Tool-use in excavation of underground food by captive chimpanzees (*Pan troglodytes*): Implication for wild chimpanzee behavior

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Spring, 2014

2014

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http://www.duo.uio.no

Print: Reprosentralen, Universitetet i Oslo

Abstract

Extractive foraging of underground storage organs (USOs) is believed to have played an important role in human evolution. This behavior is also present in wild chimpanzees (*Pan troglodytes*), who sometimes use tools in the task. Despite the importance of studying this behavior in chimpanzees to model how early hominins may have used tools in the context of USO excavation, it remains to be directly observed due to the chimpanzees' lack of habituation in the two study sites that yielded evidence of tool-use in USO excavation. Until now, no studies in captivity had been conducted to learn how chimpanzees could excavate underground food. The present experiment was designed to provide captive chimpanzees with opportunities to use tools in the excavation of artificially-placed underground food at their semi-naturally forested enclosure. The study was conducted independently with two groups of chimpanzees living at the Kristiansand Zoo, in Kristiansand, Norway. The experiment had three phases: food was placed inside holes that were 1) left open, 2) filled with regular soil, and 3) filled with clay. Materials to be used as tools were provided once during the study. The chimpanzees predominantly excavated the buried fruits manually. They used one hand to excavate soil and used both hands, alternating right and left, to excavate clay. The chimpanzees rarely used tools to excavate regular soil, while more often used tools to excavate naturally compacted soil (below the depth where the fruits were placed) and clay. In general, tool-use increased with the hardness of the soil type. The chimpanzees were selective in their choice of materials to be used as tools, preferring long and heavy sticks from trees. Even though they were observed to manufacture tools in other contexts, they were never seeing to make tools for the excavation of underground food. Only one instance of tool modification occurred. The chimpanzees gathered their own tools from the enclosure: these tools were similar in physical characteristics and material to the ones they selected from the provided materials. Some tools remained in the study area and were reused in different days. The tools that were reused more frequently were transported more. In the beginning of the study, tools were only used as investigatory probes. But later, the chimpanzees succeeded in using tools for excavation by incorporating different actions: perforate, pound, dig, shovel, and enlarge. Some individuals seemed to acquire the actions through their own trial and error, while others seemed to learn through observation of skilled individuals. It was found that excavation was not a single action, but a series of different actions all performed (manually or with tools) with the goal of extracting the underground food. Tool actions emerged sequentially and independently in the two study groups: probe, perforate, pound, dig, and shovel. Mastering one action seemed to facilitate the invention of the following action. The implications of the present study for the behavior of wild chimpanzees are discussed.

Keywords: underground food, excavating tools, captive chimpanzees

Acknowledgements

This thesis would not have been possible without the help and support of many people. I am most grateful to my advisors, who gave me the opportunity to do this project, making my dream of studying chimpanzees a reality.

- I would like to express my deepest gratitude to Dr. Adriana Hernandez-Aguilar for her continued guidance, support, and encouragement from the design of the project, all the way to the completion of this thesis. Her willingness to give her time so generously is very much appreciated.
- I owe my profound gratitude to Prof. Helene Lampe, for her constant support. I cannot adequately express my appreciation for her detailed and constructive recommendations and advise throughout this work.
- I am extremely grateful and in debt with Prof. Karl Inne Ugland for all he has done for me throughout my education at UiO, including his help with data analysis for this thesis.
- I thank very much Helene Axelsen, who granted me permission to conduct this research with the chimpanzees at the Kristiansand' Zoo, for her advise and for helping me to overcome the many logistical problems we encountered. Many thanks also to all the staff at the Zoo, in particular to Hildegunn Johannesen.
- Most importantly, I would like to thank my family for their continuous support and encouragement. Your concern for me was what sustained me this far.
- Finally, I would like to acknowledge the chimpanzees that dug out (or not!) their way into this thesis: Julius, Junior, Knerten, Miff, Binni, Josefine, Tobias, Jane, Dixi, and Yr. Working with them has been one of the most challenging experiences of my life, but also the most amazing and fulfilling.

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1 Introduction

"It's funny how humans can wrap their mind around things and fit them into their version of reality."

-Rich Riordan, *The lightning Thief*

Humans were considered unique, different from other animals, due to their abilities for tool-use (Oakley, 1956) and manufacture (Leakey, 1961). Tool-use is defined as "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 tool during or prior to use and is responsible for the proper and effective orientation of the tool" and tool-manufacture as "any structural modification of an object or an existing tool as that the objects serves, or serves more effectively as a tool" (Shumaker *et al*., 2011:5, 11). Tool-manufacture had been considered a trait that defined humans (Leakey, 1961), until chimpanzees (*Pan troglodytes*) invalidated this notion when they were observed to modify objects into tools in the wild (Goodall, 1964). This lead to Louis Leakey's famous statement: "Now we must redefine 'tool', redefine 'man', or accept chimpanzees as humans" (Peterson, 2006:212).

Today tool-use is documented in several other animals although tool-making is still rare. Egyptian vultures (*Neophron percnopterus*) drop stones on ostrich eggs to crack open the giant shell and expose its context (van Lawick-Goodall and van Lawick, 1966); Californian sea otters (*Enhydra lutris*) carry stones and pound open mollusk shells on their chest (Hall and Schaller, 1964); bottlenose dolphins (*Tursiops* sp.) wrap sponges around their beak to protect their faces when foraging on the seafloor (Smolker *et al*., 1997); New Caledonian crows (*Corvus moneduloides*) insert a number of distinct twigs in crevices to collect insects and other invertebrates (Hunt, 1996), and some populations have been reported to manufacture tools for this task (Hunt, 1996, 2000).

Orangutans (*Pongo pygmaeus*) use sticks to extract seeds from hard-shelled fruit, modify sticks to extract insects and insect products from tree-holes (van Schaik *et al*., 1996; Fox *et al*., 1999), use leafy branches to shelter from rain, leaves as gloves to handle spiny fruits (Fox *et al*., 1999) and spiny branches (Fox and Bin'Muhammad, 2002), or as napkins to wipe off dirt (MacKinnon, 1974), and hold leaves in mouth to change the pitch of warning calls (Hardus *et al*., 2009). Bonobos (*Pan paniscus*) use leaves as wipes or napkins to clean the body or as hats to protect against rain, leafy branches as fly swatters, small twigs as toothpicks, and moss sponges to get water (Ingmanson, 1996; Hohmann and Fruth, 2003). Gorilla (*Gorilla gorilla gorilla*) tool-use is anecdotal: they were observed using branches to test the depth of water and to maintain balance while foraging in swamps (Breuer *et al*., 2005). Brown capuchins (*Cebus apella*) occasionally use hammers and anvils to crack open nuts (Boinski *et al*., 2000). Bearded capuchins (*Cebus libidinosus*) possess an impressive tool repertoire: they use stones as hammer and anvils to open nuts; sticks to probe into rock cracks, tree holes, and bark to extract insects, honey, wax, or water; stones to dig underground storage organs of plants (hereafter USOs) or break wood to get insects (Fragaszy *et al*., 2004; Visalberghi *et al*., 2007; Ottoni and Izar, 2008; Mannu and Ottoni, 2009). Long-tailed macaques (*Macaca fascicularis*) use stone hammers to crack open nuts and shellfish on anvils and axe hammers to open oysters (Malaivijitnond *et al*., 2007; Gumert *et al*., 2009), and pluck human hair to use as dental floss (Watanabe *et al*., 2007). Thus several primates have been observed to use tools but only chimpanzees, orangutans, bearded capuchins and long-tailed macaques do so habitually and only the first three species have been seen to make tools.

