CHIMPANZEES, TOOLS, AND CLIMATE: A CROSS-CULTURAL COMPARISON OF CHIMPANZEE TECHNOLOGY AND ECOLOGY

A THESIS

SUBMITTED TO THE GRADUATE SCHOOL IN
PARTIAL FULFILLMENT OF THE REQUIREMENTS
FOR THE DEGREE MASTER OF ARTS

BY

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MUNCIE, INDIANA

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ABSTRACT

THESIS: Chimpanzees, Tools, and Climate: A Cross-Cultural Comparison of Chimpanzee Technology and Ecology.

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This thesis compares the tool-using behaviors and environments of nine chimpanzee study sites. In addition, tool-use in other animals is discussed, as is the social behavior of chimpanzees and the different contributions of wild and laboratory studies. Research centers on two primary questions:

- Do chimpanzee study sites differ significantly in the types of tool-using behaviors they employ?
- Is the amount of tool-using behaviors related to annual variability in rainfall or the overall wetness of a site?

No significant differences exist between the different communities being studied. A significant correlation was found between diversity of tool-using behaviors and perhumidity index, a measure of overall wetness of a particular area. Finally, no correlations were found between diversity of tool-using behaviors and annual variability and rainfall. This analysis casts further doubt on the hypothesis that hominin technology evolved as a response to living in dryer, more open environments.

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CHAPTER 1: INTRODUCTION

Tool-use in chimpanzees, like in humans, is a product of the interaction between biology, culture, and environment. It is unlikely that a single variable can explain the diversity of tool-using behaviors in chimpanzees or humans. This thesis will explore the role of environment in influencing the invention and dissemination of tool-using behaviors. Novel behaviors can arise in any environment, especially among novice tool-users. However, it is likely that novel behaviors will persist only if they prove to be advantageous in the environment in which they are invented.

An example of this is nut-cracking, a behavior that is observed mostly in West African chimpanzees (*Pan troglodytes verus*). Other sites have the necessary stones and nuts available, yet no other group has been observed exploiting this valuable resource (McGrew et al. 1997). One possible explanation is that they simply do not need to (insects provide the bulk of their protein and energy); another is that this behavior has simply not been invented by any member of these populations (McGrew et al. 1997). Nut-cracking takes many years to learn and is not likely to be quickly invented **(**Boesch and Boesch-Achermann 2000; Inoue-Nakamura and Matsuzawa 1997). However, once it is invented it opens up a new resource that an individual or group can exploit. The environment is not a causative agent in the development of a behavior, though it can exert selection pressures for particular behaviors once they are invented, similarly to how mutations occur randomly but can prove beneficial or harmful in a particular environment. In other words, the rewards of a behavior in one environment may be greater than the rewards of the same behavior in a different environment.

Environmental characteristics are important because they influence the availability of niches that organisms rely on to survive. Kamilar (2009) suggests that similar environments should have similar species compositions. The same should be true of geographically close communities as well. In general, there is a positive relationship between the number of primate species at a given site and annual rainfall, though historical factors will also influence species distribution (Kamilar 2009). This is likely due to increased plant productivity compared to dryer areas. This, in turn, should have an influence on tool use because many tools are either made out of plant materials or are used to harvest plant-based foods such as nuts or tubers.

This thesis examines whether there is a general correlation between number of tool-using behaviors and environmental variables. I hypothesize that chimpanzees living in more diverse environments, such as rainforests will have a more diverse behavioral repertoire than chimpanzees that live in less diverse locales, such as savannas. Environmental diversity will be assessed primarily using temperature and precipitation data. Relationships between seasonality will also be explored in order to test whether chimpanzees in variable environments have more tool-using behaviors than those in richer environments. Finally, I predict that variability will also influence the degree of tool use. That is, I expect more tool use among chimpanzees living in ecologically rich areas, as well as more varied tool kits than less rich regions.

Boesch-Achermann and Boesch (1994) provide compelling evidence that many of the traits that came to define hominins evolved primarily in the forest as opposed to the savanna, an idea first proposed by Frederic Wood Jones (1925). Boesch-Achermann and Boesch (1994) cite more frequent and varied tools use and increased cooperative hunting and food sharing in forest chimpanzees as opposed to those living in more open savanna-woodland environments. This thesis will explore the role of environmental and geographic variation in chimpanzee behavior in an attempt to better understand the evolution of tool-use. More specifically, the behavioral ecology of tool-use will be explored as well as how environmental diversity and variability affects access to preferred resources in an attempt to understand how different technologies and tool-using strategies might have evolved.

Behavioral ecology is, simply stated, the study of how and why an organism behaves the way it does in a particular environment and how those behaviors contribute to reproductive success (Krebs and Davies 1997) The origins of behavioral ecology can be traced to Nikolaas Tinbergan's 1963 paper *On Aims and Methods in Ethology* where he outlined the proximate and ultimate causes of behavior. As applied to tool-use behavioral ecology can help us understand how technology affects the reproductive fitness of hominoids and hominins by examining how tools allow for more efficient gathering of preferred resources as well as how technology allows organisms to cope with environmental change. I hypothesize that there will be a correlation between environmental diversity, variability, and increased reliance on tools.

This thesis will consist of five sections. The first is a brief overview of tool-use in the animal kingdom. This section will discuss how tool-use is defined, different types of tools, and the role of ecology and cognition on its development. The second section will be an overview of chimpanzee behavior, social structure, and tool-use. This section will describe the communities being examined, the scope of tool-use among wild chimpanzees, and the environmental factors that affect tool-use in their tool-use, such as resource availability, habitat and raw material availability. I will also explore how chimpanzees typically procure raw materials as well as how these behavioral traits differ between populations. In addition to examining chimpanzees, I will also discuss the tool using behavior of other animals as points of comparison. The third section provides a brief overview of studies of wild and captive chimpanzees, as well as merits and drawbacks of each approach. The fourth section examines the relationships between tool-use and the aforementioned environmental influences, and presents statistical support for these relationships. Finally, the final section discusses the findings of thesis in a broader, evolutionary context.

Phenotypic plasticity is an important concept in understanding tool-use. West-Eberhard defines phenotypic plasticity as: “the ability of a single genotype to produce more than one alternative form of morphology, physiological state, and/or behavior in response to environmental conditions” (1989:249). If an organism lives in a constantly fluctuating environment, natural selection will select the phenotype that is the most able to adapt to the changes (Potts 1998). Adapting behaviorally is likely to be a much easier and quicker task than adapting biologically in a large-brained mammal. In other words, the ability to alter behavior depending on the environment would be selected for in anthropoids living under fluctuating environmental conditions. As resource availability changes, tool-using organisms either have to adapt current technology or invent new tools in order to extract nutrients from the changing environment. This necessity to continuously adapt in order to maintain relative fitness is known as the "Red Queen Hypothesis" (Van Valen 1973). Likewise, chimpanzees living in more abundant environments will likely be more proficient tool-users than those living in less rich environments. Hypothesized reasons include: greater availability of raw materials, greater diversity of food resources, and more chances for experimentation.

Variable climates affect organisms in many different ways. Temperature and precipitation affect the availability and quality of food and water sources, as well as their distribution (Bronikowski et al. 1996). In wild baboons (*Papio cynocephalus*), for example, a general correlation was found between meteorological variation and behavioral variation, however specific behaviors differed between study groups. This suggests that baboons have a range of responses to environmental variability, and that there are often multiple valid solutions to problems encountered throughout an individual's lifetime (Bronikowski et al. 1996).

A similar conclusion was reached by McGrew and colleagues (1979) in their study of termite fishing at Gombe (Tanzania), Mt. Assirik (Senegal), and Okorobiko (Equatorial Guinea). They found that ecological differences, especially seasonality, account for some of the variation in behaviors between these groups, though other differences are likely cultural. Tool-use by chimpanzees at Gombe and Assirik were more similar to each other's than either was to that of those at Okorobiko. In general, tools used at Okorobiko were longer and stouter than those used at Gombe and Assirik. Tool-use was also found to correlate with seasonality at Gombe and Assirik; more tools being used in the month immediately after the dry season. Seasonality affects the structure of termite mounds which in turn influences the tools and strategies chimpanzees use to harvest termites. Okorobiko chimpanzees rely heavily on perforation as the mounds are soft throughout the year due to the wet climate. In dryer areas such as Assirik and Gombe, the mounds are extremely hard throughout much of the year resulting in perforation being a less useful method. In wetter climates termites are constantly rebuilding their nests, allowing chimpanzees to damage them without permanently destroying a very productive food source.

It is likely that among any organism there are multiple solutions to the same general problems and it is also likely that different communities will prefer certain solutions over others. While some tool-using behaviors may be adaptive responses to ecological problems, many of the behavioral differences between communities can be explained in terms of social custom such as differences seen in insect fishing techniques at various sites (Boesch 1995).

In terms of tool-use in chimpanzees, it is also possible that different strategies will develop to aid in solving similar problems. For example, in populations that crack nuts, there may be a relationship between time spent cracking nuts, time fishing for insects, and time hunting for meat. All three of these behaviors are important in acquiring protein. Chimpanzee populations that do not crack nuts should then spend more time gathering insects and hunting to acquire the same amount of protein. This diversification of resources among west African chimpanzees may allow them to spend less time on each sort of resource.

Behavior, like all phenotypes, is influenced by both genetics and environment (both natural and social). Tools can be seen as solutions to problems that chimpanzees encounter in their daily lives which are used to act on various parts of their environment. Cultural changes can also occur after a particular tool using behavior appears in a chimpanzee community. There is some evidence that the status of an individual who originates a behavior in a community is related to whether or not a behavioral pattern persists in the community. Boesch (1995) describes two novel behaviors observed: use of a stick to extract more of a mushroom, and leaf-clipping during resting. Only leaf-clipping spread to others in the population. The inventor of mushroom-picking was a young female with a low social ranking and it is surmised that the inventor of leaf-clipping while resting was an adult male, as they most often are seen clipping leaves during drumming displays (Boesch 1995).

Coss (1999) argues that phylogenetically ancient behavioral traits should be harder to lose than more recent traits. From a genetic perspective, ancient traits should be pretty much the same in all populations of a species, with only the more recent behavioral traits providing much of the diversity. Gene flow may limit optimal adaptation in areas with poor barriers against it. However, current research suggests that genetic differences between the various subspecies of chimpanzees are not sufficient to account for behavioral differences (Lycett et al. 2007, 2010).

A primary purpose of this thesis is to examine whether tool-use in chimpanzees is based on opportunity or necessity. In other words, is there a positive relationship between diversity and tool-use, or is the relationship negative or absent? Fox and colleagues (1999) propose two hypotheses to explain tool-use in orangutans. The necessity hypothesis states that because orangutans have strong hands and teeth with thick enamel, tools are not necessary to survival as they are biologically able to eat most foods without the need for tools. This also may explain why the tool-use repertoire of wild orangutans is so poor compared to the rich repertoire of their captive counterparts. The opportunity hypothesis argues that tool-use is facilitated by repeated exposure to favorable environments. In other words, the more opportunity an organism has to use tools, the more likely it is that tool-use will spread throughout a population. Spagnoletti and colleagues (2012) examined if bearded capuchin monkeys (*Cebus libidinosus*) used tools out of necessity during periods of resource scarcity, or used them opportunistically as they encountered preferred resources. Spagnoletti and colleagues (2012) concluded that capuchin tool use fits best with the opportunity hypothesis as the rate of tool use had no correlation with availability of fruits or invertebrates.

CHAPTER 2: TOOL-USE AND EVOLUTION

The idea that behavior could be studied from an evolutionary perspective first arose in the early 1950s (Roe and Simpson 1958). Throughout the mid-twentieth century, many different theoretical perspectives regarding behavior and evolution appeared in the evolutionary biology literature. The two most influential perspectives were sociobiology and behavioral ecology. Sociobiology was championed by Edward O. Wilson and his 1975 book *Sociobiology: the New Synthesis* was instrumental in improving its popularity. Sociobiology seeks to explain social behavior in an evolutionary context. Some argue that sociobiology is too biologically deterministic, as it suggests that genes are the major driving force in the evolution of social behaviors, with little influence by ecology or culture (Gould 1981).

Behavioral ecology is the study of how and why certain behaviors evolve in a given environment and how they contribute to reproductive fitness. A major assumption, known as the phenotypic gambit, is that genetic, intraspecific (relationships to other organisms) and cognitive mechanisms do not seriously constrain adaptive responses to ecological changes (Smith and Winterhalder 2002). In other words, this theoretical approach assumes that natural selection has favored organisms that make decisions that are adaptive to the local environment. Behavioral ecology contrasts with sociobiology in that it focuses more on the effect of environment on behavior rather than the genetics.

An important assumption in behavioral ecology is the concept of optimal foraging theory (OFT) (MacArthur and Pianka 1966). Organisms tend to optimize their foraging return in relation to the costs. In other words, organisms will employ strategies that bring in the greatest possible amount of energy and nutrients given various constraints while expending as little time or energy as possible. Optimization and efficiency are thus closely related. Optimization is gathering the best available resources while efficiency is obtaining them with minimal effort. However, complete optimization is impossible as compromises need to be made.

Another component of behavioral ecology is the concept of the phenotypic gambit. This seeks to simplify the complex relationship between behavior, ecology and genetics. The phenotypic gambit assumes that natural selection is a strong enough mechanism to override these conflicting forces and that enough genetic variation exists to allow “optimal” phenotypes to evolve. The phenotypic gambit also assumes that the genetic mechanisms behind the inheritance of these phenotypes do not significantly affect the evolutionary outcome (Smith 1992). In other words, this approach assumes that natural selection has favored organisms that perform behaviors that are adaptive to the local environment, and thus favorable to spreading that individual’s genes without directly studying the genes themselves.

Some scholars have argued that optimal approaches are not useful approaches to understanding animal behavior or biology (Gould and Lewontin 1979; Pierce and Ollason 1987). Pierce and Ollason (1987) argue that animals should not be expected to behave optimally given the large number of constraints and that it is not possible to test whether or not a particular behavior is optimal. They go so far as to call optimal foraging theory a "complete waste of time" (Pierce and Ollason 1987:111). Gould and Lewontin (1979) argue against the idea that the way a particular trait is used is the primary impetus for its evolution. They also argue that supporters of optimality theory examine discrete traits of animals as opposed to the integrated whole and that "immediate utility is emphasized over other attributes of form" (Gould and Lewontin 1979:153). However, it is important to note that this debate is still ongoing.

Though many others have argued that while it is not perfect, it is still a very useful tool (Parker and Smith 1990; Perry and Pianka 1997; Pyke 1984). Most disagreement on its utility stems from strict empiricists who argue that quantitative laboratory studies and genetics are more informative than field and behavioral studies (Perry and Pianka 1997). A similar schism can be seen in studies about the tool-using behaviors of chimpanzees. Some scholars argue that field studies are the most informative because they allow an organism to be understood in its natural habitat (Boesch 2011), while others favor laboratory studies as they allow for more control over variables, are repeatable and provide more insight into cognitive processes (Tomasello and Call 2008). Others have bridged the gap between these two approaches and have established outdoor laboratories in chimpanzee's natural habitat and tested hypotheses based on their natural behavior (Biro et al. 2003; Carvalho et al. 2008; Matsuzawa 1994). In general, most scholars believe that both approaches are useful to understanding different aspects of animal behavior.

Evolutionary Perspectives on Tool-Use

Kuhn (2004) highlights many of the important trends of which anthropologists studying technology need to be aware. Most relevant to this thesis is that an evolutionary model is especially useful when there is a direct connection between technological and biological changes. The archaeological and fossil records support an evolutionary relationship between technology and biology. Technological innovations tend to precede biological change, causing some scholars to argue that human evolution is largely self-directed (Kingdon 1993; Taylor 2010). Archaeological studies on hominid evolution, such as that of Domínguez-Rodrigo and colleagues (2005), associate increased technological complexity with more complicated subsistence patterns such as the use of sharp edged tools to butcher carcasses obtained through either active hunting or scavenging. However, it remains a mystery as to what other types of tools were used by Pliocene and Pleistocene hominids as organic objects do not preserve well. It is also likely that tool-use can be understood as evolving from prior behavioral patterns, an example being the smashing of nuts directly on rocks emerging before the use of hammer and anvil technology (Alcock 1972).

Taylor (2010) has argued that increased mastery of technology lessened the importance of natural selection on human evolution and resulted in an evolutionary trajectory that is largely self-directed. Evidence in favor of his hypothesis is the fact that new technologies tend to precede increases in brain size in the fossil record. Thus, Taylor (2010) argues that the use of tools to solve problems and the resulting selection of those with the cognitive abilities to solve those problems would be selected for, would result in an overall increase in relative brain size.

Pradhan and colleagues (2012) propose a slightly different hypothesis to explain the evolution of technology. Specifically they focus on the evolution of cumulative technology. Cumulative technology, also known as ratcheting, is the addition of new behavioral patterns to existing ones resulting in either new tools or new tool-using behaviors (Pradhan et al. 2012). Specifically they modeled variation of cumulative technology in chimpanzees and orangutans with variations in sociality and found that the technological variation between the two species is largely related to the higher degree of sociality in chimpanzees which provides more opportunities for social learning. This model suggests that cognitive changes are not essential to explain the origins of technologies more complex than those seen among chimpanzees and other animals such as the Oldowan or Acheulian. Pradhan and colleagues (2012) do suggest however, that once ratcheted technologies become a major part of hominin behavioral repertoire, natural selection may favor increased intelligence to greater facilitate the learning process. The main benefit of ratcheting is that an organism does not have to relearn a task every time it is to be performed in a new situation.

Van Schaik and colleagues (1999) argue that social tolerance is the main factor in the distribution of tool-use in the wild. They propose that the odds of an individual inventing a behavior are a function of the potential opportunities for that behavior to occur (van Schaik et al. 1999). Factors influencing these opportunities are reduced vulnerability to predators and a flexible social organization. Social tolerance was deemed especially important as it allows an individual to focus their attention on exploration without minimal interference resulting in an increased likelihood of learning or inventing new skills (van Schaik et al. 1999). It was found that mean party size did not correlate with tool-kit size; however, compiled "tolerance" scores had a strong correlation with size of the tool kit (van Schaik et al. 1999). It is possible that this "safe" learning environment is the main factor influencing the differences seen in tool-use between wild and captive populations as captive animals are freed from the constraints of predation and foraging, and are regularly presented with cognitively demanding tasks to test their tool-using or problem solving abilities.

Tool-Use in Animals

Tool-use has proven difficult to define. Schumaker and colleagues (2011) provide 15 definitions of tool-use from different authors. These definitions range from short and simple to long and complex. One of the simpler definitions is from Goodall (1986) who defines a tool as "an object held in the hand (or foot or mouth) and used in such way as to enable the operator to attain an immediate goal" (Goodall, 1986:536). This definition has few qualifiers which make it easy to work with, but difficult to use in the cases of borderline tools. Schumaker and colleagues (2011) provide a much more comprehensive definition of tool-use:

> The external employment of an unattached or manipulable attached environmental object to alter more efficiently the form, position, or condition of another object, another organism, or the user itself, when the user holds and directly manipulates the tools during or prior to use and is responsible for the proper and effective orientation of the tool. [Schumaker et al. 2011:5]

While definitions differ in the number of stipulations, they tend to have certain characteristics in common. These include the use of an external object to aid in a particular task, as well as the stipulation that the object must be manipulable. More flexible definitions allow for the inclusion of objects such as nests, burrows, and even spider webs (Pierce 1986; Reed 1985), though it is argued that this expands the pool of prospective tool-using behaviors, resulting in a definition too broad to be of any use (Schumaker et al. 2011). This thesis employs the definition put forth by Schumaker and colleagues (2011).

The use of multiple tools to accomplish a particular task is often seen in chimpanzees and other primates, these types of tools are known as associative tools. Schumaker and colleagues (2011) provide a list of 11 different associative tool types (Appendix A).

There has been a vast increase in the number of animals that have been observed using tools over the past few decades. Primates are renowned tool-users in both wild and captive settings, but many other animals have been observed using tools as well, including insects, mollusks, birds, and non-primate mammals (for a thorough review of tool-use throughout the animal kingdom refer to Bentley-Condit, 2010; Sanz et al. 2013; Schumaker et al. 2011; Seed and Byrne 2010). Primates demonstrate the most varied tool-use behaviors; they are the only order to use more than five of Bentley-Condit's (2010) ten tool-using categories. Primates make up the bulk of known tool-using behaviors in mammals, though sea otters, dolphins and brown bears have all been observed using tools to varying degrees in the wild (Deecke 2012; Fisher 1939; Smolker et al. 1997)

While tool-use is often used as evidence of advanced cognitive abilities, Hall (1963) cautions against attributing high degrees of intelligence to animals based on observations of tool-use. He suggests that many tool using behaviors are simply incidental outcomes of non-tool using behaviors and do not necessarily reflect a high intelligence. This is a view shared by Alcock (1972) who agrees that most examples of tool-use are likely to have evolved from an organism's preexisting behavioral patterns and suggests that many types of tool using behavior have their origins as lucky accidents. Seed and Byrne (2010) and Ingmanson (1996) also suggest that the use of tools is not itself indicative of cognitive abilities as bonobos and orangutans use few tools in the wild but are nonetheless highly intelligent.

Bonobos (*Pan paniscus*) are close relatives of the chimpanzee who have shown a high capacity for tool-use and tool manufacture in captivity, but have a fairly limited repertoire in the wild (Gruber et al. 2010; Ingmanson 1996; Schick et al. 1999). Ingmanson (1996) describes the tool-use of a wild population and notes that the majority of their tools are used in social or grooming contexts as opposed to feeding contexts, contrasting with how most chimpanzees use tools (though see Watts 2008). Bonobos are also not known to use tools as weapons (Ingmanson 1996). This may be related to the fact that bonobos primarily feed in rich patches and on foods that require minimal processing (White and Wrangham 1988).

Hunting is an example of a complex behavior that does not necessarily include tools, yet demonstrates a high degree of intelligence. Chimpanzees in Taï National Park are skilled hunters and hunt in groups more frequently than do chimpanzees from other sites, such as Gombe and Mahale (Boesch and Boesch-Achermann 2000). Group hunting is especially useful when hunting primarily arboreal prey in dense forest where visibility is low. Meat is divided between participants of the hunt based on an individual's contribution (Boesch and Boesch-Achermann 2000). Not only is a high degree of intelligence required to capture the prey, but also to navigate the social component of meat sharing.

Dolphins provide a good example of convergent evolution of tool-use in mammals. Like chimpanzees, dolphins live in fission-fusion social groupings. Bottlenose dolphins (*Tursiops sp.)* in Shark Bay, Australia, have been observed using sponges to protect their rostrums while foraging (Smolker et al. 1997). However, this is the only population of dolphins known to use tools, so it is currently not possible to compare their behaviors to other populations. Patterson and Mann (2011) provide an ecological incentive for this behavior. They argue that this behavior allows dolphins to exploit marine resources that they cannot hunt using echolocation, opening up a niche that would otherwise be inaccessible.

As the dolphin example illustrates, tools may allow animals to expand to other niches that they would otherwise be unable to exploit (Alcock 1972; Kingdon 2003). Kingdon (2003) advocates the concept of “niche invasion” as a means by which small bodied hominins were able to compete with larger, predatory animals for food resources. This systematic removal of obstacles (competitors) by groups of small hominins may serve as a prelude to the development of technologies such as scrapers and diggers (Kingdon 2003). Conceptually they are the same in that both acts result in the acquisition of an important resource through reduction. Removing competition results in a gain in food, while the removal and alteration of a raw material results in a functional tool (Kingdon 2003).

Alcock (1972) has also argued that tools allow for animals to invade otherwise inaccessible niches. Invasion of new niches also alters which animals an organism competes with. Alcock (1972) and Seed and Byrne (2010) stress the importance of understanding how different animals use tools. Tool-use has undoubtedly evolved convergently in many different lineages and thus understanding how animals other than primates use tools is vitally important to understanding the evolution of tool-use.

