Insectivory, termite diversity, and tool use of the Fongoli chimpanzees (Pan troglodytes verus), Senegal, West Africa

Stephanie Lynn Bogart
Iowa State University

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Insectivory, termite diversity, and tool use of the Fongoli chimpanzees (Pan troglodytes verus), Senegal, West Africa

by

Stephanie Lynn Bogart

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

MASTER OF ARTS

Major: Anthropology

Program of Study Committee:
Jill D. Pruetz, Major Professor
Matthew G. Hill
Donald Lewis

Iowa State University
Ames, Iowa
2005

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This is to certify that the Master's thesis of
Stephanie Lynn Bogart
has met the thesis requirements of Iowa State University

Signatures have been redacted for privacy
This thesis is dedicated to:

Ester Zepkin, Ileen Bogart, and Diane Bogart:

A long line of strong and independent women.
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like a second mother to me; and finally, to my best friend, Kevin McKee, who has been there through the hard times and has always believed in me.
ABSTRACT

Chimpanzees use tools to fish for termites across Africa, but the ecology of this insectivory has been largely ignored. West African chimpanzees (Pan troglodytes verus) at Fongoli, southeastern Senegal, fish for termites year-round, with peaks from April to July and in October. Data were collected on 124 termite mounds including information on nearest neighbor mound, shape, habitat-type, percent cover by woody vegetation, height, width, termite activity, chimpanzee activity, and vegetation. The presence of chimpanzee activity was assessed using ethoarchaeological methods, that is, artifacts and remnants left behind were systematically collected and measured. Tool length and plant source were recorded. Of the mounds used by chimpanzees, 59% were in open woodland. Tools were found at 29 mounds (23%), and 20 revisits also proved positive for tools, for a total of 49 assemblages of tools. A total of 401 fresh and recent (younger than 5 days old) flexible probes were analyzed. Results are compared to other sites.

At least six genera of termites occur at Fongoli. Indirect data suggest that the chimpanzees of Fongoli may fish for two of these: Macrotermes and Trinervitermes. Macrotermes subhyalinus and M. bellicosus comprise 75% of the fished mounds. Termite diet may be more diverse for the chimpanzees of Fongoli, given their long fishing season compared to other sites.
CHAPTER 1: Introduction

Importance of Chimpanzees to Understanding Human Evolution Studies

One of the principle reasons anthropologists study nonhuman primates is in regards to their role as referential models of human (*Homo sapiens*) evolution. For example, questions of human evolution initially stimulated research on our closest living relatives, chimpanzees (*Pan troglodytes*). Louis Leakey recruited Jane Goodall in the 1960s for this very purpose, to research chimpanzees in Tanzania, at the Gombe field site. Chimpanzees have been studied as referential models for human evolution, not only as analogous models but perhaps more appropriately, as inferential models for the ecology and behavior of hominids.

The chimpanzee ancestor diverged from the human ancestor about 6-8 million years ago, leaving approximately 98% of human and chimpanzee DNA identical (Navarro & Barton, 2003). Early hominid evolution following this split is thought to have occurred in a savanna-like or open habitat; this contrasts with the standard view of ancestral hominoids living in forests. Thus, studying differences of ecology and behavior in extant primates, such as chimpanzees living in savanna versus forested environments, will provide fresh information for modeling the evolution of the early hominids (Moore, 1996).

Human evolution has been modeled on many different aspects of extant primate behavior, such as diet, habitat, and predation. Research on diet in primates has been especially influential in inferring diet in early hominids. Most dietary studies of chimpanzees have concentrated on the types of fruits and plants these apes consume (see Balcomb et al., 2000; Matsumoto-Oda & Hayashi, 1997). In regards to diet, one area that has been largely ignored is insectivory. This study concentrates on the ecological context of the insectivorous diet and termite fishing behavior of chimpanzees.
Chimpanzees are often referred to as omnivores, much like humans, feeding on everything from seeds to other animals (McGrew, 1983). Although animal prey makes up a low proportion of the chimpanzee diet, fauna provide nutrients, amino acids, and proteins that cannot be acquired from plants (McGrew, 1983; Sussman, 1987). Regarding the faunivorous diet of chimpanzees, mammalian prey especially has been a focal topic of discussion among anthropologists (Stanford & Bunn, 2001). Meat-eating is appealing to anthropologists because it is often associated with hunting and sharing of food (Stanford & Bunn, 2001). However, invertebrates may be equally important in the chimpanzee diet (McGrew, 2001). The methods employed by chimpanzees for the consumption of invertebrates are of significance as well, i.e. manipulating plant material into tools to obtain otherwise unattainable insects or insects that sting or bite en masse. Chimpanzees use elementary technology for simple problem solving in order to obtain invertebrate prey (McGrew, 1992). The ecological details behind this behavior are lacking in termite fishing studies. Here I will examine these details.

Primate Insectivory

Primates are thought to exhibit a “species-specific” dietary pattern (Sussman, 1987). Most protein obtained by omnivorous primates is acquired through the consumption of insects or leaves (Sussman, 1987). Animal prey does not make up a very high proportion of the primate diet; however, it does seem to be very important (Sussman, 1987). Many studies often lump vertebrates and invertebrates together regarding their composition in the diet. However, there may be evidence missed in doing so, such as the importance of each of these categories, respectively.
Insectivory by primates is common. Insects provide high energy and offer many of the same nutrients as vertebrates (McGrew, 2001). According to studies of entomophagy (the consumption of insects) in humans, insects provide more calories (i.e. energy), essential nutrients, and sometimes protein than beef, chicken, or fish (Berenbaum, 1995). Primates consume representatives from most of the orders within the insect class, but there is preference for large-bodied social insects, either wingless or slow-moving (McGrew, 2001). Obligate insectivores include prosimians, tamarins (Saguinus spp.), and tarsiers (Tarsius spp.) (McGrew, 2001). The latter are the only truly faunivorous primate; however in that they only eat animal prey (Nash, 1984; Warren & Crompton, 1998). Monkeys, such as capuchins (Cebus sp.), baboons (Papio sp.), langurs (Colobinae), and macaques (Macaca sp.), and lesser apes (Hylobates) occasionally consume insects during opportunistic foraging (McGrew, 2001). The composition of insects in the diet of these primates can vary however. Capuchins include up to 20% of invertebrates in their diet (Freeman 1985), while invertebrates account for only 5% of the diet of long-tailed macaques (Sussman, 1987). Patas monkeys (Erythrocebus patas pyrrhonotus) consume thorn-dwelling social insects from Acacia trees, which make up approximately 36% of their diet, as well as other invertebrates, which comprise another 5% of food items (Isbell, 1998). The special and temporal availability of social insects allows a relatively large-bodied primate to exploit what is usually a costly resource to acquire. Similarly, the insectivory of large-bodied apes is largely limited to social insects.

All of the great apes consume insects and use specialized techniques to obtain them; however, the chimpanzee is the only known non-human primate to habitually use multiple types of tools to acquire insects (McGrew, 1992). Tool use of this nature has been observed
across Africa over the many years that chimpanzees have been studied in the wild (Fay & Carroll, 1994; Goodall, 1963; McBeath & McGrew, 1982; McGrew & Collins, 1985; Suzuki et al., 1995). Chimpanzees are known to be habitual consumers of insects across Africa (Collins & McGrew, 1985; Fay & Carroll, 1994; Humle & Matsuzawa, 2001; McBeath & McGrew, 1982; McGrew et al., 1979; Nishida & Uehara, 1980; Sanz et al., 2004; Suzuki et al., 1995). Chimpanzees mainly feed on social insects, such as Hymenoptera (ants, wasps and bees) and Isoptera (termites) (McGrew, 1983) and have been observed to employ various tools in order to obtain them. These patterns of tool use and other behaviors have been termed culture in chimpanzees, a feature once considered uniquely human (McGrew, 2004).

Termite fishing behavior, especially, appears to vary between sites to some degree, but detailed data regarding ecological inferences on such variance are lacking.

Termites as a taxa are very diverse across Africa (Eggleton et al., 2002). Eggleton and colleagues (2002) found approximately 133 different termite species in only two countries (Cameroon and Republic of Congo). Termite diversity may depend on the degree of habitat disturbance (Sarr et al., 1998). McGrew (1983) notes that two genera of termites are known to be consumed by chimpanzees: *Macrotermes* and *Pseudacanthotermes*. Furthermore, previous studies suggest that the termite genera *Odontotermes* is not consumed by the chimpanzees but is found at many chimpanzee sites (Collins & McGrew, 1985; 1987). This aspect of chimpanzee diet is little studied.

**Non-Human Ape Diet**

Diet among the great apes is very diverse. Divergences in diet exist even among subspecies (e.g. mountain gorilla as opposed to lowland gorilla). I present here a general breakdown of diet between species of hominoids (Table 1.1). Orangutans’ (*Pongo pygmaeus*)
diet consists mainly of fruit (54%) as well 54% fruit (Rodman, 1977) (Table 1.1). Western lowland gorillas (Gorilla gorilla gorilla) at Lope Primate research site in Gabon are characterized by a diet made up of fruit (46%), seeds (10%), leaves (22%), pith (7%), flowers (1%), animal prey (5%), and other miscellaneous items (10%) (Tutin et al., 1997). This differs slightly from another western lowland gorilla site, Bai Hokou in Central African Republic, where gorillas' diet includes 51% fruit, 26% leaves, 12% bark, and 10% herbs (Remis, 1997). Table 1.1 averages these two sites for comparison to other great apes.

Mountain Gorillas (Gorilla gorilla beringei) have a specialized diet mainly consisting of leaves, shoots, and stems (86%) and only 2% is of fruit (Fossey & Harcourt, 1977) (Table 1.1). Chimpanzee (Pan troglodytes) diet is made up of mostly fruit (60%) (averaged from 12 sites including Fongoli) (Pruetz, 2005). Animal prey in the chimpanzee diet accounts for approximately 8%, but only 2.5% is of vertebrate species (averaged from eight chimpanzees sites including Fongoli) (Pruetz, 2005). The proportion of the chimpanzee diet consisting of animal prey is greater than all other non-human hominoids. Insect eating occurs more often than vertebrate eating; the former is a daily activity while the latter may occur only a few times per year (McGrew, 1983). Of the two Orders of social insects commonly consumed by chimpanzees; Hymenoptera (ants, wasps and bees) and Isoptera (termites) (McGrew, 2001), the latter will be specifically examined in this study.
Chimpanzee insectivory

Chimpanzees vary across sites in their consumption of animal prey, especially insects. At Lope, Gabon the chimpanzee diet consists of 9.3% animal prey, including 17 invertebrate and vertebrate species (Tutin et al., 1997). The chimpanzees at Kahuzi-Biega consume animal prey as 9% of their diet, 4% of which are insect prey consumed seasonally (Basabose, 2002). Four percent of the diet of Gabon chimpanzees consists of animal foods, while up to 30% of these chimpanzees' time is spent foraging for insects (Hladik, 1977). The Gabon chimpanzees consume ant species more than termites, while Gombe, Tanzania chimpanzees consume more termites than ants (Hladik, 1977). Gombe chimpanzees spend up to 15% of their active time termite fishing (McGrew, 1983). Elsewhere in Tanzania, Mahale B group chimpanzees consume *Macrotermes* with probes and fishing techniques (McGrew & Collins, 1985), while Mahale K group chimpanzees use both hands and probes for the acquisition of the termite species *Pseudocanthotermes*, which can be found in 6.5% of fecal
data (Uehara, 1982). Tai and Budongo chimpanzees consume termites, but do not use tools to obtain them (Boesch & Boesch, 1990).

