

**A Comparison of tool using behaviour between Chimpanzees (*Pan troglodytes*) and Bonobos (*Pan paniscus*)**

**Abstract**

Chimpanzees and bonobos differ with regards to social structure, aggressive tendencies and the frequency of tool use. Chimpanzees demonstrate extensive tool usage, predominately during food acquisition, whereas bonobos show limited tool use and most often the behaviour is self directed, such as during the use of leaf rain hats. Bonobos have not been observed to use tools associated with subsistence. Conversely, chimpanzees use tools to fish for insects, to crack nuts and to obtain water. Captive chimpanzees and bonobos express similar tool using behaviour. Differences in wild habitat ecology may explain the varying tool usage between these species as bonobos experience less resource competition thus they do not need to exploit hard-to-get food by using tools. Reduced competition may also be the underlying reason for the diminished aggression seen in bonobos compared to violent-behaviour witnessed in chimpanzees.

**Introduction**

The differing behavioural activity and social dynamics between chimpanzees and bonobos has been well documented (De Waal, 1997; Stanford, 1998), especially with regards to the influence of their habitats and their contrasting aggressive tendencies. Particularly, the use of tools provides an interesting illustration of the differences in behaviour between these two primates, both in wild populations and captive groups.

Goodall (1986) defines a tool as an object that must be “held in the hand, foot or mouth and used in such a way as to enable the operator to attain an immediate goal”. Tools are used by primates to acquire food and also to complete non-subsistence objectives, such a hygiene and dentistry (McGrew, 1992). Chimpanzees demonstrate a large range of tool use by this definition, including “hammer and anvil” nut cracking (McGrew, 1992; Boesch et al., 1994), termite-fishing/ant dipping (Goodall, 1986; Boesch et al., 1990; McGrew, 1992) and pestle-pounding (Yamakoshi, 1995). The vast array of tool use is displayed in Table 1.

The list of tool usage in *Pans paniscus* is not as extensive as for *Pans troglodytes*, however in captivity twig probes, ladder props, water carriers and sponges have been observed (Jordon, 1982) and stone-tool making has be recorded (Toth et al., 1993; Schick et al., 1999). In wild populations leafy twigs have been used as tools to protect against rainfall (Kano, 1982; Ingmanson, 1996) along with leaf-sponge usage, tooth picks and tools to deter flies (Hohmann et al., 2003).

**Table 1:** The extensive range of tool use in wild chimpanzees

Tool Using Pattern	Source
Ant-dipping	Goodall (1986), Boesch et al. (1990)
Termite-fishing	Goodall (1986), McGrew (1992)
Leaf-sponges	Takeshita et al. (2001), Lanjouw (2002)
Leaf-napkin	Goodall (1986), Lanjouw (2002)
Hammer and anvil nut cracking	McGrew (1992), Boesch et al. (1994)
Pestle-pounding	Yamakoshi et al. (1995)
Honey fishing	Brewer et al. (1990)

### Study History

Chimpanzees have been the focus of many extensive field studies from the 1930s onwards, which encompass their range across Africa, as displayed in Table 2 (Goodall, 1986). Of these long-term projects, published studies by Goodall (1986), McGrew (1992) and Boesch et al. (1990, 2000) have made particular reference to the types of tool use observed. In contrast, research into bonobo behaviour only began during the mid-1970s and has been restricted to two sites in Zaire, Wamba and Lomako, which comprise the northern section of this species range (Ingmanson, 1996; Hohmann et al., 2003). Permanent research stations are present at these locations, allowing three un-provisioned groups at Lomako forest and five provisioned (when food, given at a fixed point, is used to attract apes into a clearing for closer range observations) groups at Wamba to be observed (McGrew, 1992).

**Table 2:** A selection of the major studies of chimpanzees carried out across Africa (From Goodall, 1986).

Country	Area	Date Study Commenced	Duration of Study
Guinea	Bossou	1968	Several months
Eastern Zaire	Beni	1960	Several months
Tanzania	Gombe National Park	1960	25 years (continuous)
Tanzania	Mahale Mountains	1966	19 years (continuous)
Uganda	Kibale Forest	1976	Several months
Ivory Coast	Tai Forest	1979	6 years
Gabon	Lope National Park	1983	2 years

Bonobo communities at Wamba and Lomako inhabit very similar forest habitats in close proximity and hence differences between each population are minimal (Boesch et al., 2002). This is due to the fact similar environments result in analogous adaptations from the species inhabiting them. Even so, there are some site-specific differences between each population, such as group size and social dynamics (Hohmann et al., 2002). Conversely, chimpanzees have been studied in many different forms of habitat across their distribution range and individual populations do display many differences in behaviour depending on the ecology of their environment (Goodall, 1986; McGrew, 1992; Boesch et al., 2000).

### Ecology and Distribution

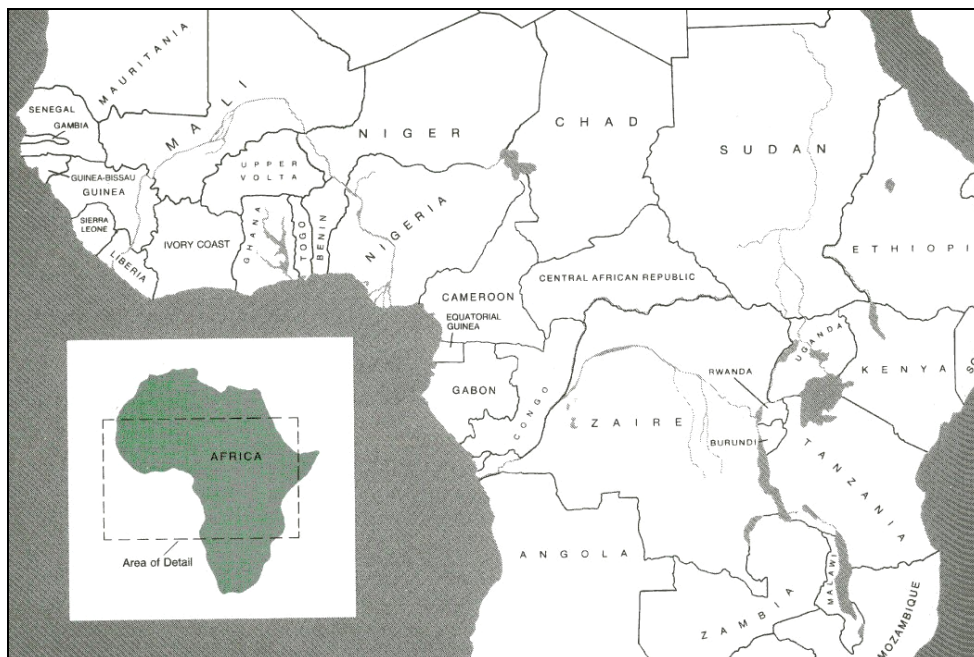
*Pan troglodytes* can be divided into three sub-species due to geographic variation in their habitats, as stated by McGrew (1992). These are *P. troglodytes schweinfurthii* (Eastern Africa, woodland living), *P. troglodytes troglodytes* (Central-western Africa, forest living) and *P. troglodytes verus* (Western Africa, savannah living). This is illustrated in Table 3, which depicts a selection of chimpanzee groups and the region they inhabit.

**Table 3:** Distribution of chimpanzee sub-species (Goodall, 1986; McGrew, 1992; Lanjouw, 2002)

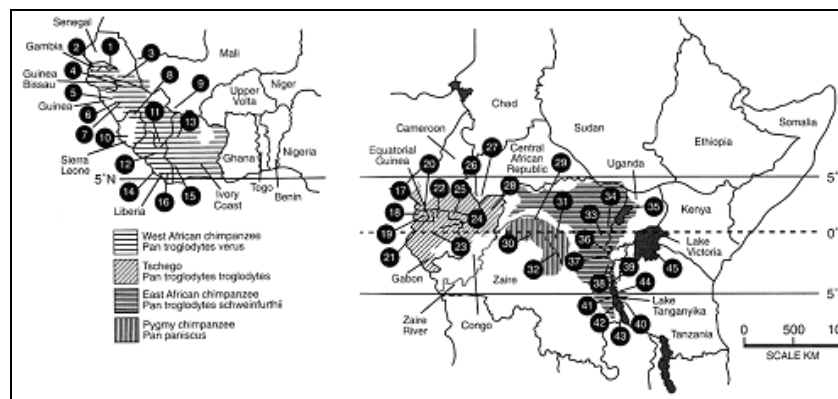
Area/Population	Country	Geographical Race	Habitat type
Beni	Zaire	<i>Pan troglodytes schweinfurthii</i> <b>(Eastern)</b>	Woodland
Budongo	Uganda		
Gombe	Tanzania		
Kasakati	Tanzania		
Kasoje	Tanzania		
Kibale (Mahale mountains)	Uganda		
Belinga	Gabon	<i>Pan troglodytes troglodytes</i> <b>(Central-Western)</b>	Forest
Campo	Cameroon		
Ipassa	Gabon		
Lope	Gabon		
Ndakan	Cental Africa Republic		
Okorobiko	Guinea		
Assirik	Senegal	<i>Pan troglodytes verus</i> <b>(Western)</b>	Savannah
Bossou	Western Guinea		
Tai	Ivory Coast		

In contrast, *Pan paniscus* distribution is limited to the Democratic Republic of Congo and they have only been studied in a small proportion of their geographical range, comprising of primary, swamp and secondary forest areas (Ingmanson, 1996; Boesch, 2002). Due to the shared ecology of the study environments (Wamba and Lomako) no sub-species of bonobos have yet been classified (Doran et al., 2002). The distribution range of *Pan paniscus* and *Pan troglodytes* across Africa is represented in Figure 1.