Chimpanzees remain the most proficient tool users and makers among animals, excluding humans (Goodall, 1986; McGrew, 1992, 2004; Wynn *et al*., 2011), excelling beyond all other non-human animals in the flexibility and complexity of these behaviors (Wynn *et al*., 2011). The similarities in tool-use and making between humans and chimpanzees (see below) should, in principle, not be surprising, as chimpanzees are (together with bonobos) the closest living relatives of *Homo sapiens*, having shared a common ancestor approximately 4 to 6 million years ago (Groves, 2001). The genomes of *Pan* and humans are over 98% identical (Cheng *et al*., 2005). Accordingly, chimpanzees not only anatomically, but also behaviorally, show striking resemblance to humans. Researchers have concluded that they have advanced cognitive abilities including self-awareness (Gallup, 1970), intentional deception (Byrne and Whiten, 1992), cooperation (Boesch, 1994), and planning for the future (Osvath, 2009). The same cognitive abilities are present in bonobos, with captive individuals matching chimpanzees in tool proficiency and complexity (Savage-Rumbaugh and Lewin, 1994), and thus researchers are puzzled as to why wild bonobos rarely use tools and have never been observed to make tools (Haslam *et al*., 2009; Wynn *et al*., 2011).

1.1 Chimpanzee tool-use and manufacture

Although the largest repertoire of chimpanzee tool use is related to feeding contexts (Goodall, 1986; McGrew, 1992), the use of tools for other purposes is also impressive and includes hygiene, investigation, intimidation, play, and gestural communication (Goodall, 1986; McGrew, 1992; Whiten *et al*., 1999, 2001; Wynn *et al*., 2011). Chimpanzees have different procedures to make tools: 1) use hands for breaking or detaching; 2) use teeth for cutting, sharpening or chewing; 3) remove bark or leaves; 4) pull while standing on objects; 5) unintentionally break stones while pounding (reviewed in Wynn *et al*., 2011).

Chimpanzee diet is diverse (Goodall, 1986) and includes hidden or embedded resources. The extraction of these out-of-sight foods is known as “extractive foraging” (Parker and Gibson, 1977, 1979). Chimpanzees engage in complex extractive foraging with tools for the purpose of obtaining insects and insect products from their nests, small mammals hidden in cervices, bone marrow from bones of prey, water concealed in tree holes or sandy riverbeds, kernels from nuts by breaking the nutshell, palm hearts by pounding the center of oil-palm trees, and USOs (bulbs, roots, tubers, and rhizomes) (reviewed in Wynn *et al*., 2011), see Appendix 7. Tools allow chimpanzees to access resources otherwise inaccessible (McGrew, 1992), and may permit them to obtain foods more efficiently and expand their diet (Moore, 1996). In fact, Wynn and colleagues (2011) argued that chimpanzees are dependent on the use of tools to function adaptively in their environment, something that was previously considered true only for humans.

Directly relevant to the present thesis is one extractive foraging behavior: the obtention of USOs by wild chimpanzees. Sporadic cases of USOs consumption were reported in different study sites based on indirect evidence (Kortlandt and Holzhaus, 1987; McGrew *et al*., 1988), but USO digging by hand was first observed in Tongo, Democratic Republic of Congo (Lanjouw, 2002) and more recently in Bossou, Guinea, (although here the chimpanzees obtain human cultivated USOs) (Hockings *et al*., 2010). Hernandez-Aguilar *et al*. (2007) discovered indirect evidence that chimpanzees in Ugalla, Tanzania, used tools to excavate USOs. Recently, Gaspersic and Pruetz (2011) also found indirect evidence of the same behavior for the chimpanzees at Bandafassi, Senegal.

Other great apes also dig for underground food: bonobos for earthworms and mushrooms (Bermejo *et al*., 1995) and gorillas for bamboo shoots (Casimir, 1975), but they have not been observed to use tools for this task. The only other non-human animal known to use tools to dig for USOs is the bearded capuchin. In Caatinga, Brasil, these monkeys dig for roots and tubers with stones (Moura and Lee, 2004).

The discovery that wild chimpanzees and capuchins use tools in USO excavation is important because before humans were considered to be the only species that exhibited this behavior (Laden and Wrangham, 2005). USOs are believed to have been an important part of the hominin diet (Hatley and Kappelman, 1980; Wrangham *et al*., 1999). There is an ongoing debate on the role that USOs versus meat may have played in human evolution, by providing the calories necessary to grow the large human brain (Aiello and Wheeler, 1995; Ungar and Teaford, 2002). Therefore, primate USO excavating behavior has important implications for early hominin USO consumption, especially of chimpanzees living in arid environments similar to those reconstructed for early hominins (Hernandez-Aguilar *et al*., 2007). Chimpanzee dietary adaptations and strategies to obtain foods in arid environments may inform about possible adaptations of early hominins that occupied similar habitats (Suzuki, 1969; McGrew *et al*., 1981; Moore, 1992, 1996; Sept *et al*., 1992; Hernandez-Aguilar *et al*., 2007; Hernandez-Aguilar, 2009).

1.1.1 Studies in Captivity

Köhler (1925) studied tool use abilities in captive chimpanzees. He designed his famous experiments so that the chimpanzees had to use tools in order to obtain desirable foods, for example piling boxes to reach overhanging food. Since then, several experiments with captive chimpanzees have been conducted to study tool-use, revealing a complexity similar to that exhibited by wild chimpanzees and even to excel them, for example, adding or combining objects to manufacture tools (e.g. Schiller, 1957; Bania *et* *al*., 2009; and Price *et al*., 2009). Some studies have focused on simulating the extractive tool-use and making behaviors observed in wild chimpanzees (e.g. Kitahara-Frisch and Norikoshi, 1982; Nash, 1982; Maki *et al*., 1989; Brent and Eicherg, 1991; Celli *et al*., 2003), but few had the goal of studying the acquisition of tool-use (e.g. Sumita *et al*., 1985; Paquette, 1992; Tonooka *et al*., 1997; Hirata and Morimura. 2000; Hirata and Celli, 2003; Hayashi *et al*., 2005; Hirata *et al*., 2009).

No study that resembled the extraction of USOs has ever been reported for captive chimpanzees. The present thesis constitutes the first one. However, there is one study with bonobos and one with brown capuchins in which the subjects had to excavate in order to get food. Roffman *et al*. (2012) presented bonobos with piles of sand or soil covering food and Westergaard and Suomi (1995) provided brown capuchins with peanuts buried in soil.

1.2 Objectives

As mentioned previously, there is indirect evidence that wild chimpanzees use tools to excavate USOs in two study sites: Ugalla, Tanzania (Hernandez-Aguilar *et al*., 2007) and Baandafassi, Senegal (Gaspersik and Pruetz, 2011). However, no one has yet observed the process of tool emergence, use and transmission in the excavation of USOs in the wild, as the chimpanzees in both study sites are non-habituated. The current study aims to understand how tool-use can develop in captive chimpanzees, in a task that simulates the excavation of USOs in the wild.

The present experiment was designed to address the following research questions:

1. How will ground-digging behavior emerge and propagate?
2. What techniques will the chimpanzees use for digging?
3. Will the chimpanzees use tools and if so, will they show selectivity and preferences in the tool materials and physical characteristics?
4. What are the underlying factors contributing to tool selectivity?

To answer these questions, an experiment was conducted with a group of chimpanzees living at the Kristiansand Zoo in Kristiansand, Norway.

2 Materials and Methods

2.1 Study Subjects

The study was conducted in a colony of chimpanzees living at the Kristiansand Zoo in Kristiansand, Norway. The colony consisted of 10 individuals: 4 adult males, 5 adult females, and 1 female infant (Figures 2.1 and 2.2). Classification of the chimpanzees' age followed Preuschoft *et al*. (2002): 10 year-olds and older were considered adult, and 3 year-olds and younger were considered infant. All except one individual were born in captivity. Demographic data are shown in Table 2.1.

2.2 Housing Conditions

The compound consists of two enclosures (indoor and outdoor) and a sleeping area (indoor). The indoor enclosure is enriched with climbing ropes and concrete poles, a metal slide, an artificial termite mound, a puzzle feeder, and an artificial waterfall (Appendix 1). The outdoor enclosure is a semi-naturally forested island of 1836 m^2 surrounded by a moat, with natural soil, rocks and vegetation including several large trees (Appendix 1, Figure 2.3). In addition, it has four large climbing wooden frames and two small shelters (wooden cabins of approximately 6 m^2, one at ground level and the other at a height of about 7 m). The sleeping area is indoors and off-exhibit, where the chimpanzees sleep in several cages alone or with others; fresh straw is provided every evening.