Questions and Goals

The questions addressed explored numerous factors relative to chimpanzee insectivory, particularly regarding termite prey. Based on McBeath and McGrew’s (1982) study of Mt. Assirik, Senegal ecology and chimpanzee termite fishing, certain questions emerged. Are Fongoli chimpanzees similar to those studies elsewhere in that *Macrotermes* is the chief genus consumed by the chimpanzees? Does termite species, in terms of diversity and abundance, influence consumption? If so, do chimpanzees consume the termites that are most abundant, or do other factors influence their choices? McBeath and McGrew (1982) addressed questions pertaining to tool material and habitat used to termite fish and found that tools were made from plants growing within two meters of the termite mounds and were often of a single species (*Grewia lasiodiscus*). Would this also be true for the Fongoli chimpanzees? Finally, I expected that the materials used for termite fishing tools at Fongoli would come mainly from the ecotone and surrounding habitat, based on McBeath and McGrew’s findings (1982). “Ecotone” habitats, defined as the transitional zone between woodland and plateau habitats containing evergreen trees, most often yielded termite fishing at Assirik (McBeath and McGrew, 1982).

To address some of these questions I replicated many methods used by McBeath and McGrew (1982). These authors, who studied at Mt. Assirik, in Parc National du Niokolo-Koba, Senegal, approximately 45 km from the Fongoli study site, calculated the proportions of various habitat types in regards to chimpanzee termite fishing. Their goal was to determine whether habitat influenced the termite fishing behavior of the chimpanzees, and their data
supported this conclusion. Habitat use related to chimpanzees termite fishing was also considered in the current study. Termite mounds are at a higher density in shrub savanna habitats when compared to gallery forest (Korb & Linsenmair, 2001). During the initial year of study at Fongoli it was found that chimpanzees spent 60% of their observed time in woodland and other open habitats (99% of study area) and 40% in the gallery forest (1% of study area) (Pruetz, unpublished data). Based on these findings, I asked whether termite fishing occurs most prominently in ecotone habitats at Fongoli. I further examined whether habitat influences termite fishing, and if so, what specific factors within the habitat are the selective pressures. Finally, I compare my findings on the physical properties of the tools used by the Fongoli chimpanzees and the termite species consumed to those findings from studies at other chimpanzee sites.

Study Site and Subjects

The study was conducted at the Fongoli study site in the Tomboronkoto Region, southeastern Senegal, West Africa (12°39 N 12°13 W) (Figure 1.1). Research was conducted from May through August in 2004. This study was conducted in a 40 square kilometer area corresponding to the chimpanzees’ core range. Study subjects included the Fongoli community of chimpanzees (Pan troglodytes verus) (Figure 1.2) and termites at the site. The chimpanzee community at Fongoli is semi-habituated with 18 identified individuals and 27 known community members (Pruetz, 2005). Observations of chimpanzees are based on ad libitum data following methods from Paterson (2001). Fongoli is important due to its location in a savanna environment, proposed to be the principal habitat in which early hominids evolved. The site is considered a mosaic habitat, including woodland, plateau, grassland, and gallery forest. Early hominids most likely lived in this type of habitat rather than dense
forested ones, e.g. Oldowan (*Australopithecus* and *Homo*) hominids (Plummer et al., 1999). Therefore, chimpanzees studied here can provide a referential model regarding the diet and behavior of those early hominids.

Dr. Jill D. Pruetz has been studying chimpanzees at the Fongoli site since April 2001 and has collected extensive data on the composition of the chimpanzee diet here. Her data is prominently from fecal analysis, supplemented by behavioral observations and feeding traces left by chimpanzees. Her data suggest that the Fongoli chimpanzees consume termites most intensively from April to July (Pruetz, unpublished data) but termites are included in the diet every month of the year (Pruetz, 2005).
Figure 1.1: Senegal, West Africa (Fongoli Chimpanzee Study Site marked).
Implications of This Research

Insects have been largely ignored as a major contributor to the diet of chimpanzees. This study will enlighten primatologists as to the importance of insects in the diet of chimpanzees, which has been argued as more important than mammal feeding (McGrew, 2001). Such significance implies that insects may also have been important to early (Pliocene) hominids and that they may have used similar technology to obtain such prey.
Termites have recently been interpreted as included in the diet of early hominids, specifically *Australopithecus robustus*, based on evidence from bone tools thought to be used to extract termites from mounds (Backwell & d’Errico, 2001). Chimpanzees use similar wooden tools to perforate termite mounds in order to clear open a ventilation hole for insertion of a flexible probe (Sanz et al., 2004). According to dental traits, gracile Australopithecines are said to have had a diet much like modern apes today, fairly omnivorous (Teaford & Ungar, 2000). Consequently, it is most likely that hominids and even protohominids used tools before this time (Beck, 1980; McGrew, 1992). However, evidence of these tools in the archaeological record is absent due to decay of organic matter such as wood, twigs, sticks, and leaves. Since tool use is found in most great apes, the assumption may be made that the last common ancestor could also have had some simple form of tool technology (about 6 million years ago). Systematic study of prehistoric diet, concentrating on insects, may allow us to make more direct inferences regarding simple forms of technology like that made from materials used by living non-human apes, e.g. in termite fishing, ant dipping and fishing, and honey extraction.

In support of the hypothesis that insectivory played an important role in early hominid evolution are data from living humans. Many modern day human societies also consume termites (McGrew, 2001). The Tiv of Nigeria gather caterpillars and termites opportunistically and will also eat the mineral-rich earth of the termite mounds (Bohannan & Bohannan, 1968). The Mbuti of Central Africa, consider termites a delicacy (Turnbull, 1965). Insects in the early hominid diet could have provided protein and nutrients that plants and fruits could not provide, especially if hunting and scavenging were limited. Early hominids may have been more reliant on insects than large vertebrates.
This thesis is laid out in terms of subject; therefore, specific methods for each subject will be presented in each chapter. Chapter 2 reviews literature relevant to this study, while the topics of focus were split into: habitat (chapter 3), termite inhabitants (chapter 4), and termite fishing tools (chapter 5). Conclusions and discussion relating to each topic are included within the chapters and, finally, chapter 6 summarizes each subject and discusses the research as a whole.
CHAPTER 2: Significance of Tool Use

"If man is to survive, he will have learned to take a delight in the essential differences between men and between cultures. He will learn that differences in ideas and attitudes are a delight, part of life's exciting variety, not something to fear." – Gene Roddenberry

What is Tool Use?

Tool use was once used as a defining criterion for humanity. More recently, the issue of culture as a hallmark of our species has been questioned. Primatologists have applied the term ‘culture’ to non-human primates, namely apes. Culture as a concept in non-human primates was introduced approximately 40 years ago following observations of Japanese macaques potato washing and rice fishing. Innovations were exhibited by one macaque and these behaviors were adopted by the rest of the troop (Kawai, 1965). This and analogous behaviors found in chimpanzees (Goodall, 1964) enticed anthropologists to consider these behaviors within the concept of culture for non-human primates. Recently there has been a move to compile all “cultural” behaviors for chimpanzees (Figure 2.1) (Whiten et al., 1999; 2002). A typical definition of culture is:

information or behavior – shared by a population or subpopulation – which is acquired from conspecifics through some form of social learning (Whitehead et al., 2004: p.427).

Social learning is included in the definition of culture used by primatologists Whiten and Ham (1992), as well as teaching and imitation.

One of the most common features of culture in non-human animals is tool use. This behavior has been suggested for many animal species, but only primates have been observed to exhibit a wide variety and complexity of tool use. Wild monkeys characteristically do not show habitual tool-use or manufacture tools as do chimpanzees (van Schaik et al., 1999, but
see Fragaszy et al., 2004). The use of tools is found in all chimpanzee communities thus far studied (McGrew, 1992; Whiten et al., 1999; 2001).

The most widely-used definition of tool use is from Beck (1980: p.10) in which a tool is:

the external deployment 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 just prior to use and is responsible for the proper and effective orientation of the tool.

He further stipulated that a tool must be an external object “free of any fixed attachment to the substrate and must be held, carried, or manipulated by the user” (Beck, 1980: p.10.).

There are four modes of tool manufacture: detach (simply separating one object into two and using the detached object), subtract (removing an object from another to use the latter), add or combine (two or more objects are connected), and reshape (reconstruction of material to
use functionally) (Beck, 1980). Tools can serve many functions: to extend reach, exert more mechanical force, elaborate on gesture in display, control liquids, intimidate predators, function as weapons, and for feeding purposes (Beck, 1980; van Schaik, 1999; Jolly, 1985).

The four levels of tool-use identified according to McGrew and Marchant (1997) are anecdotal, idiosyncratic, habitual, and customary. Anecdotal tool use is a unique or rare event that has the constraints of being an accident, mistake by the subject, or observer error (McGrew & Marchant, 1997). Idiosyncrasy is an action repeated by one individual and is constrained by limited general ability (McGrew & Marchant, 1997). Habitual tool use is when several individuals repeat an action over time, which may be constrained by context-specific explanations (McGrew & Marchant, 1997). Finally, customary tool use is a regular occurrence that all individuals of a community perform although constraints on such use include seasonality, age, or sex-specific groups and may have cross-populational differences (McGrew & Marchant, 1997). The last two levels are the most intriguing and are considered ‘cultural’ according to Whiten and colleagues (2001), who have made the first non-human attempt to map out cultural behaviors in non-humans according to similarities and differences across chimpanzee sites. Not all animal tool use qualifies as a cultural behavior according to this recent attempt to interpret behavioral variation (Whiten et al., 2001).

**Animal tool use**

**Birds (Aves)**

Numerous bird species have been observed to use tools. The Egyptian vulture (*Neophron percnopterus*) has been observed to break open ostrich eggs with stones that are thrown or hammered at the egg (Beck, 1980). The Galapagos finch (*Camarhynchus pallidus*), commonly called the woodpecker finch, will hold a twig in its bill to extract insects
from holes or hard to reach places; once insects are on the twig, the finch will hold the twig under its foot while it eats the insects from the tool (Beck, 1980). Captive Caledonian crows (Corvus monedulaeides) have demonstrated the ability to spontaneously, without human motivation and mimicry, manipulate vegetation to manufacture a probe for food (Kenwood et al., 2005).