**Figure 1a:** The countries of Africa. Chimpanzees and Bonobos are endemic to this continent (From Goodall, 1986).

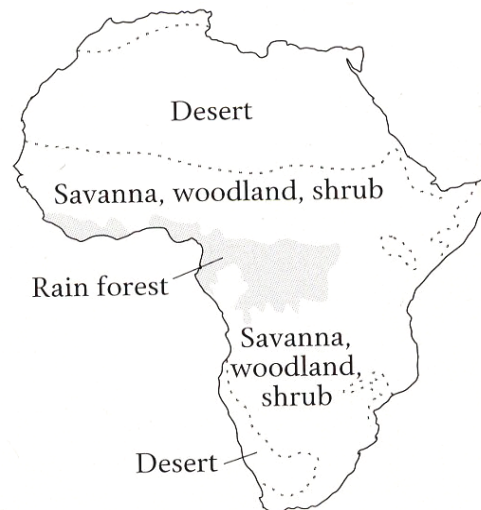


**Figure 1b:** The distribution of chimpanzees and bonobos across Western (left), Central Western and Eastern (right) Africa. The numbered arrows indicate the sites of study (From Chimpanzee Cultures, Study sites in Africa, 1994).



Bonobo populations were thought to only exist in habitats consisting of primary lowland forest within the Congo basin, as exemplified by the ecology at Wamba and Lomako, however recent studies such as Ingmanson (1996) and Myers-Thompson (2002) illustrated that bonobos appear in a wider range of environments. These include savannah and dry forest habitats similar to those of some sub-species of chimpanzee, in such sites as Lukuru in the southern periphery of the Congo Basin (Myers Thompson, 2002). Figure 2 illustrates how rainforest areas in Africa are buffered by savannah regions thus bonobos could potentially migrate to these areas.

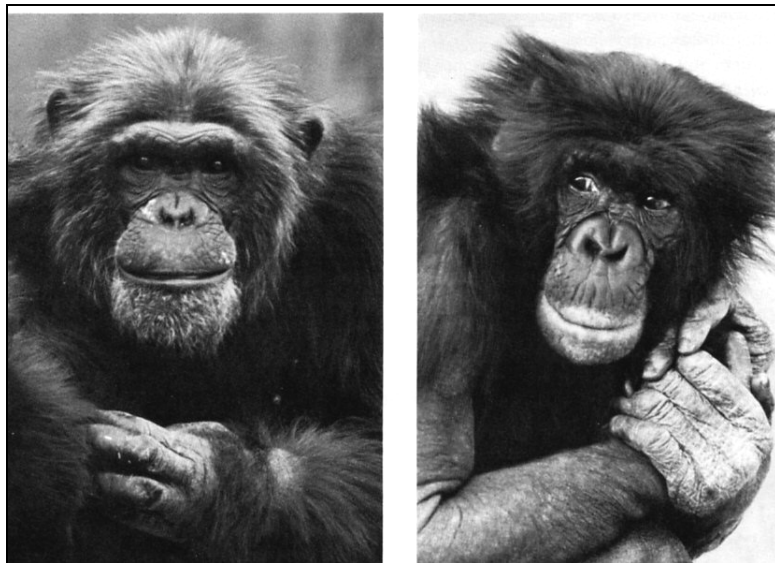
**Figure 2:** The distribution of forestation across Africa. Bonobos are mainly found in the rainforest regions whereas chimpanzees range across the continent (From De Waal, 1997).



Further field research into *Pan paniscus* may unearth populations that inhabit areas that have not as yet been included in the presently described bonobo distribution range. As stated by Hohmann et al. (2003) this may have implications regarding food availability, as social insects such as ants and termites become more accessible with increasing grassland, as opposed to dense forest habitats as seen in Wamba and Lomako. Future studies of bonobo populations in savannah habitats could investigate whether bonobos utilise these insect food sources, and if so tool usage similar to *Pan troglodytes* may be observed.

## Historical Context

Although fundamentally similar, *Pan troglodytes* and *Pan paniscus* differ morphologically in many ways, as described by De Waal (1997) and illustrated in Figure 2. Bonobos are gracile primates with slender shoulders, smaller heads and longer hair than seen in chimpanzees, which have thicker necks and broad, powerful shoulders. *Pan paniscus* have flatter faces compared to those of *Pan troglodytes*, with higher foreheads and wider nostrils. Chimpanzees and bonobos also differ with regards to posture, as epitomised by the elongated legs and elevated hips of the bonobo that allows a straighter upright position when walking or standing compared to the slightly sloped appearance of the chimpanzee. The bonobo was originally deceptively referred to as the “pygmy chimpanzee,” suggesting that this species is smaller than the “common chimpanzee”, when in fact there is a large over-lap in size between the two primates (De Waal, 1997).



**Figure 2:** Adult males of *Pan troglodytes* (left) and *Pan paniscus* (right). The bonobo has paler lips and a broader nose in comparison to the chimpanzee (From Wrangham et al., 1994).

De Waal (1997) offers a concise depiction of the history of the bonobo classification as a new primate species. He states that Bonobos were not recognised as a distinct species until 1929, when German anatomist Ernst Schwarz declared what was once thought to be the immature skull of a chimpanzee was in fact the adult skull of a new species. Behavioural scientists Robert Yerkes and Anton Portielje also deserve recognition in the discovery of *Pan paniscus* as they noted, during the early

1910s, that there were considerable differences between chimpanzees and museum specimens that are now known to have been bonobos (De Waal, 1997).

As a stark contrast to the relatively recent classification of the bonobo, the chimpanzee first arrived in Europe in 1640 to be presented to the Prince of Orange (Goodall, 1986). It was not until 1912 however that psychologist Wolfgang Kohler began an extensive study into the intellectual capabilities of *Pan troglodytes*, staging experimental scenarios in order to assess their problem solving ability, as cited in Goodall (1986). Tool construction and use was observed as solutions to various tasks, in particular linking sticks together to produce a long object capable of attaining out of range fruit. Chimpanzees were observed to use insight during problem solving, rather than just imitation behaviour. Therefore, the tool making capacity of chimpanzees were documented well before bonobos were even classified as a distinct taxonomic species.

### **Introduction to Tool Use**

Tool use occurs in chimpanzees predominantly when in the pursuit of food, usually to attain a difficult to access resource that cannot be reached by hand alone (McGrew, 1992; Yamakoshi, 2001). For example, twigs are used in honey fishing when the entry hole is too small for their fingers to obtain the resource (Brewer et al., 1990). However, no extensive tool using behaviour has been observed in *Pan paniscus* during their acquisition of food (Ingmanson, 1996). This could be due to the fact they inhabit a rich area abundant in resources, thus they have no real need to develop tools as food is relatively easy to obtain (Ingmanson, 1996; Doran et al., 2002; Myers Thompson, 2002).

This is epitomised by algae sweeping, where *Pan troglodytes verus* in Bossou use specialised tools to obtain an alga, which is similar to one ingested by Bonobos in Lukuru, allowing the chimpanzees to remain out of the water, as described by Myers Thompson (2002). This study states that, conversely, Bonobos do not use a tool to acquire the same type of resource, instead they employ an aquatic method of feeding by wading bipedally into the water waist deep, therefore no tool is needed to obtain the food so the behaviour has not developed.

## **Social Dynamics**

In order to investigate tool using behaviour in context, the diverse ecological and social-dynamic conditions experienced by chimpanzees and bonobos must be considered. Chimpanzees and bonobos demonstrate a fission-fusion social pattern where temporary groups are formed, in relation to food distribution and availability, comprising of a subsection of the community as a whole (Milton cited in Stanford, 1998; Boesch et al., 2000; Williams et al., 2002). A major difference between chimpanzees and bonobos is the social dynamics of their grouping. Bonobo groups are large and female biased whereas chimpanzee communities are small and male dominated (Hohmann et al., 2002). Females among chimpanzee societies hold equal status between each other, in contrast to the linear hierarchical structure of males, who use aggression to maintain their rank which is usually dictated by the alliances individuals have formed (Goodall, 1986). Adult males in chimpanzee groups are dominant to every female member, and will enforce punishment upon females that do not react appropriately in their presence (Wrangham et al., 1997).

Bonobos employ a more egalitarian system, with males and females sharing dominance, as exemplified by the alpha male and alpha female being co-dominant (Wrangham et al., 1997; Hohmann et al., 2002). However, female group members may collaborate to defend food resources from males (Hohmann et al., 2002) and high-ranking females can exclude males from food altogether (Williams et al., 2002), hence the power of females in bonobo societies is very evident. When food is less abundant female bonobos remain grouped and males will disperse; conversely female chimpanzees are less gregarious and spend a lower proportion of time in parties than males (Goodall, 1986; Hohmann et al., 2002; Williams et al., 2002).