Prior to this study, due to aggression from the dominant male towards the only infant of the colony (he used the infant as an object in his displays), the chimpanzees were separated into two groups. This separation continued during the present study and thus the experiment was conducted with each group independently. Each group had access to the outdoor enclosure every other day while the other remained in the inside enclosure. However, to protect the infant's health, on rainy or cold days the group without the infant was given access to the outdoor enclosure and thus the total number of days this group spent outdoors doubled the outdoor days of the group with the infant. The inside and outside enclosures are separated and it is not possible for one group to observe or have any contact with individuals of the other group.

The subjects were fed as follows. In the morning food was placed in the indoor and outdoor enclosures before the two groups of chimpanzees were given access to these enclosures from their night cages, whereas in the evening, food was served separately to each individual in his/her night cage. These meals were predominantly composed of vegetables, but also contained fruit, protein (e.g. eggs), and primate pellets. Two small snacks of fruit, nuts and seeds were given twice a day. Water was available *ad libitum* throughout the day. None of the two groups were food or water deprived during this study.

Table 2.1: Demographic data of the study subjects. Age classes followed Preuschoft *et al.* (2002).

Name	Sex	Date of Birth	Age (years)	Age Class	Origin	Human Reared	Mother/ Father's Name	Offspring
Binni	Female	Est. 1974	39	Adult	West Africa	Yes	--	Junior
Dixi	Female	1977	36	Adult	Munich Zoo	No	--	Jane/ Tobias
Julius	Male	1979	34	Adult	Kristiansand Zoo	Yes	--	Junior/ Yr
Josefine	Female	1983	30	Adult	Öland Zoo	No	--	--
Miff	Female	1987	26	Adult	Copenhagen Zoo	No	--	Knerten
Tobias	Male	1994	19	Adult	Kristiansand Zoo	No	Dixi	--
Jane	Female	1999	14	Adult	Kristiansand Zoo	No	Dixi	Yr
Knerten	Male	2000	13	Adult	Kristiansand Zoo	No	Miff	--
Junior	Male	2003	10	Adult	Kristiansand Zoo	No	Binni/ Julius	--
Yr	Female	2011	2	Infant	Kristiansand Zoo	No	Jane/ Julius	--

Binni

Julius

Julius Junior

Knerten

Miff

Figure 2.1. Indiviuals from Group 1.

Dixi

Jane

Josefine

Tobias

Yr

Figure 2.2. Individuals from Group 2.

2.3 Experimental Setting and Design

One section of the outdoor enclosure, on the southwest part, was selected as the study area (Figures 2.3 and 2.4). This study area was 24.5 m^2 and consisted of natural ground soil. Visibility, vegetation structure, ground and soil characteristics, and slope inclination were parameters considered when selecting the study area. In addition, the study area was placed at the edge of the moat in order to obtain a front view of the chimpanzees because the keepers informed that the apes did not like to sit with their backs to the water. Observations of the chimpanzees were conducted from a deck (1 m high) used by the keepers to give talks to the zoo visitors about the chimpanzees (Figure 2.3).

To provide the chimpanzees with materials to use as tools, sticks from shrubs, sticks and branches from trees, and pieces of bark from trees were gathered from a forest near Kristiansand (Figure 2.5). Before given these potential tools to the chimpanzees, their physical characteristics were recorded: length, weight, thickness (diameter at mid-section), maximum end diameter and minimum end diameter. The materials were categorized into groups (Table 2.2), and marked with an ID number. The aim was to provide the chimpanzees with appropriate materials for excavating but also inappropriate (e.g. too short with poor leverage or too thin and flimsy with poor strength) to see whether the chimpanzees would choose tools based on certain physical characteristics (e.g. longer, thicker) before using them. The materials were given in a specific stage of the experiment (see below), spread within and up to 3 meters around the study area. When the chimpanzees obtained their own tools from the enclosure, these were measured and weighted (same as the provided materials), assigned IDs with alphabetic letters (to differentiate from the ID numbers given to provided materials) and left on the same place where they were found.

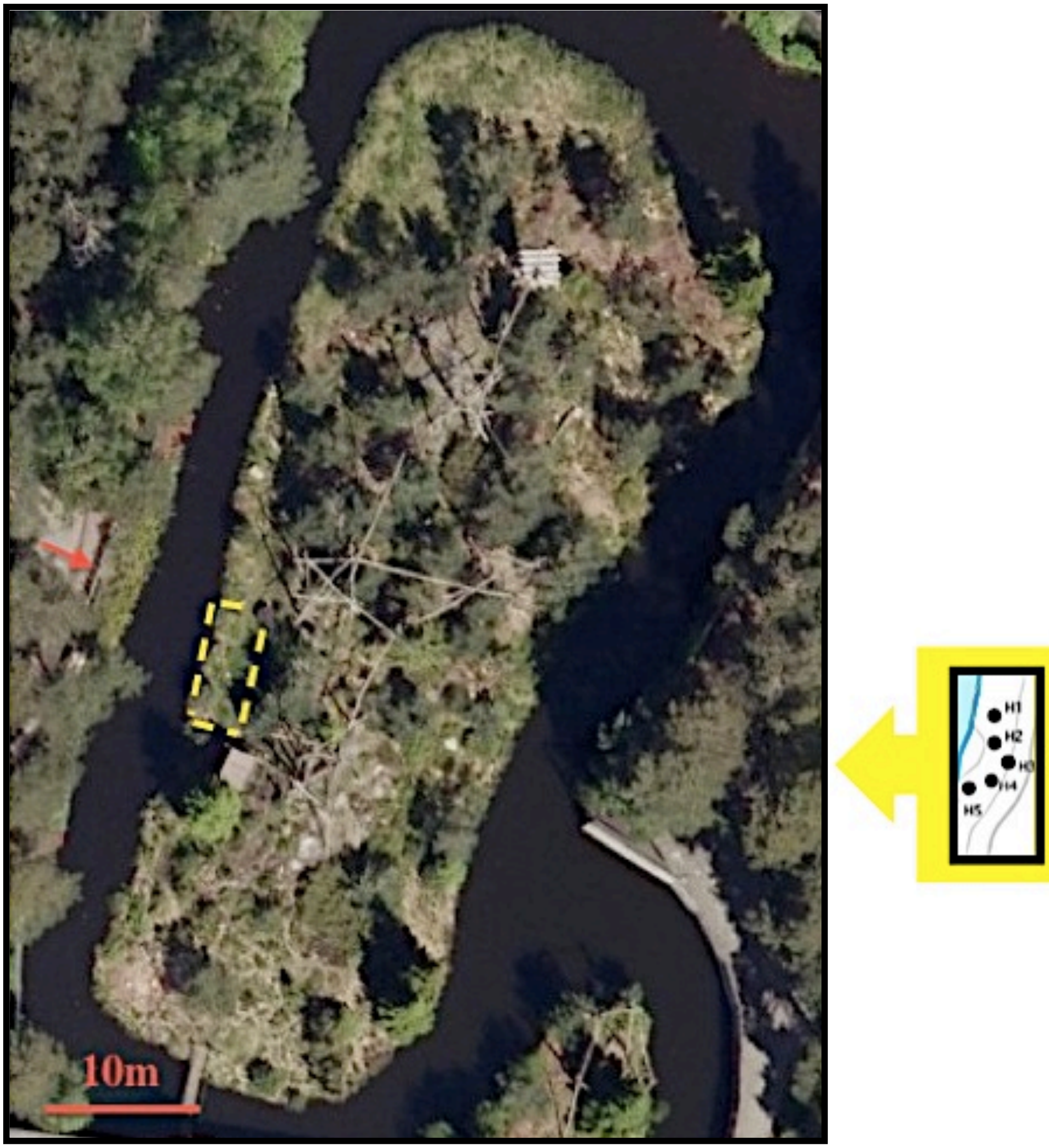

Figure 2.3. The chimpanzee island (retrived from http://www.norgeibilder.no/). The yellow rentangle indicates the location of the study area and the red arrow shows the observation deck. The drawing to the right indicates the specific location of each hole.