CHAPTER 3: CHIMPANZEE BEHAVIOR

Chimpanzees (*Pan troglodytes*) are our closest living relatives. Traditionally, chimpanzees were divided into three subspecies: the eastern chimpanzee (*Pan troglodytes schweinfurthii*), the central African chimpanzee (*P.t verus*), and the western chimpanzee (*P.t. troglodytes*). A fourth subspecies of chimpanzee (*P.t. vellerosus*, also known as *P.t. ellioti*) has recently been identified, living in the rainforests along the border of Nigeria and Cameroon (Gonder et al. 1997, 2006). However, some scholars argue that there are not enough significant genetic differences between chimpanzee groups to justify splitting them into discrete subspecies. Gonder and colleagues (2006) have argued based on analysis of mitochondrial DNA that only two subspecies should be recognized. Fischer and colleagues (2006) have argued that there is no justification of splitting chimpanzees into subspecies based on nuclear DNA analysis and behavioral similarities.

Chimpanzees live in fission-fusion social groups which is a social structure consisting of a parent group in which all members will congregate for sleeping, eating and grooming. When foraging, chimpanzees fission into smaller groups. This is an ideal foraging system in that it allows members of a species to enjoy the advantages of living in a large community while simultaneously enjoying the benefits of smaller foraging groups (Grove et al. 2012). Chimpanzee females typically leave their natal group once they reach sexual maturity. In other words, chimpanzees can be said to live in patrilocal societies. It is not uncommon for multiple parent groups to inhabit the same area and exchange members; thus sub-groups in closer proximity tend to be more genetically and behaviorally similar (Kamilar and Marshack 2012; Whiten et al. 2001).

Due to the fact that chimpanzees acquire cultural behaviors through social learning it is important to understand the role of environment in determining group size. Kamilar and Marshack (2012) argue that longitude, and thus geography, was the best predictor of behavior independent of local ecological factors. This is a logical conclusion because, as mentioned above, groups in close proximity to each other will likely behave in more similar ways than groups that are farther apart. This idea coincides with the general geographic distribution of modern chimpanzee populations.

The earliest documentation of chimpanzee tool-use dates to 16th and 17th century accounts by Portuguese missionaries and other travelers in Sierra Leone (Sept and Brooks 1994). These accounts include both naturalistic observations and far-fetched stories. The account of Manuel Álvares, a Jesuit priest, provides the most vivid depiction of nut-cracking from this period stating that “a *dari* (chimpanzee) takes a small quantity of *chaveo* (palm nuts) and with a stone in its hand breaks the nuts and eats them” (Álvares ca. 1615 [Hair 1990], cited in Sept and Brooks 1994:872). These accounts contribute significant time depth to chimpanzee behavior and indicate that chimpanzees in this region have been hammering nuts for at least 400 years. Similar accounts by Savage and Wyman (1843/1844) provide similar observations of tool use in wild chimpanzees prior to the twentieth century.

As our closest biological relatives and as proficient tool-users, chimpanzees give us the opportunity to study tool-using behaviors in ways far beyond what the archaeological record provides. We can observe the gathering, manufacture and use of tools, many of which are made out of organic materials that do no preserve in the archaeological record. The use of stone tools by chimpanzees is rare; only chimpanzees in Western Africa have been observed using stone tools to crack nuts (though see Morgan and Abwe 2007). Other primates, such as the bearded capuchin monkeys (*Cebus libidinosus)* in Brazil, and brown capuchins (*Cebus apella*) in Suriname, have been observed using percussive technology to process nuts (Boinski et al. 2000; Visalberghi et al. 2007). It is likely that tool-use goes much further back in time than the Oldowan, and understanding the relationship between chimpanzee tool-use and environment will be helpful in understanding the behavior of ancient primates.

Boesch-Achermann and Boesch (1994) and Boesch and Boesch-Achermann (2000) have studied the chimpanzees of the Taï National Park Reserve in Côte d'Ivoire since 1979 and have provided convincing evidence that many aspects of hominin evolution occurred in the rainforest as opposed to open savanna or mixed woodland environments. For much of the twentieth century, conventional wisdom held that distinctive hominid behavior was a product of evolving primarily in an open savanna environment, an idea first proposed by Raymond Dart (1925). This assumption led to a bias in chimpanzee studies in that many prior studies focused almost entirely on chimpanzees in the Gombe Stream National Park and Mahale Mountains National Park, both in Tanzania and both mixed-woodland, savanna environments (Boesch-Achermann and Boesch 1994; Goodall 1968, 1986). Boesch and Boesch-Achermann (1994) provided convincing evidence against the so-called “savanna hypothesis” by demonstrating that forest chimpanzees “use more tools, make them in different ways, hunt more frequently and more often in groups and show more frequent cooperation and food sharing" (Boesch-Achermann and Boesch, 1994:9) than do chimpanzees living in dryer, more open environments.

This makes sense from a behavioral ecological perspective. While forests have richer food resources available, these are also harder to spot due to the density of vegetation (Boesch-Achermann and Boesch 1994). The lower visibility also allows predators to lie in ambush easily. Accordingly, behaviors and tools which allow chimpanzees to efficiently gather these resources are likely to be selected for by natural selection. In addition, rich forests provide more possible raw materials than do less rich environments, possibly allowing more opportunities for innovation and experimentation. If more complex tool-use originated in a forest environment, how did hominid tool using behavior change as forest was gradually replaced by savanna?

Chimpanzees are known to sometimes use multiple tools to solve a particular task. This is known as a tool composite (Sugiyama 1997). It has been argued by some scholars that the use of multiple tools to accomplish a single task is a uniquely human characteristic (Oakley 1967). This does not appear to be the case as numerous studies now demonstrate the use of composite tools among wild chimpanzees (Boesch et al. 2009; Carvalho et al. 2008; Sugiyama 1997). Sugiyama (1997) found that there are differences between groups that use composite tools and that this behavior was completely absent from chimpanzees in Eastern Africa. This behavior does not seem to be influenced strictly by environment as there are many similarities in environments between different regions, such as the availability of nuts and stones in both east and west Africa (Sugiyama 1997). However, it is possible that the cost for learning new behaviors is greater than the benefit received by exploiting these resources. It is also possible that there is no benefit in chimpanzees taking advantage of these resources as they receive adequate nutrition from other sources.

Boesch and colleagues (2009) provided further evidence for the use of composite tools. Chimpanzees from Loango National Park, Gabon, use three-to-five element tool kits consisting of various sized and shaped sticks to extract honey from nests in trees. The use of these composite tools requires an understanding of causality and a high degree of foresight and planning (Boesch et al. 2009). These types of tool kits are employed to access resources that are difficult to reach and out of eyesight. Different approaches are employed for different species of bee. For example, more tools have found under bee's nests in Loango, Gabon, than in Goualougo, Republic of Congo. This disparity has been attributed to the chimpanzees in Loango not exploiting mason bees which construct nests on tree trunks and require fewer tools to access than do those of bees that nest deep in tree cavities (Boesch et al. 2009).

The high degree of foresight and planning required for the use and creation of tools has been argued to be the result of cooperative hunting (Boesch and Boesch-Achermann 2000). Cooperative hunting, like tool-use, involves planning and foresight (different individuals serve different roles in the hunt; movements of prey need to be anticipated), as well as an understanding of causality (e.g. performing a certain action will result in a specific outcome). In regards to tool-use, chimpanzees (and other tool-using organisms) must understand what type of tool is most adequately suited to the task, and how to use that object to attain their goal.

This seems to demonstrate that chimpanzee tool-use likely spreads through cultural learning and is not strictly influenced by the environment. No studies thus far have, however, compared technological diversity to environmental diversity. Do chimpanzees living in richer environments use more tools than those living in less rich environments? If this is the case, do tool using chimpanzees optimally select raw material or are they more opportunistic about it? Richer environments likely will have a far greater diversity of raw materials to choose from, thus increasing the likelihood for raw material preference. The application of archaeological methods to primate behavior provides valuable insight into the cognitive processes that lead to the use of an object as a tool, including raw material selection (Haslam et al. 2009).

CHAPTER 4: WILD VS. CAPTIVE STUDIES

Tool-use has been studied extensively in both laboratory and natural settings. Each of these approaches has benefits and drawbacks. The main advantage of studying animal behavior in the wild is that you can see how they react to challenges imposed on them in their natural environment. A main drawback to these kinds of studies is that researchers have limited control over the variables being observed. It is also not possible to follow all animals 24 hours a day and it is likely that some behaviors are being missed. This lack of control makes it difficult to understand the cognitive aspect of the behaviors being performed. Captive studies are well suited to examining the cognitive aspects of tool use as all aspects of the tool-using process can be controlled by the researcher. Captive studies also allow experiments to be carried out on multiple species. However, captive environments are often poor approximations of an animal's ecology and social environment.

Early studies on captive chimpanzees by Nadia Kohts, Wolfgang Köhler and Robert Yerkes vastly increased our understanding of chimpanzee intellect. Kohts was among the first psychologists to study chimpanzees and is perhaps most famous for her comparisons of her subject, Joni, to her own son, and her observations on the dependence young chimpanzees have on their mothers (Kohts 2002). Köhler studied the cognitive abilities of chimpanzees and provided early observations of captive chimpanzees' ability to use tools (Köhler 1925). Experiments performed by Köhler included providing chimpanzees with sticks of varying lengths which allowed them to reach distant objects and providing them with boxes to allow them to construct towers to aid in reaching objects located high above the ground (Köhler 1925). Yerkes started the Yerkes Primate Laboratory, the first such facility in the United States, in 1925 after purchasing two chimpanzees he raised in home, where he was the first to take an evolutionary, as opposed to a behaviorist, approach to understanding chimpanzee behavior (Yerkes 1929).

Boesch (2011) compares two approaches to understanding the evolution of social behavior: an evolutionary approach and a Cartesian approach. An evolutionary approach predicts convergence in similar environments. Increased diversity is expected in animals that face more problems. Ecological niches also affect behavioral and genetic diversity as they select different abilities in different organisms. This approach primarily seeks to find how animals are similar to others based on evolutionary relationships. The Cartesian approach, on the other hand, does not rely on understanding the relationship between behavior and environment, and focuses primarily on results from experimental studies on captive animals. Instead of focusing on the relationship between behaviors, cognition and an organism's natural environment, this approach is seeking qualitative differences among organisms (Boesch 2011).

Not surprisingly, these approaches have very different predictions about the evolution of social behavior and cognition. The Darwinian approach predicts a more analog relationship, or, in other words, more continuity. Cognitive traits are the products of adaptations to specific socio-ecological pressures. Boesch (2011) is a proponent of the Darwinian approach. All organisms learn behaviors from their interactions in a specific environment. Cognition is also related to environmental interactions as more demanding socio-ecological challenges will place more selection pressure on evolving more complex social behaviors and cognition.

Captive environments may promote tool use and behavioral innovation due to the relative safety of the environment and removal of constraints normally faced by animals such as predation, need to forage, and climate. Captive chimpanzees (and other primates) are also constantly being encouraged and rewarded by researchers for using tools or solving problems in novel ways. While they provide valuable insight into the cognitive abilities of an organism, captive studies are likely of little use to understanding behavioral evolution.

The use of field experiments bridges the gap between natural and captive studies. Outdoor laboratories are established that allow researchers to manipulate variables that may influence a chimpanzee's decision to use a particular strategy. The main advantage of field experiments is that they afford more opportunities for researchers to observe tool-use. Even if chimpanzees are followed all day, every day, there is no guarantee that they will use any tools (Matsuzawa 2011b).

Field experiments allow for daily observations of the community and often allow researchers to observe the abilities of all members of a community (Matsuzawa 2011). A second benefit of field experiments is they allow researchers to manipulate variables such as food and tool availability in order to see how scarcity or abundance affects behavior (Matsuzawa 2011). Field experiments, like laboratory experiments, allow researchers to create longitudinal records of behavior. This allows researchers to see how behaviors change over time as well as to observe how novel behaviors are spread to other members of the community (Matsuzawa 2011).

Biro and colleagues (2003) examined how chimpanzees learn tool using behavior and the extent of cultural learning among chimpanzees in Bossou. They introduced adult chimpanzees to an unfamiliar species of nut (*Coula edulis)* and examined how they would react to this new resource. All materials necessary to crack nuts was made available at the outdoor laboratory. Chimpanzee response to these nuts fell into three categories: ignore, explore, and crack. All juveniles at the site explored and cracked the novel nuts while only half of the adults did. The percentage of adults exploring and cracking these nuts gradually rose over the years from 11 percent in 1993 up to 67 percent in 2002. This was attributed to juveniles growing up exploiting this resource and adults slowly learning how to take advantage of them as they became more familiar with the nuts. Behavioral data gathered from this experiment demonstrate transmission of knowledge among adults who were well past the sensitive learning period, and that behavioral innovation is more present in juveniles than adults (Biro et al. 2003).

Another experiment was carried out by Carvalho and colleagues (2008) who applied primatological and archaeological methods to understand raw material preferences among chimpanzees at Bossou, Guinea. This experiment applied chaîne opératoire theory to understand how chimpanzees in different populations used tools. Chaîne opératoire was developed by French social anthropologists and has since been applied to Paleolithic archaeology (Bar-Yosef and Van Peer 2009). It can be translated as “operation sequence”, and refers to the entire process of tool-making; beginning with raw material selection, use, retouching, and finally its eventual discard (Bar-Yosef and

Van Peer 2009; Carvalho et al. 2008). Carvalho and colleagues (2008) carried out their experiment through direct observation, direct recording, and indirect observation. Indirect observation closely resembles archaeological approaches in that all that is observed by the researchers is the arrangement of materials after the chimpanzees have left. They found that chimpanzees show preferences for certain types of tools, as certain hammerstones were used more often than expected. A similar affinity for particular raw materials has also been shown at the 2.6 million year-old Oldowan site of Gona in Ethiopia, where it is surmised that *Australopithecus ghari* was the primary tool-maker (Semaw 2003; Stout et al. 2005).

CHAPTER 5: TOOL-USE BY CHIMPANZEES

When discussing tool-use, it is necessary to understand how frequent a particular behavior is in a chimpanzee community. Traditionally, the terms customary, habitual, and present have been used to describe how prevalent a behavior is. Customary behaviors are those that are repeatedly seen in nearly all members of a community. Habitual behaviors are those that are observed in many, but not all, individuals. Behaviors are described as present if it is observed but not seen in enough individuals for it to be customary or habitual. Appendix B contains all tool-using behaviors incorporated in this study.

Whiten and colleagues (2001) compiled a list of cultural behaviors observed in chimpanzees. In addition to customary, habitual, and present behaviors, they include three categories of labeling behaviors that are absent in a community. Behaviors are marked as absent in a community if they are not observed and no obvious ecological explanation can account for their absence. An example of this is nut-cracking; its absence in eastern and central Africa cannot be attributed to the lack of suitable materials. Behaviors are marked absent with an ecological explanation if the environment the chimps are living in lacks an essential component of the behavior. An example of this would be termite fishing being absent in a community that has no termites to fish.

Behaviors that have yet to be observed in a group due to a lack of opportunities to observe them are often assigned to the unknown category.

The most common context for using tools is feeding. The two most well studied forms of tool-use and manufacture in chimpanzees are nut-cracking and insect gathering. Nut-cracking refers to the act of smashing open nuts using a hammer and anvil. Insect gathering involves the use of a stick to extract insects from their nests. Both hammer and anvil can be made of rock, wood, or other substrate. Nut-cracking and insect fishing involve the most complex tools in the Animal Kingdom outside of those used by humans. Both involve the use of composite tools, that is, the simultaneous use of two or more tools to achieve a single outcome (Carvalho et al. 2008; Sugiyama 1997). Nut-cracking involves a hammer and an anvil, but can include up to four different elements (Carvalho et al. 2008).

Insects can be gathered through dipping or fishing. Insect fishing involves the use of a probe to extract arboreal insects while insect dipping is the use of an instrument to collect insects on the ground (Yamamoto et al. 2011). Insect gathering can involve tool manufacture, serial tools (the sequential use of two or more tools to achieve a single outcome) and the use of composite tools (the use of two or more tools at the same time to achieve a single outcome). In both insect fishing and nut-cracking, the characteristics of the tool depend on the characteristics of the target. For example, heavier hammers are used when cracking harder nuts, while longer and sturdier wands are used to extract more aggressive species of ant (Boesch and Boesch 1983; Carvalho et al. 2008; Yamomoto et al. 2011).

Tool-use will be divided into five main categories as outlined by Boesch and Boesch-Achermann (2000): pounding, extracting, probing, cleaning, and social/display. Pounding is the use of one object to smash another object, typically against an anvil. Extracting refers to the act of using a tool to extract a substance from its substrate, i.e. extracting insect grubs from their nest. Probing refers to the use of a stick to investigate some aspect of the environment, such as prodding a dead body or examining the content of a bee nest. Cleaning involves the use of a tool, such as a wad of leaves to wipe a substance, such as blood or sperm, from an individual's own body. Displaying refers to the use of objects to augment displays. Examples include, aimed throwing or dragging of branches; also included are the use of objects during play.

Pounding Tools

Pounding tools are any tools that are used to strike another object or individual. Nut-cracking and pestle pounding are two examples of pounding tools used in the feeding context. Pounding tools can also be used in non-feeding contexts such as striking another chimpanzee during fights or aggressive displays, or striking other animals in order to scare them away.

Nut-cracking

Nut-cracking in wild chimpanzees is the only tool using behavior that involves lithic technology. Nut-cracking is a four or five step process depending on whether the anvil is attached to the substrate or not. Steps include: the gathering of nuts, gathering of hammerstones, gathering of anvils, placement of the nut on the anvil, and finally the smashing of the nut with a hammer. Nut-cracking traditionally has been believed to occur only in West African chimpanzees (Boesch et al. 1994; Boesch and Boesch-Achermann 2000; Hannah and McGrew 1986), though it has recently been observed in a population of Central African chimpanzees (Morgan and Abwe 2007).

Like all tool-using behaviors, nut-cracking is acquired through social learning and it takes many years for juveniles to become proficient. Studies have shown that a critical learning period exists and if a behavior is not learned during that time, an individual is unlikely to become proficient at it (Matsuzawa 1994). There are four distinct phases of learning nut-cracking: unsuccessful attempts at hitting nuts, being able to hit them but lacking the necessary strength, development of requisite strength but still having poor technique, and finally steady progress until peak efficiency is reached (Boesch and Boesch-Achermann 2000). Mothers are actively involved in the nut-cracking process and teach their offspring how to properly crack nuts through stimulation, facilitation, and active teaching (Boesch and Boesch-Achermann 2000). Stimulation involves leaving a hammerstone on the ground, inviting the young chimpanzee to practice. Facilitation involves rewarding successful attempts with better hammers or more nuts. Teaching is the demonstration of the proper techniques when the juvenile is struggling and is the rarest form of instruction (Boesch and Boesch-Achermann 2000).

Taï chimpanzees crack five species of nut: *Panda oleosa, Pannan exceha, Sacoglottis gabonensis, Coula edulis,* and *Detanum senegalense* (Boesch and Boesch 1982). The type of nut is significantly related to the material used for an anvil; heavier nuts tended to be cracked on stone anvils (Boesch and Boesch 1982). However, distance was an important consideration, and all nuts were cracked on stone anvils if they were nearby, although wood is much more common in the forest than stone. A significant relationship also exists between nuts and material used for hammers; heavier hammers were preferred when cracking harder nuts. Finally, transfer is also related to the type of nut being cracked. Chimpanzees transfer heavier stones when cracking panda nuts. Pounders are tools chosen based on the type of nut being cracked (Boesch and Boesch 1982). Stones are rare in the forest but used far more often than would be expected by chance. Stones are optimal for hard nuts, but less so for softer ones.

There some interesting differences between populations in regards to nut-cracking. For example, Bossou chimpanzees show 100% hand preference when cracking nuts (Matsuzawa 2011c). This appears to be developmental as when chimpanzees first learn to crack nuts they show no hand preference. This preference does not appear to be genetic, though siblings tend to share hand preference (Matsuzawa 2009). Sex differences are also apparent in some communities. In Taï, for example, cracking nuts in trees or cracking open *Panda* nuts are almost exclusively performed by females (Boesch and Boesch-Achermann 2000). This is believed to be the case as males prefer social activities, while nut-cracking is largely a solitary activity (Boesch and Boesch-Achermann 2000). In contrast, Bossou chimpanzees show no sex difference in regards to nut-cracking (Humle 2011a).

Nut-cracking is an especially interesting behavior because it involves the tools most likely to be found in the archaeological record. Repeated use of anvils results in a distinctive pitting pattern that may be recognized in the archaeological record, as does repeated use of hammer stones (Sugiyama and Koman 1979). Mercader and colleagues (2002, 2007) confirmed these early observations and conclusively demonstrate that chimpanzee behavior leaves behind distinct assemblages. Mercader and colleagues

(2002) excavated an activity site of modern chimpanzees and found that chimpanzees leave behind a distinct record of tool-use and plant consumption. A more recent study by Mercader and colleagues (2007) further refined the application of archaeological techniques to primate studies by excavating a 4,300 year old chimpanzee site in the Taï National Park, the oldest known chimpanzee archaeological site. Their findings were consistent with their 2002 studies in that a distinctive assemblage of modified stones with starch residue matching that left by current chimpanzee groups was found indicating that this behavior has persisted for an appreciable period of time in this area.

Until recently, nut-cracking was only believed to exist in a few West African populations (Morgan and Abwe 2006). Boesch and colleagues (1994) hypothesized that a major drought occurred 17,000 years ago separated the forests west and east of the N'Zo-Sassandra River in Cote d'Ivoire, isolating these populations. The southern part of the river was too wide for chimpanzees to cross while the area near the narrower, northern portion lacked the large number of nut producing trees found in more southerly regions. These natural barriers impeded nut-cracking chimpanzees from crossing the river into eastern parts of the forest while chimpanzees who headed east via the northern part of the river found little utility for exploiting nuts due to their reduced presence. This demonstrates how plant distribution and geography can work together to impede the spread of chimpanzee cultural traditions. However, chimpanzees (*P.t. vellerosus*) in Cameroon have recently been observed cracking nuts, challenging this hypothesis and suggesting either independent evolution or a former link to the West African forests (Morgan and Abwe 2006).

Bossou chimpanzees are the only population known to use both mobile hammer and anvil stones (Biro et al. 2003; Carvalho et al. 2008, 2009). This is also the only population known to use stone wedges as metatools to stabilize their anvils (Matsuzawa 1994). Hammers and anvils at Bossou show evidence of reuse and frequent transport (Carvalho et al. 2009). This occurs in both the outdoor laboratory and natural settings. Carvalho and colleagues (2009) examined data collected over a five year period and found that Bossou chimpanzees systematically reused certain tool composites more often than would be expected by chance. This may indicate an understanding of hammer and anvil technology as a single nut-cracker and not as separate components, and may represent chimpanzee understanding of optimality (Carvalho et al. 2009).

Boesch and colleagues (1994) outline two common approaches to determining if a behavior is cultural. One perspective is that culture must spread through social learning. The other is that a behavior can be considered cultural if differences between populations cannot be explained by ecology or genetics. Boesch (2003) also argues for the importance of shared meaning of symbolic traits as another criterion of culture. Nut-cracking is a prime example of a cultural behavior as it fulfills both criteria. In Côte d'Ivoire, nut-cracking is seen only in populations west of the N'Zo-Sassandra River, even though the ecology on different sides of the river is nearly identical and the chimpanzees are of the same sub-species (Boesch et al. 1994). It is also known that the learning of nut-cracking is a time consuming behavior and that mothers are vitally important for the development of this behavior Matsuzawa (2001, 2011a).

Chimpanzees are not the only primate to make use of percussive technology. It is a behavior also seen in capuchin monkeys in Brazil and Suriname (Boinski et al. 2000;

Visalberghi et al. 2007). Like chimpanzees, they select particular stones for certain tasks and transport stones and nuts to sites that have suitable anvils present, indicating that the cognition for planning and foresight is not limited just to the great apes. This indicates that tool using behavior may not be an innate characteristic of great apes, but instead may have evolved numerous times in different populations due to convergent evolution (Haslam et al. 2009).

Nuts are good sources of protein, thus it may be that nut-cracking allows chimpanzees to diversify their sources of protein. During the nut season, when nuts are widely available, chimpanzees in Taï spend as much time cracking nuts as eastern chimpanzees do fishing for termites (Goodall 1986).