## **Aggression**

Aggressive tendencies differ between chimpanzee and bonobo groups, particularly with regards to infanticide, access to females and territorial defence. High-ranking male chimpanzees demonstrate higher copulation rates with parous females (Muller, 2002) therefore the reproductive benefits of attaining social dominance may justify the increased energetic and risk-taking costs of aggression. Often, ally males work together to displace a higher-ranking male, a system referred to by Frans de Waal (1982) as “Chimpanzee politics”. He describes a constant power

battle between three adult males, Luit, Nikkie and Yeroen, in Arnhem zoo (Netherlands) that took place from 1974, culminating violently in 1980. The males continually challenged the dominance position of each other, forming alliances between themselves to do so. Nikkie and Yeroen form a strong alliance in 1980, aggressively displaying against Luit, who was then the alpha male, eventually releasing a ferocious attack that resulted in his death. De Waal described the enclosure “turned red with blood” after the attack (cited in Wrangham et al., 1997) and almost as a symbolic gesture of displaced dominance both testicles of Luit were found on the ground. Nikkie then became alpha male. This attack illustrates the aggressive nature of chimpanzees, even towards their own group members.

Intercommunity aggression is rife in chimpanzee groups, with border patrols employed by males that often result in aggressive confrontations for territorial defence (Goodall, 1986; Muller, 2002). Goodall (1986) describes how attacks comprise of hitting, kicking, stamping, biting, dragging and grappling, and often if size allows the victim is lifted bodily and slammed against the ground. A specialised manner of attack occurs when adult chimpanzees, mostly males, form coalitions and invade neighbouring territories, often with lethal consequences. Muller (2002) describes how a male was found dead in Kibale National Park (Uganda) after encountering 10 males on border patrol from the neighbouring territory of Kanyawara. The victim suffered horrific injuries mainly to the ventrum, including a severed trachea, and was found with limbs out-stretched implying members of the coalition immobilised him whilst others attacked.

In stark contrast male bonobos do not patrol territory borders, nor is there any current evidence that they invade neighbouring groups or perform intra-group killings or forced copulations (Wrangham et al., 1997). Hohmann et al. (2002) states that dominance relationships between males are established and reinforced by agonistic displays, however the intensity of aggression is far less than that of chimpanzees. Usually, bonobos resolve conflict non-aggressively in contrast to the elaborate violent displays of the chimpanzee. De Waal (1997) poetically describes this dichotomy in behaviour as “the chimpanzee resolves sexual issues with power; the bonobo resolves power issues with sex”. Sex is used by bonobos to make friends, calm tense conspecifics and as a form of reconciliation (Wrangham et al., 1997) whereas chimpanzees use sex predominantly for reproductive purposes (De Waal, 1997).

Male chimpanzees have the ability to detect ovulation in females as their genitalia swell, and they compete for mating opportunities predominately at that time (Goodall, 1986; Wrangham et al., 1997). Female chimpanzees endure violent attacks and forced copulations from males during the period of monthly swelling, and are most vulnerable to male aggression (Wrangham et al., 1997). In contrast, female bonobos possess power over males as they have inconspicuous ovulation, thus males do not know when it is beneficial to compete with each other so aggression is minimal and sex occurs most of the time.

Most aggressive behaviour in chimpanzees revolves around dominance acquisition in order to gain access to females (De Waal, 1997; Wrangham et al., 1997; Muller, 2002). Wrangham et al. (1997) suggests however the root of the differing aggressive behaviour between bonobos and chimpanzees lays in the “power of female alliances” in *Pan paniscus* societies, meaning that males cannot monopolise females, thus they rarely use brute force against them. Consequently competition for mates is decreased and violence between males is thus reduced.

### **Meat Eating and Hunting**

An interesting illustration of the differences in aggressive behaviour between Bonobos and chimpanzees is that of meat eating. The frequency of hunting and killing performed by each species could be viewed as an indicator of aggression as chimpanzees will readily kill monkeys for meat whereas bonobos do not exhibit such habitual brutal behaviour. Meat eating in Chimpanzees occurs throughout their geographical range, with the hunting and consumption of their predominant prey, the Red Colobus Monkey (*Colobus badius*), arising in Kibale, Tai, Gombe and Mahale populations (Stanford, 1998; Boesch et al., 2002). Tai chimpanzees kill approximately 125 colobus monkeys a year, giving a daily average meat consumption of 186 grams for males and 25 grams for females, and similarly Gombe chimpanzees consume an average of 80 colobus per year (Boesch et al., 2000). In fact, the Colobus population in Gombe was reduced by 30 percent each year for 20 years due to the prolific killing performed by chimpanzees (Wrangham et al., 1997) therefore the lust for hunting is high in this species.

Conversely, De Waal (1997) and Stanford (1998) suggest that bonobos rarely eat meat, even though their habitat is rife with forest monkeys, such as *Colobus* and *Cephalophus* species, which chimpanzees would actively prey upon. Fruth (cited in

Stanford, 1998) argues, however, that bonobos in Lomako do in fact kill adult *Cephalophus* species regularly, although the frequency of killing is less than in chimpanzee groups.

Sabater-Pi et al. (1993), whilst observing bonobos in the Lilungu region of Zaire, noted bonobo-instigated “playful” interspecific interactions between this species and other primates, in particular *Colobus angolensis*. In contrast to how chimpanzees interact with Colobus species (hunting them as prey (Goodall, 1986; Boesch et al., 2002)) these monkeys were described by Sabater-Pi as being “handled like dolls” by bonobos and not as prey items. The bonobos seemed to view the small monkeys as objects of interest, grooming and exploring their bodies and especially enjoying any increase in activity produced by the small primates.

To provoke the monkey “toys” to move their arms and legs and interact with them, bonobos were observed to lightly hit the monkeys, only becoming aggressive if they failed to respond. Sabater-Pi observed how the bonobos swung the monkeys by their tails and tossed them into the air, often disturbingly resulting in the monkeys hitting their heads against branches. Therefore, signs of aggression, resulting from frustration, are discernible within bonobo behaviour, even if it is not as explicitly displayed as within chimpanzee communities. De Waal (cited in Stanford, 1998) reinforces this idea by stating that “bonobos are by no means lacking in aggression”, particularly with reference to food competition, but no lethal intercommunity aggression or infanticide has been observed in the field.

Often, the bonobo’s over zealous interaction with the small monkeys resulted in their death yet there was no evidence to suggest that the bonobos ate the dead monkeys, as confirmed by the lack of bone and hair in the faeces of the group studied by Sabater-Pi et al. (1993). Chimpanzees however rarely leave meat that is available for consumption, with many group members, especially adolescents, scavenging on remnants left by other individuals (Boesch et al., 2000).

Differences in diet and ecology may be factors influencing the contrast in meat consumption between chimpanzees and bonobos, rather than just differences in aggressive tendencies. De Waal (1997) describes how bonobos primarily eat ripe large fruit, such as *Anonidium* species, which can weigh up to 10kg, usually after it has fallen onto the forest floor. He also states that terrestrial herbaceous vegetation (THV) comprises the second largest proportion of the bonobo diet and this is a rich source of protein. Due to the nature of this food, the need for addition protein from

animal meat is low, thus this may explain in nutritional terms why hunting and killing for meat is rare in *Pan paniscus*.

As stated by Wrangham et al. (1997) bonobos do like eating meat such as flying squirrels and infant antelopes, and are capable of catching monkeys, as observed by Sabater-Pi et al. (1993), yet predatory violence is reduced in bonobos compared to Chimpanzees, as is inter- and intra-community aggression. Chimpanzees and bonobos inhabit lowland forest on opposite sides of the Zaire River, and Wrangham et al. (1997) suggests bonobos can afford to be more “kindly” as they are not competing with gorillas for herbaceous food sources on their side of the river as chimpanzees have to do on theirs. As Malenky et al. (1994) state “bonobos are released from feeding competition” due to the absence of gorillas. Consequently bonobos can live in large, stable groups as competition for resources are reduced (thus aggression is reduced), and therefore the need to supply extra nutrients, through such actions as hunting, is unnecessary.

Stanford (1998) suggests a political undertone to meat eating for chimpanzees, where the sharing of kills is performed strategically to reinforce alliances and also in exchange for mating opportunities. Thus, the consumption of meat may actually be of value socially and not necessarily nutritionally, reinforced by the fact males consume the largest share of the meat, approximately 48% of captures in Tai populations, whereas those requiring extra nutrients, such as growing infants and nursing females, receive only 15% (Boesch et al., 2000).

Stanford (1998) also argues that meat consumption is less in bonobos as the manipulating-power associated with meat sharing for male chimpanzees does not apply to males in bonobo societies as females can take meat freely from them. Stanford (1998) implies there are no political connotations underlying the bonobos feeding system, yet Fruth (cited in Stanford, 1998) suggests bonobos do use food sharing as a political tool; however they use *Anonidium* fruit as opposed to meat. Fruth argues that Stanford’s view of bonobos lacking “social or political ceremonies” based on the infrequent meat consumption is misinterpreted, and in fact in the same way chimpanzee meat-sharing is socially important, fruit-sharing has significant political value in bonobo societies too.

Although meat and fruit seem to play a similar role in social politics for chimpanzees and bonobos respectively, it is interesting to contrast the methods of obtaining each food item and how this reflects the nature of each species.