Figure 2.4. The study area is within the rectangle. The red arrows indicate the location of the holes.


Figure 2.5. Representative sample of the materials provided to the chimpanzees (sticks, branches and bark pieces).

Table 2.2. Categories of the materials provided (S: sticks and branches, B: bark). The values represent the number of materials in each category.

		Thickness			
		Very Thin <5 mm	**Thin 5-15 mm**	**Medium 15-25 mm**	**Thick >25 mm**
Length	**Short <20 cm**	10 S	10 S	10 S	10 S 1 B
	Medium 20-40 cm	10 S	10 S	10 S 2 B	10 S 9 B
	Long 40-60 cm	10 S	10 S	10 S	10 S 2 B

2.3.1 Stage 1: The Baseline Phase

The Baseline Phase (hereafter Baseline) was the experiment's initial stage and lasted 16 days for Group 1 (hereafter G1) and 7 days for Group 2 (hereafter G2). At the onset of this phase, five holes (15 cm in diameter and 30 cm in depth) were dug out in the study area (Figure 2.3 and Figure 2.4), where there were no large stones in the ground. A separation of at least one meter between holes was targeted to allow more than one chimpanzee to work at the same time, having free range of motion when performing the anticipated digging behavior. The distances between holes ranged from 1-3 m. Throughout this phase, the holes remained open and each day one food item (mango, nectarine, banana, or apple) was deposited into the holes. Originally, USOs such as cooked potatoes or uncooked carrots, turnip, and root beat were to be used to imitate what chimpanzees dig for in the wild. However, fruits were chosen because they comprise a smaller proportion of the chimpanzees' diet in the Zoo and consequently they are a treat for them. A stick with a yellow ribbon (hereafter referred to as stake) was placed in each hole to help the chimpanzees associate the presence of the stake and the existence of the fruit, to mimic how wild chimpanzees presumably associate the stem and leaves of a plant species with its out-of-sight USO.

2.3.2 *Stage 2: The Test Phases*

The Stage 2 consisted of two phases: Phase 1 (hereafter TP1) and Phase 2 (hereafter TP2). During TP1 (11days for G1 and 8 days for G2) a fruit was placed in each hole, the holes were filled with soil and their location marked with a stake; the provided materials were distributed within and outside the study area. During TP2 (17 days for G1 and 7 days for G2) a fruit was placed in each hole but the holes were filled with clay instead of soil and the clay was compacted with a hand tamper and by being hit several times with a foot. Clay was chosen because it compacts and hardens, thus provided a more difficult material for the chimpanzees to dig through without the aid of tools. See Table 2.3.

Throughout the study, holes were prepared in the morning prior to the chimpanzees' entrance to the outdoor enclosure (at about 8:00 am): 10 minutes before during the Baseline, and 30 and 120 minutes before during TP1 and TP2, respectively. During the Baseline, preparations consisted in placing the fruits in the holes. Throughout the Test Phases, every morning each hole was resized to its original dimensions (15 cm in diameter and 30 cm in depth, see above) before placing the fruit and filling it with soil (TP1) or Clay (TP2). It was not possible for the chimpanzees to observe the study area during these preparations. Once the group was allowed into the outdoor enclosure, all individuals had free access to the study area and could participate in the experiment if they desired.

Table 2.3. Overview of the study phases.

Phase	First Day		Last Day		Number of Days		Material	Holes	Materials to be Selected as Tools
	G1	G2	G1	G2	G1	G2			
Baseline	Jun 11	Jun 17	Jul 8	Jul 15	16	7	--	Uncovered	Not Provided
TP1	Jul 10	Jul 15	Aug 8	Aug 9	11	8	Soil	Covered	Provided
TP2	Aug 12	Aug 13	Sep 20	Oct 3	17	7	Clay	Covered	Provided

2.4 Data Collection

Data were collected from 11th of June 2013 to 3rd of October 2013. Four days when the zookeepers considered the weather too harsh, no group was allowed outdoors and therefore no data were collected. The experiment was interrupted from the 26th of August to the 10th of September due to construction for renewing the enclosure (replacing the wooden climbing frames). Behaviors were recorded with a digital video camera (Canon Legria HF M56) and later transferred to a MacBook Pro for analysis (VLC media player, Version 2.0.8 Twoflower).

Recordings started when the chimpanzees inspected the study area, which usually occurred some minutes after their entrance to the outdoor enclosure, and ended 300 minutes after. An excavation episode began with the first attempt of a chimpanzee to excavate and finished when this individual obtained the fruit or abandoned the excavating task and moved away from the hole. An episode was composed of one or a sequence of events. An event was defined as every different excavating activity exhibited by the chimpanzee throughout the episode (e.g. change of hand/foot, of tool grip, of tool used) or if the chimpanzee paused more that 3 seconds. If the same chimpanzee or another individual continued digging the same hole after the fruit had been extracted, these behaviors were also recorded.

The chimpanzees' behaviors were separated into two categories: excavating and excavating-related behaviors. The following data were collected for the excavating behaviors: name of the digger, duration of the digging episode and event, handedness (whether the right, left, or both hands were used), whether foot/feet and/or mouth were used to hold the tool, description of the excavation activity, outcome (whether the digger succeeded or failed to extract the fruit), hole number, tool ID number/letter. The following data were collected for the excavating-related behaviors: individual (reuse of tools, tool transport events, estimated distance of tool transport, tool making, tool modification) and social (if/which individual(s) observed the digger in action, stole food away from the digger, scrounged the fruit after the digger abandoned it, and if/with whom the digger shared the fruit).

To record the characteristics of the holes excavated by the chimpanzees, the depth, maximum diameter, minimum diameter, and circumference of each hole were collected every morning before the holes were re-sized prepared for the day's experimental session (see above). To identify the individual tools that the chimpanzees used in a day, the next morning the ID number/letter of each tool was recorded and its position inside the study area was mapped before the arrival of the chimpanzees. Sometimes it was possible to identify the individual tool that a chimpanzee was using from observations on-site or from the video analysis. At the end of the study the tools that could be recovered were measured again to identify breakage and were inspected to detect changes in the tool characteristics (e.g. when bark was removed).

2.5 Data Analysis

Data on the chimpanzees' behaviors at the study area were entered into Excel sheets for analysis. Statistical analysis was carried out using Microsoft Excel version 14.0.0 and program R version 2.8.0 for Mac. The relationship between 'event tool reuse' and 'tool transport distance' and between 'day tool reuse' and 'tool transport distance' were carried out with simple Regression. The results were obtained as follows:

2.5.1 Selection of tools from the provided materials

If the chimpanzees randomly selected n objects from a provided set of N objects, the null hypothesis states that all possible subsets N!/(n!(N-n)!) have the same probability of being selected. Each of the N objects has four physical characteristics: length (cm), weight (g), maximum end diameter (mm) and minimum end diameter (mm). A random selection of n objects will provide one set of four measurements of the average value of each of the four characteristics. If this selection of n objects is repeated 1000 times a sample of 1000 average numbers in a random sample of n objects is obtained. These 1000 average numbers may be used to estimate the distribution of the average size of the studied characteristics under the null hypothesis that the chimpanzees selected the tools randomly; that is, that they showed no preferences for a certain size or dimension.

In order to develop a statistical test, as an example for length, first, the 1000 average length values are sorted from the lowest to the highest value, and the 25th and 975th value is then denoted $L_{0.025}$ and $L_{0.975}$, respectively. The statistical interpretation of these two quantities is that under the null hypothesis there is a 5% chance that the average length L in a random selection of n objects from a given set of N objects is either shorter than $L_{0.025}$ or longer than $L_{0.975}$. We therefore reject the null hypothesis and conclude that the chimpanzees have length-preferences if the observed average length L is outside the interval $[L_{0.025}, L_{0.975}]$; that is, if $L < L_{0.025}$ or $L > L_{0.975}$.