**Mammals (Mammalia)**

Mammals within a number of different families have been observed to use tools. Elephants use detach and subtract strategies of manufacture, for example. This includes using twigs or branches held in their trunks to scratch parts of their bodies (Beck, 1980). Asian elephants (Elephas maximus) use branches to repel flies. They modify the branch by holding the stem with the front foot and pulling off side extensions with the trunk (Hart et al., 2001). Polar bears (Ursus maritimus) use a detach method of tool manufacture, but they have also been known to use a subtract method as well. In addition, Polar bears have been seen to use tools for weaponry purposes, where they throw chunks of ice or rocks at walruses or seals, either killing or injuring their prey (Beck, 1980). In Shark Bay, Australia, bottlenose dolphins (Tursiops truncates) use sponges on their rostra for protection against the rough seafloor. This is thought to be a foraging specialization, to prevent injury (Rendell & Whitehead, 2001).

**Primates and Tool Use**

*Cebus* is the chief tool user among New World primates in captivity (Ottoni & Mannu, 2001) and in the wild (Boinski et al., 2000). An impressive example involves an incident where a mother used simple tools (plant materials) to nurse her 6-day-old infant’s head injury (Ritchie & Fragaszy, 1988). Panger (1998) however, indicated that free-ranging
capuchins do not exhibit the amount of tool use seen in captivity. In contrast, Phillips (1998) describes a case for tool-use in a wild population of white-fronted capuchins (Cebus capucinus). They habitually use leaves to extract water from tree holes (Phillips, 1998). A recent study found capuchins (Cebus apella libidinosus) using stone hammers to crack seeds of Manihot in Caatinga dry forests and stone digging tools for digging up tubers and branches. Twigs were also used for probing of insects, honey, and water (Moura & Lee, 2004). In Piaui, Brazil, Cebus libidinosus has also been observed to use stone hammer and anvil techniques to crack nuts (Fragaszy et al., 2004). Many studies have proposed that capuchin monkeys, alongside chimpanzees, display behavioral variation among populations that cannot be explained by ecological variables (Fragaszy et al., 2004, McGrew & Marchant, 1997; Panger, 1998; Visalberghi & McGrew, 1997).

Few species have been known to use feeding tools in the wild, but among those that do are: Cebus spp., Macaca spp., Papio spp., Pongo spp., and Pan spp (van Schaik, 1999). The capacity for tool-use is thought to have evolved three times in evolutionary past, in capuchins (Cebus), cercopithecines, and apes, which are taxonomically separated and not closely related (van Schaik et al., 1999). Van Schaik et al.’s (1999) predictive model for determining likely tool-users in feeding behavior positively correlates such behavior with extractive foraging tasks, intelligence, dexterity, gregariousness, and social tolerance within primates. A primate is more likely to use tools when all of these factors are present.

**Ape tool use (Hominoidea)**

Great apes (Superfamily Hominoidea) are the only known non-human animals to use all four forms of tool manufacture as defined by Beck (1980). It is rare to find tool-use among the lesser apes, gibbons and siamangs (Hylobates spp.) (Beck, 1980). The unique
reliance on tools for specific tasks by great apes is one trait that initiates the great interest in ape behavior by anthropologists. Only studies of wild apes will be reviewed here. There is no doubt that humans are complex and intelligent apes, but to understand how we arrived here can only be determined by understanding human evolution. The apes are our closest living relatives and can help guide us to possible answers.

**Orangutans* (Pongo pygmaeus)**

Orangutans are the only habitual tool-users among primates besides chimpanzees. Orangutans use tools arboreally with their mouths (Fox & Muhammad, 2002). Suaq Balimbing orangutans use sticks or twigs to extract honey from stingless beehives in trees (van Schaik, 1999). The Suaq Balimbing orangutans also consume more insects than orangutans at other sites (Fox et al., 2004). Using short twigs, these orangutans also take seeds from *Neesia* fruits, which are protected by stinging hairs. The twigs are modified by breaking and stripping off leaves or chewing on the twig end, fraying it. Twigs are used as both a wedge and a spoon (van Schaik, 1999). Orangutans also extract termites and ants from tree holes (van Schaik et al., 2003a) using unmodified twigs.

An orangutan cultural database was recently initiated, modeled after that of Whiten and colleagues for chimpanzees (1999; 2001). Van Schaik and colleagues (2003b) compiled a list of behaviors interpreted as cultural using a similar definition to the one described earlier for chimpanzees. Some of the tool use behaviors include leaf wipe (wiping face with leaves), sun cover (building a cover on nests), scratch stick (using detached stick to scratch body parts), branch as swatter (leafy branch swatting at bees/wasps), tree hole tool use, seed extraction tool, and branch scoop (drinking water extracted from a tree hole with a leafy branch) (van Schaik et al., 2003b).
Gorillas (*Gorilla gorilla*)

A few instances have been described for tool-use among wild gorillas; however, none are interpreted as habitual for any community. Mountain gorillas have been said to use just as much skill with their hands, if not more, in processing thistles than is seen with chimpanzee tool use. Gorillas, according to Byrne and colleagues (2001), do not have any need for tools. Byrne and colleagues (2001) suggested that this complexity in processing food shows that gorillas have a great cognitive capacity.

Bonobos (*Pan paniscus*)

Little is known about the tool-use behavior of bonobos (*Pan paniscus*) due to the lack of study of wild populations. In the wild, leafy twigs are used to cover the body from the cold (Lomako) and twigs are used to shelter nests/beds (Wamba) (Fruth et al., 1999). Branches are also used in display behaviors. In the wild, bonobos display little material culture when compared to chimpanzees, however (Fruth et al., 1999).

Chimpanzees (*Pan troglodytes*)

The chimpanzee (*Pan troglodytes*) is the only extant non-human primate known to use a tool-kit (McGrew et al., 2003). A tool kit is the sum total of tools used or the repertoire possessed by a population, while a tool set is the sequential use of tools. An example of both is when chimpanzees probe for honey: they first use a stick chisel; a slimmer chisel is used next; third, they puncture a hole, and finally use a dip stick to retrieve the goods.

Chimpanzees exhibit a wide variety of tool using behavior (Beck, 1980; Whiten et al., 2001). They have been observed to do everything from throwing (aimed and unaimed) to nut cracking, using the same hammer and anvil technique that hominids have been characteristically said to exhibit. Chimpanzee tool-use can be divided into three categories:
social (antagonistic and non-antagonistic), subsistence, and maintenance (McGrew et al., 2003). To illustrate the diversity among chimpanzees, Tai, Ivory Coast chimpanzees have 20 different tools in their tool kit, while Budongo, Uganda chimpanzees have only five. There are no ecological explanations as to why tools of the type used by Tai chimpanzees do not appear at Budongo (Whiten et al., 2001).

Under certain environmental conditions (i.e. dry forests at Bossou, Guinea), wild chimpanzees depend on tool use for the acquisition of reliable food resources (Yamakoshi, 1998). Subsistence technology is most representative of chimpanzee ‘culture’. Of 39 behavior patterns judged to be cultural, 22 are used for subsistence (Whiten et al., 2001). Chimpanzees spend 15% of their daily time budget at some sites using tools to fish for termites and an equal amount of time nut cracking at other sites (McGrew, 1992).

**Termite Fishing**

My research concentrates on termite fishing for several reasons. First, termites are a substantive food that may exceed in quantity all other vertebrates consumed in the rainy season (McGrew, 2003). Second, termites provide a substantial source of nutrition. The use of tools for termite fishing will be the main target of this study.

Gorillas and bonobos do not use tools for termite fishing (McGrew, 2001). Orangutans use probes for bees and honey, but use a ‘smash and grab’ technique for termites, ants, wasps, and bees (van Schaik, 1999; van Schaik et al., 2003a). Chimpanzees customarily use probes to fish for termites (Figure 2.2) or ants. Both chimpanzees and orangutans exhibit a female dietary preference for insects and a male preference for mammalian protein intake (McGrew, 2001). When chimpanzees customarily use probes to fish for termites or ants, these activities give them many more kilocalories than the energy invested in the activity
Thus, termites are a high-value food that is obtainable using a simple technology.

Termite fishing involves using probes made of twigs, stems, bark, leaves, or vines; these are then inserted into a ventilation hole of a termite mound; termites attack the intruding object, and the chimpanzee carefully withdraws the probe from the hole and eats the affixed termites (Goodall, 1963; 1968). Termite fishing is habitual at the Assirik, Senegal site and customary at Gombe and Mahale (Whiten et al., 2001). This pattern is also found at the Fongoli, Senegal site and is the focus of the current study.

Termite fishing is practiced at many sites across Africa: Assirik, Senegal (McGrew et al., 1979; McBeath & McGrew, 1982); Rio Muni, Equatorial Guinea (McGrew et al., 1979); Gombe, Tanzania (McGrew et al., 1979); Mahale, Tanzania (McGrew & Collins, 1985); Ndakan, Congo (Fay & Carroll, 1994); Ndoki, Congo (Suzuki et al., 1995); Goualougo, Republic of Congo (Sanz et al., 2004). McBeath & McGrew (1982) found that, at Mt. Assirik the majority of termite fishing occurs in an ecotone habitat. This is the zone between plateau and woodland where water drainage produces an area characterized by evergreen vegetation. They concluded that habitat was influential on this behavior. Such ecological influences are important to consider when attempting to assess the cultural versus ecological aspects of non-human primate behavior.
Implications for Culture?

Tools are considered an important part of the chimpanzee cultural database proposed by Whiten et al. (1999, 2001). Such cultural implications are remarkable, considering humans were thought to be the only extant animal to possess culture for many decades. The only known animals to habitually use different and multiple tools are chimpanzees and humans (Boesch, 2003). Therefore, research on chimpanzee tool use may provide referential models for hominid (early human) tool evolution where fossil evidence is lacking.

Five types of evidence are used in order to make inferences about hominid life: fossilized bones and teeth, artifacts, ecofacts, etc.; flora and fauna fossilized in association with hominid dwellings; extant traditional societies (i.e. hunter-gatherers); and behavior of extant non-human primates. Tools first appear in the hominid fossil record about 2.5 million years ago, although new reports may suggest even earlier evidence (see Blackwell & d’Errico, 2001). It is still debated as to whether the first tool users were *Homo* or *Australopithecus*. However, it is likely that hominids and even protohominids used tools
before this time (Beck, 1980; McGrew, 2001). The evidence for particular tools in the fossil record are absent due to ecological decay of organic matters such as wood, twigs, sticks, and leaves.

Regarding the evolution of tool-use, it appears that, with an increase in intelligence and plasticity, there was an associated increase in the technology of tools (Rightmire, 2004). Humans have more interest in objects for the purposes of tool use in all areas, whereas non-human primates use tools primarily for feeding purposes. No one can deny that humans have a superior knowledge and use of tools and technology than any other species on earth. Yet we cannot ignore where that knowledge has come from and that we are not as unique as we may think. Human technology has evolved to the level of computers and airplanes. Our technology has had a massive impact on the biological and physical environment to an extent of which we are only starting to become aware. It may be ironic that tool-use is considered one of the main shapers of our species but may ultimately may end up being our downfall (Beck, 1980). Perhaps to understand this eventual destruction we have to examine how tool use was created.