Chimpanzees brutally hunt down their prey, echoing their aggressive nature, whereas bonobos will gain fruit from the forest floor and thus obtain an important social tool in a non-aggressive way. This reiterates the notion of the bonobo nature to “make love not war” in contrast to chimpanzees being “red in tooth and claw” (Milton, cited in Stanford, 1998).

### **Tool Use => Levels of association**

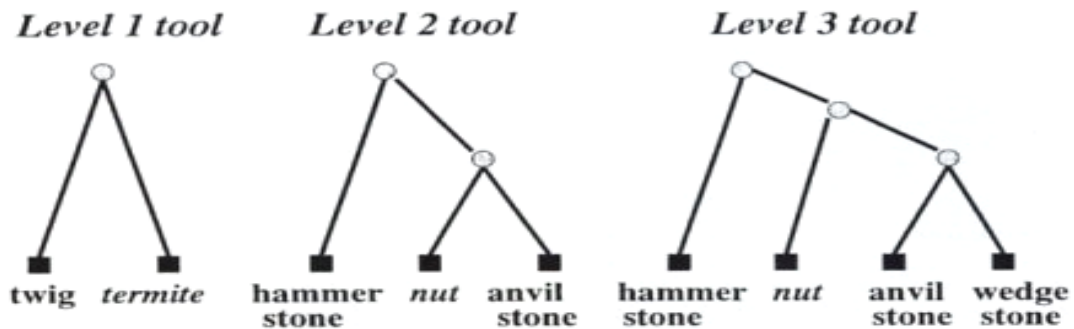
Matsuzawa (2001) classified tool-using behaviour into a three-levelled hierarchy, depending on the components involved. He states that the relation of two unrelated objects (the tool and target) is the underlying feature of tool use, as exemplified by using a stick to access ants. Singularly, the stick is not a tool, yet when the chimpanzee manipulates it to obtain a goal (ants) it becomes one. The number of objects and associations between those objects form the basis of Matsuzawa’s classification system, as displayed in Figure 4. “Level One” tool use is when one of two objects is related to the other in an adaptive manner, that is when individual’s fitness is increased by the action, such as obtaining a food source previously unattainable. Using sponges to obtain water is an example of this type of tool use as a single relationship exists between two single objects. Most observed chimpanzee tool use predominantly falls into this category.

When two associations are made between objects, in more complex tool usage, Matsuzawa defines this as “Level Two”. Nut cracking is representative of this level as there are two phases involved, the positioning phase and cracking phase, where in the former the nut is related to the anvil and in the latter the hammer is related to the nut. These events must follow a hierarchical order thus the nut and anvil form one cluster of association and a second relationship occurs between the clustered objects and the hammer (Figure 4).

The most complex tool usage is classified as “Level Three” and involves the concept of “metatools”, where a tool is used to assist another tool (Matsuzawa, 1991, 2001; McGrew, 1992). For example, an anvil stone may have a slanting edge, which results in the nut rolling off and preventing effective hammering. In this instance another stone may be used as a wedge-tool, as demonstrated by chimpanzees over the age of six years old – an “anvil for another anvil” (Matsuzawa, 1991, 2001). A three tiered relationship can be deduced as the wedge supports the anvil producing a flat surface, the nut is placed on the anvil and the hammer stone is used to crack the nut

(Figure 4). Metatool behaviour involves solving spatial problems along with the ability to perform complex manipulation of several objects in the right order (Matsuzawa, 1994).

**Figure 4:** Hierarchical levels of tool use (From Matsuzawa, 2001)



No evidence to date has suggested bonobos demonstrate metatool usage. As metatools are predominately used during nut-cracking behaviour (Matsuzawa, 1991; McGrew, 1992), which has not been observed in the studied populations of bonobos (Igmanson, 1996), there may be no opportunity for this complex problem solving tool use to develop. Chimpanzee populations that crack nuts (some Western African groups) obtain a vast amount of energy from this resource (Yamakoshi, 2001) and so metatool usage has developed in order to optimise the methods of attaining this nutritional food. Bonobos in contrast gain adequate energy and nutrients from the abundant THV and fruit within their habitat (De Waal, 1997), thus nut cracking may not occur as there is no need to exploit hard-to-get resources (such as hard-shelled nuts) when easily attainable food is available. If the initial nut cracking tool use is not present, metatool development is unlikely and therefore bonobos may not adopt this behaviour due to lack of opportunity, not ability.

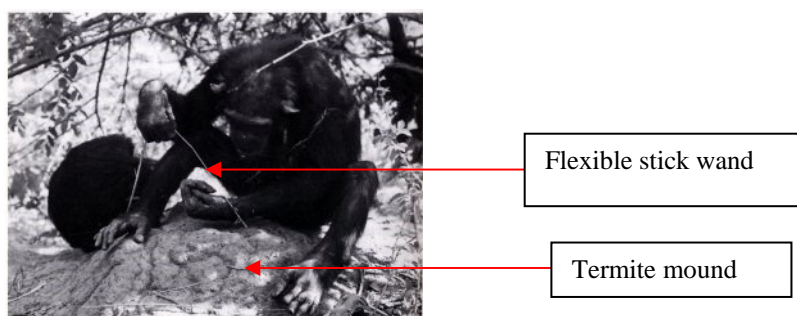
This idea is reiterated by Takeshita et al. (1996) in a study that compared object manipulation capabilities between *Pan paniscus* and *Pan troglodytes*, as a precursor for tool use. The researchers introduced four objects (spoon, bowl, plastic boxes and cotton towels) to subjects of each species and recorded the manipulations performed. They found no significant difference between the species in the variety of manipulation undertaken, or the proportion of simple verses complex motor patterns observed. Bonobos were observed to use both hands more often when manipulating objects compared to chimpanzees, although unimanual manipulation does not imply

inefficiency (wild chimpanzees often use one hand to perform efficient tool use). This study concluded that bonobos do have the capability to manipulate objects as tools so the absence of tool usage in wild populations is not due to motor inability.

Takeshita et al. (1996) noted the predominant difference between chimpanzees and bonobos, with regards to object manipulation, lay in the fact chimpanzees' preferred orienting manipulation of objects towards a substrate whereas bonobos preferred orientating to their own body. This corresponds with the tool usage observed in captive and wild populations of *Pan paniscus*, as most tools are used in self directed behaviours, such as rain hats and tooth picks (Kano, 1982; Jordon, 1982; Ingmanson, 1996) where the tool has to be directed towards the bonobos own body. In contrast, chimpanzees use tools predominately in food acquisition (Goodall, 1986; McGrew, 1992) and thus object manipulations towards substrates, such as nuts and inaccessible nests, are required.

### Subsistence Tool Use

Chimpanzees use tools to obtain food that is difficult to access without the use of such technology. Ants, termites and honey are prime targets for tool using by *Pan troglodytes* as they are enclosed by nest or mounds, consequently chimpanzees cannot utilise them as a food source with their hands alone (Yamakoshi, 2001). A variety of materials are used to access social insects depending on the nature of the nest or mound. Flexible wands are used to enter the intricate, winding ant/termite nests (see Figure 5) whereas stout sticks are used to penetrate the hard outer surfaces of well protected colonies (Goodall, 1986; McGrew, 1992; Yamakoshi, 2001). Intraspecific variation within this tool use behaviour exists between subspecies of chimpanzee.



**Figure 5:** Female chimpanzee fishing for termites in Gombe, Tanzania (From McGrew, 1992).

## Termites Fishing

There are several species of termites preyed upon by chimpanzees; predominately the large mound-building members of the genus *Macrotermes* are eaten, with up to 2 million insects in any single colony (McGrew, 1992). There is seasonal variation with regards to accessibility as the termites remain deep within the sun-baked hardened mound during the dry season and move closer to the surface during the wet season; Gombe chimpanzees fish for termites predominantly at this time (Goodall, 1986; McGrew, 1992; Yamakoshi, 2001). Termite fishing offers a high protein intake for the tool user and thus fitness is increased through this behaviour (Yamakoshi, 2001).

Termite fishing has not been observed in chimpanzees inhabiting the Tai forest, and with *Macrotermes* species being restricted to savannah areas this is not surprising (Boesch et al., 1990). Thus, the distribution of termites can influence which subspecies use fishing tools. Cultural variation also plays a role in this tool use as Central Western chimpanzee populations perform a specific type of termite fishing. This is described by Suzuki et al. (1995) who observed the usage of a tool set by *Pan troglodytes troglodytes* (Central Africa) in the Ndoki forest to obtain termites, consisting of a mound “perforating stick” and a “fishing probe”. Brewer et al. (1990) defines a tool set as the sequential use of two or more tools to obtain a goal objective. This behaviour shows impressive cognitive foresight and problem solving abilities. The perforating sticks used were stout and straight (52.7cm long, 10.9cm diameter) with any small leaves being removed prior to use. The fishing probes comprised of flexible stems and were of similar lengths to the perforating tools; however they were much thinner (5mm diameter). The probes were also frayed at the end, forming a brush-like tool.

A further study by Sanz et al. (2004) described the complex method of manufacture and use of this termite fishing tool-set. Fishing probes underwent complex manipulation to formulate the brush-like structure. Firstly, trimming down the stalk section altered the length of the stick and any leaves were removed. Secondly, the brush tip was formed by pulling one end of the stick through the chimpanzee’s partially closed teeth, resulting in fraying of fibres that were then separated using the incisors.