The critical values for the four characteristics were as follows:

- Length (cm): 24.648----33.488
- Weight (g): 21.00----47.52
- Maximum end diameter (mm): 12.72 ----19.68
- Minimum end diameter (mm): 11.00----17.28

2.5.2 Selection of tools from the provided materials and tools gathered by the chimpanzees

In the present experiment, the chimpanzees were given the option to select their tools from the provided materials. They also had the possibility to gather tools from the vegetation in the outdoor enclosure. In this case, we will test whether these two options produced differences in tool choice. Again, we explain the statistical procedure in terms of length. Assume n and m objects are selected from respectively the provided materials and the outdoor enclosure, and denote the length of the tools by respectively $x_1, x_2, \ldots, x_n$ and $y_1, y_2, \ldots, y_m$. Under the null hypothesis of no preferences of length, the distribution of the length of the tools from the provided materials and the outdoor enclosure should have the same expectation, that is, H_0: $E(X) = E(Y)$. Since these length values do not have a normal distribution or equal variances, it is recommended to apply the nonparametric Mann-Whitney test with modification for ties (Conover, 1980).

3 Results

During the 66 days of the study (44 days for G1 and 22 days for G2) 9 out of the 10 chimpanzees were seen to excavate. These chimpanzees used only hand, only tool, or a combination of hand and tool in excavation. Seven of them were observed to use tools in excavation.

3.1 Characteristics of the tools used

Out of 110 provided stick and branch materials the chimpanzees selected 25 (23%) and used them as tools. These tools were all tree branches and ranged in length from 25.2 cm to 57.5 cm and in weight from 1 g to 159 g (see Table 3.1 for descriptive statistic of the measurements). These tools were significantly longer (41.06±9.69 cm, $P<0.05$) and heavier (50.28±43.40 g, $P<0.05$) than the potential stick and branch tools that were not selected. But selected versus non-selected did not differ in maximum end diameter (16.88±8.28 mm, $P>0.05$) and minimum end diameter (14.08±7.54 mm, $P>0.05$), Figure 3.1. None of the bark materials provided were selected (n=14; length: $\bar{x}$ =28.87 and SD=7.66 cm, weight: $\bar{x}$ =142.14 and SD= 73.45 g, and thickness: $\bar{x}$ =30.64 and SD=6.34 mm).

During the Baseline, when materials to use as tools were not provided, and during the two test phases (TP1 and TP2) when these materials were available, four of the chimpanzees (Julius and Junior from G1 and Josefine and Tobias from G2) gathered sticks, a piece of grass, and a plastic tube from the enclosure and transported them up to 10 m to the study area to use them as tools (see Table 3.2 for descriptive statistic of the measurements of these gathered tools). The gathered tools did not differ in physical characteristics (length, weight, maximum end diameter and minimum end diameter) from the selected tools (the respective P values of the nonparametric Mann-Whitney test are 0.31, 0.49, 0.22 and 0.48); see Figure 3.2. In other words, the tools the chimpanzees gathered by themselves and the ones they selected from the provided materials shared the same characteristics.

Table 3.1. Descriptive statistics of the materials (sticks and branches) provided (mean ± SD (range).

	Provided materials		
	Selected (tools) (n=25)	Non-selected (n=85)	All (n=110)
Length (cm)	41.06±9.69 (25.2-57.5)	25.50±10.57 (11.5-55.7)	29.04±12.24 (11.5-57.5)
Weight (g)	50.28±43.40 (1-159)	28.31±35.62 (1-206)	33.30±38.44 (1-206)
Maximum end diameter (mm)	16.88±8.28 (4-32)	15.64±10.58 (4-46)	15.92±10.08 (4-46)
Minimum end diameter (mm)	14.08±7.54 (3-29)	14.04±10.06 (2-43)	14.05±9.51 (2-43)

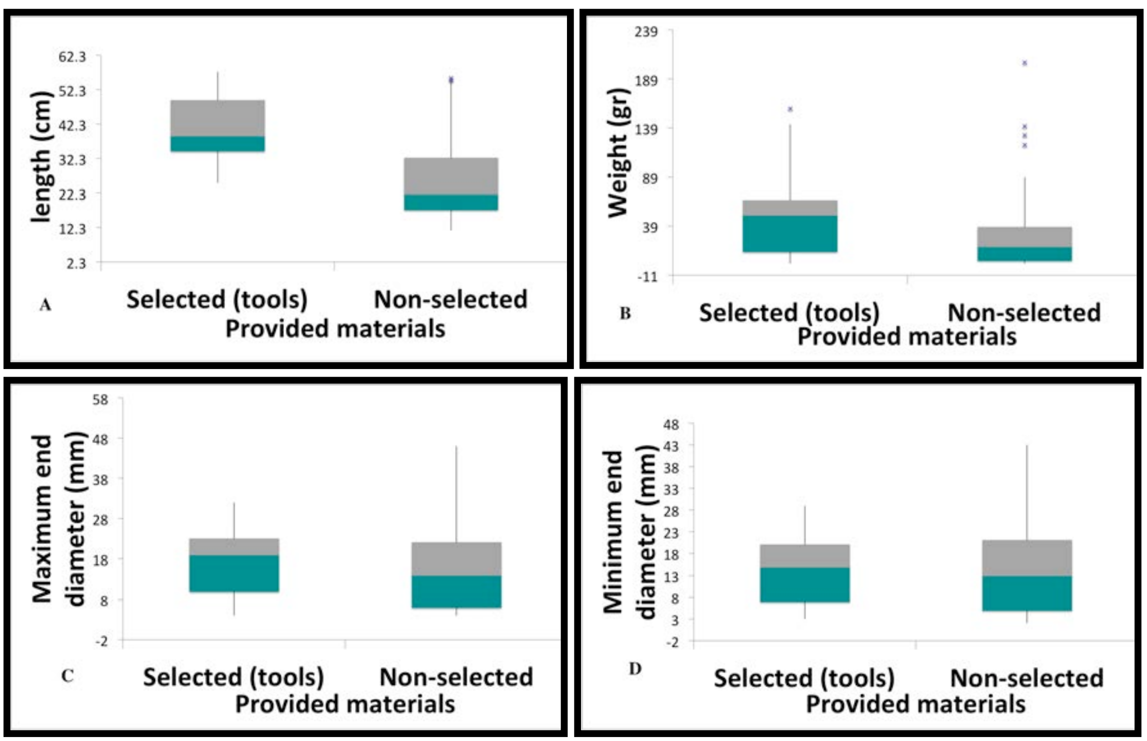

Figure 3.1. Boxplots of the selected and non-selected provided materials (A: Length (cm), B: Weight (g), C: Maximum end diameter (mm), and D: Minimum end diametr (mm); $n_{selected\ (tools)}$=25 and $n_{non\text{-}selected}$=85).

Table 3.2. Descriptive statistics of the tools gathered by chimpanzees (mean ± SD (range). First column: all gathered tools; Second column: without the grass tool.

	Gathered tools	
	(n=11)	(n=12)
Length (cm)	51.29±20.11 (24.5-81)	48.43±21.58 (17-81)
Weight (g)	56.04±59.97 (9-189.1)	52.03±58.84 (8-189.1)
Maximum end diameter (mm)	24.18±10.42 (6-40)	--
Minimum end diameter (mm)	15.27±11.75 (3-36)	--