Pestle Pounding

Bossou chimpanzees are so far the only group observed to practice pestle-pounding, a behavior that they practice habitually (Sugiyama 1994; Yamokoshi 2011). This behavior involves a chimpanzee climbing into the crown of an oil-palm tree and exposing the top of the trunk where new shoots are growing. Once the top is exposed an extracted shoot is inserted into a hole and pounded several times deepening the hole. Once the hole is suitably deep the chimpanzee sticks its arm into the hole, extracting the juice and pulpy material within (Yamakoshi 2011).

This is a multi-component behavior consisting of two distinct phases. The first, petiole-feeding, does not involve the use of tools while the second phase, pestle-pounding does (Humle and Matsuzawa 2004). Not all petiole-feeding events lead to pestle pounding; in fact, nearly half of them end without resulting in pestle-pounding (Yamakoshi 2011). The actual tool used during pestle-pounding is by far the largest used by chimpanzees with a length typically in the one-to-three meter range (Yamakoshi and Sugiyama 1995).

Extracting Tools

Extracting tools refer to any object used to aid in removing an object or substance from its substrate. Examples include the use of tools to extract insects and insect products from their nests, as well as extracting water from ponds, tree hollows or other contexts, extracting algae from the surface of ponds, and extracting marrow from bones.

Termite fishing

Jane Goodall's first observation of tool-using in Wild chimpanzees at Gombe was of a male fishing for termites (Goodall 1964). At Gombe, termites are gathered almost exclusively with tools during the main termite fishing season (Goodall 1986). Prior to the actual gathering of termites, a chimpanzee will first gather suitable material (usually a leaf stem or flexible stick) and dip it into the entrance to the termite mound. Many times, the tools need to be modified in order to make them useful for this task.

Different strategies are employed depending on whether termites are gathered during the wet or dry season. In Gombe, for instance, termites are far more aggressive during the wet season and will thus be quick to bite and cling to any invading object (Goodall 1986). During the dry season, however, termites are located deeper underground and are less aggressive, thus necessitating the use of longer tools and different techniques to bring them to the surface (Goodall 1986).

At Goualougo Triangle, Republic of Congo, chimpanzees are known to use two tools to extract termites from their nests (Sanz and Morgan 2007; Sanz et al. 2004). A stick is used to open entrances on the surface of the nest followed by the use of a fishing probe to extract the termites. Goualougo chimpanzees are thus far the only population to use serial tools to extract termites from elevated termite nests (Sanz and Morgan 2007).

Similar use of serial tools to extract termites has also been observed at the site of Ndoki Forest, Congo (Suzuki et al. 1995). Chimpanzees use a stick to make small, yet deep, holes in the exterior of the termite mounds. After perforation, a smaller fishing probe was then used for termite extraction (Suzuki et al. 1995). On occasion, chimpanzees left their perforators protruding from the mound acting as a stopper. Termites will repair destroyed parts of their mounds, and the use of stoppers may be a method to maintain access to the mound without opening up a new hole, though it is only speculation as this behavior has yet to be directly observed (Suzuki et al. 1995). At Ndoki, termite fishing was not observed to be seasonal, as similar percentages of termites were found in fecal samples analyzed during the dry and rainy seasons (Suzuki et al. 1995). Termites are more likely to be gathered from underground nests than from aboveground swarms. Seasonality affects the behavior of the termites as they are more active aboveground during the rainy season (Suzuki et al. 1995).

Chimpanzees at Ndoki also seem to show preference for particular raw materials as they use fewer raw materials than chimpanzees at other study sites, though the tools are otherwise similar in terms of size and shape (Suzuki et al. 1995). This is likely not determined by ecology as species used at other sites for tools are also available at Ndoki.

Ant dipping/fishing

Tools are also used by chimpanzees to gather ants. Like termites, many species of ants live in underground nests. There are also species that live predominantly in trees and thus require different techniques to gather. In Taï National Park, chimpanzees exploit two species of ant, *Dorylus nigricans* and *Dorylus gerstaeckeri*, both of which live in underground nests, filling the entrance with loose sand (Boesch and Boesch 1990). Chimpanzees gather ants by digging the nest entrance with their hands and inserting their arm into the larger hole, or through the use of sticks (Boesch and Boesch 1990). If sticks are used, the stick is held with one hand and inserted into the opening of the nest. Once extracted, the chimpanzee eats the ants directly off the stick (Boesch and Boesch 1990). *D. gerstaeckeri* are smaller and are extracted with tools more frequently than *D. nigricans* (Boesch and Boesch 1990).

Chimpanzees in Taï National Park and Gombe both use tools to dip for ants, but differences exist in terms of frequency of tool-use and techniques used. As mentioned previously, Taï chimpanzees eat the ants directly off the stick when they use tools to gather ants. In Gombe, however, they use their hands to scoop the ants off of the stick before ingesting them (McGrew 1974). Chimpanzees at Gombe almost always use tools to gather ants while chimpanzees at Taï National Park only use tools when extracting one species (Boesch and Boesch 1990; McGrew 1974). Chimpanzees at Goualougo Triangle have also been observed eating ants directly off of the probe as well as scooping ants into their hands before eating (Sanz and Morgan 2007).

Differences in tool length may be related to the type of insect prey being extracted. Ants are classified as either epigaeic or intermediate. Epigaeic ants create large nests, hunt in large swarms both on the ground and in vegetation, and tend to have longer legs and larger mandibles (Möbius et al. 2008; Schöning et al. 2008). Intermediate ants, however, hunt only in the leaf litter, not in vegetation, and produce less conspicuous nests (Möbius et al. 2008). The more aggressive epigaeic ants tend to be swept into the hand before the mouth, likely in an effort to avoid the more painful bites. Shorter tools and the "direct mouthing" technique are used more often on the less aggressive, intermediate species of ants (Schöning et al. 2008).

Bossou chimpanzees employ both the direct-mouthing technique as and the pull-through technique depending on which types of ants are being harvested (Humle 2011b). They also employ different strategies depending on whether the ants are harvested from nests or swarm trails. When dipping for ants at nests, the chimpanzees use either longer tools or position themselves higher off the ground (Humle 2011b). No significant differences in tool length were observed when harvesting ants at swarm trails (Schöning et al. 2008). The pull-through method was also used more often on the more aggressive ants than on less aggressive ants (Humle 2011b).

Differences in ant dipping behavior are apparent between study sites. Chimpanzees at Taï do not dip epigaeic species at the nest, nor do they harvest any ants at swarm trails (Schöning et al. 2008). Bossou chimpanzees also use longer tools than Taï chimpanzees when dipping for the less aggressive intermediate ants (Schöning et al. 2008). No significant differences in availability and density of army ant nests or trails were found between Taï National Park and Bossou, suggesting that differences in the tool-using repertoires of these populations are likely cultural (Möbius et al. 2008).

These results demonstrate the role of both environment and culture on the development of a particular technology. In regards to ant dipping, the ecology between the two regions is similar in terms of availability and density, suggesting the choice of which ant to harvest is largely cultural. However, for the ants that are dipped, common trends are observable at each site. More aggressive ants tend to be harvested with larger sticks and less aggressive ones with shorter ones. Taï chimpanzees also extract ant larvae more often than do Bossou chimpanzees, further supporting a cultural explanation for ant choice (Möbius et al. 2008).

In Mahale (Tanzania), chimpanzees use tools to fish for arboreal ants (Nishida and Hiraiwa 1982; Nishida 1973). Ants from the genus *Camponotus* are the most widely spread genus of ant in Africa and demonstrate a high degree of behavioral and ecological diversity (Nishida and Hiraiwa 1982). These ants tend to construct their nests in tree trunks, dry branches and hollow stalks of grass (Nishida and Hiraiwa 1982). Tools are only used to gather ants if the openings are too small for them to fit their hand (Nishida 1973). The size of the hole dictates the type of tool that is used. For holes that are only slightly too small to use their hands they break a branch off its substrate, remove excess leaves and stems if necessary, and insert it into the hole. The smallest holes require more specific modifications and materials; chimpanzees strip the bark from twigs using their incisors before inserting the modified stick into the nest. The tool is continuously modified until it is the proper size to accomplish the task at hand (Nishida and Hiraiwa 1981).

Honey Extraction

Chimpanzees also use extractive technology to gather honey from bees' nests. In Loango National Park, Gabon, they have been observed using three- to five-element tool sets in order to access honey (Boesch et al. 2009). Tools were used sequentially in order to break open the entrance to the hive, to enlarge the opening, and to collect honey from hives in trees, as well as to open the ground, locate the honey chamber, and to scoop the honey out of the chamber (Boesch et al. 2009).

Bee species vary greatly across study sites. In Assirik, *Apis mellifera* is extremely aggressive: chasing and stinging anything that comes within 25 meters of their nest. They are slightly less aggressive at Gombe; stinging only those chimpanzees that attempt to access their hives. At Lopé, Gabon, they are fairly docile; attacking only in self-defense (Tutin et al. 1995).

Algae Scooping

Similar to insect fishing, a chimpanzee finds a stick or stem, modifies its length, and removes excess leaves. The tool is then placed in the water and used to scoop algae off the surface (Humle 2011a). The chimpanzee either consumes the algae by licking the length of the tool or removes the algae using its hand and then licking its hand (Humle 2011a). Both of these techniques are similar to those seen in ant-dipping, indicating a possible shared origin between these two behaviors.

Water extraction

Chimpanzees from nearly every long term study site have been observed using leaves as water sponges to either collect drinking water or to clean their bodies (Boesch and Boesch 1990; Goodall 1986; Nishida 1990; Reynolds 2005; Sanz and Morgan 2007; Sousa 2011; Watts 2008). This behavior involves crumpling up leaves and inserting them into a water source that cannot be drunk directly. The sponge is then removed from the source and the water is squeezed into the mouth (Goodall 1986). On occasion, chimpanzees have been seen to use a stick to push the sponge into a deep hollow that they would not be able to reach with just the sponge (Sugiyama 1997; Whiten et al. 2011).

Marrow extraction

Chimpanzees in Taï National Park have been regularly observed eating marrow from the long bones of monkeys (Boesch and Boesch 1990). The ends of the bone are first bitten off before a small stick is used to extract the marrow. They are the only group observed thus far enacting this behavior.

Probing Tools

Probing tools involve tools used primarily for investigation. Chimpanzees from Taï National Park, for example, make extensive use of grubs and honey. In order to gather these resources, however, they need to first infiltrate bees' nests. A probe is first inserted into the entrance of the nest to gauge the presence of adult bees. If present, adult bees will swarm and block the entrance with their stingers facing outwards. The chimpanzee then uses the probe to smash the bees and then quickly eats them. After the adult bees are eaten or disabled, the chimpanzee then cracks open the branch where the nest is located and eats the larvae and honey (Boesch and Boesch 1990).

Investigation

Investigative tools are those that are used to gather more information about an individual's surrounding. During termite probing for example, a chimpanzee will insert a blade of grass into the opening of the nest, remove it, and smell the end (Goodall 1986). After smelling it the chimpanzee will either enlarge the opening for fishing, or move on to another one, indicating that this is likely done to assess the productivity of the particular nest (Goodall 1986). A similar behavior is performed on holes in trees and dead wood, probably to determine the presence of insect larvae (Goodall 1986). Probes are often used to touch objects that chimpanzees are afraid to touch with their bare hands, such as a leopard or snake carcass (Goodall 1986).

At Bossou, chimpanzees have been observed using a stick to hook a branch and move it closer to enable climbing (Sugiyama and Koman 1979). The hook is manufactured by taking a stick and removing the thorn bark and extraneous side-branches. The tool is then used in an attempt to bring the branch closer, and the chimpanzee may create numerous tools in order to find one that is sufficient for the task at hand.

Cleaning Tools

Cleaning tools involve the use of objects, typically leaves, to clean substances off an individual’s body. Insects and parasites are sometimes placed on leaves and squashed during bouts of grooming at some sites.

Body Care

In addition to gathering food, tools are also used for personal grooming. In Gombe, chimpanzees use leaves to wipe debris and liquids off their bodies, dab bleeding wounds, and dry themselves after it rains (Goodall 1986). Chimpanzees have also been known to wipe themselves after contacting strangers, possibly suggestive of social class (Goodall 1986). A chimpanzee from Mahale was once observed using a blade of grass or small twig to stimulate sneezing during a bout of illness in order to clear his nasal passages (Nishida and Nakamura 1993). Similarly, a chimpanzee at Gombe was once observed using a stick as a toothpick (Goodall 1986).

Social/Displaying Tools

Objects incorporated during displays or social activities are grouped into this category. Chimpanzees often incorporate objects such as branches or stones into their aggressive displays. Juveniles use objects such as sticks and leaves during play sessions and sometimes carry around stick "dolls" as toys (Goodall 1986).

Aggression

During aggressive displays chimpanzees sometimes drag, wave, or hurl branches to increase their effectiveness. Rocks may also be rolled or thrown at the target of the display (Goodall 1986). Tools can also be used to inflict physical harm on a target. Victims can be whipped with a branch or sapling as well as clubbed by a stout stick (Goodall 1986). Objects, such as stones and branches are also thrown at targets (Goodall 1986; Sugiyama and Koman 1979). This behavior is seen in males more than females. The frequency of this behavior is increased if feeding competition increases (i.e. more chimpanzees feeding in a patch than resources would allow) (Goodall 1986). Throwing is also observed during play (Sugiyama and Koman 1979). A low-ranking male at Gombe, Mike, made extensive use of empty kerosene containers in his displays, allowing him to quickly move up the social hierarchy and become the alpha male (Goodall 1986).

Play

Chimpanzees often use tools prior to, or during play sessions. Infants and juveniles spend a lot of time observing tool use by their mothers and other older members of the community, and attempt to copy them (Myowa-Yamakoshi and Yamakoshi 2011). Oftentimes juveniles will manipulate tools in novel ways because they do not yet know how to properly use them (Myowa-Yamakoshi and Yamakoshi 2011). Play behaviors may provide opportunities for young chimpanzees to learn how to use tools in a safe manner (Myowa-Yamakoshi and Yamakoshi 2011).

Solitary play is the use of an object by a lone chimpanzee. This can involve both detached and attached objects (Myowa-Yamakoshi and Yamakoshi 2011). The most common types of material used during this kind of play are branches, vegetation bundles, and vines (Myowa-Yamakoshi and Yamakoshi 2011). Different materials are used more often by different age groups and the use of detached objects increases significantly in individuals older than five years (Myowa-Yamakoshi and Yamakoshi 2011). An example of this would be self-tickling, a form of solitary play in which a juvenile or adolescent chimpanzee uses a stone or stick to tickle themselves (Goodall 1986).

Hunting Tools

Chimpanzee groups in the mixed-savanna environments of Fongoli, Senegal, are known to sharpen sticks into hunting spears which they use to aid in capturing bush babies (*Galago senegalensis*) (Pruetz and Bertolani 2007). The creation of these tools is a multi-step process. It is also a flexible one in which one or more steps can be omitted or repeated depending on the context. While many populations have been observed using sticks and other similar objects to investigate the environment, this is the first recorded case of chimpanzees using objects with the intent of injuring and capturing prey. While hunting is typically a male oriented activity at other sites such as Taï National Park and

Gombe (Boesch and Boesch-Achermann 2000; Goodall 1986), juveniles and females were observed hunting with spears far more often than males.

Fongoli chimpanzees also participate in much less meat sharing than do other groups, which may have prompted females and juveniles, groups not normally associated with hunting, to hunt their own meat (Pruetz and Bertolani 2007). While males in the group who coordinate and hunt green monkeys (*Chlorocebus aethiops*) often share the meat, females and juveniles who hunt bush babies typically do not. The authors attribute this to the fact that the prey is small and rarely requires collaboration to catch. Regardless, savanna dwelling chimpanzees are especially important to our understanding of hominid behaviors due to the similar environments and likely similar resources that extinct hominids and modern chimpanzees had available.

Other Contexts

Leaves are commonly used as tools in various contexts. For example, a chimpanzee at Gombe was observed picking up some leaves, holding them in its hand, and defecating on them (Goodall 1986). Leaves are also known to be used as protection from insects while feeding on their nests as well as to wipe food remains from bones and fruits (Boesch and Boesch 1990; Goodall 1986).

CHAPTER 6: ENVIRONMENT, STUDY SITES, AND METHODS

Ecologists studying species richness and biodiversity typically offer two explanations to account for the distribution of species richness. One group of hypotheses is that there should be a strong correlation between species richness and climatic variables such as temperature and precipitation (Francis and Currie 2003). The other contends that species richness is more influenced by historical factors such as extinctions and migrations than by climate (Latham and Richards 1993).

In reality, both factors play important roles in influencing species richness. Wiens and Donoghue (2004) argue that ecologists and biogeographers, while both contributing much to our understanding of biodiversity, tend to focus too narrowly on their particular discipline. An increase of species richness within a particular region can occur when new species migrate into a region or through speciation. However, each environment has a carrying capacity that limits the number of different species that can coexist in a particular region (Wiens and Donoghue 2004). Dispersal is also linked to ecological processes such as the availability of food and water.

Phylogenetic niche conservatism determines which environmental conditions particular organisms can tolerate, where they can disperse, and the various factors that constrain dispersion (Wiens and Donoghue 2004). Niche evolution is what enables an organism to spread to new habitats or climatic zones. Specifically, niche evolution should enable an organism to migrate to a region which would have previously deterred that organism from dispersing to that particular region based on changes in the organism's niche or biology.

The tropical conservation hypothesis predicts high species richness in regions characterized by warmer temperatures and abundant rainfall (Francis and Currie 2003). Francis and Currie (2003) sought to determine whether species richness of angiosperms was related to climate in a consistent manner throughout the globe. They found that in regions where water deficit is low, richness increases strongly with temperature (Francis and Currie 2003). Richness is best understood by examining it in relation to both water availability and temperature. Both variables have a strong combined influence on species richness and neither should be examined in isolation (Francis and Currie 2003).

Eeley and Foley (1999) examined the relationships between species richness, range size and specialization in African primates. Generalists tend to be more widespread than specialists, which is not surprising considering specialists are adapted to specific ecological niches and would be far less likely to survive outside of them. Catarrhine richness is concentrated primarily in equatorial regions of western Africa. Catarrhines are characterized by low average range size and narrow habitat and diet breadth (Eeley and Foley 1999). Richness was found to decrease with distance from the equator and thus is strongly correlated with latitude. Mean range size and mean dietary breadth increase significantly with latitude, as does mean habitat breadth.

Mean range size, habitat breadth, and dietary breadth are negatively correlated with species richness (Eeley and Foley 1999). The overall distribution of range size is right skewed; most catarrhines have small ranges and few have exceptionally large ones.

Overall, catarrhine richness is concentrated at the equator, while range size is at its lowest at the equator.

Study Sites

The following section provides a brief description of each of the study sites employed in this thesis. All climatic data was collected from the literature, with a preference given to data provided by scholars studying chimpanzees. In such cases where climatic data was not provided, research conducted by other scholars was incorporated into the study. For example, long term data for Kibale was collected over a 50 year period from the nearby town of Fort Portal, which is located 10km west of the forest (Wing and Bus 1970). Long term data was preferred, but this is not realistic as this data was simply not available. This study is also somewhat biased in terms of geographic breadth. Included in this study were three groups from western Africa (Bossou, Taï, and Assirik), five groups from eastern Africa (Budongo, Gombe, Kibale, Mahale K, and Mahale M), and only one group from central Africa (Lopé).

Assirik

Assirik is located in the southeastern portion of the Parc National du Niokolo Koba in Senegal. A small community of chimpanzees lives near Mont Assirik. The study area consists of five main vegetation types: Gallery forest, woodland, bamboo thicket, grassland and plateau (Hunt and McGrew 2002). It is the driest chimpanzee study site, receiving a mean annual rainfall of around 954 mm, with a range of 824 – 1,224mm (McGrew et al. 1981). Assirik experiences five completely dry months and a mean of 84 days of rain per year (McGrew et al. 1981). The beginning of the rainy season is very consistent; the first major rains of the wet season occur during the last week of May or first week of June (McGrew et al. 1981). Assirik also experiences more seasonal extremes than other sites with a mean maximum temperature of 35°C and a mean minimum temperature of 23°C (Hunt and McGrew 2002).

Food and water sources at Assirik are highly variable and seasonal. Streams typically dry out during the December – May dry season. During the wet season from June to November, water courses flow down the slopes of Mont Assirik, creating an important water source (Hunt and McGrew 2002). The only major permanent water source, the Gambia River, is located 20km away from Assirik at its closest point (Hunt and McGrew 2002). Due to the extreme dryness of the region, Assirik chimpanzees spend most of their time in the gallery forests which are only a small portion of the habitat (Hunt and McGrew 2002). However, they do spend more time in more open areas during the rainy season (Hunt and McGrew 2002). Assirik chimpanzees are also sympatric with more potential predators, including lions, leopards, hyenas and African hunting dog, than chimpanzees from any other study site (Hunt and McGrew 2002).

Assirik chimpanzees live with more potential predators than chimpanzees at other study sites (Hunt and McGrew 2002). They also tend to have larger mixed parties and nest in larger groups than other chimpanzee communities, possibly as a result of increased predation pressure. Assirik chimpanzees also have the largest home range size, which may be a result of the relative scarcity and high seasonality of preferred food patches (Hunt and McGrew 2002). Finally, Assirik chimpanzees spend far less time hunting than chimpanzees in other regions.

Assirik chimpanzees have the smallest tool-using repertoire after Lopé. They have a total of nine tools, of which four are used in the feeding context. A complete breakdown of Assirik chimpanzee tool use is presented in Table 1.

Table 1: Tool-using behaviors at Assirik

Behavior	Frequency	Category	Feeding?	Manufacture?
Branch shake	Habitual	Display	No	No
Ant dip wipe	Habitual	Extract	Yes	No
Fluid dip	Habitual	Extract	Yes	No
Ant fish	Habitual	Extract	Yes	Yes
Termite fish-leaf mid-rib	Habitual	Extract	Yes	Yes
Termite fish-non leaf	Habitual	Extract	Yes	Yes
Play start*	Present	Display	No	Yes
Aimed throw*	Present	Display	No	Yes
Leaf napkin*	Present	Clean	No	Yes

*Only observed once

Bossou

The site of Bossou is located in the Republic of Guinea on the west coast of Africa. It is one of six long term chimpanzee study sites in Africa and one of only two in West Africa. This community is unique because of its close proximity to human settlement. The village of Bossou is home to around 2,500 people (Humle 2011c). A small community of 13 chimpanzees lives in the forests outside the village. The Bossou chimpanzees have a unique relationship with the people of the village and often share the same resources with little to no conflict (Humle 2011c). Many Manon people hold the belief that chimpanzees are the reincarnation of their ancestors and are their families' totem animal (Humle 2011a).

The climate is divided into two seasons: a dry season from November to February and a wet season from March to October. The most rain tends to fall from July to

September with the least amount of rain occurring from January to February (Humle 2011c). Monthly precipitation ranges from 0 mm in the dry season to over more than 700 mm in the wet season. Bossou is one of the wettest chimpanzee sites, receiving an average of 2,272mm of rainfall per year (Matsuzawa et al. 2011). Temperature ranges from as low as 12°C to as high as 43°C in the dry season. Daily fluctuations in temperature are less common during the rainy season as are extremely hot or cold temperatures (Humle 2011c).

Bossou chimpanzees spend most of their time within a core area of around 6 km^2 in the hills surrounding the community (Humle 2011c). The Bossou chimpanzees have been habituated without provisioning since 1976 and were first studied in 1942 (Humle 2011c).

Bossou chimpanzees are well known for using stone hammer and anvil technology to crack open oil-palm nuts (*Elaeis guineensis*). The most common behaviors observed at Bossou in addition to nut-cracking are ant-dipping and algae scooping (Humle 2011a). In all, 24 different tool-using behaviors have been observed at Bossou, of which 71% are related to subsistence, 13% related to defense and 4% related to communication, exploration and comfort (Humle 2011a). Half of the tools used in the feeding context are used to enable access to insects or insect products (Humle 2011a). Fourteen of the 24 observed behaviors are customary or habitual. Sixty-five percent of these customary behaviors are performed in the feeding context and 21% are related to communication, exploration and comfort (Humle 2011a). However, one third of the observed behaviors in this group have been seen only once, possibly because they did not diffuse to other members of the community (Humle 2011a).