The study by Sanz et al. (2004) states that inspection of the termite mound occurs first, followed by the selection of a target insertion point. The chimpanzee then pushes the stout perforating tool into the ground, often using a two-handed method, resulting in the creation of a deep insertion hole. The tool is withdrawn and inspected for dead termites, therefore indicating whether the nest has been penetrated. If this is the case, the second fishing probe tool is inserted into the mound tunnels, with the brush-like end collecting the termites. A specific technique was observed for insertion of the fishing probe as the brush section was flexible and thus difficult to manoeuvre. The fibres were compacted and straightened by moistening the tip with saliva and pulling the brush through the primates' hands. If an insertion was unsuccessful, the chimpanzees were observed to repeat the "brush straightening" procedure before trying again. Therefore, they demonstrated a high cognitive ability to understand the cause and effect of the object manipulation, resulting in the more efficient use of the tool. By using their mouth to pick off termites from the brush, or sweeping their hand along the length of the fishing tool, the chimpanzees ingested the large, nutritious termites.

Termite fishing has not been witnessed in wild bonobo populations. However the motor capacity to investigate holes with sticks has been observed in captive populations (Jordon, 1982), thus ecological factors, such as insect distribution and an abundance of easy-to-get foods, could explain the absence of this tool using pattern in this species.

### **Honey Extraction**

Honey is a naturally high source of energy, and this, combined with the substantial protein and fat obtained from ingested larvae and bees, makes a hive an attractive target for subsistence exploitation (McGrew, 1992). Hives are often inaccessible as a result of anti-predatory strategies employed by the bee species targeted, which include sting-less *Meliponini* and stinging *Apis* or *Xylocopa* (Brewer et al., 1990). Consequently, tools are used to help "fish" for this resource as recorded in chimpanzees at Cameroon, Tanzania, Senegal and Ivory Coast, thus this behaviour occurs across all three geographical sub-species (Boesch et al., 1990; Brewer et al., 1990; McGrew, 1992).

Reflecting the tool set usage observed in termite fishing, Brewer et al. (1990) recorded a chimpanzee from a free-ranging group in Gambia demonstrating

impressive technological skill whilst extracting honey, using tools sequentially depending on the results achieved by the previous instrument. Firstly, a stout “chisel” branch tool was used (35-40cm long, 20mm thick) to repeatedly deliver powerful blows to the batumen (waxy resin that seals the nest wall) and once this layer crumbled the tool was discarded. A sharper, more precise chisel tool was then employed (25cm long, 15mm thick) to widen the previously produced hole, gouging away more batumen. The chimpanzee then inspected this hole by inserting its finger and sniffing it.

The second tool was abandoned and a thin green branch (30cm long, 10mm thick) was used as a “bodkin” tool to puncture the seal of the nest. Again, this third tool was examined after insertion. The final tool was used as a fishing probe (75-80cm long, 8mm thick) to extract large amounts of dripping honey. Each type of tool required different manipulation (e.g. differing grips) thus the chimpanzee demonstrated complex motor abilities as well as cognitive insight to incorporate many objects together (Takeshita et al., 1996).

Bonobos have not been recorded to display this type of tool-set usage, even though the cognitive ability to use tools sequentially has been illustrated in captivity by Toth et al. (1993) and Schick et al. (1999). Therefore, the likely explanation for the absence of this tool use may be due to diet variation. Bonobos ingest many high protein foods such as THV, fruit and caterpillars (De Waal, 1997) hence exploiting highly defended hives may not be so appealing and thus not targeted for subsistence.

### **Ant Dipping**

Ant dipping has been observed within *P. t. schweinfurthii* species, such as Gombe (Goodall, 1986) and Mahale (Boesch et al., 1990) groups, and *P. t. verus* populations in Bossou (Yamakoshi, 2001), Assirik (McGrew, 1992; Hunt et al., 2002) and Tai regions (Boesch et al., 1990). There is no evidence to suggest it occurs in Semliki chimpanzees, Uganda, even though it has emerged in other eastern populations, suggesting this tool use is not ecologically determined (Hunt et al., 2002).

McGrew (1992) describes the method of this tool use, stating that chimpanzees modify a branch to create a long flexible wand that they then insert into the underground nest of Driver ants, after initially digging into it by hand. Modification involves stripping an appropriate branch of its leaves, peeling away the bark and reducing the tool to the correct length (Goodall, 1986; McGrew, 1992). As a

defensive strategy ants swarm up the stick tool, which is then removed quickly and the individual sweeps its' hand along the stick to collect a jumbled mass of ants to be ingested. At Kasoje (Tanzania) Wood-boring ants are predominantly eaten, with chimpanzees using thin branch tools to fish them out of tree-holes (McGrew, 1992).

The methods employed for ant-dipping differ between groups, as exemplified by Gombe chimpanzees, which insert probes into driver ants' nests and disregard provisional exploration with their hands, whereas Tai populations will use their hand predominately and only utilise tools if necessary. Increased sensitivity to driver ant bites may have arisen in Gombe chimpanzees, thus due to this increased susceptibility tools are used immediately (Boesch et al., 1990).

This behaviour has not been witnessed in bonobos, which may be due to the fact ants are a very low source of nutrition (Matsuzawa et al., 1996). For an average one hour fishing episode in Mahale (Tanzania) 600 ants were obtained by a chimpanzee, yielding only 1gram of protein (Yamakoshi, 2001). Bonobos live in an environment with nutritious food such as fruits (Myers Thompson, 2002), thus there is no need to exploit a poor food source so ant-dipping behaviour has not evolved.

### **Intraspecific differences: Nut Cracking/ Stone Tool Use**

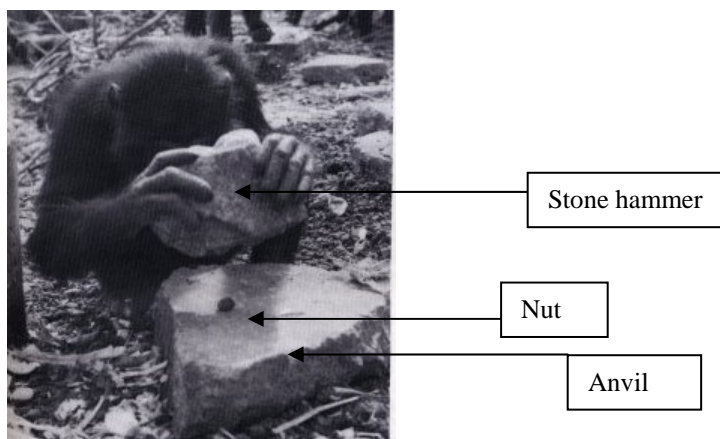
Tool use not only differs between *Pan troglodytes* and *Pan paniscus*, it also varies within individual species populations, as exemplified by the behavioural differences between bonobo groups at Wamba and Lomako, Zaire (Ingmanson, 1996), and between geographical races of chimpanzee (Boesch et al., 1990; McGrew, 1992; McGrew et al., 1997). Nut cracking behaviour is a good illustration of tool-using diversity across the *Pan troglodytes* sub-species. Central-western (*P. t. troglodytes*) and eastern (*P. t. schweinfurthii*) populations, including Gombe (tanzania), Mahale (tanzania) and Lope (Gabon) show no signs of this tool use, and only some western (*P. t. verus*) groups, such as Bossou (Guinea) and Tai (Ivory coast), demonstrate this behaviour (McGrew et al., 1997). The eastern border of this tool using pattern is the Sassandra River, west Cote d'Ivoire (Boesch et al., 2000).

Hard-shelled nuts, predominantly oil-palm nut (*Elaeis guineensis*), Coula nut (*Coula edulis*) and Panda nut (*Panda oleosa*), are present in most chimpanzee habitats (Matsuzawa et al., 2001) and contain a highly nutritious kernel (Matsuzawa et al., 2001). Tools, either wooden or stone, are used by chimpanzees to crack open the hard shell and access the edible kernel. This tool use is extremely beneficial as it exploits a

high energy food, as exemplified by Tai chimpanzee populations that obtain 3762 kcal from 2.3 hours of nut cracking, which is nine times more than that that is expended through this activity (Yamakoshi, 2001).

This behaviour requires an “anvil” to support the “goal-object”, that is the hard-shelled nut to be cracked (McGrew, 1992; Matsuzawa et al., 1996). A wooden or stone “hammer” is needed to apply a downward force on to the nut (see Figure 6) (McGrew, 1992; McGrew et al., 1997) and the species of nut determines which type of hammer is selected. Soft shelled nuts at Tai (Ivory Coast) were cracked with wooden hammers 62% of the time and 99% of hard shelled nuts were cracked using stone hammers (Boesch et al., 2000).

Suitable hammers are scarce therefore they are generally transported between sites of nut-cracking if energetically beneficial, as Boesch et al. (2000) state heavier tools for larger nuts (more energy gain) are carried over greater distances. Chimpanzees also transport nuts to the location of the anvil (McGrew et al., 1997; Boesch et al., 2000). The ability to perform this tool usage increased as a function of age, with chimpanzees under 3.5 years old unable to demonstrate an appropriate hierarchical understanding of action-object association, only acquiring the basic components of nut-cracking (picking a nut, holding it, hitting it with a hammer) after observing other members of the group perform this tool use (Inoue-Nakamura et al., 1997).