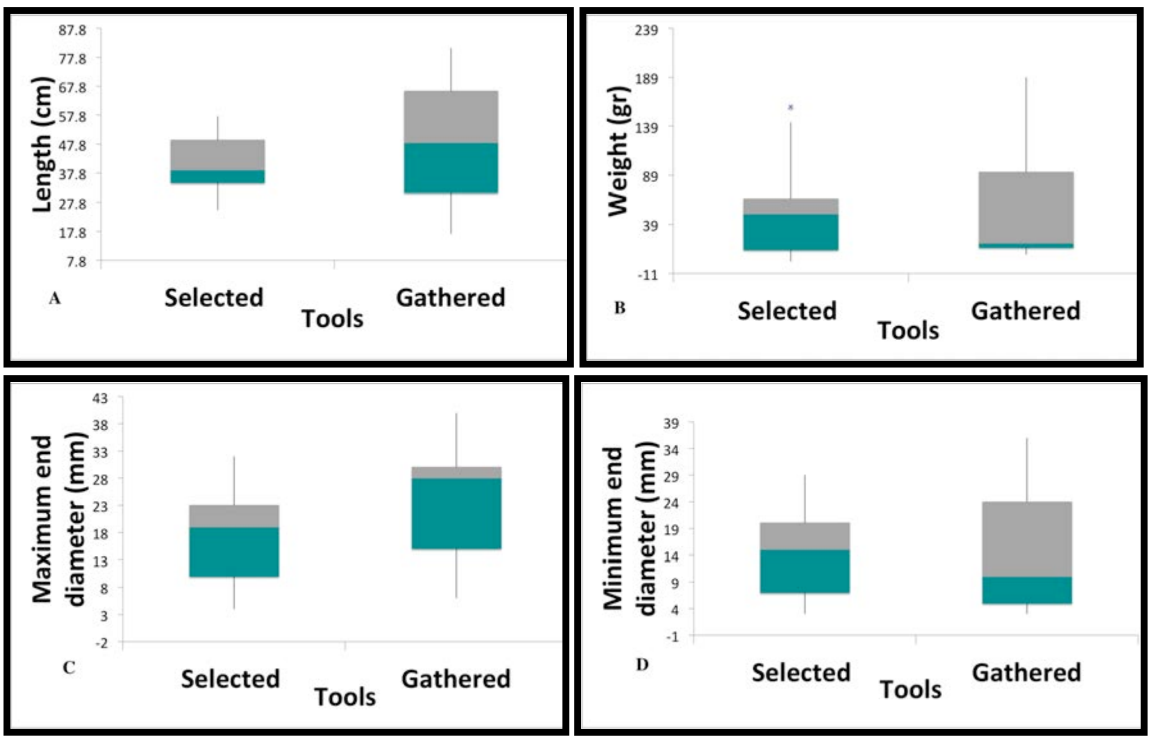

Figure 3.2. Boxplots of the selected and gathered tools (A:length (cm), B: weight (g), C: maximum end diameter (mm), and D: minimum end diametr(mm); $n_{selected}$=25 and $n_{non-selected}$=12).

3.2 Tool reuse

Out of the 25 tools selected by the chimpanzees, 16 (64%) were reused in different events and days throughout the study. These tools were reused in a total of 266 events: 61 during TP1 and 205 during TP2 ($\bar{x}$ = 16.62, SD= 20.54, range= 2-75). Similarly, 6 out of 12 tools gathered by the chimpanzees were also reused, in a total of 40 events: 2 during the Baseline, 11 during TP1, and 27 during TP2 ($\bar{x}$ = 6.66, SD= 6.91, range= 2-17). Tools 108, 102, and 103 exhibited the highest number of event reuse (Figure 3.3). In addition, 14 of the selected tools and 2 of the gathered tools were reused in different days ($\bar{x}$ =7, SD=5.58, range=2-22). Tools 108, 102 and 104 had the highest number of day reuse (Figure 3.4). Sample pictures of the reused and non-reused tools can be seen in Appendix 2.

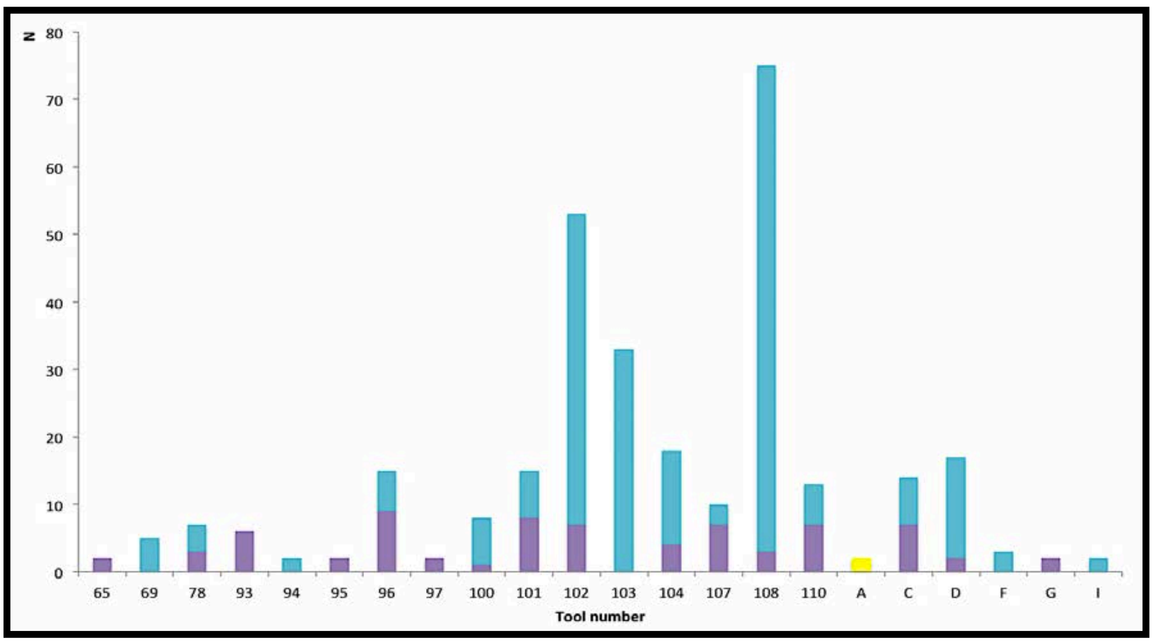

Figure 3.3. Tool (provided and gathered) event reuse throughout the study (■B= Baseline, ■TP1= First Test Phase, ■TP2= Second Test Phase).

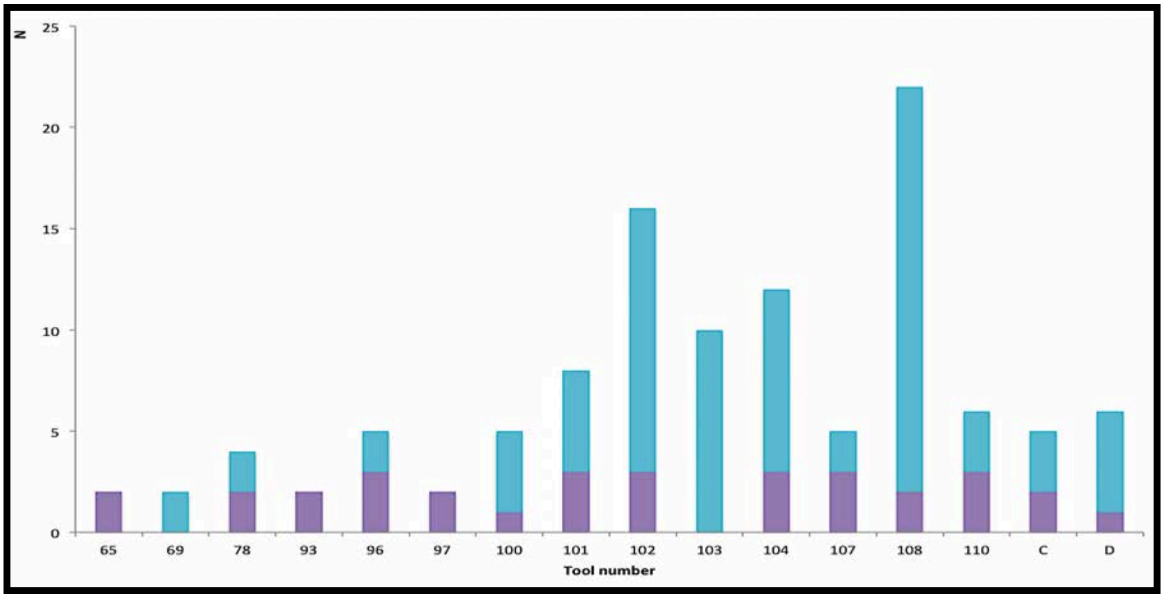

Figure 3.4. Tool (provided and gathered) day reuse throughout the study (■TP1= First Test Phase, ■TP2= Second Test Phase). Tools during Baseline were not used in different days.