Only one observed behavior appears to be biased towards one sex. Males have been observed algae scooping more than females. Age differences do appear in this community. With the exception of nut-cracking, juveniles use more tools than do adults (Humle 2011a)

Bossou chimpanzees have also been seen employing five different tool composites, one of which (the use of a stone hammer and anvil to crack nuts) is customary (Humle 2011a). Use of non-customary composites include that of digging sticks and dipping wands to extract diver ants, the use of a leaf tool and stick to collect water from tree hollows, the use of pestle-pounding and fiber sponge to collect palm hearts and sap, and finally the use of a stone hammer, anvil and wedge to crack open nuts (Humle 2011a).

All chimpanzee populations have their own suite of cultural behaviors that differentiate them from other communities (see Whiten et al. 1999, 2001). In Bossou, eight tool-using behaviors appear only in this community: branch-haul, gum-collect, digging tool, push-pull, pestle pound, anvil-prop, leaf-fold, and algae scoop (Humle 2011a). The Bossou chimpanzees have one of the richest tool kits when compared to those from the other long term study sites. Bossou chimpanzees have a higher percentage of behaviors related to subsistence, more unique customary complex behaviors, and no tools used for grooming (Humle 2011a). Bossou is also unique because, as mentioned previously, there is no sex difference in tool-using frequency. Taï National Park chimpanzees, for example, show a marked female bias in terms in nut-cracking (Boesch and Boesch-Achermann 2000). Table 2 provides a complete breakdown of tool-using behaviors at Bossou.

Table 2: Tool-using behaviors at Bossou

Behavior	Frequency	Category	Feeding?	Manufacture?
Drag branch	Habitual	Display	No	No
Investigatory probe	Habitual	Probe	No	No
Anvil prop	Habitual	Misc	Yes	No
Shrub bend	Habitual	Display	No	No
Branch shake	Customary	Display	No	No
Leaf sponge	Customary	Extract	Yes	Yes
Algae scoop	Customary	Extract	Yes	Yes
Pestle pound	Customary	Pound	Yes	Yes
Nut hammer (stone hammer/stone anvil)	Customary	Pound	Yes	No
Ant dip single	Customary	Extract	Yes	Yes
Aimed throw	Customary	Display	No	No
Leaf-clip - mouth	Customary	Display	No	Yes
Branch slap	Customary	Display	No	No
Play start	Present	Display	No	No
Sponge push pull	Present	Extract	Yes	Yes
Dig	Present	Extract	Yes	No
Insect pound	Present	Pound	Yes	Yes
Resin pound	Present	Pound	Yes	Yes
Branch hook	Present	Probe	No	Yes
Nut hammer (Stone hammer/wood anvil)	Present	Pound	Yes	No
Seat-vegetation	Present	Clean	No	No
Club	Present	Display	No	No
Ant dip wipe	Present	Extract	Yes	Yes
Ant fish	Present	Extract	Yes	Yes
Termite fish-leaf mid-rib	Present	Extract	Yes	Yes
Leaf strip	Present	Display	No	Yes

Budongo Forest

Budongo Forest is a 435 km^2 forest located in western Uganda on the Albertine Rift and home to 584 chimpanzees (Plumptre et al. 2003; Reynolds 2005). The Sonso community consists of 59 individuals as of 2003 (Reynolds 2005). It is located at medium altitude, around 1100 m above sea level on average (Reynolds 2005). Rainfall is abundant, ranging from 1,240 mm to 2,187 mm per year with an average yearly rainfall of 1,600 mm (Reynolds 2005). There are two dry seasons between mid-December and mid-February, and between June and July, where rainfall is typically less than 50 mm per month (Reynolds 2005). Temperature is fairly stable throughout the year. Monthly maximum and minimum temperatures typically range from 19°C to 32°C (Reynolds 2005).

The first study of the chimpanzees of Budongo Forest took place in 1962 and was conducted by Vernon and Frankie Reynolds (Reynolds and Reynolds 1965). Research was then interrupted for 25 years because of political unrest. Habituation began in 1990 and took five years of daily observation for the chimpanzees to become habituated enough to allow a census to be taken (Reynolds 2005). Like at Taï, Budongo chimpanzees were not provisioned during the habituation process (Reynolds 2005).

Budongo Forest is especially rich in fruiting trees due to the prevalence of mixed-forest, which makes around 50% of the forest (Reynolds 2005). In total, Budongo chimpanzees have been observed eating 103 different species of plant (Reynolds 2005: Appendix B). Diet is also supplemented with meat, insects, and honey (Reynolds 2005). A total of 16 tool-using behaviors are present at Budongo, of which only one is used to gather food (fluid-dip for honey). A complete breakdown is illustrated in Table 3.

Table 3: Tool-using behaviors at Budongo

Behavior	Frequency	Category	Feeding?	Manufacture?
Play start	Habitual	Display	No	No
Drag branch	Habitual	Display	No	No
Rain dance	Habitual	Display	No	No
Fly whisk	Habitual	Misc.	No	No
Branch shake	Customary	Display	No	No
Leaf sponge	Customary	Extract	No	Yes
Leaf clip - fingers	Customary	Display	No	Yes
Leaf clip - mouth	Customary	Display	No	Yes
Branch slap	Customary	Display	No	No
Shrub bend	Customary	Display	No	No
Leaf napkin	Customary	Clean	No	No
Leaf inspect	Customary	Clean	No	No
Comb	Present	Clean	No	No
Aimed throw	Present	Display	No	No
Leaf groom	Present	Display	No	No
Fluid dip	Present	Extract	Yes	Yes

Gombe

Gombe Stream National Park, located on the eastern shore of Lake Taganyika is the home of the longest ongoing chimpanzee research project; it has been continuously studied since 1960, though studies were briefly halted in 1975 when four researchers were kidnapped by rebels from eastern Zaire (Goodall 1986). Gombe is home to around 160 chimpanzees (*P.t. schweinfurthii*). It is a mixed-forest/savanna woodland environment (Goodall 1986). There are two main seasons: a rainy season extending from mid-October to mid-May with the heaviest rain fall occurring between December and March, and a dry season which spans the rest of the year (Goodall 1986). Temperatures are fairly stable at Gombe: average maximum temperature during the dry season ranges from 27° C to 30 C° and from 25°C to 26.5°C during the wet season (Goodall 1986). August and September are the hottest time of the year with maximum daily temperatures typically hovering around 30°C (Goodall 1986). Minimum daily temperatures are consistently between 18.5°C and 21°C through the year (Goodall 1986).

The chimpanzees at Gombe were habituated through the process of provisioning. Bananas were left out in a designated area in order to encourage chimpanzees to come to the camp so researchers could closely observe their behavior (Goodall 1986). However, provisioning began to have a negative impact on the behavior of the community as ranging and feeding patterns began to be noticeably altered. This led to a change in the provisioning process; chimpanzees were given fewer bananas, given bananas less often, and given bananas only when they were alone, resulting in less aggression and fewer visits by chimpanzees (Goodall 1986).

The chimpanzees at Gombe have the largest tool-kit of any chimpanzee group studied thus far. A total of 28 behaviors have been observed, of which 14 are customary. Data is summarized in Table 4.

Table 4: Tool-using behaviors at Gombe

Behavior	Frequency	Category	Feeding?	Manufacture?
Club	Habitual	Pound	No	No
Self-tickle	Habitual	Misc.	No	No
Leaf squash	Habitual	Clean	No	No
Leaf strip	Habitual	Display	No	Yes
Branch shake	Customary	Display	No	No
Play start	Customary	Display	No	No
Drag Branch	Customary	Display	No	No
Leaf sponge	Customary	Extract	No	Yes
Investigatory probe	Customary	Probe	No	No
Aimed throw	Customary	Display	No	No
Ant dip wipe	Customary	Extract	Yes	Yes
Fluid dip	Customary	Extract	No	Yes
Lever open	Customary	Extract	No	No
Expel stir	Customary	Extract	No	Yes
Leaf groom	Customary	Display	No	Yes
Rain dance	Customary	Display	No	No
Termite fish-non leaf	Customary	Extract	Yes	Yes
Leaf napkin	Customary	Clean	No	No
Sponge push pull	Present	Extract	No	Yes
Leaf wipe	Present	Extract	No	No
Leaf brush	Present	Misc.	No	No
Container	Present	Misc.	No	No
Leaf mop	Present	Extract	No	No
Ant dip single	Present	Extract	Yes	Yes
Ant fish	Present	Extract	Yes	Yes
Leaf dab	Present	Clean	No	No
Fly whisk	Present	Misc.	No	No
Leaf inspect	Present	Clean	No	No

Kibale

Kibale National Park is located just east of the Ruwenzon Mountains in western Uganda and is characterized by a mix of mature lowland and evergreen forest, swamp, grasslands and secondary forests (Chapman et al. 1999; Watts 2008). The Kanyawara region receives on average about 1,700 mm of rain per year. Mean daily minimum is

15.5°C and the mean daily maximum is 23.7°C based on readings taken between 1990 and 1996 (Chapman et al. 1999). The Ngogo region of the forest has a mean annual rainfall of approximately 1,500mm. Mean daily minimum temperature is 16.7°C and the mean daily maximum is 24.2° C (Chapman et al. 1999). The site has been continuously studied since 1995 (Watts 2008).

The Ngogo community in Kibale Forest, western Uganda is the largest known chimpanzee community, numbering between 140 and 150 individuals (Watts 2008). Unlike most other chimpanzee communities, tools used in the foraging context make up the smallest portion of the Ngogo community's tool kit. In all, 16 different tool using behaviors were performed with nine different tools (Watts 2008). Tools were most often used in a grooming or hygienic context in Ngogo; 276 (47.75%) of the 578 observed cases of tool use involved the use of a leaf napkin to clean the user's body (Watts 2008b).

The Kanyawara community, which is included in the present study, employs 15 different tool-using behaviors, none of which are used to obtain food. Tools for displaying make up the largest percentage of their repertoire, (9/15 or 60%). Table 5 provides a breakdown of the tool-use of Kanyawara chimpanzees.

Table 5: Tool-using behaviors at Kibale

Behavior	Frequency	Category	Feeding?	Manufacture?
Branch shake	Habitual	Display	No	No
Drag Branch	Habitual	Display	No	No
Fluid dip	Habitual	Extract	No	Yes
Leaf clip - fingers	Habitual	Display	No	Yes
Leaf clip - mouth	Habitual	Display	No	Yes
Leaf strip	Habitual	Display	No	Yes
Play start	Customary	Display	No	No
Leaf sponge	Customary	Extract	No	Yes
Leaf groom	Customary	Display	No	Yes
Rain dance	Customary	Display	No	No
Leaf napkin	Customary	Clean	No	No
Leaf dab	Customary	Clean	No	No
Investigatory probe	Present	Probe	No	No
Aimed throw	Present	Display	No	No
Seat-vegetation	Present	Clean	No	No

Lopé

Lopé Reserve is located in Central Gabon. It consists predominantly of semi-deciduous forest with smaller areas of savanna and gallery forest north and west of the study site (Tutin et al. 1995). Mean annual rainfall is approximately 1,511mm, with a distinct dry season that lasts from mid-June to mid-September (Tutin et al. 1995). Mean monthly minimum temperatures range from 20.1 – 23.2°C and mean monthly maximum temperatures range from 27-32.8°C (Tutin et al. 1995).

Studies have been carried out at Lopé since 1983. Lopé is an especially interesting site because it is one of the few where chimpanzees and gorillas are sympatric. The gorillas at Lopé are partially habituated, while the chimpanzees are only poorly habituated. The chimpanzees are very shy and thus direct observations of their behavior are limited compared to other sites that have been studied for a comparable period of time

(Tutin et al. 1995). Only six tool-use behaviors were observed at Lopé, likely due to the community's lack of habituation. Of these six behaviors, two are performed in the feeding context. A complete breakdown of tool-use at Lopé is illustrated in Table 6.

Table 6: Tool-using behaviors at Lopé

Behavior	Frequency	Category	Feeding?	Manufacture?
Branch shake	Habitual	Display	No	No
Play start	Habitual	Display	No	No
Drag Branch	Habitual	Display	No	No
Fluid dip	Customary	Extract	No	No
Lever open	Customary	Extract	Yes	No
Ant fish	Customary	Extract	Yes	Yes
Leaf sponge*	Present	Extract	No	Yes

*observed only once; modifications not mentioned.

Mahale Mountains

Mahale Mountains National Park is located on the eastern shore of Lake Taganyika in western Tanzania. The first scientific studies on the chimpanzees commenced in 1965 by a team lead by Junichiro Itani, The habituation process began the same year (Nishida 1990). Like at Gombe, habituation of chimpanzees was attempted through provisioning. A sugarcane plantation was planted at the foot of the mountains by Nishida and people from the village of Kasoje in order to attract chimpanzees to the area for study (Nishida 1990).

The Mahale Mountains Chimpanzee Research Project began in 1975 with funding by the Japan International Cooperation Agency (Nishida 1990). The main goal of this project was the conservation of Mahale chimpanzees. The Tanzanian government established the Kasoje Chimpanzee Research Station the same year and worked together with Japanese researchers on studying the chimpanzees. Mahale Mountains National

Park officially opened in 1985. An unfortunate side-effect of this was the displacement of the local residents of the site, who were transferred to nearby villages in 1974 (Nishida 1978).

The most prominent features of Mahale are the large mountain peaks that dominate the landscape. The tallest peak in the park, Mt. Nkungwe, stands 2,460 m above sea level (Nishida 1990). The park is characterized as a mixed-woodland environment, containing a mixture of gallery forests, open savanna, and drier woodland (Nishida 1990). Mahale is the most isolated chimpanzee study site, and is accessible by researchers only by boat, and once there researchers must travel by foot, as there is no access for motor vehicles at the site (Nishida 2012). Mahale is especially notable for its large population of chimpanzees, estimated to be 30% of the total population of chimpanzees in Tanzania (Kano 1972).

Mahale is home to at least six communities of chimpanzees (Nishida 1968), the longest studied and most well-known groups are the K and M groups, named after the Kansyana and Myako camps respectively (Nishida 1990). K group was habituated in 1966 and M group fully habituated by 1968. Provisioning was reduced by 1975 due to its influence on the overall ranging and feeding behavior of chimpanzees. In general, chimpanzees at Mahale were provisioned far less than those at Gombe, and provisioning was completely abandoned in 1987 (Nishida 1990).

Records from Kansyana Camp recorded between 1975-1978 show an average rainfall of 1,878mm of rain per year with an average minimum temperature of 18.31°C and an average maximum temperature of 28.98°C (Nishida 1990). Myako receives slightly less rain per year, experiencing a mean annual rainfall of 1653.23mm based on data collected between 1977 and 1984. Mean minimum temperature is around 21°C while the mean maximum temperature is around 29.03°C (Nishida 1990). K and M group employ 14 and 20 types of tool-using behaviors, respectively (Tables 7 and 8). K group uses tools during feeding far more than M group and both groups modify similar numbers of tools.

Table 7: Tool-using behaviors at Mahale K

Behavior	Frequency	Category	Feeding?	Manufacture?
Investigatory probe	Habitual	Probe	No	No
Fluid dip	Habitual	Extract	No	Yes
Expel stir	Habitual	Extract	Yes	Yes
Branch shake	Customary	Display	No	No
Play start	Customary	Display	No	No
Drag Branch	Customary	Display	No	No
Leaf clip - mouth	Customary	Display	No	Yes
Leaf groom	Customary	Display	No	Yes
Ant fish	Customary	Extract	Yes	Yes
Rain dance	Customary	Display	No	No
Termite fish-leaf mid-rib	Customary	Extract	Yes	Yes
Termite fish-non leaf	Customary	Extract	Yes	Yes
Leaf mop	Present	Extract	Yes	No
Bee probe	Present	Probe	Yes	Yes

Table 8: Tool-using behaviors at Mahale M

Behavior	Frequency	Category	Feeding?	Manufacture?
Investigatory probe	Habitual	Probe	No	No
Fluid dip	Habitual	Extract	No	Yes
Expel stir	Habitual	Extract	Yes	Yes
Branch shake	Customary	Display	No	No
Play start	Customary	Display	No	No
Drag Branch	Customary	Display	No	No
Aimed throw	Customary	Display	No	No
Leaf clip - mouth	Customary	Display	No	Yes
Leaf groom	Customary	Display	No	Yes
Ant fish	Customary	Display	Yes	Yes
Shrub bend	Customary	Display	No	No
Rain dance	Customary	Display	No	No
Leaf sponge	Present	Extract	No	Yes
Sponge push pull	Present	Extract	No	Yes
Nasal probe	Present	Probe	No	No
Club	Present	Pound	No	No
Leaf clip - fingers	Present	Display	No	Yes
Branch slap	Present	Display	No	No
Leaf napkin	Present	Clean	No	No
Leaf strip	Present	Display	No	Yes

Taï National Park

Taï National Park is located in southwestern Cote d'Ivoire and the largest remnant of tropical rainforest in West Africa (435,000 hectares) (Boesch and Boesch-Achermann 2000). Taï and other tropical rainforests are characterized by heavy rainfall throughout the year. At Taï, the heaviest rainfall is experienced from March-July and September to December, with an annual rainfall of around 1800mm (Boesch and Boesch-Achermann 2000). However, the amount of rainfall has seen a steady decline over the past 40 years. The forest belt has fluctuated over the past million years and more recently has had to cope with increasing deforestation and increasing numbers of people settling in the region. The dry seasons range from July to August and from November to March (Anderson et al. 2005). As a whole, this region of Africa has experienced a marked decrease in total precipitation over the last 50 years and is trending towards increased seasonality (Boesch and Boesch-Achermann 2000).

Studies at Taï National Park, Cote d'Ivoire, challenged many early assumptions about chimpanzees living in rainforest habitats. Telaki (1975) stated that chimps in the forest did not hunt, but studies at Taï clearly show that this is false; there they hunt often and cooperatively. While most chimpanzee studies have focused on Mahale and Gombe, both mixed-woodland sites in Tanzania, most chimpanzees live in tropical forest environments (Boesch and Boesch-Achermann 2000). The Taï National Park research project is also noteworthy because researchers did not provision the chimpanzees with food as at other sites, in order to habituate them to human presence.

As of the publication of Boesch and Boesch-Achermann (2000), there were 123 identified individuals at Taï National Park with 77 females and 46 males. Like all known chimpanzee groups they live in a flexible social system known as a fission-fusion society. Fission-fusion societies in chimpanzees consist of a main social group containing all members of a particular community and smaller foraging groups which break apart from, or fission from, the main social group and later return. Chimpanzee communities are multi-male and multi-female groups, with females typically leaving their natal group once they reach sexual maturity.

This community is well-known for their large, cooperative hunts, and nut-cracking behavior. They have the second largest tool repertoire (tied with Bossou) and have a larger number of customary behaviors. Table 9 illustrates the extent of their tool-kit.

Table 9: Tool-using behaviors at Taï National Park

Behavior	Frequency	Category	Feeding?	Manufacture?
Nut hammer (other)	Habitual	Pound	Yes	No
Lever open	Habitual	Extract	Yes	No
Play start	Habitual	Display	No	No
Seat-vegetation	Habitual	Clean	No	No
Club	Habitual	Pound	No	No
Leaf clip - fingers	Habitual	Display	No	Yes
Rain dance	Habitual	Display	No	No
Fly whisk	Habitual	Misc	No	No
Nut hammer (stone hammer/stone anvil)	Customary	Pound	Yes	No
Ant dip single	Customary	Extract	Yes	Yes
Bee probe	Customary	Probe	Yes	Yes
Nut hammer (Stone hammer/wood anvil)	Customary	Pound	Yes	No
Nut hammer (Wood hammer/wood anvil)	Customary	Pound	Yes	No
Nut hammer (Wood hammer/stone anvil)	Customary	Pound	Yes	No
Marrow pick	Customary	Extract	Yes	Yes
Fluid dip	Customary	Extract	Yes	Yes
Expel stir	Customary	Extract	Yes	No
Branch shake	Customary	Display	No	No
Drag Branch	Customary	Display	No	No
Leaf sponge	Customary	Extract	No	Yes
Investigatory probe	Customary	Probe	No	No
Aimed throw	Customary	Display	No	No
Leaf clip - mouth	Customary	Display	No	Yes
Branch slap	Customary	Display	No	No
Sponge push pull	Present	Extract	Yes	Yes
Leaf wipe	Present	Extract	Yes	No

Methods

Tool-using behaviors were first separated from all candidate cultural behaviors described by Whiten and colleagues (2001). A total of 55 tool-using behaviors were considered for the present study (Appendix 1). The list was updated with current observations if applicable using the modes of tool-use and manufacture presented by Schumaker and colleagues (2011). Customary and habitual tool-using behaviors were the subject of environmental analysis. The numbers of habitual, customary, and present tool behaviors of each site are illustrated in Figure 1.

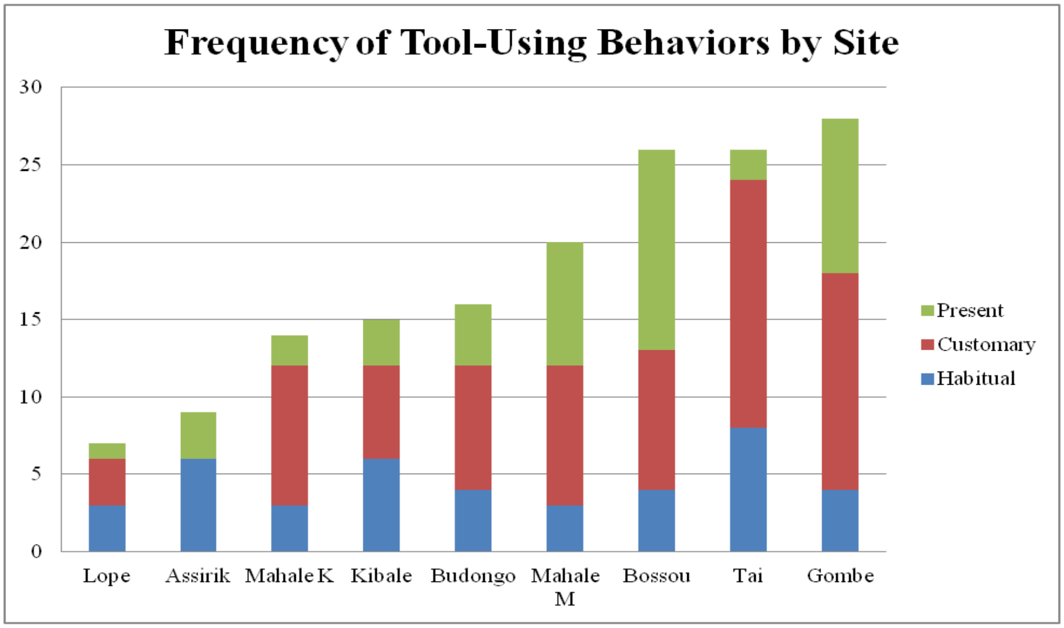

Figure 1: Frequency of Tool-Using Behaviors by Site

Each of these study sites demonstrates differential availability of resources as well as differing degrees of seasonality. Some sites, such as Assirik, are highly seasonal with marked wet and dry seasons. Other sites, such as Taï National Park and Bossou, receive a more constant supply of rain. For this study, seasonality will be measured using the average mean monthly precipitation standard deviation as well as the mean annual precipitation standard deviation. Monthly rainfall and temperature means were calculated and standard deviations between each of them will be calculated to assess climatic variability. This will allow comparisons to be made between tool use and monthly fluctuations in rainfall as well as yearly fluctuations in rainfall.