**Figure 6:** A chimpanzee using hammer and anvil nut cracking tools (From McGrew, 1992)

McGrew et al. (1997) investigated the environmental factors underlying the lack of nut cracking tool use in Lope chimpanzees (*P. t. troglodytes*), Gabon, concluding that materials required for this behaviour, such as suitable nuts, anvils and

hammers, are present in their habitat. Also the dietary intakes of Bossou groups, who do exhibit nut cracking behaviour, and Lope populations, do not significantly differ. Thus, it is not the case that higher quality food sources are causing the exclusion of nut kernels from the non-nut cracking individuals' diets. This study also states that lope chimpanzees have the cognitive ability to manipulate tools, as they perform ant-fishing and honey-dipping, which in fact shows more complex object manipulation as sticks have to be modified for the purpose whereas hammer and anvil tools are not.

## Culture

If differences between populations are independent of ecological or genetic factors, as in the case of the Lope chimpanzee population, they can be considered to be culture-related (Boesch et al., 1994). Therefore, McGrew et al. (1997) suggested that nut-cracking behaviour is cultural, a tradition learned from other individuals within the group and transmitted between generations, and at present no member in Lope has discovered that the kernel within the nut is edible or formulated the technology to obtain it. Boesch et al. (1994) reached the same conclusion with regards to nut-cracking behaviour being a culturally derived practice.

However, this study proposes that culturally transmitted tool use may not be optimally adaptive for the environment as it is a case of “do what others do [and not] search for the best solution”, as illustrated by ant dipping tool use. Boesch et al. (1994) suggest the lengths of dipping sticks used by Tai chimpanzees are much less efficient than those used by Gombe groups due to the culturally derived nature of this behaviour. In respect to nut cracking, Niagre forest chimpanzees (Ivory Coast), 50km from Tai populations, would benefit from this tool use yet this it has not developed even though ecological similarities occur between the two sites; lack of cultural transmission may explain this (Boesch et al., 1994). Table 4 displays the types of tool use that are considered to be culturally derived.

Immigrating females, who leave their natal group and join neighbouring communities, from populations who do practice nut cracking may enter a group which do not demonstrate this behaviour, and thus nut-cracking techniques can be observed and imitated by the naive group members. In general, the method of nut-cracking and the tools involved are consistent between communities of *P. t. versus*, however the nut species used differ, regardless of whether they are present or not within the habitat (Matzusawa, 1994).

**Table 4:** Cultural differences in tool-using behaviour within populations of chimpanzee and bonobo (Adapted from Boesch et al., 1994; Ingmanson, 1996)

Tool Use Pattern	West Africa (chimpanzee)		East Africa (chimpanzee)		Bonobos	
	Bossou	Tai	Gombe	Mahale	Wamba	Lomako
Ant-dip	+	+	+	-	-	-
Honey-dip	-	+	+	-	-	-
Leaf-napkin	-	-	+	-	+	+
Leaf-sponge	+	+	+	-	?	?
Nut crack	+	+	-	-	-	-
Termite fish	-	-	+	+	-	-
Rain hats	?	?	?	?	+	-
Fly whisk	+	+	+	-	+	+

+ indicates behaviour is present, - indicates behaviour is absent, ? indicates unknown

Matsuzawa et al., (2001) demonstrated the concept of cultural transmission by introducing Coula and Panda nuts to Bossou chimpanzees, which usually only cracked oil-palm nuts. At first most members of the group treated the unfamiliar nuts with neophobia. However, an immigrant adult female, without hesitation, proceeded to crack the novel nuts, obviously familiar with this resource from her natal community where Coula nuts were abundant, and observing juvenile individuals then cracked these nuts as well. The process of behavioural patterns being spread between communities is referred to as “diffusion” (McGrew, 1992) and often there is a “cultural zone” comprising of several neighbouring communities where similar traditions occur due to the migration of individuals between them (Matsuzawa et al., 2001).

Bonobos have not been observed to use nut-cracking tools, even though the tree species (e.g. *Panda oleosa*) that produce hard-shelled fruits cracked open by chimpanzees are present in their habitats (Ingmanson, 1996; Hohmann et al., 2003). The explanation for intraspecific differences in tool using behaviour in this case may be that suitable material for tool construction is not abundant in bonobo areas. In Lomako stones are too soft and scarce for nut cracking to be effective, thus this tool use has not been developed (Hohmann et al., 2003).

Although stone tool use has never been documented in the wild, Toth et al. (1993) demonstrated that a captive bonobo had the capability to strike stones together with precision and force to remove flakes that can then be used to cut a cord, thus illustrating stone tool use. The cord was attached to a box that opens a door to reveal a reward. The bonobo even demonstrated the capacity of insight, not just imitation, by developing a technique to fracture stones that had not been displayed for him, by

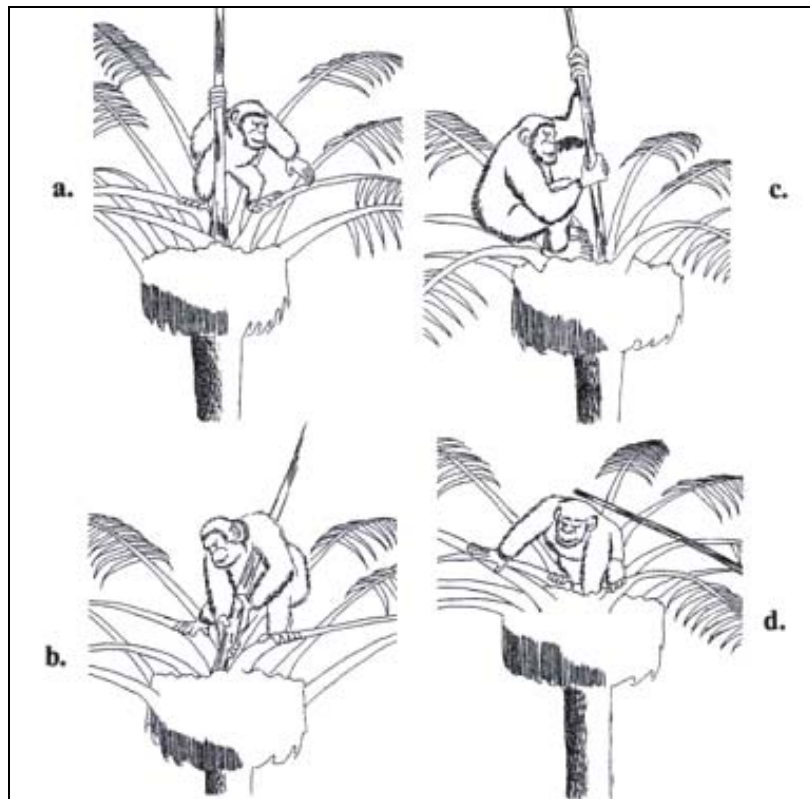
throwing them hard against a floor. This idea echoes the results of a similar study by Sumita et al. (1985) on the acquisition of stone tool use in captive chimpanzees, where demonstrations of nut-cracking with stone hammers resulted in chimpanzees imitating this behaviour, but in addition the subjects modified their methods themselves to become more proficient, again illustrating insight and a causal understanding of their goal-directed behaviour.

Although extensive stone tool use as seen in some chimpanzee groups has not been documented in wild bonobos populations, Toth et al. (1993) have demonstrated that the motor skills and cognitive abilities required performing complex tool-manipulation tasks do exist in *Pan paniscus*.

### **A recently discovered tool use**

Yamakoshi et al. (1995) observed a new type of tool use in Bossou, Guinea, that incorporates similar motor co-ordination to that required by honey fishing but with much greater force. Pestle pounding is this newly documented behaviour, where the tough petiole of a leaf from an Oil-palm tree (*Elaeis guineensis*) is used as a pestle to pound the centre of the palm crown. This exposes the stem apex at the bottom of the radiating leaves, which is then ingested by the chimpanzees. This process is comprised of discrete motor components, as represented in Figure 7. The chimpanzees expose the young shoots at the crown by moving away the radiating mature leaves with their hands and feet (Figure 7a), and then using great force they pull out the shoots to be used as a pestle-tool (Figure 7b). The removal of a young shoot leaves a vertical hole in the crown which is then deepened by pounding with the hard petiole of the extracted leaf (Figure 7c). Pounding results in a well of juicy fibrous food in the hole of the apical bud in the centre of the crown. This part of the tree would not be accessible without the use of tools. The chimpanzees then discard the leaf-tool to use their arms to access the nutritious resource (Figure 7d). Chimpanzees have also been observed to use a chewed fibre mass as a sponge-tool to obtain the juicy liquid (Yamakoshi et al., 1995).

**Figure 7:** Diagrammatic representations of Pestle pounding tool use (From Yamakoshi et al., 1995)



Environmental factors affect the frequency of this tool-using behaviour as when fruit is ripe and plentiful (dry season), the occurrence of pestle-pounding decreases whereas in the wet season, when ripe fruit is less available, pestle-pounding behaviour increases (Yamakoshi et al., 1995). The apical bud is highly nutritious, and the abundance of young shoots in oil-palm trees is high throughout the year therefore pestle-pounding behaviour may have developed so that this resource can be exploited effectively when fruit is not abundant.