3.3 Tool modification

Except in one occasion, the chimpanzees were never observed to intentionally modify the tools. On September 12th Julius was using tool 108 to excavate filled hole (H3), he stopped, looked at the tool and at 10:14:13 started to strip the bark from the tool peeling it down with one hand. This modification was clearly intentional. However, it was not clear that Julius' goal was to enhance the tool's function.

3.4 Tool transport

Two kinds of tool transport by the chimpanzees were observed: 1) they gathered materials in the outdoor enclosure and transported them to the study area to be used as tools, or 2) they transported tools between the empty or filled holes, within and outside of the study area. Throughout the duration of the study the total transport distance of all tools was 174.5 meters. During the Baseline the shortest total distance of transport occurred: the subjects transported the tools they gathered (A, B, and E) for a total of 9 meters (n= 4, $\bar{x}$ = 2.25 m, SD=1.32, range= 1-4 m). During TP1 tools were transported for a total of 34.5 meters (n= 15, $\bar{x}$ = 2.30 m, SD= 2.32, range= 1-10 m). During TP2 the longest total distance of transport occurred: 131 meters (n= 74, $\bar{x}$ = 1.77 m, SD= 1.58, range= 1-10 m). The longest single tool transport distance (10 meters), which occurred three times: one time in TP1 and two in TP2.

The linear model of the relationship between tool transport distance and tool event reuse was statistically significant (Figure 3.5; linear regression, $F_{1,16}$=105.6, $P<0.05$). Tool event reuse explained 87% of the variability in tool transport distance. Similarly, the linear model of the relationship between tool transport distance and tool day reuse was statistically significant (Figure 3.6; linear regression, $F_{1,14}$=49.6, $P<0.05$). Tool day reuse explained 78% of the variability in tool transport distance.

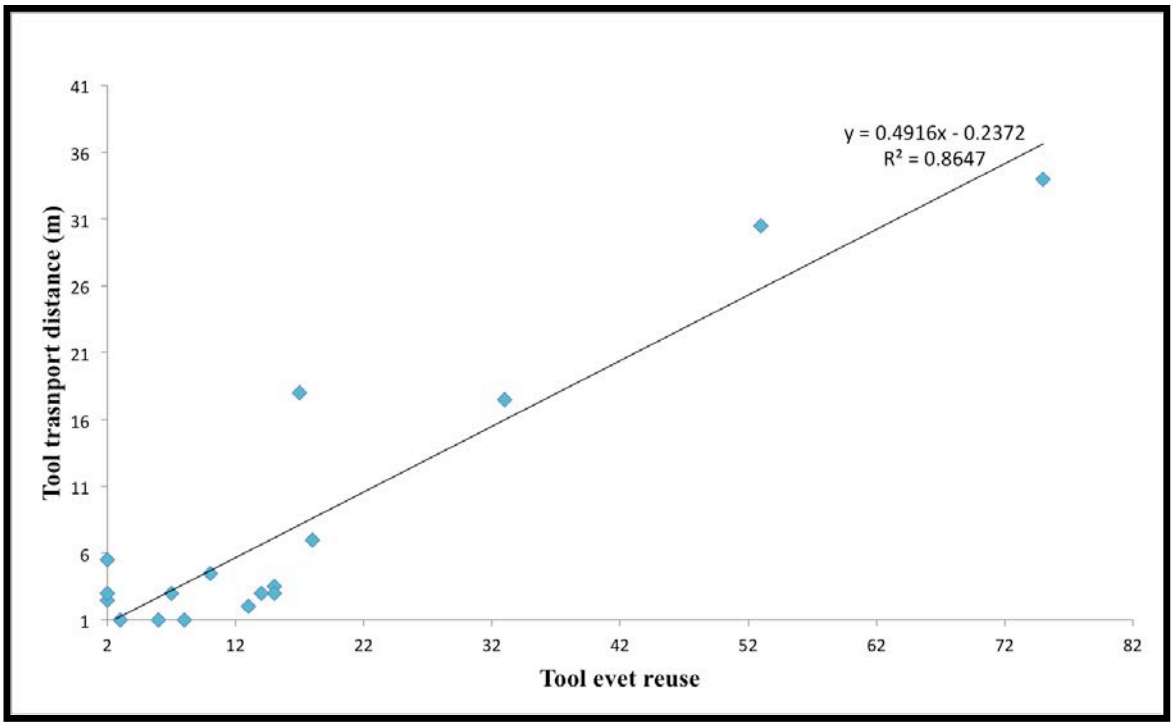

Figure 3.5. The regression between tool event reuse and tool transport distance. The highest values belong to tools 108 and 102, respectively.

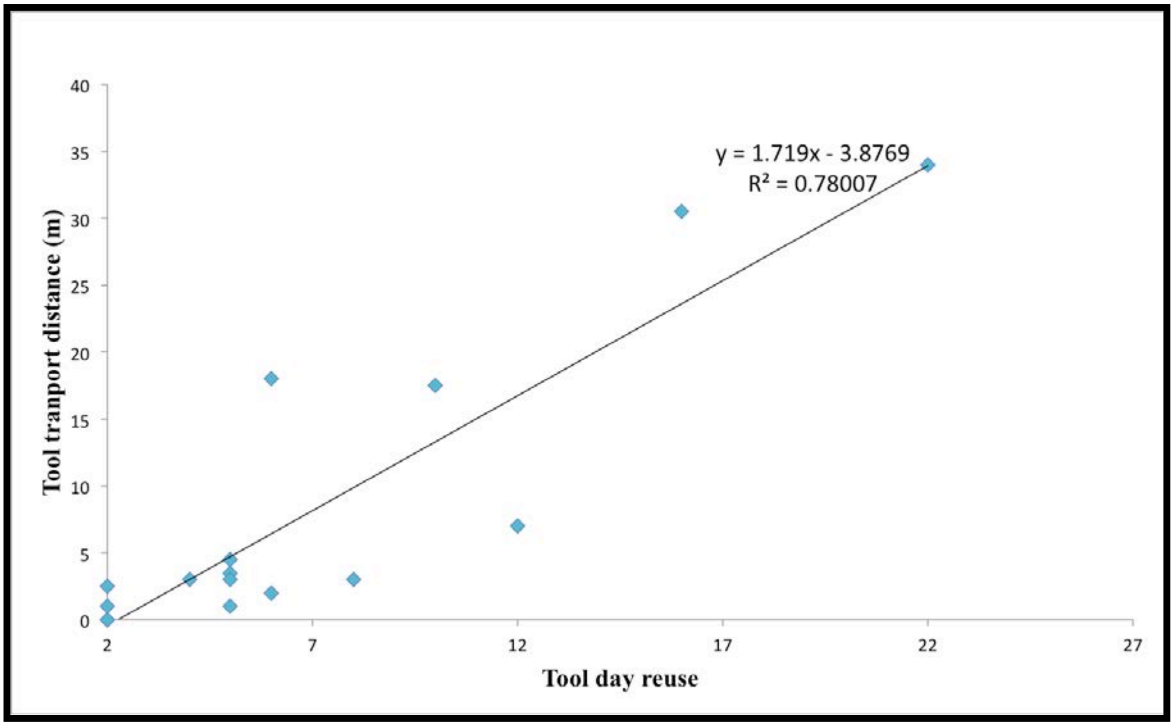

Figure 3.6. The regression between tool day reuse and tool transport distance. The highest values belong to tools 108 and 102, respectively.

3.5 Excavation-related techniques and actions observed over the study

The chimpanzees were seen to perform different techniques and actions during excavation. When excavating manually, the chimpanzees were never observed to use both hands at the same time. An ethogram of the tool-use actions involved in excavation was produced based on the data collected both from video records and from in situ observations (Table 3.3). The timing of emergence of tool-use actions per group is shown in Figure 3.7. See Appendix 3 and Figure 3.8 for photos of the chimpanzees preforming the different actions.

Table 3.3. Ethogram of the tool-use actions involved in excavation.