Whitehead and colleagues (2004) suggest that cultural diversity should be a promotion for conservation efforts in all animals (see also Norris, 2002). For example, the evolution of culture is proposed to be very important in the Order Cetaceans due to the constant change in marine ecosystems, allowing whales and dolphins to be able to move monthly (Rendell & Whitehead, 2001; Norris, 2002). Cultural behavior in terms of travel routes provide a way to cope with the changing environment as well as a patchy food resource distribution (Rendell & Whitehead, 2001; Norris, 2002). Cetaceans also follow
general rules for models of culture: large brain, long gestation, sexual maturity age, and long lifespan (Rendell & Whitehead, 2001).

Culture as we know it may exist all around us, not just in our own species, but in others as well. Why has human culture evolved to what it is? Does it flaunt our superior intelligence? Or does it disprove our intelligence if we ultimately destroy ourselves? If chimpanzees have culture it cannot be known for certain. This lies in the minds of our subjects and it is left to primatologists to make inferences. However, with the increasing information from not only chimpanzees but also other primates, whales, and dolphins, this possibility is difficult to ignore. There is much to justify the role of culture studies within primatology, resulting in a new subfield: cultural primatology.

Tool use is an important component in cultural studies. This research attempts to examine specific features of tool use in chimpanzees. The habitat and vegetation, termite diversity and abundance, and characteristics of tools are examined here to further our knowledge of the ecology of termite fishing.
CHAPTER 3: Ecology of Study Site

Introduction

Senegal, West Africa is located in the region stretching across northern Africa from the west (Senegal) to the east (Ethiopia) known as sub-Saharan Africa. Southeastern Senegal is described as having a long dry season (November to April/May) and a short wet/rainy season (May to October) (Carter et al., 2003). Temperatures at Fongoli reach their highest peaks in the dry season (>37°C) (Pruetz, unpublished data). This region represents a semi-arid, open environment between the Sudanian and Sudo-Guinean vegetative belts (Carter et al., 2003). It has been suggested that chimpanzees in dry habitats are more affected by seasonality than chimpanzees living in more forested habitats (Hunt & McGrew, 2002). This led to the question of how such a habitat would affect the chimpanzee insectivorous diet in terms of context. Would habitat also affect where chimpanzees eat?

The Fongoli site is similar to that of Assirik, with a habitat that is more open compared to other chimpanzee study sites in Africa (McGrew et al., 1981). Baldwin and colleagues (1982) found the Mt. Assirik chimpanzees to utilize woodland and forest habitats significantly more than plateau habitats, which were mainly used for travel. Seasons affected use of habitat, when temperatures rose in the dry season, vegetation coverage and water resources became more important for the chimpanzees at this time (Baldwin et al., 1982; Tutin et al., 1983). This need for water and shaded areas was interpreted as correlated with thermoregulation issues in the dry season, but was not thought to be related to food availability (Baldwin et al., 1982; Tutin et al., 1983). Fongoli's chimpanzees, 45 km southeast of Mt. Assirik, are described as using habitat comparable to that of Mt. Assirik (Pruetz, unpublished data). Preliminary data indicate similar selective use of certain habitats.
During the initial year of study, at Fongoli it was found that chimpanzees spent 60% of their time in woodland and other open habitats (99% of study area) and 40% in the gallery forest (1% of study area) (Pruetz, unpublished data). Given the ecological similarities at these two sites, chimpanzee behavioral similarities are also expected.

McBeath and McGrew (1982) found that habitat at Mt. Assirik influenced chimpanzees’ termite fishing behavior. It was hypothesized that habitat would be influential to the eating habits of the chimpanzees, and that habitat would most likely provide the vegetation needed for making tools and for coverage from the sun. Ecotone habitat, defined as the transitional zone between woodland and plateau habitats, was the habitat that yielded most termite fishing (McBeath and McGrew, 1982).

Methods

To address the possibility that habitat use may influence termite fishing at the Fongoli site I replicated many methods of McBeath and McGrew (1982). Based on their findings, the question of whether termite fishing occurs most prominently in ecotone habitats is addressed here. Additionally I asked if habitat influences termite fishing, and subsequently, what specific factors within the habitat are the selective pressures promoting this behavior.

Fongoli is a mosaic habitat much like that of Mt. Assirik (McGrew et al., 1981; Tutin et al., 1983) but different from most other chimpanzee sites (Pruetz, 2005). The site includes woodland (Figure 3.1d), bamboo woodland, plateau (Figure 3.1b), grassland, ecotone (Figure 3.1c), and gallery forest (Figure 3.1a). Definitions of the habitat follow Pruetz et al. (2002; Table 3.1). Open habitat includes grassland, plateau, and woodland, following Pruetz (2005) where open habitat is defined by the nature of the canopy and vegetation coverage. Closed habitat includes ecotone and gallery forests habitats.
Table 3.1: Definitions of habitat types (from Pruetz et al., 2002)

<table>
<thead>
<tr>
<th>Habitat</th>
<th>Definition</th>
</tr>
</thead>
<tbody>
<tr>
<td>Bamboo</td>
<td>&quot;Flat-leaved savanna with isolated palms and deciduous trees&quot;.</td>
</tr>
<tr>
<td>Ecotone</td>
<td>&quot;Where water runoff from plateau edge produces a strip of evergreen woody vegetation&quot;.</td>
</tr>
<tr>
<td>Gallery forest</td>
<td>&quot;Tropical semi-deciduous lowland forest&quot;.</td>
</tr>
<tr>
<td>Grassland</td>
<td>&quot;Narrow-leveled savanna with isolated deciduous trees&quot;.</td>
</tr>
<tr>
<td>Plateau</td>
<td>&quot;Narrow-leveled savanna with isolated deciduous shrubs&quot;.</td>
</tr>
<tr>
<td>Woodland</td>
<td>&quot;Drought-deciduous lowland woodland&quot;.</td>
</tr>
</tbody>
</table>

Figure 3.1: Habitats of Fongoli a.) Gallery forest, b.) Plateau, c.) Ecotone, d.) Woodland.

Data collection

Eight transects, each approximately one kilometer in length, were surveyed to assess habitat and termite mound distribution. Any termite mound found within 20m (total transect
width of 40m) either side of the transect line was recorded along with habitat to determine mound density. The habitats were recorded for analyses of termite mound density according to habitat. Termite mounds (both unused and used by chimpanzees) were marked with the assistance of field assistants, and mapped using a Global Positioning System (GPS: Magellan model). A total of 124 mounds were marked and monitored. To determine chimpanzee activity at termite mounds, indirect evidence was used according to ethoarchaeology methods following McGrew et al. (2003). Characteristics recorded included vegetation around mound, percent vegetation coverage of mound, habitat, characteristics of mounds (shape, width, height, and activity) evidence of tools use (discarded probes used by chimpanzees), and distance to nearest neighbor mound.

**Analyses**

Every change of habitat along each transect was used in the estimation of habitat distribution. Mound density was estimated using transect data and habitat proportions; a grid of 100m by 100m (1 hectare) was used to estimate the relative densities of termite mounds. Nearest neighbor methods (following Cottam & Curtis, 1956) were used to give an estimate of total mound density at the site; this method could not be used within each habitat due to low sample size. Finally, analyses were done of characteristics on mounds used by chimpanzees for termite fishing to compare with all mounds sampled.

**Results**

Mound distribution is shown in Figure 3.2. Termite mounds were marked and monitored within the core study area of 40 square kilometers at Fongoli. The average distance between mounds is 29 meters, with a range of 2-85m.
Figure 3.2: Recorded termite mound distribution on GPS Magellan (UTM units).
Transect data revealed a habitat that is diverse. Open woodland accounts for the majority of area (32%) (Figure 3.3). Grassland and plateau each accounted for 24% of the total area sampled (Figure 3.3). Another 13% was bamboo woodland (Figure 3.3). Both ecotone and cultivated fields accounted for small percentages of the site (Figure 3.3). Finally, gallery forest is only 1% of Fongoli’s surface area (Figure 3.3). These findings are comparable to Pruetz’ (2005) findings using quadrat methods.

Of the 124 mounds marked and monitored, 43% were in open woodland. A total of 49 tool assemblages at 29 mounds were recorded. Mounds used by chimpanzees were found in woodland (59%), ecotone (21%), bamboo (10%), and gallery forest (10%); none were found in grassland or plateau (Figure 3.4). Chimpanzees termite fish in woodland significantly more than in other habitats ($X^2=18$, df=3, p-value=0.0004, two-tailed). Gallery and ecotone habitats are also used by Fongoli chimpanzees for termite fishing more than expected given the availability of these habitats (ecotone $X^2=7.68$, df=6, p-value=.0014, two-tailed; gallery $X^2=23.04$, df=6, p-value=<.0001, two tailed).

![Figure 3.3: Fongoli Habitat distribution.](image-url)
Figure 3.4: Habitat distribution at Fongoli and location of termite mounds used by chimpanzees.

Termite mound density (based on transect data) was the highest in plateau and grassland habitat, numbering approximately 10 mounds per hectare (Table 3.2). Ecotone was characterized by the next highest termite mound density, followed by woodland and bamboo. Cultivated fields yielded fewer mounds per hectare at Fongoli, but gallery forest exhibited the lowest termite mound density, with approximately one mound per hectare. Figure 3.5 demonstrates the habitats used by chimpanzees to termite fish in relation to the mound density proportions at Fongoli.
Table 3.2: Mound density (per hectare) at Fongoli for each category of habitat.

<table>
<thead>
<tr>
<th>Habitat</th>
<th>Mound density (per hectare)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Woodland</td>
<td>7</td>
</tr>
<tr>
<td>Ecotone</td>
<td>8</td>
</tr>
<tr>
<td>Gallery</td>
<td>1</td>
</tr>
<tr>
<td>Bamboo</td>
<td>7</td>
</tr>
<tr>
<td>Plateau</td>
<td>10</td>
</tr>
<tr>
<td>Grassland</td>
<td>10</td>
</tr>
<tr>
<td>Field</td>
<td>5</td>
</tr>
</tbody>
</table>

Figure 3.5: Termite mound density proportion versus termite fished habitat used by chimpanzees at Fongoli.

Nearest neighbor analyses indicate that the mean distance between two termite mounds in all habitats is 28.8 meters, with an expected value of 9.5 m based on nearest neighbor analysis (Cottam and Curtis, 1956). According to a Poisson analysis, this finding is significantly higher than expected (Poisson, p-value=0.0018, two-tailed). Therefore, termite mounds are more widely distributed than expected for Fongoli. Lee and Wood (1971)
however, state that nearest neighbor analyses are not appropriate measures of termite mounds because they are not randomly distributed.