All statistics were calculated using Microsoft Excel and Graphpad InStat. A level of significance of $p<.05$ was applied to all statistics employed in this study. Primarily three types of statistical tests were carried out for this project: Pearson correlations, analysis of variance (ANOVA), and chi-square tests. The Pearson correlation "measures the degree and direction of the linear relationship between two variables" (Gravetter and Wallnau 2005:415). In other words, it measures the likelihood that a change in the independent variable will be accompanied by a change in the dependent variable. Pearson correlations were first used to determine if any correlations existed between tool-using behaviors and ecological variables. They were also used to determine if the correlations still held after removing tool-using behaviors marked as "present" at each site as these behaviors are those that have been rarely observed, sometimes only seen performed one time by a single member of a community. A drawback of using Pearson correlations, however, is they are susceptible to being heavily influenced by outliers.

ANOVA is primarily used to determine if the variability is greater within a sample or between different samples. The chi-square test for independence compares a group of variables to each other to determine if they are related.

The perhumidity index (PI) was devised by Walsh (1992) and incorporates climate diagrams, developed by Walter and Lieth (1960). These diagrams graph monthly temperature and monthly precipitation together on the same graph. The temperature scale ranges from 0-50°C and is twice that of the rainfall scale from 0-100 mm, with increments of ten (Walsh 1996, see figure 5.2). Climate diagrams classify months into three types: wet months (rainfall over 100mm), drought months (where monthly rainfall falls below the temperature scale), and dry/intermediate months (rainfall between temperature scale and 100mm) (Walsh 1996). Appendix C contains all climatic data incorporated in this study.

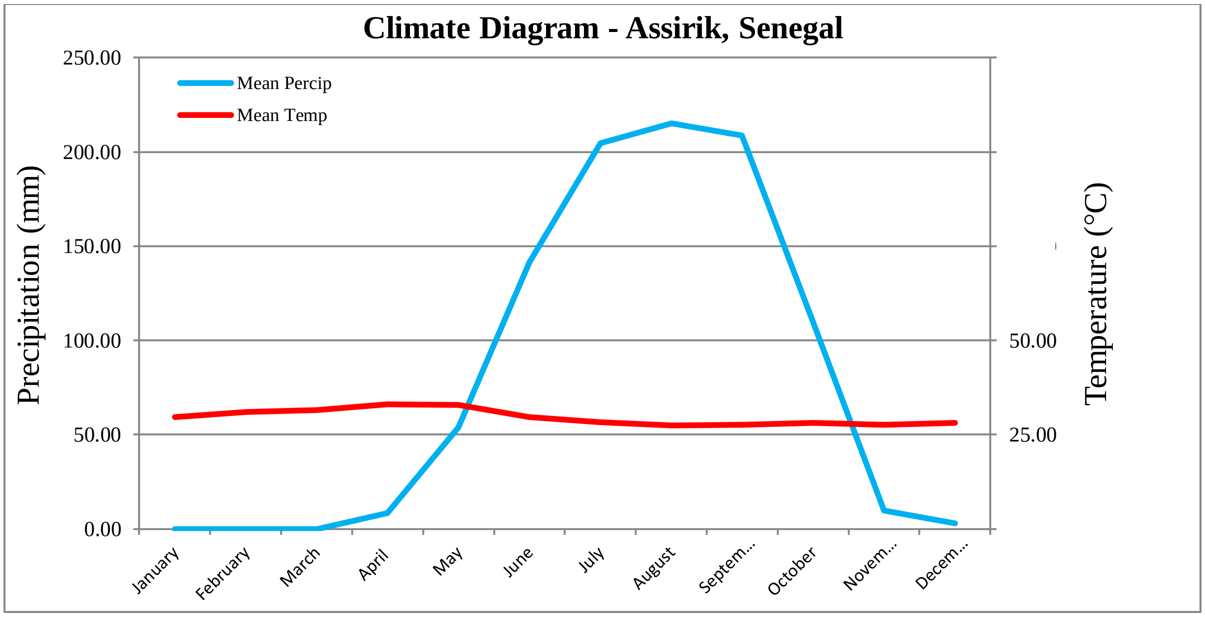

Figure 2: Example of a climate diagram. Data from the site of Assirik, Senegal

The PI is used to summarize dry and wet months into a single value by assigning weights to months based on precipitation and temperature data. Months are classified as either very wet (more than 200 mm of rainfall), wet (100-199 mm of rainfall), dry months (50-99 mm of rainfall) and drought months (typically less than 50 mm of rainfall). Each month is assigned a score based on these classifications: 2.00 for very wet months, 1.00 for wet months, -1.00 for dry months, and -2.00 for drought months. Dry months are given a value of -.50 if they follow a wet month and drought months are given a value of

-1.5 if they follow a wet month. The logic behind this is that soil water availability should still be relatively high in dryer months following a wet month (Walsh 1996). The perhumidity index is, in essence, a measure of total productivity of a particular region by accounting for total water availability and water retention. The use of averages results in slightly lower PI values than the use of actual monthly data (Walsh 1996). However, this study employs primarily monthly average data due to its greater availability. Figure 3 provides a graph of rainfall at each site, as well as providing the mean monthly temperature, number of tool-using behaviors, and perhumidity index.

Ecological diversity will be indirectly assessed through the use of perhumidity index. Diversity is strongly correlated with total moisture availability (Francis and Currie 2003), thus sites with high amounts of precipitation and low amounts of evaporation will be considered the most diverse while study sites with lower precipitation and higher amounts of evaporation will be considered less diverse. Precipitation and temperature are only one component of total productivity of a region. A higher PI score will be used to assess the overall diversity of a site.

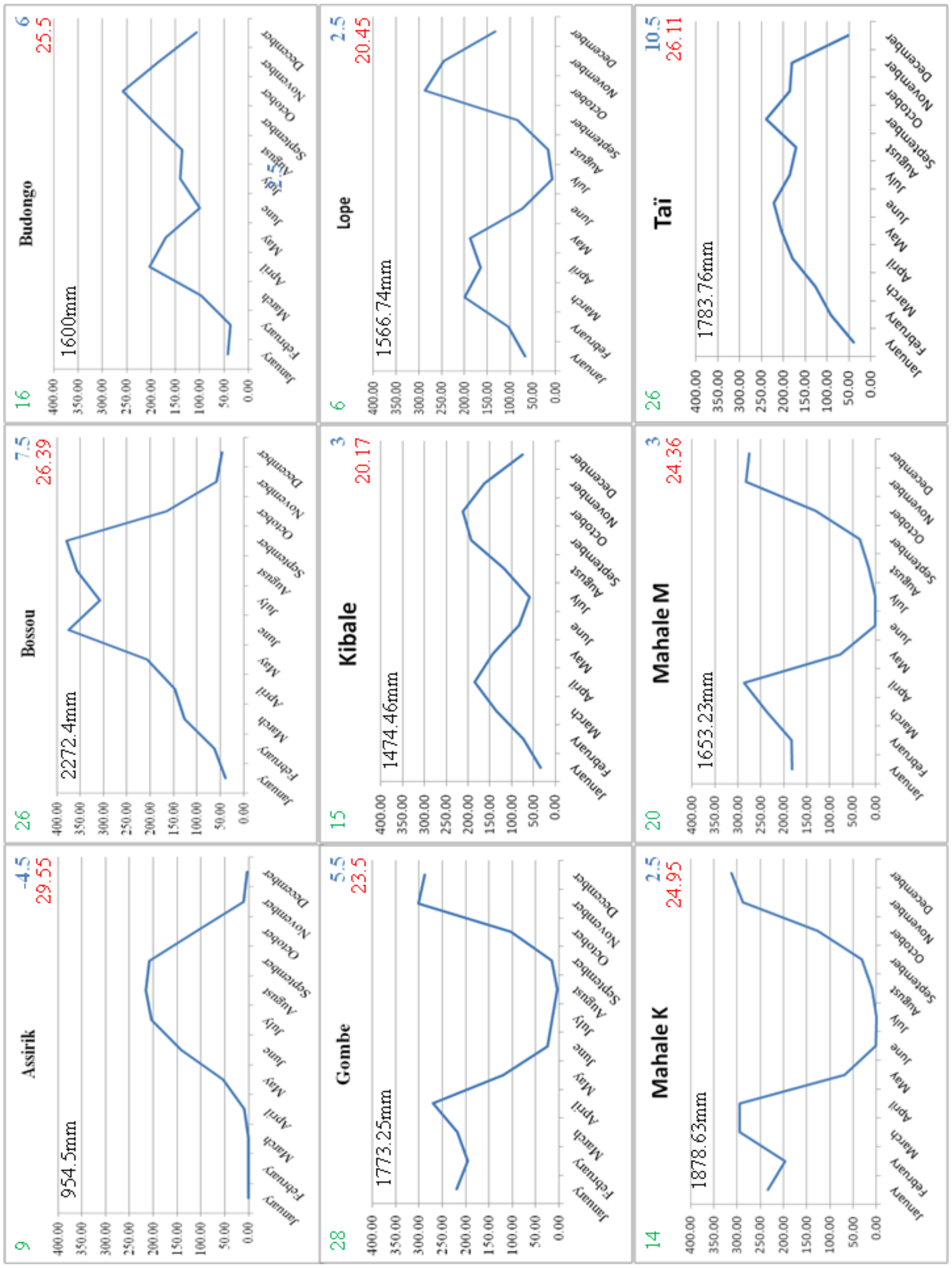

Figure 3: Rainfall, number of tools, mean monthly temperature, and perhumidity index at each site.

The green number is the number of tool-using behaviors at the site, red is the mean monthly temperature (°C), and blue is the perhumidity index.

CHAPTER 7: RESULTS

Schumaker and colleagues (2011) was consulted for defining which behaviors fit the category of tool-use. The list of tool-using behaviors (Appendix 1) was broken down into various categories to explore if certain classes of behaviors were more common in particular environments (i.e. pounding, probing, extracting, extracting, and grooming). Analysis of variance (ANOVA) was used to determine if the sites differed significantly from each other as well as if the relative proportions of tool-using behaviors at each site differed significantly.

Table 10: ANOVA summary table comparing tool-using behavior across all nine sites

Source of Variation	*SS*	*df*	*MS*	*F*	*P-value*	*F crit*
Between Groups	72.58	7	10.37	0.88	0.53	2.31274
Within Groups	375.20	32	11.73			
Total	447.78	39.00				

Table 10 illustrates that no significant differences exist between the study sites in terms of the overall tool-using repertoire. The ANOVA summary table comparing the frequencies of the different types of tool-using behaviors is presented in Table 11. These results clearly demonstrate that there are significant differences between the number of different tools used throughout the study sites. Post-hoc testing using Tukey’s Honestly

Significance Difference (HSD) test reveals significant differences between ten of the fourteen pairings (Table 12).

Table 11: ANOVA summary table comparing frequency of the five categories of tool use

Source of Variation	*SS*	*df*	*MS*	*F*	*P-value*	*F crit*
Between Groups	275.24	4	68.81	12.32	0	2.61
Within Groups	223.33	40	5.58			
Total	498.58	44				

Table 12: Results of Tukey's HSD Test

Comparison	**Mean Difference**	**q**	**P value**	
Extract vs Probe	4.556	5.784	**	P<.01
Extract vs Clean	3.889	4.937	**	P<.01
Extract vs Display	-1.556	1.975	ns	P>.05
Extract vs Pound	4.000	5.078	**	P<.01
Probe vs Clean	-0.667	0.846	ns	P>.05
Probe vs Display	-6.111	7.759	***	P<.001
Probe vs Pound	-0.556	0.705	ns	P>.05
Clean vs Display	-5.444	6.912	***	P<.001
Clean vs Pound	0.111	0.141	ns	P>.05
Display vs Pound	5.556	7.053	***	P<.001

Table 12 shows that significant differences exist between the number of extraction tools and every other category with the exception of displaying tools. This is not surprising as the extraction and display categories have the most behaviors seen at all sites. Figure 3 illustrate the proportion of each tool-using behavior observed at each study site.

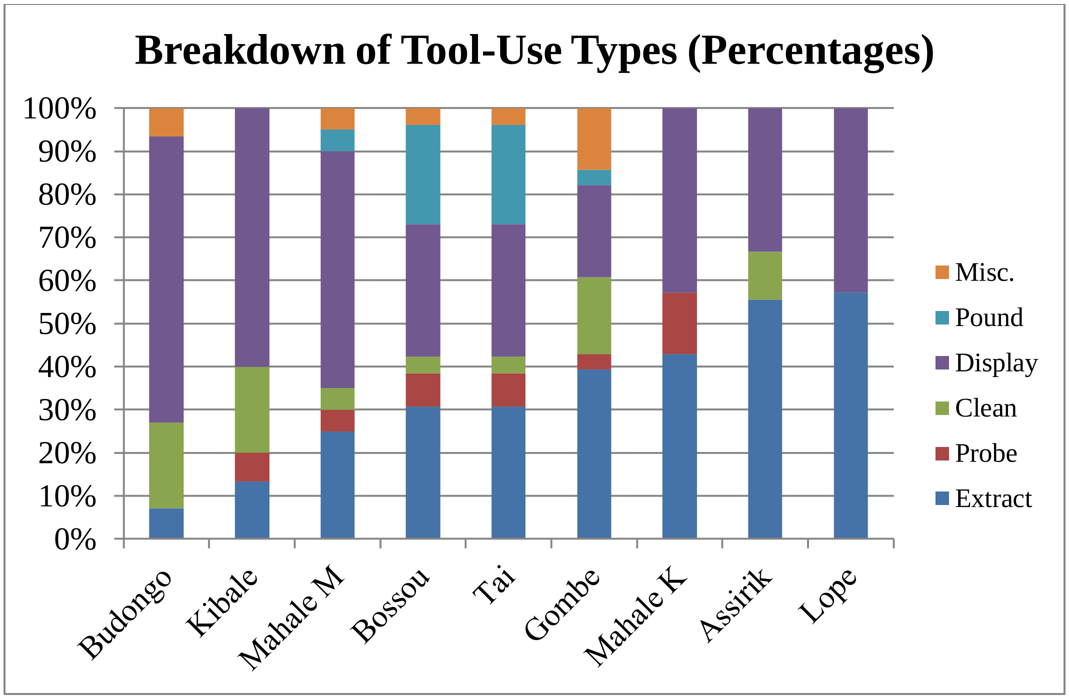

Figure 4: Percentages of the different categories of tool-using behaviors at each study site.

The next step in this analysis was to see if any correlations existed between tool-using behaviors and the environment. Tool-using behaviors were compared to the following ecological variables: mean annual precipitation, mean annual precipitation standard deviation (monthly standard deviations), mean annual minimum temperature, mean annual maximum temperature, mean annual minimum-maximum range, mean monthly standard deviation (month-month temperature variation) and the perhumidity index.

Significant positive correlations were found between diversity of tool-using behaviors and perhumidity index (r=.71, n=9, p=.03, two-tailed test), and is illustrated in Figure 4. This suggests that as total moisture of a study site increases, so does the number of tool-using behaviors in that site. A significant correlation was found between diversity of tool-using behaviors and number of very wet (>200mm) months (r=.81, n=9, p=.0098, two-tailed test), however when tool-using behavior is compared to very wet months plus wet months, the correlation is not significant at the p<.05 level (r=.62, n=9, p=.0664, two-tailed test).

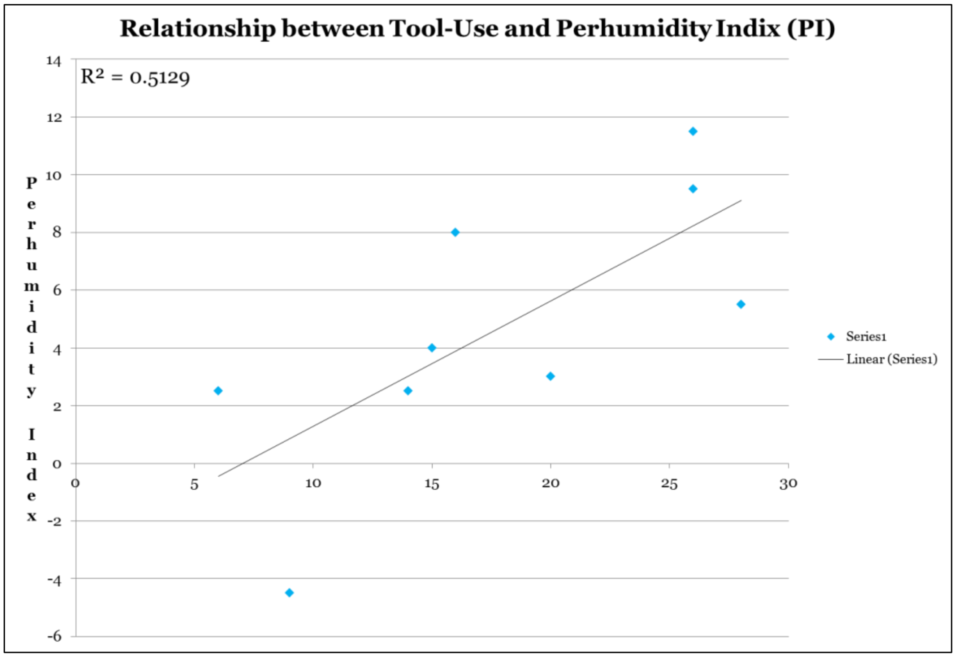

Figure 5: Scatter plot demonstrating relationship between number of tool-using behaviors and perhumidity index. Perhumidity index is illustrated on the y-axis, with amount of tool-using behaviors on the x-axis.

Comparisons were then made between feeding tools and ecological factors. Figure 6 compares the number of behaviors used for feeding across the study sties. No significant relationships were found between tools used for feeding and any ecological variables.

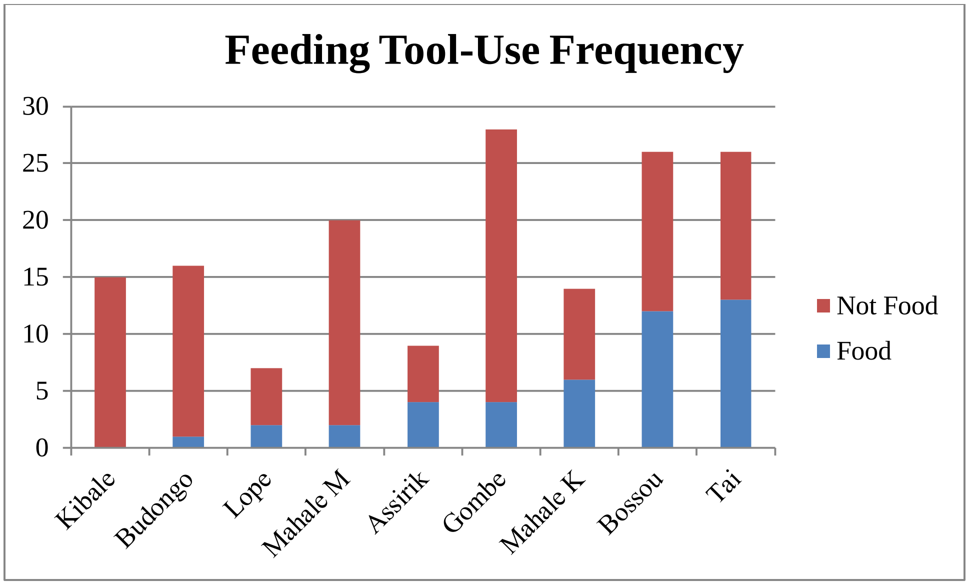

Figure 6: Graph illustrating the relative frequencies of feeding tool-using behaviors at each study site.

The number of manufactured tools was also compared to ecological variables. Definitions of manufacture largely followed the conventions outlined by Schumaker and colleagues (2011). However, the manufacture category "detach" was not included in this study. Detach refers to objects that are removed from their substrate and then either used directly as tools or further modified. I feel the category "detach" is far too vague and results in far too large a sample of manufactured tools. Any behavior that involved a chimpanzee altering the shape or form of a detached or found object was classified as manufacture. Chimpanzees sometimes use a tool as is or modify it to aid in a particular task depending on different variables (Nishida and Hiraiwa 1981). For example, the chimpanzees of Mahale only modify ant dipping tools if necessary, for instance if the entrance to the nest is very small they will peel off park from a dipping wand, whereas if it is only moderately small they simply detach a branch and insert it into the hole as is. In these situations, the behavior will simply be categorized as manufacture.

Some tools are not necessarily manufactured, but are combined or used in series to achieve a particular goal. For example, nut-cracking involves the use of a hammer and anvil, neither of which is itself manufactured. However, they are used in concert to accomplish the task of cracking open a nut. This type of technology is known as a tool-composite (Carvalho et al. 2008; Schumaker et al. 2011). Tool composites are one type of associative tool. Associative tools refer to behaviors that involve the use of multiple tools, either in tandem or sequentially. A full list of associative tools is provided in Appendix A.

One question posed for this study was does tool-manufacture increase with increased moisture availability? A significant correlation exists between activities involving manufactured tools and mean annual precipitation (r=.81, n=9, p<.01, two-tailed). No significant correlation was found between number of tool behaviors that involved modification and perhumidity index.

The tool-using behaviors of eastern and western chimpanzees (*P.t. schweinfurthii* and *P.t. verus*) were compared using a chi-squared test for independence, which measures the likelihood that the variables being measured are related. Central African chimpanzees (*P.t. troglodytes*) were not included because Lopé was the only central African site included in this study. A significant association was found between sub-species and tool-use (χ^2=17.4, n=145, p<.01). Table 13 illustrates the differences between the sub-species.

Table 13: Comparison of tool-using behaviors employed by eastern and western chimpanzees.

	Extract	Probe	Clean	Display	Pound
P.t. schweinfurthii	25	5	12	42	2
P.t verus	21	4	3	19	12

No significant correlations were found between tool-use and mean monthly rainfall standard deviation or mean annual rainfall standard deviation. Temperature readings were gathered from the literature, with preference given to studies that included multiple years of data. Environments with higher standard deviations were deemed more variable than environments with lower ones.

Finally, all cultural behaviors listed by Whiten and colleagues (2001) were incorporated into the study to determine if the overall behavioral diversity was related to moisture availability as a point of comparison. The correlations between total behavioral repertoire and precipitation was not significant, while the correlation between total behaviors and PI was significant (r=.72, n=9, p=.03, two-tailed) and is illustrated in Figure 7. Interestingly, this is the same correlation seen in the comparison of tool-using behaviors to PI. A slight correlation (r=.41) existed between non tool-using behaviors and PI or percentage of tool-using behaviors and PI or precipitation.

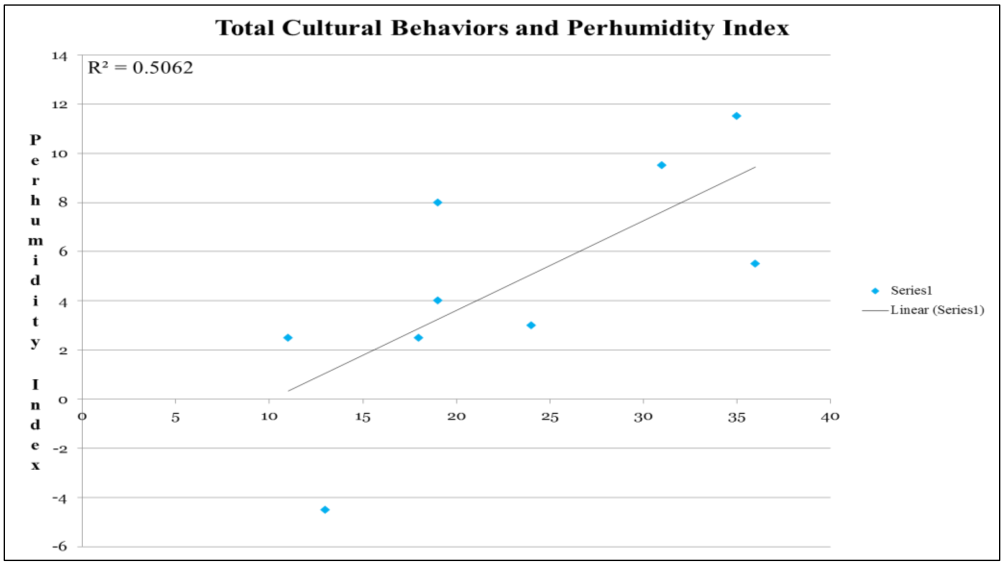

Figure 7: Scatterplot comparing total cultural behaviors to perhumidity index. Perhumidity index is listed on the y-axis while number of cultural behaviors are on the x-axis.