Bonobos predominately feed on THV when fruit is not abundant (De Waal, 1997) as this resource is not affected by seasonal change, and it was assumed that chimpanzees at Bossou followed the same pattern as THV is present in their habitat (Yamakoshi et al., 1995). However, interspecific competition from other THV consumers, such as gorillas (Wrangham et al., 1997), may have forced chimpanzees to exploit another non-seasonal food supply, the consequence being the intake of oil-palm shoots and apical buds, and the subsequent tool use required to access them. As bonobos can feed on abundant supplies of THV in their habitats there has been no selective pressure to find other sources of nourishment, and this lack of requirement may explain why no pestle pounding has been observed.

### **Tool use in wild bonobos**

In contrast to chimpanzees, the tools used by bonobos are rarely in the context of food acquisition; instead they are often used in self-directed behaviour and communication (Ingmanson, 1996). The absence of subsistence-related tool use in bonobos observed at Wamba may be related to the ecology of the area. Food of high nutritious quality, such as fruit and THV, is plentiful and easily obtained (Ingmanson, 1996). Therefore, there is no selective advantage to utilise hard-to-access foods like nut kernels or insects within a nest and as such no advanced tool using technology has been developed.

The tool use exhibited by wild bonobos is described by Ingmanson (1996). Branches were used as tools at Wamba (Congo basin) in “branch dragging” to communicate group movement and also to convey dominance, although during these displays observing bonobos did not show fear or flee from the branch dragging individual. Only 3% of branch dragging reported by Ingmanson (1996) were in association with threat displays compared to 64% that signified group movement. Hence, this type of tool was not used aggressively, contrasting with chimpanzees which used branch dragging in violent displays (Goodall, 1986).

Branch dragging (illustrated in Figure 8) behaviour has been observed in Lomako as well as Wamba, with the context again being mainly communicative rather than agonistic (Hohmann et al., 2003). This type of tool use requires the cognitive ability to select branches that are most effective, motor skills to remove branches off trees and co-ordinated locomotion to run with the tool. There are many opportunities for cultural variations in technique between these sites but as of yet no research has investigated this potential diversity (Hohmann et al., 2003).

Environmental factors can dictate the type of tool using behaviour observed, and bonobos inhabiting the rainforest at Wamba have developed a way of protecting themselves from the heavy rainfall that is endured there by utilising leaves as rain hats (Kano, 1982; Ingmanson, 1994, 1996). Leafy branches are used either as umbrellas, held above their heads, or as rain coats, draped over their head, shoulders or back if the tool-user was lying down (Kano, 1982; Ingmanson, 1996). Sometimes the branches were not completely detached but bent slightly, resulting in a tent like structure being formed, and branches were often transported to other locations to be

utilised as rain-protecting devices (Ingmanson, 1996). This tool-using behaviour has never been observed in chimpanzee populations (Kano, 1982; Ingmanson, 1994).



**Figure 8:** A male bonobo dragging a branch. Leafy ones were preferred as these create more noise to attract the attention of the group (From De Waal, 1997).

Ingmanson (1996) states that rain hat tool use requires a hierarchical cognitive process, in the same way nut-cracking behaviour in chimpanzees follows a sequential thought pattern. A concept of requiring a protective mechanism from the rain is needed followed by the selection of materials to fulfil this purpose. The foresight of arranging branches and leaves effectively is then required. This learning process takes years to perform efficiently as Ingmanson (1996) remarked that no bonobo under the age of ten was observed using rain hats efficiently, echoing the findings of Matsuzawa (1994) regarding chimpanzee metatool use, where juveniles were not seen to perform complex tool using behaviour.

An important component of rain hat tool use, as stated by Ingmanson (1996), is the behaviour of the individual using them. Non-using bonobos were observed to move around, shaking the rain off their skin, whereas individuals utilising rain coverings remained still so as not to disturb the deliberately placed leaves. Kano (1982) often witnessed bonobos replacing leaves that had slipped off and one individual even held several leaf-covers in place for four minutes, demonstrating a full understanding of the relationship between action, object manipulation and the resulting consequence (i.e. protection from the unpleasant effects of rain).

Ingmanson (1996) also reported wild bonobo populations at Wamba using leaves to wipe faeces and urine off their bodies, thus serving as a napkin. Goodall (1986) also viewed this behaviour within chimpanzee groups at Gombe, Tanzania,

with males fastidiously using leaves to clean their penises after mating. Ecological factors do not affect this type of tool use so it is interesting to observe the pattern appearing in both *Pan troglodytes* and *Pan paniscus* species as this illustrates behavioural similarities in tool use do occur when environmental elements are irrelevant.

Bonobos at Wamba also used twigs as toothpick tools; one male even modified the twig with his teeth before use to create a more pointed appliance (Ingmanson, 1996). This behaviour has been detected in Gombe, where a female chimpanzee was observed to use a twig tool to pick at her teeth where it appeared some food had got stuck (Goodall, 1986). At Wamba branches were used as fly squatters on numerous occasions and this tool use was also observed in chimpanzee populations at Bossou, Tai and Gombe (Goodall, 1986; Boesch et al., 1990; McGrew, 1992; Boesch et al., 1994; Ingmanson, 1996).

Cultural differences occur within tool using behaviour in bonobo populations as they do in chimpanzee societies. Toothpicks and napkins leaf tools have not been recorded at Lomako whereas Ingmanson (1996) observed this behaviour in Wamba. Rain hats are not constructed by bonobos at Lomako in the same way Wamba groups manipulate branches, however they have developed a different way to protect themselves from rainfall by placing twigs and leaves over their bodies when in the nest at night (Hohmann et al., 2003). Environmental factors between Lomako and Wamba are very similar, and this combined with the fact both types of rain covering require non-specific leaf materials suggests that any difference in this tool using behaviour may be cultural.

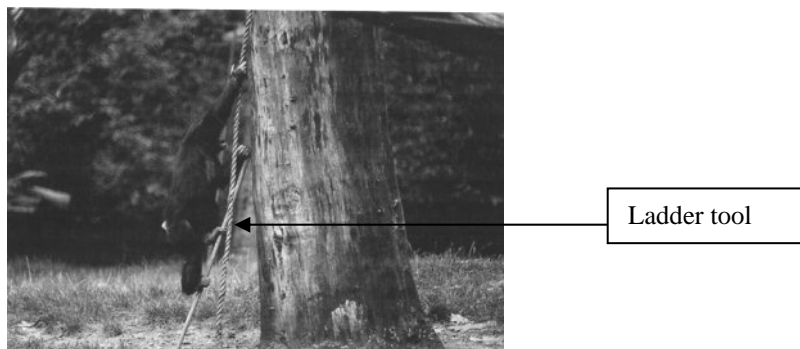
### **Captive Studies of Bonobos and Chimpanzees**

Studies of captive bonobo and chimpanzee populations have illustrated a remarkable similarity in tool use between these two primate species. Captive surroundings and food provisioning eliminate the natural variation in habitat ecology that occurs between wild groups of *Pan troglodytes* and *Pan paniscus*, thus allowing behaviour to be independent of factors such as interspecific competition and food availability. De Waal (1982) and Takeshita et al. (2001) observed tool use in chimpanzees inhabiting the Arnhem Zoo, Netherlands, and similarly, Jordon (1982), whilst monitoring object manipulation of captive bonobo groups in Frankfurt, Stuttgart and Antwerp, observed many instances of tool use. Gold (2002) also

recorded tool using activity in captive bonobo communities in the Apenheul Primate Park, Netherlands.

The enclosures at Arnhem Zoo and Apenheul Primate Park share many common features, such as large open and varied terrain, trees to climb and trees protected by electric fences or plastic cylinders. Both environments are surrounded by a moat of approximately 2 metres in depth (Takeshita et al., 2001; Gold, 2002). The similarity of habitat may be the underlying reason for the echoing behaviours observed between these two species.

De Waal (1982) often observed two male chimpanzees in Arnhem Zoo manufacturing ladder tools by deliberately breaking off branches from dead oak trees in the enclosure, often forcing apart forked branches 20 metres above ground level. The ladder-branches (see Figure 9) were then propped against trees that were protected by electric wire 2 metres up the trunk from the base. One male held the branch against the tree whilst the other climbed up it, therefore avoiding the electrified section of the trunk, and accessing the non-protected canopy. The primary motivation for this ladder-using tool was to obtain the fresh tender leaves on these living trees. This type of tool usage illustrates the chimpanzees manufacturing capacity as well as co-operation between individuals to use the tool effectively to obtain a goal (the succulent leaves), which were then shared among the helpers.



**Figure 9:** Chimpanzee using a branch as a ladder tool to climb the tree (From Takeshita et al., 2001).

This behaviour reflects that observed by Gold (2002) in a captive bonobo community, where a female dragged a 4 metre long-branch to a living tree protected by a plastic cylinder. She then proceeded to use the branch as a ladder to climb up and overcome the plastic cylinder section of the tree. Co-operative behaviour was then observed as she hoisted up four other bonobos whilst balancing on a lower branch of

the “forbidden” tree. Again, as in the chimpanzee example, the underlying motive for this tool use was to obtain fresh leaves to eat. Captive bonobo population studies have thus illustrated that the tool-using individual intentionally selected objects with the foresight that they will be used as a tool, exemplified by the fact the bonobo removed the branches from one site and transported them to another area of use (Gold, 2002).