**Discussion and Conclusions**

The Fongoli study site consists mainly of open habitat (including woodland), which limits the chimpanzees’ availability of water and thermoregulation abilities especially in the dry season. Ecotone habitat, a closed habitat, was characterized by 21% of the total chimpanzee fishing assemblages. Ecotone only makes up 3% of the site. Gallery forest habitat was used in 10% of termite fishing instances and only makes up 1% of area (Figure 3.1). Both of these habitats were used significantly more than what would be expected at Fongoli. In contrast to Mt. Assirik (McBeath & McGrew, 1982), the Fongoli chimpanzees did not use ecotone most often for termite fishing; instead they used open woodland. This may be due to the reduced proportion of ecotone at Fongoli.

The termite data presented here indicate that Fongoli chimpanzees are using the habitats with low to medium densities of mounds for termite fishing. Therefore, termite mound density does not influence the termite fishing behavior of the Fongoli chimpanzees. The termite mound density at Fongoli is characteristic of an open mosaic habitat (Korb & Linsenmair, 2001; Lee & Wood, 1971). Entomology studies indicate that *Macrotermes bellicosus* has a higher density in open habitats in Cote d’Ivoire and lower densities in the gallery forests (Korb & Linsenmair, 2001). It has been estimated that Macrotermitinae have a density of less than 10 mounds per hectare in Africa (Lee & Wood, 1971). Collins and McGrew (1987) estimated the density of termite mounds using transect data at Mahale. The density of termite mounds was 10.6 mounds per hectare at Kasoje and 13.5 mounds per hectare at Bilenge, with a total of 15.6 mounds per ha overall in open woodland. Fongoli
termite mound density is comparable to that found at Mahale, although the habitats are different. Mahale is characterized as having denser forest (Collins & McGrew, 1987), compared to the mosaic of open habitats at Fongoli. At another Tanzanian site of Gombe, mound density was only 5.6 per ha. Collins and McGrew (1987) attribute this low density to the steep slopes found in Gombe. No other chimpanzee site provides data for comparison.

Senegal's open environment has been used in reference to understanding early hominids behavior and ecology during the Plio-Pleistocene (McGrew et al., 1981). Habitats in eastern Africa are more forested and comparable for adaptations of Miocene primates in a forest-woodland habitat (Collins & McGrew, 1988). Data presented here provide evidence for the selective use of woodland and forested habitats by the chimpanzees for a food resource (termites), in comparison with grassland and plateau habitats. Thus, habitat rather than termite mound density influences chimpanzee termite fishing. Mound density is high in plateau and grassland habitats, where the chimpanzees do not consume termites (Figure 3.5). However, termite species diversity does differ between habitats, and this could also be a factor in chimpanzee termite feeding behavior. I address this issue in the following chapter.
CHAPTER 4: Fongoli Termites

Introduction

Here I present an in-depth analysis of the termite species, their mound characteristics, and their importance in the diet of the Fongoli chimpanzees. McGrew (1983) noted that mainly two genera of Isoptera (termites) are consumed by chimpanzees: *Macrotermes* and *Pseudacanthotermes*. Previous studies suggest that the termite genus *Odontotermes* is not consumed by chimpanzees, although they are found at several chimpanzee sites (Collins & McGrew, 1985; 1987). Most sites only report the species that are included in the diet of the chimpanzees (Table 4.1). This study went further to record all termite species at the site in order to determine availability of the species chimpanzees select for consumption. The only comparable data come from Collins and McGrew (1985; 1987) for the Tanzanian sites of Mahale Bilenge, Mahale Kasoje, and Gombe.

The questions addressed here explored numerous factors relative to insectivory of chimpanzees, particularly termites. Based on McBeath and McGrew (1982) questions included: Is *Macrotermes* the chief genus consumed by the Fongoli chimpanzees? Does termite species, in terms of diversity and abundance, influence consumption? If so, do chimpanzees consume the termites that are most abundant, or do other factors influence their choices?

Methods

Multiple termite samples were collected at mounds with tools and at non-tool mounds. A total of 39 termite samples were collected using chimpanzee tool extraction techniques and forceps (Figure 4.1), then preserved in vials of 85% ethanol. An attempt was made to sample all species and castes (workers, immatures, reproductives, and both minor
and major soldiers) of termites. Dr. Rudolf Scheffrahn from the University of Florida identified the samples.

Termite species are reviewed in terms of habitat, abundance, and whether chimpanzees consume them. Mound characteristics are analyzed according to mound shape and height. Shape categories were innovated by the author to include convex, castle, mushroom, and miscellaneous. Convex is a mound that is dome shaped and may have satellite mounds, smaller mounds less than 5m distant (Figure 4.2a). Castle mounds can be several meters tall, with intricate towers, and resembling a castle. Mushroom mounds are low mounds less than one meter in height with a narrow stem that domes out at the top (Figure 4.2b, c). Miscellaneous mounds are those mounds that did not seem to take a particular shape or were on a slope, which resulted in a misshapen structure. Some structures can have multiple shapes; these generally had double inhabitant genera (Figure 4.3). In these cases the dominant structure was used for analyses.

Figure 4.1: Author and Mbouli Camera (field assistant) collecting termites.
Figure 4.2: Mounds at Fongoli a) convex mound under Saba vine in ecotone habitat b) mushroom mounds on plateau c) Mushroom mound close up

Figure 4.3: Double inhabitant mound (convex with mushroom) in woodland habitat.
Results

Mound characteristics

No evidence was found to suggest that Fongoli chimpanzees ever fished at the mushroom shaped mounds; instead all mounds used had convex, castle, or miscellaneous shapes. Convex mounds were used significantly more by the chimpanzees than all other shapes ($X^2=20$, df=2, $p=0.0001$, two-tailed). All termite mounds recorded for the study had an average height of 97 cm. Fished mounds used by chimpanzees had an average height of 100 cm, and a range of 25-215 cm.

Termite distribution

Termite species varied within the study site: at least six different genera of termites were recorded at Fongoli: Cubitermes (2 species), Microcerotermes (1 species), Amitermes (1 species), Trinervitermes (3 species), Macrotermes (2 species), and unidentified species of Termitinae (Table 4.1). Cubitermes are mostly found associated with mushroom shaped mounds on the plateau and grassland, while Macrotermes are associated with a convex mound shape and are generally in woodland or forested habitats. However, Trinervitermes is likely to be found in all habitats and associated with convex or mushroom shaped mounds.

Termites were collected at 29% of all mounds recorded; another 7% were abandoned of termite inhabitants and 64% were not identified. Most of the termites found at Fongoli were Macrotermes sp (36%) and Trinervitermes sp (36%), followed by Cubitermes, Microcerotermes, and Amitermes (Figure 4.4). In 18% of cases, more than one termite genus inhabited a mound. Two genera and four species were found in association with termite tools: Macrotermes subhyalinus, M. bellicosus, Trinervitermes togoensis, and T. geminatus. These termites were sampled at mounds where tools were found. Multiple species inhabiting
termite mounds and few direct observations of termite fishing made it difficult to determine which termite species are being consumed by the chimpanzees. However, *Macrotermes* species were most often (75% of cases) found in association with tools. There were three instances where *Trinervitermes* was associated with tools, but two of these were double inhabitant mounds with *Macrotermes* also resident. Figure 4.5 illustrates termite soldiers of the species associated with tools.

Figure 4.4: Termites diversity at Fongoli.
The Fongoli chimpanzees may rely on termites more than chimpanzees at other sites. They are one of a few known wild populations to eat these social insects year-round. Data from fecal analyses indicate termites are present in the chimpanzee diet in all months of the year (Pruetz, 2005).

Both *Macrotermes* spp. and *Trinervitermes* spp. were found in association with tools at Fongoli. However, since there are instances of multiple inhabitants at a mound, it cannot be conclusively said that *Trinervitermes* are eaten by the Fongoli chimpanzees. Further
micro-fecal analyses could remedy this lack of evidence. Other sites have reported the consumption of multiple termite genera however. Table 4.1 lists the termite species known to be consumed or found in association with termite fishing tools at sites across Africa. The Mahale B group seems to select *Macrotermes* from a number of possible species; however the Mahale K group consumes *Pseudacanthotermes springier* apparently due to the absence of *Macrotermes* in the area (Collins & McGrew, 1985). At Gombe, the chimpanzees fish for *Macrotermes* and use their hands to opportunistically acquire *Pseudacanthotermes* (McGrew, 1992). Fongoli chimpanzees could use this same technique with *Trinervitermes* when at a mound that houses both this species and *Macrotermes*. More data are needed to determine conclusively which termite species are eaten by Fongoli chimpanzees. In fact, Fongoli chimpanzees have been observed to use tools to termite fish as well as their hands to capture termite prey at the same mound (Pruetz, personal communication).

Termite fishing in the dry season at Fongoli may be related to the behavioral characteristics of *Trinervitermes*. *Trinervitermes* are more active in the dry season (Ohiagu, 1979), when *Macrotermes* is more difficult to obtain from mounds. *Trinervitermes* are a grass-harvesting termite (Ohiagu, 1979), which may provide chimpanzees with certain nutrients that wood-eating *Macrotermes* do not provide (Pearce, 1997). Effects on the soil acidity and moisture or the activity of the termites may be affected by having double occupants such as *Trinervitermes* and *Macrotermes*. Different kinds of soil are used by different termite species. Also, *Trinervitermes* often forages on the surface (Ohiagu, 1979), which provides easy access for chimpanzees. *Trinervitermes* secretes a toxic substance that immobilizes other insect enemies (Lee & Wood, 1971); whether or not this toxin is secreted on tools and whether it affects an animal the size of a chimpanzee is unknown.
Table 4.1: Termite genera and species at chimpanzee sites across Africa.