CHAPTER 8: SUMMARY AND CONCLUSIONS

This thesis provided a brief overview of tool-use in the Animal Kingdom, with a focus on chimpanzees. Theories for its evolution as well as the benefits and drawbacks of wild and captive studies were discussed, as were ecological factors that may influence its development. Chimpanzees are socially complex primates that live in fission-fusion societies and, after humans, make the most extensive use of tools in the Animal Kingdom.

Some scholars have argued that technology and other "human" characteristics such as cooperative hunting primarily evolved out of necessity to cope with drier, more open savanna environments (Dart 1925; Leakey 1981; though see Wood-Jones 1925). More recent data, however, casts doubt on this hypothesis. This is supported by data from chimpanzee studies, as well as paleontological evidence. *Ardipithecus ramidus*, for example, is known to have inhabited woodland environments based on fossilized wood, seeds, paleosols, and a faunal assemblage including bovids and monkeys (White et al. 2009). Stable isotope analysis of the teeth indicates a high reliance on C3 plants which further support a forest origin for this species (White et al. 2009). Fossils of *Australopithecus anamensis* from the Middle Awash region of Ethiopia dating to around 4.1 to 4.2 million years ago were excavated from strata that strongly suggested a woodland habitat (White et al. 2006). Analysis of bovid fauna from the Tanzanian Plio-Pleistocene site of Laetoli was also predominately woodland around 3.5-3.8 million years ago before shifting to a more mosaic, open habitat around 2.66 million years ago (Kovarovic and Andrews 2007)

Anatomy of *Australopithecus* and early *Homo* still reflect many adaptations to forested environments such as longer arms, fingers, and shorter legs. Susman and Stern (1982) have argued that *Homo habilis* was possibly still partially arboreal based on the curvature and robustness of the middle phalanges. Morphological and paleoecological data strongly suggests that many hominin traits evolved when hominins still spent considerable time in or near wooded environments and have remained adaptive. Orangutans provide a modern example of an organism that moves bipedally through the trees. In their study of Sumatran orangutans, Thorpe and colleagues (2007) observed orangutans tend to move more bipedially on small, flexible branches. This form of locomotion allows for an ape to support itself both from below, with its feet, and above, with its hands (Thorpe et al. 2007).

Boesch-Achermann and Boesch (1994) were among the first to call for an increased focus on forest chimpanzees and cited more tool-use and cooperative hunting among Tai Forest chimps when compared to chimpanzees at Mahale and Gombe. Over the past 20 years, long term data from other forested sites, such as Budongo and Bossou, as well as dry habitat chimpanzees in Assirik, have furthered our knowledge about tool-use in forest chimpanzees. The archaeological record may be biased against preserving skeletal remains from the rainforest due to its wet climate and soil acidity.

Results from this thesis suggest a relationship between tool-use and environmental productivity. This supports the opportunity hypothesis explored in orangutans and capuchin monkeys (Fox et al. 1999; Spagnoletti et al. 2012). This hypothesizes that sufficient environmental conditions encourage development of tool use by providing many opportunities for tool-using behaviors to develop. This may partially contribute to the discrepancies seen in tool-use among captive and wild populations. Captive animals of any species typically show a higher tool-using proficiency than do their wild counterparts. A combination of ample food, no predation pressure, and ample opportunity to use and make tools may be the primary factor in this proficiency. Forest chimpanzees may on average use more tools than those in dry or mixed habitats because there are more resources available to make tools (i.e. more incentive), lower predation pressure, and more stable food supplies.

This research further discredits the hypothesis that technology evolved primarily as a means of coping with dryer, more seasonal environments. An interesting area of future study would be to compare technological diversity to density of tree cover. It is likely that a similar relationship exists between tree density and tool-use as wetter regions are more likely to have more tree cover. The “rainforest hypothesis” postulated by Boesch-Achermann and Boesch (1994) seems to be the most well supported hypothesis on the origins of hominid technology. Most early studies on hominid tools relied extensively on stone artifacts which likely represented only a portion of the total tool-using repertoire of hominids. Increased opportunity to experiment as well as increased availability of raw materials in wetter environments likely had a more significant relationship on tool development. It is possible that increased reliance on stone technology during the early Paleolithic could have resulted from hominins spending more time in dryer, open environments as stone resources may have been more available than plant-based resources.

It is important to note that this thesis is not demonstrating or advocating an environmentally deterministic view on tools, nor is it arguing that ecological richness or overall wetness is the main factor in the evolution of tool-use among chimpanzees, but one of many. Chimpanzees, like humans, are cultural animals, and thus their social environment is instrumental in the innovation and dissemination of novel behaviors. Kamilar and Marshack (2012) have argued that behavioral variation among chimpanzees is best explained by geography. Communities that are closer to each other tend to be more behaviorally similar to each other than those that are far apart. This is true regardless of local ecology. They incorporated the same list of behaviors used in this thesis, but included non-tool using behaviors as well. Their paper primarily explored the role of cultural diffusion in chimpanzee behavioral diversity while this thesis explored the role of environment on the overall richness of chimpanzee tool-using behavior.

Directions for future research

Future cross-cultural research on the relationship between chimpanzee tools and environment would benefit greatly from comparing the number of tool-using behaviors directly to a measure of ecological richness such as tree species richness. The scale of study is also important. Research on chimpanzee predation on army ants and termites demonstrates the adaptation of technology to ecological problems such as insect aggression, seasonality, hardness of nests, and prey species (Goodall 1986; Humle 2011b;

Nishida and Hiraiwa 1982; Schöning et al. 2008). Similar trends are seen in nut-cracking, as chimpanzees carefully choose the material of their hammers and anvils based on the characteristics of the nut (Boesch and Boesch 1982) In other words, the characteristics of tools are tailored to suit the particular needs of the chimpanzee. While technological richness may increase with ecological richness, it is likely that the ecological components of the individual tools and associated behaviors are more likely to be influenced by local factors.

The present study could be improved through the use of better ecological data. While some sites have extensive climatic information over a long period of time, other sites only have averages over only a couple years in some cases. Most resources consulted for this study often only included generic data such as mean annual rainfall and temperatures without including monthly averages or the time period for which data is available. Finally, it is likely that as chimpanzees continue to be studied, more tool-using behaviors will be discovered. Increases are likely to be most obvious in communities that are not currently well habituated.

The relationship of tool-use and climatic variability also deserves future investigation. Some studies have demonstrated the seasonal influence on certain tool-using behaviors such as nut-cracking and insect fishing though this information has not been examined for all study sites (Boesch and Boesch-Achermann 2000; Goodall 1986). This is an especially interesting area of future research because it could help explain how behaviors which are more common in wet, rainforest environments became adapted to dryer, more open habitats.

LITERATURE CITED

Alcock, John

1972 The Evolution of the Use of Tools by Feeding Animals. Evolution 26(3): 464–473.

Alp, Rosalind

1993 Meat Eating and Dipping by Wild Chimpanzees in Sierra Leone. Primates 34:463-468.

1997 ‘Stepping-Sticks’ and ‘Seat-Sticks’: New Types of Tools Used by Wild Chimpanzees (*Pan troglodytes*) in Sierra Leone. American Journal of Primatology 41:45-52.

Álvares, Manuel

1615 Etiópia Menor E Descripção Géografica Da Província Da Serra Leoa. Transcription from an Unpublished Manuscript by the Late Avelino Teixeira Da Mota.

Anderson, D.P., and E.V. Nordheim

2005 Factors Influencing Tree Phenology in Taï National Park, Côte d’Ivoire. Biotropica 37(4): 631–640.

Bar Yosef, Ofer, and Philip Van Peer

2009 The Chaîne Opératoire Approach in Middle Paleolithic Archaeology. Current Anthropology 50(1):103–131.

Bentley-Condit, Vicki, and E.O. Smith

2010 Animal Tool Use: Current Definitions and an Updated Comprehensive Catalog. Behaviour 147(2):185–32A.

Bermejo, Magdalena, and German Illera

1999 Tool-set for Termite-fishing and Honey Extraction by Wild Chimpanzees in the Lossi Forest, Congo. Primates 40:619-627.

Biro, Dora, Noriko Inoue-Nakamura, Rikako Tonooka, Gen Yamakoshi, Claudia Sousa, and Tetsuro Matsuzawa

2003 Cultural Innovation and Transmission of Tool Use in Wild Chimpanzees: Evidence from Field Experiments. Animal Cognition 6(4):213–23.

Boesch, Christophe

1995 Innovation in Wild Chimpanzees. International Journal of Primatology 16(1):1-16.

2003 Is Culture a Golden Barrier Between Human and Chimpanzee? Evolutionary Anthropology 12(2):82–91.

2011 The Ecology and Evolution of Social Behavior and Cognition in Primates. *In* The Oxford Handbook of Comparative Evolutionary Psychology. J. Vonk and T. Shackelford, eds.

Boesch, Christophe, and Hedwige Boesch

1982 Optimisation of Nut-cracking with Natural Hammers by Wild Chimpanzees. Behaviour 83:265–286.

1990 Tool Use and Tool Making in Wild Chimpanzees. Folia Primatologica 54(1-2):86–99.

Boesch, Christophe, and Hedwige Boesch-Achermann

2000 The Chimpanzees of the Taï Forest: Behavioural Ecology and Evolution. New York: Oxford University Press.

Boesch-Achermann, Hedwige, and Christophe Boesch

1994 Homininization in the Rainforest: The Chimpanzee's Piece of the Puzzle. Evolutionary Anthropology 3(1):9–16.

Boesch, Christophe, Paul Marchesi, Nathalie Marchesi, and Barbara Fruth

1994 Is Nut Cracking in Wild Chimpanzees a Cultural Behaviour? Journal of Human Evolution 26:325–338.

Boesch, Christophe, Josephine Head, and Martha M Robbins

2009 Complex Tool Sets for Honey Extraction Among Chimpanzees in Loango National Park, Gabon. Journal of Human Evolution 56(6):560–9.

Boinski, Sue, R.P. Quatrone, and Hilary Swartz

2000 Substrate and Tool Use by Brown Capuchins in Suriname: Ecological Contexts and Cognitive Bases. American Anthropologist 102(4):741–761.

Brewer, Stella M. and W.C. McGrew

1990 Chimpanzee Use of a Tool-Set to Get Honey. Folia Primatologica 54(1-2): 100-104.

Bronikowski, A.M., and J. Altmann

1996 Foraging in a Variable Environment: Weather Patterns and the Behavioral Ecology of Baboons. Behavioral Ecology and Sociobiology 39(1): 11–25.

Carvalho, Susana, Eugénia Cunha, Cláudia Sousa, and Tetsuro Matsuzawa
2008 Chaînes Opératoires and Resource-exploitation Strategies in Chimpanzee (Pan Troglodytes) Nut Cracking. Journal of Human Evolution 55(1):148–63.

Carvalho, Susana, Dora Biro, William C. McGrew, and Tetsuro Matsuzawa
2009 Tool-composite Reuse in Wild Chimpanzees (Pan Troglodytes): Archaeologically Invisible Steps in the Technological Evolution of Early Hominins? Animal Cognition 12(1):S103–14.

Chapman, C.A., R.W. Wrangham, L.J. Chapman, D.K. Kennard, and A.E. Zanne
1999 Fruit and Flower Phenology at Two Sites in Kibale National Park, Uganda. Journal of Tropical Ecology 15(2): 189–211.

Collias, N., and E. Collias
1967 External Constructions by Animals. Stroudsburg PA: Dowden, Hutchinson, and Ross.

Coss, Richard G.
1999 The Effects of Natural Selection on the Evolution of Behavior. *In* Geographic Variation in Behavior. Susan A. Foster and John A. Ender, eds. Pp. 180–208. New York: Oxford University Press.

Dart, Raymond
1925 *Australopithecus africanus*, the Man-Ape of South Africa. Nature 115:195-199.

Davies, Nicholas B. and John R. Krebs (eds.)
2007 An Introduction to Behavioural Ecology. Third Edition. Oxford: Blackwell Science.

Deecke, Volker B.
2012 Tool-use in the Brown Bear (*Ursus arctos*). Animal Cognition 15(4):725–30.

Domínguez-Rodrigo, Manuel, Travis Rayne Pickering, Sileshi Semaw, and Michael J Rogers
2005 Cutmarked Bones from Pliocene Archaeological Sites at Gona, Afar, Ethiopia: Implications for the Function of the World's Oldest Stone Tools. Journal of Human Evolution 48(2):109–121.

Deblauwe, Isra, Patrick Guislain, Jef Dupain, and Linda Van Elsacker
2006 Use of a Tool-Set by *Pan troglodytes troglodytes* to obtain termites (*Macrotermes*) in the Periphery of the Dja Biosphere Reserve, Southeast Cameroon. American Journal of Primatology 68(12):1191-1196.

Eeley, Harriet A.C., and Robert A. Foley
1999 Species Richness, Species Range Size and Ecological Specialisation among African Primates: Geographical Patterns and Conservation Implications. Biodiversity and Conservation 8:1033–1056.

Fay, J. Michael, and Richard W. Carroll
1994 Chimpanzee Tool Use for Honey and Termite Extraction in Central Africa. American Journal of Primatology 34(4):309-317.

Fischer, Ann, Joshua Pollack, Olaf Thalmann, Brigit Nickel, and Svante Pääbo
2006 Demographic History and Genetic Differentiation in Apes. Current Biology 16:1133–1138.

Fisher, Edna M.
1939 Habits of the Southern Sea Otter. Journal of Mammology 20(1):21-36.

Fox, Elizabeth A., Arnold F. Sitampul, and Carel P. van Schaik
1999 Intelligent tool use in wild Sumatran orangutans. *In* The Mentality of Gorillas and Organutans, pp.99–116. S.T. Parker, L. Miles, & R. Mitchell (Eds). Cambridge: Cambridge University Press.

Francis, Anthony P., and David J. Currie
2003 A Globally Consistent Richness-climate Relationship for Angiosperms. The American Naturalist 161(4):523–36.

Gonder, M. Katherine, John F. Oates, Todd R. Dissotell, Michael R. Forstner, Juan Carlos Morales, and Don J. Melnick
1997 A New West African Chimpanzee Subspecies? Nature 388: 337.

Gonder, Mary K., Todd R. Disotell, and John F. Oates
2006 New Genetic Evidence on the Evolution of Chimpanzee Populations and Implications for Taxonomy. International Journal of Primatology 27:1103–1127.

Goodall, Jane
1964 Tool-Using and Aimed Throwing in a Community of Free-Living Chimpanzees. Nature 201:1264-1266.

1968 Behaviour of Free-Living Chimpanzees of the Gombe Stream Area. Animal Behaviour Monographs 1:163-311.

1971 In the Shadow of Man. London: William Collins.

1986 The Chimpanzees of Gombe: Patterns of Behavior. Cambridge: Belknap Press of Harvard University Press.

Gould, Stephen J.
1981 The Mismeasure of Man. New York: W.W. Norton & Company.

Gould, S.J. and R.C. Lewontin
1979 The Spandrels of San Marco and the Panglossian Paradigm: A Critique of the Adaptationist Programme. Proceedings of the Royal Society B: Biological Sciences 205(1161):581–598.

Gravetter, Frederick J., and Larry B. Wallnau
2005 Essentials of Statistics for the Behavioral Sciences. 5th edition. Belmont: Wadsworth.

Grove, Matt, Eiluned Pearce, and R.I.M. Dunbar
2012 Fission-fusion and the Evolution of Hominin Social Systems. Journal of Human Evolution 62:191-200.

Gruber, Thibaud, Zanna Clay, and Klaus Zuberbühler
2010 A Comparison of Bonobo and Chimpanzee Tool Use: Evidence for a Female Bias in the Pan Lineage. Animal Behaviour 80(6): 1023–1033.

Hair, Paul E. H.
1990 Manuel Alvares: Ethiopia Minor and a Geographical Account of the Province of Sierra Leone (c. 1615). Liverpool: Department of History, University of Liverpool.

Hall, K.R.L.
1963 Tool-Using Performances as Indicators of Behavioral Adaptability. Current Anthropology 4(5): 479–494.

Hanna, Allison C., and W.C. McGrew
1987 Chimpanzees Using Stones to Crack Open Oil Palm Nuts in Liberia. Primates 28: 31–46.

Haslam, Michael, Adriana Hernandez-Aguilar, Victoria Ling, Susana Carvalho, Ignacio de la Torre, April DeStefano, Andrew Du, Bruce Hardy, Jack Harris, Linda Marchant, Tetsuro Matsuzawa,William McGrew, Julio Mercader, Rafael Mora, Michael Petraglia, Hélène Roche, Elisabetta Visalberghi and Rebecca Warren

2009 Primate Archaeology. Nature 460(7253):339-344.

Hirata, Satoshi, Masako Myowa, and Tetsuro Matsuzawa

1998 Use of Leaves as Cushions to Sit on Wet Ground by Wild Chimpanzees. American Journal of Primatology 44:215-220.

Humle, Tatyana

2011a The Tool Repertoire of Bossou Chimpanzees. *In* The Chimpanzees of Bossou and Nimba. Tetsuro Matsuzawa, Tatyana Humle, and Yukimaru Sugiyama, eds. Pp. 61–71. Toyko: Springer.

2011b Ant-Dipping: How Ants Have Shed Light on Culture. *In* The Chimpanzees of Bossou and Nimba. Tetsuro Matsuzawa, Tatyana Humle, and Yukimaru Sugiyama, eds. Pp. 97–106. Tokyo: Springer.

2011c Location and Ecology. *In* The Chimpanzees of Bossou and Nimba. Tetsuro Matsuzawa, Tatyana Humle, and Yukimaru Sugiyama, eds. Pp. 3–12. Tokyo: Springer.

Hunt, Gavin R., and Russell D. Gray

2004 The Crafting of Hook Tools by Wild New Caledonian Crows. Proceedings of the Royal Society B-Biological Sciences 271(Suppl. 3):S88-S90.

Hunt, Kevin D., and William C. McGrew

2002 Chimpanzees in the Dry Habitats of Assirik, Senegal and Semliki Wildlife Reserve, Uganda. *In* Behavioural Diversity in Chimpanzees and Bonobos. Christophe Boesch, Gottfried Hohmann, and Linda F. Marchant, eds. Pp. 35–51. Cambridge: Cambridge University Press.

Inoue-Nakamura, Noriko, and Tetsuro Matsuzawa

1997 Development of Stone Tool Use by Wild Chimpanzees (*Pan Troglodytes*). Journal of Comparative Psychology 111(2):159–173.

Jones, Clyde, and Jorge Sabater Pi

1969 Sticks Used by Chimpanzees in Rio Muni, West Africa. Nature 223:100–101.

Jones, Frederic W.

1925 Arboreal Man. London: Edward Arnold.

Kano, Takayoshi
1972 Distribution of the Primates on the Eastern Shore of Lake Tanganyika. Primates 12(3-4):281-304.

Kamilar, Jason M.
2009 Environmental and Geographic Correlates of the Taxonomic Structure of Primate Communities. American Journal of Physical Anthropology 139(3):382–93.

Kamilar, Jason M., and Joshua L. Marshack
2012 Does Geography or Ecology Best Explain “Cultural” Variation Among Chimpanzee Communities? Journal of Human Evolution 62:256–260.

Kingdon, Jonathan
1993 Self-Made Man: Human Evolution from Eden to Extinction? New York: John Wiley & Sons, Inc.

2003 Lowly Origins. Princeton: Princeton University Press.

Kitahara-Frisch, J.
1993 The Origin of Secondary Tools. *In* The Use of Tools by Human and Non-Human Primates. Anne Berthelet and Jean Chavaillon, eds. Pp. 239-246. Oxford: Claredon Press.

Kitahara-Frisch, J., K. Norikoshi, and K. Hara.
1987 Use of a Bone Fragment as a Step Towards Secondary Tool-Use in Captive Chimpanzees. Primate Report 18:33-37.

Köhler, Wolfgang
1956 The Mentality of Apes. Translated from the 2d Rev. Ed. by Ella Winter. 2nd edition. London: Routledge & Kegan Paul LTD.

Kohts, Nadia N.L.
2002 Infant Chimpanzee and Human Child: A Classic 1935 Comparative Study of Ape Emotions and Intelligence. Translated by Boris Vekker. Oxford: Oxford University Press.

Kortland, A., and M. Kooij
1963 Protohominid Behaviour in Primates. Symposium of the Zoological Society of London 10:61-88.

Kovarovic, Kris, and Peter Andrews
2007 Bovid Postcranial Ecomorphological Survey of the Laetoli Paleoenvironment. Journal of Human Evolution 52(6):663–80.

Kuhn, Steven

2004 Evolutionary Perspectives on Technology and Technological Change. World Archaeology 36(4):561–570.

Lycett, Stephen J., Mark Collard, and William C. McGrew

2007 Phylogenetic Analyses of Behavior Support Existence of Culture Among Wild Chimpanzees. Proceedings of the National Academy of Sciences of the United States of America 104(45):17588–92.

2010 Are Behavioral Differences Among Wild Chimpanzee Communities Genetic or Cultural? An Assessment Using Tool-use Data and Phylogenetic Methods. American Journal of Physical Anthropology 142(3):461–467.

Leakey, Richard E.

1981 The Making of Mankind. New York: E.P. Dutton

MacArthur, Robert H., and Erick R. Pianka

1966 On Optimal Use of a Patchy Environment. The American Naturalist 100(916):603–609.

Mannu, M., and E.B. Ottoni

1991 [Posture and Laterality in Spontaneous Cracking of Palm Fruits by a Group of Tufted Capuchins (*Cebus apella*) in Semi-Captive Conditions]. *In* Livro de Resumos do IX Congresso Brasileiro de Primatological. Santa Teresa, Brazil: Congresso Brasileiro de Primatological, 31.

2009 The Enhanced Tool-Kit of Two Groups of Wild Bearded Capuchin Monkeys in the Caatinga: Tool Making, Associative Use and Secondary Tools. American Journal of Primatology 71(3):242-251.

Matsuzawa, Tetsuro

1991 Nesting Cups and Metatools in Chimpanzees. Behavioral and Brain Sciences 14(4):570-571

1994 Field Experiments on Use of Stone Tools by Chimpanzees in the Wild. *In* Chimpanzee Cultures. Richard W. Wrangham, McGrew W.C., Frans B.M. de Waal, and Paul G. Heltne, eds. Pp. 351–370. Cambridge: Harvard University Press.

2011a Education by Master-Apprenticeship. *In* The Chimpanzees of Bossou and Nimba. Tetsuro Matsuzawa, Tatyana Humle, and Yukimaru Sugiyama, eds. Pp. 201–210. Tokyo: Springer.

2011b Field Experiments and Tool Use. *In* The Chimpanzees of Bossou and Nimba. Tetsuro Matsuzawa, Tatyana Humle, and Yukimaru Sugiyama, eds. Pp. 157–164. Tokyo: Springer.

2011c Stone Tools for Nut-Cracking. *In* The Chimpanzees of Bossou and Nimba. Tetsuro Matsuzawa, Tatyana Humle, and Yukimaru Sugiyama, eds. Pp. 73–84. Tokyo: Springer.

McGrew, William C.

1974 Tool Use by Wild Chimpanzees in Feeding Upon Driver Ants. Journal of Human Evolution 3:501-508

1992 Chimpanzee Material Culture. New York: Cambridge University Press.

2004 The Cultural Chimpanzee: Reflections on Cultural Primatology. New York: Cambridge University Press.

McGrew, W.C., C.E.G. Tutin, and P.J. Baldwin

1979 Chimpanzees, Tools, and Termites: Cross-Cultural Comparisons of Senegal, Tanzania, and Rio Muni. Man 14(2):185–214.

McGrew, W.C., P.J. Baldwin, and C.E.G. Tutin

1981 Chimpanzees in a Hot, Dry, Open Habitat: Mt. Assirik, Senegal, West Africa. Journal of Human Evolution 10(3):227-236.