Jordon (1982) also states the use of ladder tools in captive bonobos, as well as wooden blocks that were used to reach out of range objects or to see over the cage wall. Takeshita et al. (2001) recorded this type of tool usage in captive chimpanzees, where boxes were used as steps to reach a windowsill that allowed a view from the outside enclosure to the inside one. The chimpanzees seemed highly motivated to perform this tool-using behaviour, maybe due to the fact they could see the keepers working or because the window sill offered a solitary refuge away from the other group members (Takeshita et al., 2001).

Tools were used in an aggressive capacity in chimpanzees and, surprisingly, bonobos in captivity. Gold (2002) observed a branch being used as a club by a female bonobo against a peahen. The bird in question had just hatched a clutch of peachicks in the bonobo enclosure. The intensely curious bonobos chased the chicks; however the mother peahen tried to defend her chicks by attacking the bonobos, much to the annoyance of one female who then retrieved a branch (105cm long) and transported it to the peahen mother. She then proceeded to beat the mother with the branch, striking 40 blows in eight minutes, pursuing her to the moat where the clubbing attack continued until the bird was killed. As with *Colobus* monkeys fatally injured by wild bonobo individuals, no attempt was made to eat the deceased animal.

Jordon (1982) also observed agonistic displays involving sticks, boughs and chains performed by bonobos, along with the use of wooden blocks and sticks as tools to throw at conspecifics, humans and birds. Chimpanzees were observed to throw stones, sticks and sand at conspecifics by Takeshita et al. (2001) and more aggressive tool use was seen as branches were used to flail and club other individuals, echoing the behaviour recorded in captive bonobos.

The aggressive tendency of bonobos has been portrayed as inferior to that of chimpanzees on the basis of the lack of violence seen in the two long-term studied populations in the wild at Wamba and Lomako (De Waal, 1997; Wrangham et al., 1997). However, under captive conditions bonobos have shown the same aggressive

behaviour with regards to tool use and object manipulation as chimpanzees (Jordon, 1982; Gold, 2002).

Both chimpanzee and bonobo captive communities illustrated the use of tools as sponges and containers for water. Takeshita et al. (2001) observed chimpanzees using introduced objects as ladles to collect water, such as a bowl, spoon and even a volleyball, which had been deflated and transformed into a bowl shape after a male had displayed with it. The chimpanzees would typically collect water in their container tool from one location but drink in another (Takeshita et al., 2001).

Captive bonobos have also been observed to use tools as containers, including red-pepper halves (*Capsicum* spp.) that were taken to the surrounding moat to scoop up water (Jordon, 1982). A juvenile female in one captive population studied by Jordon (1982) consistently carried a plastic canister over three metres to a lawn sprinkler within the enclosure, watched and waited for it to fill up then selected a dry location in the cage to drink it. By transporting the containers to and from the source of water, each species has demonstrated the cognitive ability of foresight in their objectives and chosen tools accordingly.

Chimpanzees and bonobos have demonstrated the ability to imitate behaviour of humans and conspecifics in captivity (Sumita et al., 1985; Toth et al., 1993) and as Takeshita et al. (2001) state captive apes have the opportunity to watch human actions. Thus they would be familiar with the concept of a container as this is what their food would be carried to their enclosure in and therefore it is not surprising that this tool-use behaviour is replicated by captive populations of bonobo and chimpanzee.

In Arnhem Zoo, chimpanzees used paper, stuffed toys and towels as sponges to absorb water (Takeshita et al., 2001) which they then sucked out, and in captive bonobo groups this same principle was applied only with different materials, such as wood-wool and leaves (Jordon, 1982). Tennis balls were also used by bonobos as sponges, with the primates submerging them in water before sucking them to obtain the liquid (Jordon, 1982). Captive populations of these species would not have been exposed to the idea of sponges by human keepers and therefore each species is responding to their environment and developing tools that increase their own fitness within it.

This is echoed in wild populations where chimpanzees at Tongo (eastern Zaire) have adapted to their dry forest environment by developing tools to obtain moisture, as described by Lanjouw (2002). If pools of water that had collected on branches were

unattainable directly, chimpanzees prepared moss “sponge” tools by rolling the plant into a bundle, then inserting them into the hollows of branches to absorb the water, which they sucked out. Often sponges were pre-made before visiting a tree illustrating the chimpanzees had the direct intention to drink and use their tools accordingly. Goodall (1986) observed similar behaviour in Gombe chimpanzees, except in this region leaves were chewed to create an absorbent sponge, which again was sucked to obtain the water within. Evidence for sponge tool use has also been recorded in eastern chimpanzee groups at Semliki (Uganda) and western at Assirik (Senegal) (Hunt et al., 2002).

Ingmanson (1996) performed an extensive study of wild bonobo populations at Wamba (Zaire) and yet found not sponge tool use, however this rainforest environment does not suffer from water scarcity thus tools adapted to dry conditions are not advantageous, and consequently have not developed. As previously described, sponge tools were utilised in captive bonobo groups (Jordon, 1982) therefore the ability to execute this behaviour exists but their natural habitat does not require its use.

## **Conclusion**

Using tools requires the cognitive ability to understand causal relationships between actions and the motor abilities to manipulate objects (Tonooka, 2001), both of which have been demonstrated to exist in chimpanzees and bonobos (Takeshita et al., 1996). Even though the prerequisites are present in *Pan paniscus*, this species has not been recorded to use tools to obtain food in the wild (Ingmanson, 1996) in stark contrast to chimpanzees, which use highly advanced tool technology in the pursuit of subsistence (McGrew, 1992; Yamakoshi, 2001). Bonobos do utilise objects as tools, however this behaviour is often self directed, as exemplified by the use of rain hats, fly squatters and leaf-napkins (Jordon, 1982; Ingmanson, 1996).

Takeshita et al. (1996) propose that gaining adequate nutrition is problematic for chimpanzees therefore a need to manufacture tools for subsistence has arisen whereas bonobos inhabit an environment where they do not need to use tools to forage efficiently so tools for this purpose are unnecessary (Ingmanson, 1996; De Waal, 1997). In captivity food is provisioned therefore the need to use tools in food acquisition is reduced; hence chimpanzees and bonobos have the same opportunities to develop and use tools for other purposes, and this may be why each species illustrates similar tool using behaviours in this situation.

Ingmanson (1996) interestingly observed the absence of weapon tools in wild bonobo groups at Wamba, even though it is seen in captive groups, with behaviours such a branch dragging used to promote group cohesion by communicating directions of movement. Conversely, chimpanzees in Gombe were observed by Goodall (1986) to use branch dragging in an aggressive context during dominance displays and as a way of intimidation others and distancing themselves from individuals. Food competition may play a role in this behavioural variation as Gombe chimpanzees have a selective pressure to forage singularly due to resource competition whereas this is not the case for bonobo populations that live in habitats of abundant resources (Wrangham et al., 1997; De Waal, 1997).

Although there are signs of aggressive tendencies in bonobos, chimpanzees are by far more violent. Chimpanzees also perform more tool use, especially with regards to food acquisition and thus the two dispositions may be related. In order to perform aggressive advances, which are energetically costly (Muller, 2002), an individual must be well-fed, and obtaining more food from an environment where resources are low is advantageous. Hence, subsistence tool use may have developed as an adaptation to fuel the increased aggressive tendencies of this species. Bonobos live in an abundantly resourced habitat and there is no selective advantage for subsistence tool use to develop as adequate nutrition can be gained without it. Also aggression is low due to the reduced competition for food; as Wrangham et al. (1997) states bonobos live in a “kindly” habitat thus they can afford to be more “kind”.

It could be suggested that due to the fact bonobos spend less time in aggressive confrontations compared to chimpanzees they may have more time to develop tool using behaviour. Even though it may appear that chimpanzees use more tools, bonobos have formulated them in response to issues associated with their habitats such as rainfall (rain hats) and communication problems (branch dragging) so when tools are advantageous bonobos have developed them.

The lack of tool usage in wild bonobos may be attributed to the fact they are still relatively understudied compared to chimpanzees. De Waal (1997) states that judgement should be reserved on the perceived notion that bonobos do not use tools, on the basis that larger populations must be studied to obtain a more accurate view of their behaviour. He reinforces this argument with the example of orangutans, a species that for many years were classed as substandard tool users in comparison to the extensive technology used by chimpanzees. However, van Schaik et al. (1996), as

cited by De Waal (1997), discovered that orangutans used tools for honey extraction and insects foraging in much the same way chimpanzees do. Previous to this discovery orangutans were known to hold leaves above their heads to protect them from rain and use sticks to scratch places they were unable to reach (De Waal, 1997). This echoes the described view of bonobo tool use to date, with Ingmanson (1994) observing the use of “rain hats” in Wamba, and Jordon (1982) and Gold (2002) noting the use of sticks to obtain out of reach items in captive bonobo populations. The lack of extensive research into bonobos may erroneously imply more behavioural differences between this species and chimpanzees than are actually present (Hohmann et al., 2002). Therefore, there is a strong possibility that with more field research tool technology similar to chimpanzees may be observed.

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