<table>
<thead>
<tr>
<th>Genus</th>
<th>Species</th>
<th>Fongoli, Senegal</th>
<th>Mt. Assirik, Senegal</th>
<th>Gombe, Tanzania</th>
<th>Mahale - Bilenge, Tanzania</th>
<th>Mahale - Kasoje, Tanzania</th>
<th>Budongo Forest, Uganda</th>
<th>Rio Muni</th>
</tr>
</thead>
<tbody>
<tr>
<td>Cubitermes</td>
<td>sankurensis</td>
<td>X</td>
<td>X</td>
<td>X</td>
<td>X</td>
<td>X</td>
<td>X(-)</td>
<td></td>
</tr>
<tr>
<td></td>
<td>loubetsiensis</td>
<td>X</td>
<td>X</td>
<td></td>
<td>X</td>
<td></td>
<td>X</td>
<td></td>
</tr>
<tr>
<td>Microceroterme</td>
<td>parvus or other</td>
<td>X</td>
<td>X</td>
<td>X</td>
<td>X</td>
<td></td>
<td>X</td>
<td></td>
</tr>
<tr>
<td></td>
<td>spp.</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Macrotermes</td>
<td>bellicosus</td>
<td>X</td>
<td>X</td>
<td>X</td>
<td>X</td>
<td></td>
<td>X</td>
<td></td>
</tr>
<tr>
<td></td>
<td>subhyalinus</td>
<td>X</td>
<td>X</td>
<td>X</td>
<td>X</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Other spp?</td>
<td>X</td>
<td>X</td>
<td></td>
<td>X</td>
<td>X</td>
<td>X</td>
<td></td>
</tr>
<tr>
<td>Trinerviterme</td>
<td>geminatus</td>
<td>X</td>
<td>X</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>occidentalis</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Amitermes</td>
<td>evuncifer</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>family Termitidae</td>
<td>spp?</td>
<td>X</td>
<td>X</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Pseudacanthoterme</td>
<td>spiniger or spp?</td>
<td>X</td>
<td>X(-)</td>
<td>X</td>
<td>X</td>
<td>X</td>
<td>X(-)</td>
<td></td>
</tr>
<tr>
<td>Odontoterme</td>
<td>spp?</td>
<td>X</td>
<td>X</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

P = Present; C = Consumed with or without tools (-) or found in association with tools

Collins and McGrew (1987) found 16% of termite mounds in Gombe, Mahale (Bilenge), and Mahale (Kasoje) to have more than one species of termites in residence. Another 6.5% of mounds had more than two species resident. Table 4.1 describes termites known to be present and eaten at chimpanzee sites. Only Collins and McGrew (1987) presented comparable data on termite species abundance. They compared Kasoje, Bilenge, and Gombe, Tanzanian sites. Kasoje and Gombe were characterized by a greater percentage of *Pseudacanthotermes*, while the most common termite species at Bilenge was *Odontotermes* (Collins and McGrew, 1987). At all sites, *Macrotermes* were uncommon, which may explain the defined seasonality of termite fishing at these sites. At Fongoli, however, *Macrotermes* is one of the most common termite genera at the site, which may explain the chimpanzee’s year-round termite fishing. Collins and McGrew (1987) found that termite species’ distribution affected chimpanzees’ termite fishing, which may also be true for Fongoli. The Fongoli chimpanzees termite fish in woodland more than any other habitat, which may potentially be correlated with *Macrotermes* distribution in woodland habitats. Thus, habitat does influence termite fishing at Fongoli. Although, seasonality was found to be important at Mt. Assirik, termite abundance and distribution were not calculated (McBeath & McGrew, 1982).

Termite consumption by Fongoli chimpanzees is an important factor when compared to other sites, due to Fongoli’s year-around termite fishing behavior. In terms of food scarcity at Fongoli, the period of lowest fruit availability is July–August (Pruetz, 2005). Fruit scarcity does not seem to correlate with termite abundance in the diet (Pruetz, unpublished data). Termites therefore, may not be a fall-back food resource for Fongoli chimpanzees. Rather,
the chimpanzees consume termites throughout the year at this site, with a few peaks from April to July and in October (Pruetz, unpublished data).

At other sites such as Mt. Assirik (McGrew et al., 1979), Gombe (McGrew et al., 1979) and Mahale (McGrew & Collins, 1985), seasonality in termite fishing coincides with the initial months of the wet season. At Okorobiko, Rio Muni, there is no seasonality in this behavior, and termite fishing tools are found throughout the year (McGrew et al., 1979). Ndoki forest, Congo, also exhibits a lack of seasonal variation in termite fishing behavior, and there was no correlation with rainfall in the months that provided the most tools (Suzuki et al., 1995). Suzuki and colleagues (1995) concluded that the termite soldiers at Ndoki must be available to eat throughout the year for the chimpanzees. The same seems to be true at Fongoli.

Eggleton et al. (2002) recorded at least 133 different termite species in western Africa. If Fongoli chimpanzees are only consuming *Macrotermes*, they may be exploiting only a small proportion of the known termite species found here. More research on relative abundance of termite species needs to be conducted. Further investigation into whether or not the chimpanzees are consuming only one of the species inhabiting a mound also needs to be done. If two species are present, yet only one is consumed, this would then suggest that the chimpanzees are selective regarding the termites they consume. Also, as a caveat, the observed indisputable evidence of termites in the diet of chimpanzees is the hard mandibles and heads of the *Macrotermes* soldiers in feces. The consumption of workers and possibly other species of termites is difficult to discern based on this type of macro-analysis. More extensive methods that sample termite diversity at a site will give a better understanding of the relation between termite availability and consumption, especially related to seasonality.
Micro-analysis of termite remains in the feces may help to give more detailed results of chimpanzee invertebrate diet.
CHAPTER 5: Chimpanzee Termite Fishing Tools

Introduction

Termite fishing is labeled a 'cultural' behavior by primatologists and has been observed at many chimpanzee sites across Africa (Whiten et al., 2001). This behavior set a major course in anthropology, where tool use was once thought to be a uniquely human characteristic (Goodall, 1964). The chimpanzee study sites that exhibit termite fishing or consumption were outlined in the previous chapter (Table 4.1). The only site where chimpanzees have been studied and are known to consume termites but not use tools is Budongo Forest. Here, the chimpanzees knock over mounds to eat *Cubitermes* (Newton-Fisher, 1999). *Cubitermes* are not known to be eaten by chimpanzees elsewhere. Such behavior at Budongo may be due to a low frequency of *Macrotermes* (Newton-Fisher, 1999), but these analyses have yet to be done. This case is isolated, and most chimpanzees consume *Macrotermes* species and use tools to obtain them.

Fongoli is the one of two dry savanna habitat sites where chimpanzees are known to termite fish. It may be assumed that this site will produce different results compared to most other sites based on significant habitat and climatic differences. One difference is that the Fongoli chimpanzees termite fish throughout the year (Pruetz, 2005). Therefore, many factors examined in this study were included in order to examine whether there is a difference between dry and wet season termite fishing, how tools compare to other sites, and what the selective pressures for this behavior at Fongoli may be. For example, McBeath and McGrew (1982) found that termite fishing tools were most often made from plants growing within two meters of chimpanzee termite mounds and were often of the species *Grewia lasiodiscus*. It was therefore expected that the materials used for termite fishing tools by
Fongoli chimpanzees would come mainly from the *Grewia*, due to the similarities in habitat between these two sites.

**Data Collection**

Chimpanzee termite-fishing tools were collected when found and further analyzed regarding plant material, lengths, diameters, and characteristics of the proximal and distal ends. Tool lengths and characteristics were analyzed for comparison to other sites. The distance from the mound to the tool was measured. The tools found at these mound sites were classed as fresh (less than 24 hours old), recent (2-4 days old), or old (more than 4 days old) (McBeath & McGrew, 1982), based on color and the use of a reference collection by the author. Age of assemblage was also determined from assessing the archaeology of the site, using indicators such as associated feces freshness, and freshness of breaks on the plant material used as a tool (McGrew et al., 2003). Tools were made from six possible types of raw materials: twig, vine, bark, leaf-stalk, grass, and palm-frond (McGrew et al., 1979). Species of plant was noted if known. Availability of vegetation around the mound was recorded as well as its distance from the mound, and percent coverage from vegetation above the mound was assessed. Seasonality was determined by rainfall: the dry season ended on June 25th when rain became frequent (daily) and heavy (ground flooding and river flow); the wet season began on June 26th.

**Results**

**Plant material and vegetation**

Of the vegetation around fished termite mounds, a few species were prominent. *Saba senegalensis* (22%), *Grewia* sp (19%), and *Hexalobus monopetalus* (15%) were the plants most frequently encountered. However, there was no significant difference across species of
plants in frequency found in proximity to termite fished mounds (GLM procedure f=0.59, df=19, p=0.9, two-tailed). Figure 5.1 shows a chimpanzee with a plant in his mouth, ready to modify it.

The raw material sources for tools (Figure 5.1) were all within 10 meters of the mounds. *Grewia* grew a mean distance of 2.5 meters (range 0-10m) from the mound, while *Hexalobus* had a mean of 0.7 m (range 0-5m) and *Saba* 1.1 meters (range 0-10 m) from the mound.

The average percent foliage coverage for all mounds recorded is 41%, with a range of 0-100%. Of the fished mounds, the average foliage cover is 63%, with a range of 15-100%. Termite mounds selected for fishing were never completely in the open (i.e. without tree coverage).

Figure 5.1: Chimpanzee holding plant material in mouth.
Fishing probes were aged when collected; 401 of 533 (75%) were fresh or recent, and only these will be used for analysis. Figure 5.2 illustrates a fresh find of tools made from Saba, and Figure 5.3 shows a tool kit for that particular find. Tools were most commonly made from Grewia, Hexalobus, and Saba plants (77%). Plant sources for tools were, on
average, 1.3 m from the termite mound (range 0-10 m). The average distance between tools and the mound is 36.5 cm with a range of 0-224 cm (Table 5.1). All tools were found within 2.5 meters of a mound. All 401 fresh tools were flexible probes, with a mean length of 29.5 cm (range 9-106 cm) (Table 5.1) made of wood, twig, or vine materials, but not grass (Figure 5.4a). Dry season tools had a mean length of 31.3 cm with a range of 11.9-106 cm. Wet season tools were characterized by a mean length of 26.7 cm with a range of 9.2-72.3 cm. However, there was no significant difference between tools from the different seasons (Poisson analysis, p-value=0.5434, two-tailed). Frayed distal ends of tools occurred on 61% of all flexible probes (Figure 5.4b), while the proximal ends were stripped or clipped (Figure 5.4c). The average diameters of the proximal and distal ends did not differ greatly (Table 5.1).

On June 30th of 2004, a perforating stick made from bamboo that was 20.5 cm in length with a 0.7 cm diameter was found next to a mound with 36 flexible probes (mound TM152) (Figure 5.5 shows perforating stick). This is one of two perforating sticks found at Fongoli (Pruetz, unpublished data).

Table 5.1: Flexible probe measurements (cm).

<table>
<thead>
<tr>
<th>Tool length</th>
<th>Dry season</th>
<th>Wet season</th>
<th>Proximal end</th>
<th>Distal end</th>
<th>Distance from mound</th>
</tr>
</thead>
<tbody>
<tr>
<td>Average</td>
<td>29.5</td>
<td>31.3</td>
<td>26.7</td>
<td>0.027</td>
<td>0.021</td>
</tr>
<tr>
<td>Max</td>
<td>106</td>
<td>106</td>
<td>72.3</td>
<td>1</td>
<td>0.5</td>
</tr>
<tr>
<td>Min</td>
<td>9</td>
<td>11.9</td>
<td>9.2</td>
<td>0.1</td>
<td>0.1</td>
</tr>
</tbody>
</table>
Figure 5.4: Tool characteristics a.) flexible probe of twig material from mound 124NN b.) frayed distal end of 124NN tool c.) stripped proximal end of Grewia tool at mound 103NN.