McGrew, W.C, R.M. Ham, L.J.T. White, C.E.G. Tutin, and M. Fernandez

1997 Why Don't Chimpanzees in Gabon Crack Nuts ? International Journal of Primatology 18(3):353–374.

Mercader, Julio, Melissa Panger, and Christophe Boesch

2002 Excavation of a Chimpanzee Stone Tool Site in the African Rainforest. Science 296(5572):1452–5.

Mercader, Julio, Huw Barton, Jason Gillespie, Jack Harris, Steven Kuhn, Robert Tyler and Christophe Boesch

2007 4,300-Year-Old Chimpanzee Sites and the Origins of Percussive Stone Technology. Proceedings of the National Academy of Sciences of the United States of America 104(9):3043–8.

Morgan, Bethan J., and Ekwoge E Abwe

2006 Chimpanzees Use Stone Hammers in Cameroon. Current Biology 16(16):R632–633.

Möbius, Yasmin, Christophe Boesch, Kathelijne Koops, Tetsuro Matsuzawa, and Tatyana Humle

2008 Cultural Differences in Army Ant Predation by West African Chimpanzees? A Comparative Study of MicroecologicalVariables. Animal Behaviour 76(1):37–45.

Myowa-Yamakoshi, Masako, and Gen Yamakoshi

2011 Play Behaviors Including the Use of Objects in Young Chimpanzees at Bossou. *In* The Chimpanzees of Bossou and Nimba. Tetsuro Matsuzawa, Tatyana Humle, and Yukimaru Sugiyama, eds. Pp. 231–240. Tokyo: Springer.

Nishida, Toshisada

1968 The Social Group of Wild Chimpanzees in the Mahili Mountains. Primates 9: 167–224.

1973 The Ant-Gathering Behavior by the Use of Tools among Wild Chimpanzees of the Mahale Mountains. Journal of Human Evolution 2:357-370.

1980 The Leaf-Clipping Display: a Newly Discovered Expressive Gesture in Wild Chimpanzees. Journal of Human Evolution 9:117-128.

1990 A Quarter Century of Research in the Mahale Mountains: An Overview. *In* The Chimpanzees of the Mahale Mountains: Sexual and Life History Strategies. Toshisada Nishida, ed. Pp. 3–36. Tokyo: University of Tokyo Press.

1997 Sexual Behaviour of Adult Male Chimpanzees of the Mahale Mountains National Park, Tanzania. Primates 38:379-398.

2012 Chimpanzees of the Lakeshore: Natural History and Culture at Mahale. Cambridge: Cambridge University Press.

Nishida, Toshisada and Mariko Hiraiwa

1982 Natural History of a Tool-Using Behavior by Wild Chimpanzees in Feeding upon Wood-Boring Ants. Journal of Human Evolution 11:73-99.

Nishida, Toshisada and M. Nakamura

1993 Chimpanzee Tool Use to Clear a Blocked Nasal Passage. Folia Primatologica 61:218-220.

Oakley, Kenneth P.

1967 Man the Tool-Maker. British Museum, London

Odell, George H.
2004 Lithic Analysis. New York: Kluwer Academic/Plenum.

Parker, G.A., and J. Maynard Smith
1990 Optimality Theory in Evolutionary Biology. Nature 348:27–33.

Patterson, Eric M., and Janet Mann
2011 The Ecological Conditions That Favor Tool Use and Innovation in Wild Bottlenose Dolphins (*Tursiops Sp.*). PloS One 6(7):e22243.

Perry, Gad, and Eric R. Pianka
1997 Animal Foraging: Past, Present and Future. Trends in Ecology & Evolution 12:360–364.

Pierce, G.J., and J.G. Ollason
1987 Eight Reasons Why Optimal Foraging Theory Is a Complete Waste of Time. Oikos 49(1): 111–117.

Plumptre, A.J., D. Cox, and S. Mugume
2003 The Status of Chimpanzees in Uganda. Albertine Rift Technical Report Series No. 2, Wildlife Conservation Society.

Potts, Richard B.
1998 Variability Selection in Hominid Evolution. Evolutionary Anthropology 7:81-96.

Pradhan, Gauri R., Claudio Tennie, and Carel P. van Schaik
2012 Social Organization and the Evolution of Cumulative Technology in Apes and Hominins. Journal of Human Evolution 63(1):180-190.

Pruetz, Jill D, and Paco Bertolani
2007 Savanna Chimpanzees, *Pan Troglodytes Verus*, Hunt with Tools. Current Biology: 17(5):412–7.

Pyke, Graham H.
1984 Optimal Foraging Theory: A Critical Review. Annual Review of Ecology and Systematics 15(1984):523–575.

Reynolds, Vernon
2005 The Chimpanzees of Budongo Forest: Ecology, Behaviour, and Conservation. Oxford: Oxford University Press.

Reynolds, Vernon and Frankie Reynolds
1965 Chimpanzees of the Budongo Forest. *In* Primate Behavior: Field Studies of Monkeys and Apes. I. DeVore, editor. New York: Holt, Rinehart, and Winston.

Roe, Anne, and George Gaylord Simpson (eds)
1958 Behavior and Evolution. New Haven: Yale University Press.

Russon, Anne E.
2006 Acquisition of Complex Foraging Skills in Juvenile and Adolescent Orangutans (*Pongo pygmaeus*): Developmental Influences. Aquatic Mammals 32(4):500-510.

Sanz, Crickette M., and David B. Morgan
2007 Chimpanzee Tool Technology in the Goualougo Triangle, Republic of Congo. Journal of Human Evolution 52(4):420–33.

Sanz, Crickette, Casper Schöning, and David B. Morgan
2009 Chimpanzees Prey on Army Ants with Specialized Tool Sets. American Journal of Primatology 71:1-8.

Sanz, Crickette, Dave Morgan, and Steve Gulick
2004 New Insights into Chimpanzees, Tools, and Termites from the Congo Basin. The American Naturalist 164(5):567–81.

Sanz, Crickette, Josep Call, and Christophe Boesch, eds.
2013 Tool Use in Animals: Cognition and Ecology. Cambridge: Cambridge University Press.

Sargeant, Brooke L., Aaron J. Wirsing, Michael R. Heithaus, and Janet Mann
2006 Can Environmental Heterogeneity Explain Individual Foraging Variation in Wild Bottlenose Dolphins (*Tursiops Sp.*)? Behavioral Ecology and Sociobiology 61(5):679–688.

Savage, T., and J. Wyman
1843/1844 Observations on the External Characters and Habits of the Troglodytes Niger. Boston Journal of Natural History 4:362–386.

Schick, Kathy D., Nicholas Toth, Gary Garufi, Sue Savage-Rimbaugh, Duane Rimbaugh, and Rose Sevcik
1999 Continuing Investigations into the Stone Tool-making and Tool-using Capabilities of a Bonobo (*Pan Paniscus*). Journal of Archaeological Science: 821–832.

Schöning, Caspar, Tatyana Humle, Yasmin Möbius, and W.C. McGrew
2008 The Nature of Culture: Technological Variation in Chimpanzee Predation on Army Ants Revisited. Journal of Human Evolution 55(1):48–59.

Seed, Amanda, and Richard Byrne
2010 Animal Tool-use. Current Biology 20(23):R1032–9.

Sept, Jeanne M, and George E Brooks
1994 Reports of Chimpanzee Natural History, Including Tool-Use, in 16th- and 17th-Century Sierra Leone. International Journal of Primatology 15(6):867–878.

Shumaker, Robert W., Kristina R. Walkup, and Benjamin B. Beck
2011 Animal Tool Behavior: The Use and Manufacture of Tools by Animals. Baltimore: The Johns Hopkins University Press.

Smith, Eric A.
1992 Human Behavioral Ecology I. Evolutionary Anthropology 1(1):20–24.

Smith, Eric A., and Bruce Winterhalder
2002 Evolutionary Social Science: The Behavioral Ecology Approach. Samfundsøkonomen 4:13–21.

Smolker, Rachel, Andrew Richards, Richard Connor, Janet Mann, and Per Berggren
1997 Sponge Carrying by Dolphins (*Delphinidae*, *Tursiops sp.*): a Foraging Specialization Involving Tool Use? Ethology 103(6):454–465

Sousa, Cláudia
2011 Use of Leaves for Drinking Water. *In* The Chimpanzees of Bossou and Nimba. Tetsuro Matsuzawa, Tatyana Humle, and Yukimaru Sugiyama, eds. Pp. 85–96. Tokyo: Springer.

Spagnoletti, Noemi, Elisabetta Visalberghi, Eduardo Ottoni, Patricia Izar, and Dorothy Fragaszy
2011 Stone Tool Use by Adult Wild Bearded Capuchin Monkeys (*Cebus Libidinosus*). Frequency, Efficiency and Tool Selectivity. Journal of Human Evolution 61(1):97-107.

Spagnoletti, Noemi, Elisabetta Visalberghi, Michele P. Verderane, Eduardo Ottani, Patricia Izar, and Dorothy Fragezy
2012 Stone Tool Use in Wild Bearded Capuchin Monkeys, *Cebus Libidinosus*. Is It a Strategy to Overcome Food Scarcity? Animal Behaviour 83(5):1285–1294.

Stout, Dietrich, Jay Quade, Sileshi Semaw, Michael J. Rogers, and Naomi E. Levin
2005 Raw Material Selectivity of the Earliest Stone Toolmakers at Gona, Afar, Ethiopia. Journal of Human Evolution 48(4):365–80.

Sugiyama, Yukimaru
1969 Social Behaviour of Chimpanzees in Budongo Forest, Uganda. Primates 10: 197-225.

1985 The Brush-Stick of Chimpanzees Found in South-West Cameroon and their Cultural Characteristics. Primates 26:331-342.

1994 Tool Use by Wild Chimpanzees. Nature 367:327.

1997 Social Traditions and the Use of Tool-Composites by Wild Chimpanzees. Evolutionary Anthropology 6(1):23–28.

Sugiyama, Yukimaru, and Jeremy Koman
1979 Tool-Using and -Making Behavior in Wild Chimpanzees at Bossou, Guinea. Primates 20(4):513–524.

Sugiyama, Yukumaru, Jeremy Koman, and Mo. Bhoye Sow
1988 Ant-Catching Wands of Wild Chimpanzees at Bossou, Guinea. Folia Primatologica 51:56-60

Susman, Randall L., and Jack T. Stern
1982 Functional Morphology of *Homo habilis*. Science 217(4563):931–934.

Suzuki, Shigero, Suehisa Kuroda, and Tomoaki Nishihara
1995 Tool-set for Termite-fishing by Chimpanzees in the Ndoki Forest, Congo. Behaviour 132(3):219–235.

Taylor, Timothy
2010 The Artificial Ape. New York: Palgrave MacMillan.

Teleki, Geza.
1974 Chimpanzee Subsistence Technology: Materials and Skills. Journal of Human Evolution 3:575-594.

1975 Primate Subsistence Patterns: Collector - Predators and Gatherer - Hunters. Journal of Human Evolution1 3:574–594.

Thorpe, S.K.S., R.L. Holder, and R.H. Crompton
2007 Origin of Human Bipedalism as an Adaptation for Locomotion on Flexible Branches. Science 316(5829):1328–31.

Tinbergen, Nikolaas
1963 On Aims and Methods of Ethology. Zeitschrift Für Tierpsychologie 20(4):410–433.

Tomasello, Michael, and Josep Call
2008 Assessing the Validity of Ape-human Comparisons: a Reply to Boesch (2007). Journal of Comparative Psychology 122(4):449–52.

.

Toth, Nicholas., Kathy D. Schick, E.Sue Savage-Rumbaugh, Rose A. Sevcik, and Duane M. Rumbaugh
1993 *Pan* the Tool-Maker: Investigations Into the Stone Tool-Making and Tool-Using Capabilities of a Bonobo (*Pan paniscus*). Journal of Archaeological Science 20(1):81-91.

Tutin, Caroline E.G., Rebecca Ham, and Dorothea Wrogemann
1995 Tool-Use by Chimpanzees (*Pan t. troglodytes*) in the Lope Reserve, Gabon. Primates 36(2):181–192.

Van Schaik, C.P., E.A. Fox, and A.F. Sitompul
1996 Manufacture and Use of Tools in Wild Sumatran Orangutans: Implications for Human Evolution. Naturwissenschaften 83(4):186-188.

Van Schaik, Carel P., Robert O. Deaner, and Michelle Y. Merrill
1999 The Conditions for Tool Use in Primates: Implications for the Evolution of Material Culture. Journal of Human Evolution 36(6):719–41.

Van Valen, Leigh
1973 A New Evolutionary Law. Evolutionary Theory 1:1-30.

Visalberghi, E., D. Fragaszy, E. Ottoni, P. Izar, M.G. Oliveira and F.R.D. Andrade
2007 Characteristics of Hammer Stones and Anvils Used by Wild Bearded Capuchin Monkeys (*Cebus libidinosus*) to Crack Open Palm Nuts. American Journal of Physical Anthropology 132:426–444.

Walsh, Rory P.D.
1996 Climate. *In* The Tropical Rainforest. 2nd edition. P.W. Richards, ed. Pp. 159–205. Cambridge: Cambridge University Press.

Walter, H. and Lieth H.
1960 Klimadiagramm-Weltatlas. Jena: G. Fischer.

Watts, David P.
2008 Tool Use by Chimpanzees at Ngogo, Kibale National Park, Uganda. International Journal of Primatology 29(1):83–94.

West-Eberhard, Mary Jane
1989 Phenotypic Plasticity and the Origins of Diversity. Annual Review of Ecology and Systematics 20(1989):249–278.

White, Francis J, and Richard W. Wrangham
1988 Feeding Competition and Patch Size in the Chimpanzee Species *Pan paniscus* and *Pan troglodytes*. Behaviour 105(1/2):148–164.

White, Tim D., Giday WoldeGabriel, Berhane Asfaw, Stan Ambrose, Yonas Beyene, Raymond L. Bernor, Jean-Renaud Boisserie, Brian Currie, Henry Gilbert, Yohannes Haile-Selassie, William K. Hart, Leslie J. Hlusko, F. Clark Howell, Reiko T. Kono, Thomas Lehmann, Antoine Louchart, C. Owen Lovejoy, Paul R. Renne, Haruo Saegusa, Elisabeth S. Vrba, Hank Wesselman, and Gen Suwa.
2006 Asa Issie, Aramis and the Origin of Australopithecus. Nature 440(7086): 883–9.

White, Tim D., Berhane Asfaw, Yonas Beyene, Yohannes Haile-Selassie, C. Owen Lovejoy, Gen Suwa, and Giday WoldeGabriel,
2009 *Ardipithecus ramidus* and the Paleobiology of Early Hominids. Science 326:75–86.

Whiten, A., J. Goodall, W.C. McGgrew, T. Nishida, V. Reynolds, Y. Sugiyama, G. Tutin, R.W. Wrangham, C. Boesch.
2001 Charting Cultural Variation in Chimpanzees. Behaviour 138(11/12): 1481–1516.

Wiens, John J. and Michael J. Donoghue
2004 Historical Biogeography, Ecology and Species Richness. Trends in Ecology & Evolution 19(12):639–44.

Wilson, Edward O.
1975 Sociobiology: The New Synthesis. Cambridge: Harvard University Press

Wimpenny, Joanna H., Alex A.S. Weir, Lisa Clayton, Christian Rutz, and Alex Kacelnik
2009 Cognitive Processes Associated with Sequential Tool Use in New Caledonian Crows. PLOS One 4(8):e6471.

Wrangham, Richard W., W.C. McGrew, Frans B.M. de Waal, and Paul G. Heltne, eds.
1994 Chimpanzee Cultures. Cambridge: Harvard University Press.

Wright, R.V.S.
1972 Imitative Learning of a Flaked Stone Technology: The Case of an Orangutan. Mankind 8:296-306.

Yamakoshi, Gen, and Yukimaru Sugiyama

1995 Pestle-pounding Behavior of Wild Chimpanzees at Bossou, Guinea: A Newly Observed Tool-using Behavior. Primates 36(4):489–500.

Yamamoto, Shinya, Gen Yamakoshi, and Tetsuro Matsuzawa

2011 Ant Fishing in Trees: Invention and Modification of a New Tool-Use Behavior. *In* The Chimpanzees of Bossou and Nimba. Tetsuro Matsuzawa, Tatyana Humle, and Yukimaru Sugiyama, eds. Pp. 123–130. Tokyo: Springer.

Yerkes, Robert

1929 The Great Apes: A Study of Anthropoid Life. New Haven: Yale University Press.

APPENDIX A: ASSOCIATIVE TOOL-USE

Associative Tool-Use (Table 1.2 in Schumaker et al. 2011:19)

Term	Definition	References
Associative tool	Tools used in any combination to achieve an outcome. Includes all other categories in this table except Tool Kit, Tool Assemblage, Tool Crafting and Construction.	Sugiyama 1997; Schumaker et al. 2011
Sequential Tool	A tool used to acquire another tool.	Wimpenny et al. 2009
Tool Set	Two or more tools used sequentially, usually each in a different mode, to achieve a single outcome. See Serial Tool, below.	Bermejo and Illera 1999; Brewer and McGrew 1990; Deblauwe et al. 2006; Mannu and Ottoni 2009; McGrew 2004; Sanz and Morgan 2007; Sanz et al. 2009; Suzuki et al. 1995; Wimpenny et
Serial Tool	Synonymous with Tool Set	Sanz and Morgan 20007
Tool Composite	Two or more tools used simultaneously, usually each in a different mode, to achieve a single outcome, where the first tool is not used to manufacture the second. May include Metatools.	Carvalho et al. 2008, 2009; McGrew 2004; Sugiyama 1997
Metatool	A tool used simultaneously with a second tool to increase the efficiency or effectiveness of the second tool, where the first tool (the Metatool) acts directly on the second. The scond tool could not function as a tool on its own; the Metatool makes it a better too. Every Metatools is a part of a Tool Composite. The use of a Metatool is not Tool Manufacture.	Matsuzawa 1991, 1994; Sousa and Matsuzawa 2004; Sugiyama 1997
Tool Kit	All of the various tools known to be used by a single individual, a single population, a species, or a genus, as specified by the author.	Mannu and Ottoni 2009; McGrew 1992, 2004; Russon 2006; van Schaik et al. 1996; Teleki 1974
Tool Assemblage	All of the tools found in the same context at a particular site that are presumed to have been used by the same group or population. Assemblages may accumulate over time.	Carvalho et al. 2009; Odell 2004
Multi-Function Tool	A single, specific tool used in two different modes and/or for two different functions.	Bermejo and Illera 1999; Boesch et al. 2009; Fay and Carrol 1994; Sanz and Morgan 2009; Tutin et al. 1995
Secondary Tool	A tool used to manufacture (structurally modify) another tool. The usual mode of manufacture is Subtract. Differs from Metatool, in which no tool manufacture is involved.	Kitahara-Frisch 1993; Kitahara-Frisch et al. 1987; Mannu and Ottoni 2009; Schick et al. 1999; Sugiyama 1997; Toth et al. 1993; R. Wright 1972

APPENDIX B: LIST OF TOOL-USING BEHAVIORS

Appendix B: Tool-Using Behaviors (Adapted from Whiten et al. 2001, Table 1)

Behavior	Description	Source
Investigatory probe	Probe used to examine location (usually hole/recess), then sniffed.	Goodall 1968:206
Play-start	Initiate play, incorporating an object.	Goodall 1986:560
Drag-branch	Dragging a large branch while running, as part of an aggressive display.	
Leaf-sponge	Wad of leaves/vegetation chewed and used to collect water, then squeezed into mouth.	Goodall 1964
Branch-shake	A branch is shaken to attract attention, such as in courtship.	Goodall 1968:217
Nasal probe	Use of a small stick to clear the chimpanzees own block nasal passage.	Nishida and Nakamura 1993
comb	A leaf stem is used to comb through body hair.	
Insect-pound	Probe used to retrieve insect by prodding it.	Sugiyama and Koman 1979
Resin-pound	Probe used to obtain resin by pounding it.	Sugiyama and Koman 1979
Branch-hook	Branch with twig(s) used to catch and pull closer another branch.	Sugiyama and Koman 1979
Perforate	Stout stick used to make probing holes in termite nests (termites then extracted with smaller probes).	Jones and Sabater Pi 1969; McGrew et al. 1979; Suzuki et al. 1995
Dig	Use of a stick as spade to dig away part of a (termite) nest mound	Jones and Sabater Pi 1969; McGrew et al. 1979; Suzuki et al. 1995
Brush-stick	Use of a stick for digging, making the end brush like. Tools identified but behaviour not observed; probably for termite digging and/or termite catching; "brush end 2-10 cm wide.	Sugiyama 1985
Seat-stick	Branch broken from a tree and sat upon (to provide protection from an uncomfortable surface).	Alp 1997:48
Stepping-stick	Branch broken from a tree and placed under the sole of the foot as protection.	Alp 1997:48
Container	Leaves used to catch/hold material.	Goodall 1986:546
Leaf-mop	Leaves used to mop up insects.	Nishida 1973:364
Leaf-wipe	Leaves used to wipe out food from skulls, fruits.	Boesch and Boesch 1990
Leaf-brush	Leaves used to brush bees, etc. away from an entrance surface.	Goodall 1986
Open-and-probe	Use of strong tools to probe and harvest food (chiseling and gouging followed by dipping; perforating followed by fishing.	Brewer and McGrew 1990; Suzuki et al. 1995; see also Sugiyama 1997
Sponge push-pull	Use of a stick to push leaf-sponge into a hole and withdraw it.	Matsuzawa 1991, cited by Sugiyama 1997
Algae-scoop	Use of a stem, stripped of leaves, to scoop surface vegetation like algae from water surface.	

