH, Partridge TC, Burckle LH, editors. Paleoclimate and Evolution, with Emphasis on Human Origins New Haven, Connecticut: Yale University Press. p. 356-368.
- Whiten A, Goodall J, McGrew WC, Nishida T, Reynolds V, Sugiyama Y, Tutin CEG, Wrangham RW, Boesch C. 1999. Cultures in chimpanzees. Nature 399:682-685.

- Whiten A, Goodall J, McGrew WC, Nishida T, Reynolds V, Sugiyama Y, Tutin CEG, Wrangham RW, Boesch C. 2001. Charting cultural variation in chimpanzees. *Behaviour* 138:1481-1516.
- Whiten A, Goodall J, McGrew WC, Nishida T, Reynolds V, Sugiyama Y, Tutin CEG, Wrangham RW, Boesch C. 2001. Charting cultural variation in chimpanzees. *Behaviour* 138:1481-1516.
- Wich SA, Geurts ML, Setia TM, Utami-Atmoko SS. 2006. Influence of fruit availability on Sumatran orangutan sociality and reproduction. In: Boesch C, Hohmann G, Robbins MM, editors. *Feeding Ecology in Apes and Other Primates*. Cambridge: Cambridge University Press. p. 337-358.
- Wilson 1975 *Sociobiology: A New Synthesis*. Cambridge, Massachusetts: The Belknap Press of Harvard University Press.
- Wrangham RW. 1977. Feeding behaviour of chimpanzees in Gombe National Park, Tanzania. In: Clutton-Brock TH, editor. *Primate Ecology: Studies of feeding and ranging behaviour in lemurs, monkeys and apes*. London, New York: Academic Press. p. 503-538.
- Wrangham RW. 1980. An ecological model of female-bonded primate groups. *Behaviour* 75:262-299.
- Wrangham RW. 1986. Ecology and social relationships in two species of chimpanzee. In: Rubenstein DI, Wrangham RW, editors. *Ecological Aspects of Social Evolution: Birds and Mammals*. Princeton, NJ: Princeton University Press, p. 352-378.
- Wrangham RW. 1999. The evolution of coalitionary killing: the imbalance-of-power hypothesis. *Yearbook of Physical Anthropology* 42:1-30.
- Wrangham RW, Conklin NL, Chapman CA, Hunt KD, Milton K, Rogers E, Whiten A, Barton RA. 1991. The significance of fibrous foods for Kibale forest chimpanzees [and discussion]. *Philosophical Transactions: Biological Sciences* 334:171-178.
- Wrangham RW, Conklin NL, Etot G, Obua J, Hunt KD, Hauser MD, Clark AP. 1993. The value of figs to chimpanzees. *International Journal of Primatology* 14:243-256.
- Wrangham RW, McGrew WC, de Waal, F, Heltne PG. 1994. *Chimpanzee Cultures*. Cambridge, MA: Harvard University Press
- Wrangham RW, Chapman CA, Clark-Arcadi AP, Isabirye-Basuta G. 1996. Social ecology of Kanyawara chimpanzees: implications for understanding the costs of great ape groups.

- In: McGrew WC, Marchant LF, Nishida T, editors. Great Ape Societies. Cambridge: Cambridge University Press. p. 45-57.
- Wrangham RW, Conklin-Brittian NI, Hunt KD. 1998. Dietary response of chimpanzees and cercopithecines to seasonal variation in fruit abundance: I Antifeedantes. *International Journal of Primatology* 19:949-970.
- Wynn JG. 2000. Paleosols, stable carbon isotopes, and paleoenvironmental interpretation of Kanapoi, Northern Kenya. *Journal of Human Evolution* 39:411-432.
- Yamagiwa J, Mwanza N, Yumoto T, Maruhashi T. 1994. Seasonal change in the composition of the diet of eastern lowland gorillas. *Primates* 35:1-14.
- Yamagiwa J. 2004. Diet and foraging of the great apes: ecological constraints on their social organizations and implications for their divergence. In Russon AE, Begun DR, editors. *The evolution of thought: Evolutionary origins of great ape intelligence* Cambridge, U.K.: Cambridge University Press. p. 210-233.
- Yamagiwa J, Basabose AK. 2006. Effects of fruit scarcity on foraging strategies of sympatric gorillas and chimpanzees. In: Boesch C, Hohmann G, Robbins MM, editors. *Feeding Ecology in Apes and Other Primates*. Cambridge: Cambridge University Press. p. 73-96.
- Yamakoshi G. 1998. Dietary responses to fruit scarcity of wild chimpanzees at Bossou, Guinea: possible implications for ecological importance for tool use. *American Journal of Physical Anthropology* 106:283-295.
- Yamamoto S, Yamakoshi G, Humle T, Matsuzawa T. 2008. Invention and modification of a new tool use behavior: ant-fishing in trees by a wild chimpanzee (*Pan troglodytes verus*) at Bossou, Guinea. *American Journal of Primatology* 70:699-702.

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- Bogart SL, Pruett JD, McGrew WC. 2005. Termite de jour: termite fishing by West African chimpanzees (*Pan troglodytes verus*) at Fongoli, Senegal. *American Journal of Physical Anthropology* Suppl 40:75. [Abstract]