Figure 5.5: Perforating stick of Bamboo from mound TM152.
Discussion and Conclusions

Fongoli resembles Mt. Assirik in the types of material used by chimpanzees for termite fishing. At Fongoli, grass was not a material source in this study due to season. Grass was not tall enough at the end of the dry season and at the beginning of the wet season for tool material. McGrew and colleagues (1979) found twigs to be the prominent material of choice at Mt. Assirik in Senegal. At Assirik, 97% of tools made were of twigs, leaf-stalks, and vines (McBeath & McGrew, 1982), while at Gombe the majority of tools were made from grass (McGrew et al., 1979). At Mahale the majority of tools were made of bark (75%) (McGrew & Collins, 1985). Ecology may be a factor contributing to these differences, but this possibility has not been discussed in detail regarding these sites.

Termite fishing tools were mostly made from three plant species typically found around mounds used for termite fishing. These were species that the chimpanzees also consumed (Pruetz, 2005). *Grewia, Hexalobus*, and *Saba* combined were most often selected for source material at Fongoli. However, this finding differs from data recorded at Mt. Assirik, in which *Grewia lasiodiscus* (twig) alone was the species of plant that the chimpanzees used most often (McGrew et al., 1979; McBeath & McGrew, 1982).

*Saba* at Fongoli was found on average 1.1 meters (range 0-10m) from fished mounds. McGrew and colleagues (1979) found that 94% of the tools originated from plants within two meters of the mounds at Mt. Assirik, Gombe, and Rio Muni. This study shows that tools can originate from sources up to 10 meters away, but on average the distance to source was only 1-2m. This suggests that chimpanzees have plentiful raw materials for probes at Fongoli, similar to what has been reported for other sites.
The Fongoli chimpanzees select termite mounds that are generally well shaded from direct sunlight. This could be a thermoregulatory factor for the chimpanzees, or it may be a by-product of the frequency with which the chimpanzees’ use woodland versus closed habitats. Shade is not considered to be a selective pressure for termite fishing here, but is a secondary characteristic resulting from habitat selectivity.

Flexible probe length (all tools found) reported in this study did not differ significantly (Poisson t-test with 95% CI, p-value=0.27, two-tailed) from the preliminary study done at Fongoli (McGrew et al., 2005). However, grass material was used in the latter study, which was not found to be used for tools here. This discrepancy is due to seasonality. In the dry and early wet seasons in which this research was done, the grass was not tall enough to make fishing probes. The range of tool lengths was also greater in this study, possibly reflecting the greater number of tools found versus the preliminary study done by McGrew and colleagues (2005). There was no significant difference between tools from the dry season and the wet season (Poisson analysis, p-value=0.5434, two-tailed). However further investigation and greater sample sizes could prove otherwise; dry season tools exhibit a trend toward a longer range and average compared to the wet season. Data on dry season tools are limited and should be further researched. Shorter probes had been clipped and the ends were left as debitage at mounds. Tool lengths from sites are compared in Table 5.2. Shorter probes may indicate easier access to termites.

The perforating stick found is anecdotal in this study due to the small sample size (McGrew & Marchant, 1997), but the awareness that the Fongoli chimpanzees may use perforating sticks allows us to look for it in the future. These sticks are not used at every site characterized by termite fishing and they are hypothesized to be replacements for manual
removal of the termite soil to uncover holes. Some sites that use perforating sticks include Ndoki, Goualougo, and the Ndakan and Bai Hokou sites in Congo (Suzuki et al., 1995; Sanz et al., 2004; Fay & Carroll, 1994).

Termite fishing was observed three times during this study. These observations gave evidence as to the technique used by the Fongoli chimpanzees (Pruetz, unpublished data). The probe is inserted into the termite mound after opening a hole with the fingers, and after extraction the chimpanzees often support the probe on the opposite wrist and pick off the termites with their lips. Picking of termites between two fingers (not thumbs) off of mounds was observed. A male was observed to bring a tool from at least 6 meters away to a mound. A total of 5 individuals were observed termite fishing (3 males, 2 females, 1 infant watching mother and attempting to fish with her discarded tool). Fongoli chimpanzees’ technique resembles that described for Gombe and (Figure 5.7) (Goodall, 1963; 1968) Mahale, Tanzania (McGrew & Collins, 1985), and Goualougo, Congo Basin (Sanz et al., 2004).

Table 5.2: Flexible probe lengths of chimpanzee sites.

<table>
<thead>
<tr>
<th>Site</th>
<th>Tool length mean (cm)</th>
<th>Source</th>
</tr>
</thead>
<tbody>
<tr>
<td>Fongoli</td>
<td>29.5</td>
<td>This study</td>
</tr>
<tr>
<td>Mt. Assirik</td>
<td>32.5</td>
<td>McGrew et al., 1979</td>
</tr>
<tr>
<td>Gombe</td>
<td>30.7</td>
<td>McGrew et al., 1979</td>
</tr>
<tr>
<td>Mahale</td>
<td>37.7</td>
<td>McGrew &amp; Collins, 1985</td>
</tr>
<tr>
<td>Rio Muni</td>
<td>49.7</td>
<td>McGrew et al., 1979</td>
</tr>
<tr>
<td>Ndoki</td>
<td>50.8</td>
<td>Suzuki et al., 1995</td>
</tr>
<tr>
<td>Goualougo</td>
<td>43.1</td>
<td>Sanz et al., 2004</td>
</tr>
</tbody>
</table>
Figure 5.6: Gombe chimpanzees termite fishing.
CHAPTER 6: Conclusions and Summary

Termite Fishing Behavior of Fongoli Chimpanzees

Fongoli chimpanzees consume insects mainly in woodland habitats. However, they also termite fish in the ecotone and gallery forest habitats significantly more than would be expected based on availability of these sites. These findings contrast with Assirik’s chimpanzees termite fishing mainly in ecotone habitats (McBeath & McGrew, 1982). This could be because Assirik has more ecotone (5%) (McBeath & McGrew, 1982) compared to Fongoli (3%). Assirik’s ecotone is characterized by a clear transition between habitats and is easy to see, whereas at Fongoli it is more subtle (Pruetz, personal communication). This may be a factor in the selection of ecotone at Fongoli as well. The available vegetation may also be a factor. Fongoli chimpanzees select three plant species predominantly for making tools over all others, while chimpanzees at Assirik select one species of plant material over all others (McBeath & McGrew, 1982). This selection may be due to the fact that these plants are abundant around the mounds.

Termite species play an important role in determining termite fishing behavior of Fongoli chimpanzees. Two genera and four species of termites were found in association with tools at Fongoli. Such diversity is greater than that associated with tools at any other chimpanzee site. However, direct evidence for chimpanzee consumption of 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 have been found through direct evidence to be eaten (observation and feces). 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 not indigestible like those of *Macrotermes* or that it is difficult to discern the smaller heads of *Trinervitermes* through macro-analyses of feces. Further research could be conducted to examine this possibility.

The Fongoli termite fishing tool kit does not differ significantly from that of most other termite fishing chimpanzee sites. Based on direct observation, the technique used by Fongoli chimpanzees is similar to Gombe (Goodall, 1963; 1968) and Mahale, Tanzania (McGrew & Collins, 1985), and Goualougo, Congo Basin (Sanz et al., 2004). However, the dry season tools do exhibit a trend towards a longer length than those of the wet season. Such a trend may be due to *Macrotermes*’ habit of retreating further underground in the dry season (Noirot & Darlington, 2000). Another factor may be terrestriality. At Bossou, Guinea, chimpanzees were observed to spend more time on the ground during the dry season and more time arboreal in the wet season, which was attributed to a reduction of thermoregulation costs by resting in trees during the cooler months (Takemoto, 2004). Since the treetops would have a higher concentration of heat from the sun than the forest floor in the dry season, terrestriality is increased (Takemoto, 2004). If this were true for Fongoli, the chimpanzees may consume termites in the dry season due in part to their increased terrestrial activity.

Termite mound density does not seem to influence termite fishing at Fongoli, but rather the habitat is an important influence on this behavior in chimpanzees. Vegetation
surrounding fished mounds was proportionately more shaded from direct sunlight, which may also be a by-product factor of the habitat influencing chimpanzee termite fishing selection. *Macrotermes* are more prominent in woodland habitats and this may also be a selecting factor for the Fongoli chimpanzees. Therefore, many selective pressures influence the Fongoli chimpanzees as to where and what they termite fish.

The Fongoli chimpanzee diet consists of 5.4% invertebrates (Pruetz, 2005). The consumption of insects does not increase during times of fruit scarcity (Pruetz, 2005). Thus, termites at Fongoli are not considered a fallback food. Further research would provide evidence as to whether termites are a staple in the diet.

**Benefits from Eating Termites**

In terms of nutrition, Wrangham (1977) found that *Macrotermes* workers and immatures provide the greatest amount of protein (68.4%), while reproductive individuals provided the highest percentage of lipids (52.8%); soldiers fell between the two castes on both accounts (Figure 6.1). Termites are high in protein, rich in fat, and provide a high caloric intake (Berenbaum, 1995). Insects are especially important in compensating for dietary deficiencies. Many of the nutrients found in termites are used by African peoples who are malnourished (Berenbaum, 1995). Table 6.1 displays the various nutrients and their content for a termite species compared to beef, chicken and fish (taken from Berenbaum, 1995: p.179, Table 6.1). A lack of iron can produce anemia (growth and blood loss require the nutrient iron). The nutrient thiamine helps the nervous system, synthesis of collagen, improving cognitive function, and maintaining memory, while also playing a role in promoting growth and repair of all body tissues. Riboflavin is used in body growth and red blood cell production and helps in releasing energy from carbohydrates. Niacin reduces the
amount of cholesterol and certain fatty substances in blood. Iron, thiamine, riboflavin, and niacin are all used to aid an inadequate diet in humans (Berenbaum, 1995), and would thus also provide chimpanzees nutrients important for growth and maintenance of health (Wrangham, 1980).

Insects are eaten throughout most of the world by human populations living in Africa, Asia, and Latin America (DeFoliart, 1999). It has been suggested that Western populations (Europeans and North Americans) do not consume insects due to the unpredictability of supply and a constant supply from other sources (DeFoliart, 1999). Insects have been an important food throughout human history. In ancient human societies, such as those of the Greeks and Romans, insects were cooked and considered a delicacy, prominent among upper class society (DeFoliart, 1999).

Figure 6.1: *Macrotermes* sp. soldier and immatures.
Table 6.1: Protein, vitamins, and nutrients in termites, beef, chicken, and fish (/100g).