Appendix B: Tool-Using Behaviors (Adapted from Whiten et al. 2001, Table 1) - Continued

Behavior	Description	Source
Anvil-prop	Putting a small stone under one end of an anvil stone to keep it more level.	Matsuzawa 1994
Nut-hammer, wood hammer/wood anvil	Use of a piece of wood to crack nuts on a wooden anvil (e.g. tree root).	Boesch and Boesch 1983
Nut-hammer, wood hammer/stone anvil	Use of a piece of wood to crack nuts on a stone anvil.	
Nut-hammer, stone hammer/wood anvil	Use of a piece of stone to crack nuts on a wooden anvil.	
Nut-hammer, stone hammer/stone anvil	Use of a piece of stone to crack nuts on a stone anvil.	
Nut-hammer, other	Same as above, but using alternate materials (e.g. hard ground as anvil).	
Pestle pound	Palm petiole used to pound and deepen hole in crown of palm tree.	Yamakoshi and Sugiyama 1995
Club	Striking forcefully with one end of a stick, the other held in the hand.	Kortland and Kooij 1963
Termite fishing using leaf midrib	Leaf midrib used to extract termites from tunnel.	Goodall 1964; McGrew et al. 1979
Termite fish using non-leaf materials	Probing instrument, sometimes modified, used to extract termites from tunnel.	Goodall 1964
Ant-fish	Probes used to extract arboreal ants from tunnels.	Nishida 1973; Nishida and Hiraiwa 1982
Ant-dip-wipe	Use of wand to collect safari ants that swarm up it, ants then manually wiped off in a cluster and eaten.	McGrew 1974; see also Goodall 1968
Ant-dip	Use of stick to collect safari ants that swarm up it, ants then picked off with lips and eaten.	Boesch 1996; see also Sugiyama et al. 1988
Fluid dip	Use of probe to extract fluid, including honey.	Boesch and Boesch 1990:89
Bee probe	"First tests for the presence of adults by probing the nest entrance with a stick. If present, adult bees block the entrance with their abdomens, ready to sting. The chimpanzee then disables them with the stick to make them fall out and eats them rapidly."	Boesch and Boesch 1990:89
Marrow-pick	Use of probe to extract contents of bone/skull.	Boesch and Boesch 1990:90
Expel/stir	Vigorous insertion, probing and removal of stick used in attempt to expel or stir up insects or other animals in hole.	Nishida 1973:364
Seat-vegetation	A few large, detached leaves placed on the ground and sat upon.	Hirata et al. 1998
Fly-whisk	Leafy twig used to fan away flies.	Sugiyama 1969:216
Self-tickle	An object is used to probe ticklish areas on self.	Goodall 1986:559

Appendix B: Tool-Using Behaviors (Adapted from Whiten et al. 2001, Table 1) - Continued

Behavior	Description	Source
Aimed-throw	Throwing of object with clear (even if inaccurate) tendency to aim.	Goodall 1964; Sugiyama and Koman 1979
Leaf-napkin	Leaves used to clean body surface.	Goodall 1964
Leaf-dab	Wound inspected by touching leaves to it, then examining leaves (leaves may be chewed).	Wrangham, unpublished
Leaf-groom	Chimpanzee picks up one or more leaves and grooms them, sometimes while lip smacking.	Goodall 1986:391; Goodall1968; Nishida 1980
Leaf-clip, mouth	Noisy ripping of leaf with mouth, to gain attention.	Nishida 1980
Leaf-clip, fingers	Noisy ripping of leaf with fingers, to gain attention.	Nishida 1980
Leaf-strip	"Leaves torn off stem by fingers, generally by thumb and fingers encircled around stem and swept off end of stem in violent move that tears at several or many leaves simultaneously."	Wrangham, unpublished
Leaf-squash	Squashing of ectoparasites on leaves used in leaf groom.	Boesch 1995
Leaf-inspect	Ectoparasite placed on leaf on palm of hand, visually inspected, then eaten or discarded.	Assersohn, unpublished
Branch slap	Sitting on and slapping a branch with a hand to attract another's attention. May be used in courtship.	
Shrub bend	Putting stems under foot and squashing to attract attention of potential mating partner.	Nishida 1997:385
Rain dance	At the start of heavy rain, several adult males perform vigorous charging displays. Displays tend to return the males to their starting position, to be coordinated or in parallel, may include slow charges as well as rapid, and may involve a variety of display patterns. May include objects.	Goodall 1971; Schumaker et al. 2011; Wrangham unpublished

APPENDIX C: CLIMATE DATA

Appendix 2.1: Mean Monthly Preciptiation, Minimum Temperatures, and Maximum Temperatures at Assirik, 1976-1979 (from McGrew et al. 1981)

	1976			**1977**			**1978**			**1979**		
	Percip	**Min temp**	**Max temp**	**Percip**	**Min temp**	**Max temp**	**Percip**	**Min temp**	**Max temp**	**Percip**	**Min temp**	**Max temp**
January				0.00	23.10	35.10	0.00	23.70	36.30	0.00	23.10	36.30
February		23.70	36.60	0.00	23.70	39.00	0.00	22.80	39.30	0.00	23.70	39.30
March	0.00	23.70	36.60	0.00	25.20	39.90	0.00	23.70	38.70	0.00	25.80	38.40
April	33.00	23.70	38.10	1.00	27.60	39.90	0.00	26.40	41.40	0.00	25.80	41.40
May	64.00	24.60	38.10	52.00	26.70	39.90	30.00	26.40	40.20	69.00	26.70	39.60
June	87.00	25.80	36.30	140.00	24.60	33.30	156.00	24.60	34.80	183.00	24.60	33.60
July	169.00	24.30	32.40	147.00	24.60	31.80	331.00	23.70	31.80	171.00	24.60	32.70
August	154.00	24.30	32.40	170.00	23.70	31.80	297.00	23.70	28.80	239.00	23.70	30.60
September	195.00	24.30	32.40	278.00	23.70	30.60	269.00	23.70	30.60	93.00	23.70	31.80
October	154.00	24.60	31.80	36.00	23.70	32.70	130.00	23.70	31.80	119.00	23.70	32.70
November	34.00	21.60	31.80	0.00	20.70	35.40	0.00	20.70	33.60	5.00	21.60	34.80
December	1.00	21.00	33.60	0.00	22.80	35.40	11.00	20.10	33.60	0.00	22.80	35.70
Total:	891.00			824.00			1224.00			879.00		
Mean:	89.10	23.78	34.55	68.67	24.18	35.40	102.00	23.60	35.08	73.25	24.15	35.58
SD:	73.44	1.37	2.58	92.84	1.80	3.50	130.57	1.86	4.09	86.90	1.43	3.47
Range:	195.00	4.80	6.30	278.00	6.90	9.30	331.00	6.30	12.60	239.00	5.10	10.80
Median:	75.50	24.30	33.60	18.50	23.70	35.25	20.50	23.70	34.20	37.00	23.70	35.25

Appendix 2.2: Mean Rainfall and Temperature at Bossou, 1996-1998. From Matsuzawa et al. (2011, Appendix C)

	1996 Rainfall	1997 Rainfall	1998 Rainfall	Mean Temp	PI
January	18.30	58.00	0.00	25.83	-2
February	125.90	0.00	9.90	27.58	-1
March	166.50	88.00	103.50	28.05	1
April	124.60	168.80	212.20	27.33	1
May	172.70	241.60	191.50	26.9	2
June	316.80	432.20	266.90	25.67	2
July	300.90	315.50		24.78	2
August	286.10	428.50		25.13	2
September	460.40	298.90		25.15	2
October	188.30	143.30		25.33	1
November	19.40	96.50		25.23	-0.5
December	60.00	33.60		24.67	-2
Total:	2239.90	2304.90	784.00	N/A	7.5
Mean:	186.66	192.08	130.67	25.97	0.63
SD:	133.25	149.40	110.73	1.17	1.58
Range:	442.10	432.20	266.90	3.38	4
Median	169.60	156.05	147.50	25.5	1

Mean Monthly Rainfall, Minimum Temperature, Maximum Temperature and Perhumidity Index at Budongo from 1993-2000. From Reynolds (2005)

Month	Mean Percipitation (mm)	Mean Min. Temp	Mean Max. Temp	Mean Temp	PI
January	42.00	22.20	31.20	26.70	-2
February	37.00	20.70	31.20	25.95	-2
March	97.00	21.90	29.10	25.50	-1
April	202.50	21.90	27.30	24.60	2
May	170.00	21.30	27.30	24.30	1
June	100.00	21.00	26.40	23.70	1
July	139.50	20.40	24.90	22.65	1
August	126.00	19.80	25.20	22.50	1
September	197.50	19.80	26.40	23.10	1
October	258.00	21.00	26.40	23.70	2
November	184.00	21.60	29.40	25.50	1
December	106.50	21.60	31.20	26.40	1
Total:	1660.00	N/A	N/A	N/A	6.00
Mean:	138.33	21.10	28.00	24.55	0.5
SD:	66.69	0.80	2.34	1.17	1.38
Range:	221.00	2.40	6.30	3.38	4
Median:	132.75	21.15	27.30	25.50	1

Mean Monthly Rainfall and Perhumidity Index at Gombe from 1973-1975 and 1978. From Goodall (1986)

Month	1973	1974	1975	1978	PI
November	390.00	210.00	170.00	435.00	2
December	270.00	280.00	255.00	345.00	1
January	140.00	270.00	170.00	300.00	2
February	130.00	130.00	140.00	380.00	2
March	140.00	230.00	140.00	360.00	1
April	175.00	300.00	20.00	585.00	-1.5
May	190.00	160.00	80.00	50.00	-2
June	5.00	40.00	5.00	50.00	-2
July	4.00	30.00	20.00	4.00	-2
August	3.00	3.00	3.00	4.00	1
September	2.00	30.00	15.00	15.00	2
October	60.00	90.00	175.00	90.00	2
Total:	1509.00	1773.00	1193.00	2618.00	5.5
Mean:	125.75	147.75	99.42	218.17	0.46
SD:	121.25	108.86	86.08	203.75	1.78
Range:	388.00	297.00	252.00	581.00	4
Median:	135.00	145.00	110.00	195.00	1

Mean Monthly Rainfall, Temperature and Perhumidity Index at Port Royal. From Wing and Bus (1970)

Month	Mean Percip.	Mean Temp	PI
January	33.02	20.64	-2
February	73.66	21.28	-1
March	136.14	20.94	1
April	185.17	20.64	1
May	143.76	19.68	1
June	83.31	20.00	-0.5
July	59.44	20.48	-1
August	117.60	21.60	1
September	192.28	12.48	1
October	212.34	20.16	2
November	163.32	21.28	1
December	74.42	20.32	-0.5
Total:	1474.46	N/A	3.00
Mean:	122.87	19.96	0.25
SD:	58.32	2.42	1.20
Range:	179.324	9.12	4
Median:	126.873	20.56	1

Mean Rainfall, Minimum Temperature, and Maximum Temperature at Kibale from 1976-1978. From Ghiglieri (1984)

	1976			**1977**			**1978**		
Month	Rainfall	Min. temp	Max. temp	Rainfall	Min. temp	Max. temp	Rainfall	Min. temp.	Max. temp
January	141.56			57.00	15.36	27.20	39.00	14.40	25.60
February				78.00	16.00	28.16	153.00	12.16	28.80
March				141.00	15.36	28.80	69.00	14.00	25.60
April				153.00	14.40	26.56	255.00	14.40	27.20
May				84.00	15.36	24.96	132.00	14.40	24.00
June				207.00	16.00	24.00			
July				54.00	16.00	24.96			
August				162.00	16.00	27.20			
September				153.00	15.36	9.60			
October				192.00	15.36	24.96			
November				231.00	16.00	26.56			
December	57.00	14.40	25.26	138.00	14.40	27.20			
Total:	57.00	N/A	N/A	1650.00			648.00	N/A	N/A
Mean:	N/A	14.40	25.26	137.50	15.47	25.01	129.60	13.87	26.24
SD:	N/A	N/A	N/A	53.38	0.58	5.06	83.90	0.97	1.82
Range:	N/A	N/A	N/A	177	1.60	19.20	216.00	2.24	4.80
Median	N/A	N/A	N/A	147	15.36	26.56	132.00	14.40	25.60

Mean Monthly Rainfall and Perhumidity Index at Lopé Reserve from 1984-1990. From Tutin and Fernandez (1993)

Month	1984	1985	1986	1987	1988	1989	1990	PI
January	18.00	72.00	63.00	18.00	85.50	126.00	85.50	-1.00
February	94.50	40.50	126.00	121.50	126.00	58.50	157.50	1.00
March	234.00	171.00	180.00	202.50	157.50	220.50	234.00	1.00
April	148.50	207.00	229.50	216.00	135.00	99.00	117.00	1.00
May	324.00	207.00	135.00	139.50	148.50	198.00	157.50	1.00
June	166.50	3.15	54.00	3.15	193.50	63.00	31.50	-0.50
July	40.50	4.50	0.00	3.15	0.00	0.00	0.00	-2.00
August	90.00	18.00	0.00	3.15	1.58	0.00	0.00	-2.00
September	99.00	90.00	18.00	126.00	36.00	58.50	157.50	-1.00
October	198.00	355.50	216.00	315.00	414.00	252.00	256.50	2.00
November	157.50	306.00	148.50	144.00	369.00	351.00	247.50	2.00
December	130.50	126.00	54.00	81.00	193.50	108.00	229.50	1.00
Total:	1701.00	1600.65	1224.00	1372.95	1860.08	1534.50	1674.00	2.50
Mean:	141.75	133.39	102.00	114.41	155.01	127.88	139.50	0.21
SD:	84.33	117.78	81.55	98.88	129.22	107.22	94.08	1.44
Range:	306.00	352.35	229.50	311.85	414.00	103.50	256.50	4.00
Median:	139.50	108.00	94.50	123.75	141.75	351.00	157.50	1.00

Monthly Rainfall and Perhumidity Index at Mahale Mountains, Kansyana Camp 1975-1988. Nishida 1990 Table A.1a

Year	January	February	March	April	May	June	July	August	September	October	November	December
1975					26.10	4.90	2.90	0.00	83.60	118.30	129.60	203.00
1976	147.3	195.6	212.9	238.3	66.4	0	0	6.8	11.8	96.3	539.5	278.1
1977	330.6	140.3	169.1	461.8	104.1	2.1	0	0	2.8	101.6	310.3	384.8
1978	209	140.3	227.6	187.2	14.8		0	37.4	61.2	288.7	336.8	400.5
1979	212.1	176.3	305.8	447.1	170.6	0	0	0	0	78.3	247.4	259
1980	320.9	335.2	131.9	210.3	78.7	0	0	0	87.9	82.3	268.7	379
1981	184.9	153	380.4	255.8	78.7	0	0	13.5	0	39.5	110.3	318.9
1982	147.1	199.4	259.9	267	146.7	0	0	0	30.4	239.8	395	377.4
1983	169.4	100	546.5	381.4	20	0	0	54.4	2.6	222	279.2	276.2
1984	218.8	168.8	287.4	212.9	22.5	0	0	0	1.7	86.5	406.8	251.5
1985	306	322.1	345.5	255.8	56.1	0	0	5	8	3.6	256.8	354.3
1986	203.3	322.7	359.6	245.8	135.5	2.5	0		68.6	130.4	318.1	322.4
1987	389	155.4	395.1	405	48.8	0	0	0	87.8	173.5	193.7	255
1988	211.4	146.1	202.3	264.1	0	2.1	0	5.1	5.1	110.5	240.9	307.4
Mean	234.60	196.55	294.15	294.81	69.21	0.89	0.21	9.40	32.25	126.52	288.08	311.96
PI	2.00	1.00	1.00	1.00	-0.50	-2.00	-2.00	-2.00	-1.00	1.00	2.00	2.00
SD	76.66	78.46	112.18	94.21	53.27	1.55	0.78	17.05	36.67	78.88	112.13	60.70
Range	241.9	235.2	414.6	274.6	170.6	4.9	2.9	54.4	87.9	285.1	429.2	197.5
Median	211.4	168.8	287.4	255.8	61.25	0	0	0	9.9	106.05	273.95	313.15

Monthly Mean Daily Minimum Temperature °C at Mahale Mountains, Kansyana Camp, 1976-1988 Nishida 1990 Table A.4b

Year	January	February	March	April	May	June	July	August	September	October	November	December
1976												18.6
1977	18.4	18.7	19.2	19.1	18.4	16.5	15.6	17	18.5	19.8	20.3	19.2
1978	19.5	19.3	19.3	19.6	18.5	16.3	15.4	16.6	18.1	18.3	18.8	18.8
1979	19.5	19.1	18.7	19.4	18.5	16.3	15.3	16.3	17.4	19	19.5	19.3
1980	19.5	19.3	19.4	19.7	19	17	16.3	17.6	18.4	19.2	18.9	18.9
1981	19.1	18.9	19	19.3	18.3	16.7	16	17.3	18.3	19.7	19.3	18.9
1982	19	19	18.8	19.2	19.2	17.4	15.8	16.6	18.2	19.2	18.6	19.4
1983	19.3	19.9	19.8	19.9	19.5	17.5	16.8	17.5	17.6	18.7	18.5	18.4
1984	18.4	18.7	18.7	18.8	18	16.3	16.3	16.3	17.2	18.6	18.7	18.6
1985	18.8	18.7	19	19.1	18.3	16.1	15.4	16.5	17.8			
1986	18.9	18.3	18.5	19.3	18.6	15.9	14.7		17.4	20	19.5	19.1
1987	18.7	19	19.4	19.4	19.4	16.5	15.9	17.3	19		19.3	19.3
1988	19	19.2	19.3	19.5	18.2	17.4	16.5	17.4	17.8	19.1	18.8	18.5
Mean	19.01	19.01	19.09	19.36	18.66	16.66	15.83	16.95	17.98	19.16	19.11	18.92
SD	0.39	0.41	0.38	0.30	0.49	0.54	0.59	0.50	0.53	0.55	0.53	0.34
Range	1.10	1.60	1.30	1.10	1.50	1.60	2.10	1.30	1.80	1.70	1.80	1.00
Median	19.00	19.00	19.10	19.35	18.50	16.50	15.85	17.00	17.95	19.15	18.90	18.90

Monthly Mean Daily Maximum Temperature °C at Mahale Mountains, Kansyana Camp, 1976-1988 Nishida 1990 Table A.4a

Year	January	February	March	April	May	June	July	August	September	October	November	December
1976												27.3
1977	27.5	28.2	27.9	26.7	27.1	27.5	28.1	29.3	31.4	32.7	30.2	28.7
1978	28.2	28	28.6	27.7	28.5	28.7	28.4	30	31.4	31.6	27.3	27.3
1979	28.1	28.5	28.9	26.9	28.4	27.7	28.5	31.1	33.8	31.6	29.1	28.8
1980		26.1	27	26.7	27.5	28.9	28.3	28.5	28.4	28.6	26.8	25.9
1981	26.6	27.5	25.5	26.3	26.7	27	26.8	28.3	30.3	31.1	29.4	26.8
1982	27.5	26.8	27	26.6	26.9	28.2	28.7	31	31.9	29	27	27.4
1983	28.2	29.9	28.9	28.3	28.3	29.5	30	29.3	32.1	29.4	29	27.7
1984	27.8	28	28.3	28.8	30.3	29.3	29.4	31.1	31.6	30.2	27	26.9
1985	27.1	27.3	28.1	28.9	31	31.7	31	32.1	30.6			
1986	27.8	28.5	28.1	30.1	30.6	30.9	30.7		31.6	29.5	26.8	24.7
1987	27	27.9	27.9	29	31.5	32.8	32.7	33	33		28.5	27.9
1988	27.3	28.8	30.4	31	33.5	33.6	32.6	32.3	33.5	32.5	27.7	26.1
Mean	27.55	27.96	28.05	28.08	29.19	29.65	29.33	30.55	31.63	30.62	28.07	27.13
SD	0.52	0.98	1.21	1.52	2.15	2.14	1.66	1.58	1.47	1.48	1.21	1.17
Range	27.68	3.80	4.90	4.70	6.80	6.60	5.90	4.70	5.40	4.10	3.40	4.10
Median	27.50	28.00	28.10	28.00	28.45	29.10	29.05	31.00	31.60	30.65	27.70	27.30

Mean Minimum Temperatures at Mahale Mountains, Myako Camp 1975-1984. Nishida 1990 Table A.5b

Year	January	February	March	April	May	June	July	August	September	October	November	December
1977									22.00	23.00	21.10	20.80
1978	21.20	21.30	20.50	21.20	20.70	19.60	18.60	20.10	21.10	21.20	20.40	20.70
1979	21.00	21.10	20.80	20.80	20.40	19.10			20.60	21.50	20.90	20.30
1980	20.80	20.90	20.20	20.60	20.50	18.70	18.90	19.70	20.90	21.20		20.50
1981	20.60	20.60	20.90	21.20								
1982	21.30	21.20	21.20	20.80	20.50	19.80	20.70	21.50		21.90	21.00	21.80
1983	21.30	22.00	21.80	21.40	21.60	20.70	20.10	20.70	21.40	21.00	20.90	20.50
1984	20.30	20.80	20.80	20.80	21.40	20.50	19.80	20.20	21.30	21.70	20.70	21.00
Mean	20.93	21.13	20.89	20.97	20.85	19.73	19.62	20.44	21.22	21.64	20.83	20.80
SD	0.38	0.45	0.51	0.29	0.52	0.78	0.86	0.69	0.48	0.68	0.25	0.50
Range	1	1.4	1.6	0.8	1.2	2	2.1	1.8	1.4	2	0.7	1.5
Median	21	21.1	20.8	20.8	20.6	19.7	19.8	20.2	21.2	21.5	20.9	20.7

Mean Maximum Temperatures at Mahale Mountains, Myako Camp 1977-1984. Nishida 1990 Table A.5b

Year	January	February	March	April	May	June	July	August	September	October	November	December
1977									34.40	33.80	30.70	30.70
1978	31.10	31.30	30.40	30.40	33.30	32.50	31.50	31.80	31.40	31.60	27.30	27.30
1979	31.70	31.10	30.50	30.50	31.60	31.10			34.00	33.60	30.40	31.20
1980			29.20	29.20	28.80	30.00	30.30	31.00	31.60	29.70		25.90
1981	26.40	28.40	27.60	27.60	29.20	30.80	30.70	30.80	33.30			
1982		28.80	28.50	28.50	29.40	31.60	31.20	32.30	32.40	31.10	26.70	26.70
1983	27.20	28.90	28.40	28.40	30.70	32.00	32.20	31.70	33.30	30.90	26.80	26.80
1984	27.00	27.30	28.50	28.50	31.40	31.10	30.80	32.10	34.00	33.00	27.00	
Mean	28.68	29.30	29.01	29.01	30.63	31.30	31.12	31.62	33.05	31.96	28.15	28.10
SD	2.51	1.58	1.09	1.09	1.61	0.82	0.67	0.60	1.13	1.54	1.87	2.26
Range	5.30	4.00	2.90	2.90	4.50	2.50	1.90	1.50	3.00	4.10	4.00	5.30
Median	27.20	28.85	28.50	28.50	30.70	31.10	31.00	31.75	33.30	31.60	27.15	27.05

Mean Monthly Rainfall, Minimum Temperature, and Maximum Temperatures, Tai Forest. From Anderson and Nordheim (1995)

	1995			**1996**			**1997**			**1998**			**1999**		
Month	Percip.	Mean min	Mean max	Percip.	Mean min	Mean max	Percip.	Mean min	Mean max	Percip.	Mean min	Mean max	Percip.	Mean min	Mean max
January				0.69	21.50	31.50	126.00	21.75	30.50	3.50	22.00	32.75	22.50	21.25	30.75
February				126.00	22.00	34.25	36.00	22.25	33.75	58.50	23.50	34.25	144.00	21.50	31.50
March				171.00	22.25	33.25	193.50	22.25	33.50	63.00	24.50	33.00	81.00	22.25	33.50
April				261.00	22.75	30.75	103.50	22.25	31.25	220.50	23.00	31.50	130.50	22.25	31.25
May				207.00	22.00	30.50	207.00	22.25	31.25	189.00	22.75	30.75	216.00	22.00	30.00
June				216.00	21.75	28.50	189.00	22.00	27.75	211.50	22.25	29.25	274.50	22.00	28.75
July	189.00	22.00	28.50	346.50	21.50	27.75	27.00	22.00	27.75	157.50	22.00	28.00	207.00	21.25	28.50
August	319.50	22.25	28.50	324.00	22.00	28.00	202.50	22.25	28.00	67.50	22.00	27.75	90.00	21.50	28.50
September	288.00	22.25	29.50	126.00	22.00	28.75	243.00	22.75	29.25	396.00	22.25	28.75	193.50	22.00	29.25
October	382.50	21.75	30.00	247.50	22.00	29.25	139.50	22.25	30.50	261.00	22.50	30.00	94.50	22.00	30.50
November	99.00	21.50	30.00	139.50	22.25	28.75	189.00	22.00	30.00	202.20	22.00	30.00	189.00	21.50	30.00
December	139.50	21.50	30.50	58.50	22.25	28.75	13.50	19.25	30.50	54.00	21.50	30.50	81.00	21.25	29.50
Sum:	1417.50			2223.69			1669.50			1884.20			1723.50		
Mean:	236.25	21.88	29.50	185.31	22.02	30.00	139.13	21.94	30.33	157.02	22.52	30.54	143.63	21.73	30.17
SD:	110.84	0.34	0.84	102.57	0.34	2.09	78.49	0.88	1.99	112.30	0.82	2.03	73.18	0.39	1.46
Range:	283.50	0.75	2.00	345.81	1.25	6.50	229.50	3.50	6.00	392.50	3.00	6.50	252.00	1.00	5.00
Median:	238.50	21.88	29.75	189.00	22.00	29.00	164.25	22.25	30.50	173.25	22.25	30.25	137.25	21.75	30.00

Mean Rainfall and Perhumidity Index at Tai Forest

Year	January	February	March	April	May	June	July	August	September	October	November	December
1995							189.00	319.50	288.00	382.50	99.00	139.50
1996	0.69	126.00	171.00	261.00	207.00	216.00	346.50	324.00	126.00	247.00	139.50	58.50
1997	126.00	36.00	193.50	103.50	207.00	189.00	27.00	202.50	243.00	139.50	189.00	13.50
1998	3.50	58.50	63.00	220.50	189.00	211.50	157.50	67.50	396.00	261.00	202.00	54.00
1999	22.50	144.00	81.00	130.50	216.00	274.00	207.00	90.00	193.50	94.50	189.00	81.00
Mean	38.17	91.13	127.13	178.88	204.75	222.63	185.40	200.70	249.30	224.90	163.70	69.30
PI	-2.00	-1.00	1.00	1.00	2.00	2.00	1.00	2.00	2.00	2.00	1.00	-0.50