<table>
<thead>
<tr>
<th>Nutrient</th>
<th>Energy (kcal)</th>
<th>Protein (g)</th>
<th>Calcium (g)</th>
<th>Phosphorus (mg)</th>
<th>Iron (mg)</th>
<th>Thiamine (mg)</th>
<th>Niacin (mg)</th>
<th>Riboflavin (mg)</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Macrotermes subhyalinus</strong></td>
<td>613</td>
<td>14.2</td>
<td>0.04</td>
<td>0.438</td>
<td>7.5</td>
<td>0.13</td>
<td>9.5</td>
<td>1.15</td>
</tr>
<tr>
<td>Beef</td>
<td>219</td>
<td>27.4</td>
<td>0.012</td>
<td>0.23</td>
<td>3.5</td>
<td>0.09</td>
<td>6</td>
<td>0.23</td>
</tr>
<tr>
<td>Chicken</td>
<td>166</td>
<td>31.6</td>
<td>0.011</td>
<td>0.265</td>
<td>1.3</td>
<td>0.04</td>
<td>10.7</td>
<td>0.1</td>
</tr>
<tr>
<td>Fish</td>
<td>170</td>
<td>28.5</td>
<td>0.032</td>
<td>0.274</td>
<td>1</td>
<td>0.08</td>
<td>3</td>
<td>0.11</td>
</tr>
</tbody>
</table>

Termites diversified in the Cretaceous along with angiosperms (Thorne et al., 2000). The diversification of angiosperms has been proposed to correlate with primate origins by Sussman (1987) while visual predation on insects was proposed by Cartmill (1972).

Angiosperm diversification and insect predation are considered to be evolutionary explanations for primate specializations in vision (color, stereoscopic vision) and grasping abilities. Social insects, such as termites, may have been important in the diet of primates throughout this lineage's existence.

Figure 6.2: *Macrotermes* sp. workers and soldiers.
Macrotermes

Macrotermes (Figure 6.2) are consumed at most sites by chimpanzees (see Table 4.1). Macrotermes is the largest social insect in Africa and mounds contain an impressive number of individuals (Howse, 1970). One mound can contain up to 2 million Macrotermes (East Africa: Harris, 1955; West Africa: Luscher, 1955). During the dry season, termites retreat far underground to escape the heat of the sun because of susceptibility to water loss (Noirot & Darlington, 2000). Soil moisture affects the activity of all termite species; heavy rainfall will often cause termites to retreat further underground as well (Ferrar, 1982). Macrotermes have been known to descend to depths of greater than 40 m (Lepage et al., 1974). Macrotermes' underground passages are complex, consisting of three different kinds: radial, big cross and small cross passages (Jmhasley & Leuthold, 1999). These passages can extend up to 30 meters from the mound, and will often cross with those of other termite mound passages (Jmhasley & Leuthold, 1999).

Hominid Insectivory?

Termite fishing in savanna chimpanzees is especially relevant to the study of early hominid behavior and ecology. Termites have recently been inferred as included in the diet of Australopithecus robustus, based on evidence from bone tools thought to be used to extract termites from mounds (Backwell & d'Errico, 2001). According to dental traits, gracile australopithecines are said to have had a diet much like modern apes today, i.e. fairly omnivorous (Teaford & Ungar, 2000). It is most likely that hominids and even protohominids used tools before such evidence appears in the fossil record at about 2.6 mya (Beck, 1980; McGrew, 1992; Sigaut, 1993). Tool use by early hominids has been hypothesized as an important development in the evolution of human diet (Ungar & Teaford,
Tools used by nonhuman primates for food procurement that were made of organic materials would not survive fossilization (Teaford et al., 2002). Evidence of these tools in the archaeological record is absent due to decay of organic matter such as, wood, twigs, sticks, and leaves. It is conceivable that early hominid tools were similar to what we find in extant nonhuman primates (Teaford et al., 2002). Since tool use is found in great apes, it is not unreasonable to assume that the last common ancestor may have had some simple form of tool technology (about 6 million years ago). Stone and bone tools of early hominids may have been used similar to those of nonhuman primates; however functional interpretation is difficult (Teaford et al., 2002). Could such tool use have led to the evolution of stone tools? Stone tools have been recorded in the Tai community of chimpanzees for the cracking of nuts (Boesch et al. 1994), and attempts have been made to relate this behavior to early hominid stone tool techniques (Joulian, 1996; Panger et al., 2002). Early hominids may have used similar methods of extracting invertebrates, cracking nuts, and other food related tool use like that observed in non-human apes today (Foley & Lahr, 2003; Panger et al., 2002). Panger and colleagues (2002) suggest that, while direct evidence for stone tools dates to 2.6 million years ago, *Australopithecus* may have had the manipulative capabilities for tool making and using around 3.2 million years ago. Systematic study concerning the prehistoric diet, especially regarding insects and nuts, may allow more direct inferences for simple forms of technology made from materials like that used by living non-human apes. Such materials may have been used for termite fishing, ant dipping and fishing, nut cracking, and honey extraction. Insects in the early hominid diet could have provided protein and nutrients that plants and fruits could not provide, especially if hunting and scavenging were limited. Early hominids may have been more reliant on insects than large vertebrates. Later hominids might
have been characterized by a decrease in invertebrates and an increase in vertebrate prey, which would also be significant in the evolution from simple forms of tools to complex tools. Some believe that a significant change in human diet occurred between *Australopithecus* and *Homo*, with the latter having a dramatic increase in meat procurement (Milton, 1999). Perishable tools may have assisted early *Homo* in food processing and procurement, allowing a variable diet (Teaford et al., 2002). As tooth size and enamel thickness decreased, the use of tools for food processing likely became even more important (Teaford et al., 2002).

Isotopic analyses done on *Australopithecus africanus* and *robustus* demonstrate that early hominids exploited open habitats for food, such as woodland and grassland (Sponheimer & Lee-Thorp, 1999). This conclusion may also lead to further investigation of whether early hominids consumed a higher intake of animal prey than once believed (Sponheimer & Lee-Thorp, 1999). It may be that open habitats do not provide as much fruit as do more forested ones. Fongoli’s mosaic habitat and the chimpanzees that live there will help in providing referential models for the Paleolithic diet of early hominids.

The impact of Fongoli chimpanzees’ emphasis on invertebrates may be interpreted regarding the early hominid diet in terms of an important resource that has been ignored quite frequently by researchers (see Ungar & Teaford, 2002). Fongoli is only one of a few dry savanna habitats where chimpanzees have been studied and provides evidence for the chimpanzees’ reliance on termites throughout the year. Fongoli and Assirik have environments similar to those that have been proposed for Plio-Pleistocene hominids in East Africa (McGrew et al., 1981). Considering the environment at Fongoli, chimpanzees here may provide insight into early hominid life. Consuming insects throughout the year rather
than as a fallback food may also characterize the diet of early hominids. This study suggests that insects may have been a crucial element in early hominid diet.

Questions of Culture

Whiten and colleagues (2001) have mapped out what they define as cultural variation among chimpanzees from different sites across Africa. As of 2001, a total of nine sites are considered. A recent conference was held in order to add more sites, which will include Fongoli (Pruetz, personal communication). This charting of cultural behaviors illustrates the differences between communities of chimpanzees. Chimpanzee site directors are given a list of behaviors to record for at their respective sites (Whiten, 2001; Whiten et al., 2001). These behaviors are then assigned patterns of representation: not known, not possible, absent, present, habitual, and customary (Whiten, 2001; Whiten et al., 2001). There are a total of 39 'cultural' behaviors recorded so far (Whiten et al., 2001), and more may be added in the next attempt. From this effort, primatologists can now compare behaviors found at their chimpanzee sites to those of others. This attempt is similar to what anthropologists have been doing with modern humans for centuries. Since this initial effort to chart culture in non-humans, there are now moves to do so among dolphins, whales (Whitehead et al., 2004), capuchins (Fragaszy et al., 2004) and orangutans (van Schaik et al., 2003b).

The identification of chimpanzee culture helps to illustrate their welfare and significance to humans who may not be aware of the chimpanzee’s impeding threat, with the ultimate goal of conservation in mind. Today, the greatest threat to primate populations is habitat destruction (Hill, 2002). According to a recent survey, as of 2003, the western subspecies of chimpanzee is now extinct in at least two countries in which they once resided: Benin and Togo (Butynski, 2003). Estimates in 2003 estimate a population of 200,000 for all
subspecies of *Pan troglodytes* combined, and all species and subspecies of *Pan* are considered “endangered” according to the United States Endangered Species Act of 1973 (Butynski, 2003). Nigerian (*Pan troglodytes vellerosus*) and Western chimpanzees (*Pan troglodytes verus*) (Figure 6.3) have the lowest population numbers and are currently at the greatest risk (Butynski, 2003). Senegal is reported to have between 100 and 300 Western chimpanzees left in the wild (Carter et al., 2003). Thus, research on these chimpanzees is greatly needed before they disappear. Chimpanzees live a tenuous existence in the “marginal” habitats of Fongoli (Pruetz, unpublished data). Research on diet in chimpanzees is beneficial in terms of conservation of habitat. This research shows the importance of closed habitats (ecotone and gallery forests) as well as open habitats (woodland) in the consumption of termites, which is also a major contributor to the Fongoli chimpanzee diet. Thus, conservation of these habitats is important for the survival and diet of the chimpanzees.

Many questions addressed here have yet to be answered but are on-going questions that drive anthropologists to conduct research. We may never understand completely how human culture evolved. However, we are aware that our own culture may eventually destroy us. Looking for answers to how and why human culture evolved may provide answers that help us stop the destruction. Anthropologists using paleo-studies and extant primate studies may hold keys to the answers. We can make inferences on cultures from the past and from non-human primates, and we can only hope that we get close enough to the truth with our knowledge to get a better picture of human evolution. With such knowledge it may be possible to understand where the human species is headed.
Much debate has been on whether non-human animals can have culture (Foley & Lahr, 2003; Laland & Hoppitt, 2003). As more information is compiled it will be difficult to deny it any longer, and the human species will again theoretically decrease regarding our superiority that we believe we hold in this universe. It is a fact that people are not ready to accept, but it may be too late when they do, for all creatures and environments that have fascinated us may be gone by then.

**Future Research**

I will continue my research into the insectivorous diet of chimpanzees in search for answers to hominid evolution and chimpanzee habitat conservation. Forested habitats are extremely important for chimpanzee diet, as I have illustrated here and others have shown regarding the frugivorous diet of the chimpanzee (Pruetz, 2005; Wrangham et al., 1993; Sugiyama & Koman, 1992).
Fongoli is a dry mosaic habitat that is not often found associated with chimpanzees. Another site, Semliki, Uganda is similar to Fongoli’s habitat, but the chimpanzees have not shown any evidence for the consumption of invertebrates such as termites (Hunt & McGrew, 2002). Research into this area has not been completed. A possible explanation may be that the knowledge of termite fishing is absent; however there are ways of obtaining termites and other invertebrates without the use of tools (Newton-Fisher, 1999; McGrew, 1992), which should be examined further.

I propose a more extensive methodology examining termite diversity across sites to give a better understanding of the relation between termite availability and consumption. Termite mound density and species composition at other termite fishing chimpanzee sites would give the necessary tools for comparison across sites to determine variations. Micro-analysis of termite remains in the feces may help to give more detailed results of chimpanzee invertebrate diet. Further observational data on Fongoli chimpanzee termite fishing may give us a better understanding of the diversity of termite species in the diet and the importance of termites in the diet overall.
REFERENCES CITED


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