Probe/Investigate	The chimpanzee held one end of a stick and placed the other end in the entrance of the open, or of the completely or partially excavated holes. Then the tool was withdrawn gently and the inserted end was visually inspected and smelled.
Perforate	The chimpanzee inserted a stick perpendicular to the ground and applied force pushing the end of the stick into the ground with both hands or a hand and a foot. The tool was retrieved and the end that went into the ground was then usually smelled and visually inspected.
Pound	The chimpanzee held a stout stick with both hands and with poweful back and forth movements of the tool hit the ground repeteadly. The forceful blows weakened the soil in the hole, facilitating access to the fruits.
Dig	The chimpanzee held a stick with both or either hand and inserted it into the ground out from where he/she stood. Then, while pressing the tool in the ground, moved it powefully inward towards him/herself. The repeated movement of the tool broke up the earth and loosened the soil.
Shovel	The chimpanzee held the midsection of the tool with one hand and with the other hand, or the opposite leg, held the upper end of the stick. Then he inserted the lower end of the stick into the ground and forced it in until about half of the tool had penetrated. He then withdrawed the tool outward, which resulted in the removed materials deposited outside of the excavated area.
Enlarge	The chimpanzee made a small hole on the surface using fingers or tool. Then he inserted a stick into this hole and with sweeping, circular motions of the tool widened the opening. Tool stayed in contact with the ground while rotating.

3.5.1 *Baseline*

During Baseline the holes were left open and fruits were deposited on the bottom. Chimpanzees predominantly investigated the holes manually (mainly through poking), visually and olfactorily. However, despite the fact that the chimpanzees had not been provided with tool materials yet, two of them (both from G1) gathered their own tools. The first chimpanzee (Junior) got tools A and B and the second (Julius) got tool E, transporting them to the study area: 4m (tool A), 2.5m (tool B) and 1m (tool E). Both chimpanzees used their tools to investigate the holes by probing. In addition, Junior used tool A to perforate at the bottom of two holes (H2 and H5).

3.5.2 *Test Phase 1*

During this phase the holes were filled with non-compacted regular soil. The buried fruits were obtained shortly after the chimpanzees arrived to the study site. However, the chimpanzees revisited the holes and excavated later in the day even though there were no more fruits left. The following are the techniques and actions observed in both instances:

1) When fruits were available:

The chimpanzees predominantly (96% of events) used either hand to excavate the fruits. Two different manual excavation techniques were observed: a) the chimpanzee inserted a hand in the hole up to the wrist and with back and forth movements of the hand continuously searched for the fruit without taking the soil out of the hole, b) the chimpanzee removed handfuls of soil until the fruit was exposed, piling the soil at any side of the holes (Appendix 4). In addition to manual excavation, the use of only tool or of hand and tool were observed in 3% and 1% of the excavation events, respectively. The only tool actions observed were probing partially excavated holes and digging. Digging was done once, on the second last day, by one chimpanzee (G1: Knerten).

2) When no more fruits were available:

The chimpanzees revisited the study area and excavated the partially filled holes by hand, tool, or both (85%, 10%, and 5% of the events, respectively). Both manual excavation techniques described above (a and b) were observed. However, in b) the chimpanzees excavated the soil below the level where the fruits had been placed. Tools were used only below this level, where the soil was naturally compacted and thus harder than the non-compacted soil used to fill up the holes. The tool actions observed in this phased were: probing, perforating, pounding, digging and enlarging (30%, 31%, 7%, 30% and 2% of the tool-use events, respectively). Probing emerged in G2 during this phase but the chimpanzees of this group were not observed to perform any other action. Pounding, digging and enlarging emerged in G1 and probing and perforating (both of which had emerged in Baseline) continued in this group.

Regarding tool-use actions in this phase, 5 out of 7 tool users probed (3 from G1 and 2 from G2), and 2 perforated and pounded (both from G1). Digging was done by 3 of the tool users (all from G1). Enlarging was only seen once and was done by one chimpanzee (from G1), Table 3.4.

3.5.3 Test Phase 2

During this phase the holes were filled with clay. Unlike in the previous phase (TP1), not all buried fruits were excavated shortly after the chimpanzees entered the study area. As a result, the chimpanzees regularly revisited the area to excavate the remaining fruits. The following are the techniques and actions observed in both instances:

1) When fruits were available:

The chimpanzees used either hand to excavate the fruits in most (81%) of the events. They initiated excavation using two different techniques: a) the chimpanzee opened the entrance above the filled hole with one finger (index or middle) and then inserted the remaining fingers to widen the hole, or b) the chimpanzee inserted all the fingers forcefully in the hole and with a circular motion of the hand took out a pile of clay. After using techniques a) or b), the chimpanzee continued to withdraw clay from the hole, continuously alternating the left and right hand in the task. On occasions, the chimpanzee was seen to scrape the clay at the surface before applying any of the techniques (Appendix 4). In addition to manual excavation, the chimpanzees were observed to excavate the fruits using only tool or hand and tool (8% and 11% of the events, respectively). A tool was used together with one hand to facilitate the excavation using different techniques: a) the chimpanzee perforated the clay filled hole with a tool, and then used fingers to widen the entrance; b) pounded the clay with a tool and used the tool as a hoe or either hand to take the clay out; c) dug the clay with a tool and then used either hand to take the clay out. The main tool-use action in this instance was digging (67% of the tool-use events), which emerged in G2 on the first day of this phase and continued in G1 (digging had emerged in G1 during TP1). However, tools were also used in probing, perforating, pounding, and enlarging actions (8%, 7%, 11%, and 2% of the tool-use events, respectively). In addition, during the excavation of the fruits, a new technique emerged: shoveling, which was performed by only one chimpanzee (G2: Julius). The shoveling action comprised 5% of the tool-use events. Perforating, pounding, and enlarging actions emerged in this phase in G2 and continued in G1 (these had emerged in G1 during TP1). See Figure 3.7.

2) When no more fruits were available:

The chimpanzees dug further, below the soil level where the fruit had been placed by a) continuously withdrawing the naturally compacted soil using one hand (76% of events), or by 2) using a tool alone or a tool in combination with one hand (24% of events, each 12%). Tools were used in probing, perforating, pounding and digging actions (16%, 10%, 8% and 66% of the tool-use events, respectively).

Regarding tool-use actions in this phase, 5 out of 7 tool users probed and perforated (3 from G1 and 2 from G2). Pounding was done by 4 (2 from G1 and 2 from G2), whereas digging was done by 6 of the tool users (4 from G1 and 2 from G2). Enlarging was only seen in 3 tool users (2 from G1 and 1 from G2), Table 3.4.

3.6 Sequence for the emergence of tool actions

Both groups achieved the use of tools in the excavation of the underground placed fruits (Figure 3.7, Table 3.4). The timing when tool-use emerged differed between the two groups: all tool-use actions emerged earlier in G1 (from Baseline) than in G2 (Figure 3.7). However, tool actions emerged in a similar sequence in both groups (except for shoveling, which was unique to G1). Considering both groups together, 6 out of the 7 tool users performed at least two actions (Table 3.4). Four of these 6 seemed to have acquired the actions through their own trial and error, in other words, "invented" the action (Julius and Junior from G1, and Josefine and Tobias from G2) while the other two (Knerten and Miff from G1) seemed to have learnt the actions by observing the skilled individuals, except for digging which was first observed to be performed by Julius and learnt by Junior. An example of observational learning can be found in Appendix 5.

All 7 tool users began by probing (first action), except for Miff (G1) who started tool use until TP2 and learnt only two actions: perforate and dig. Out of the 4 chimpanzees that seemed to have acquired the tool actions by their own trial and error (Julius and Junior from G1 and Josefine and Tobias from G2), 3 acquired perforate (second action), all 4 acquired pound (third action), then dig (fourth action) and 1 finally acquired shovel (fifth action). Thus the sequence for the emergence of tool actions was: probe, perforate, pound, dig, and shovel (Figure 3.7). Mastering one action seemed to facilitate the invention of the following action. Enlarge is not considered part of the sequence because out of the 3 chimpanzees seen to perform this action (Knerten and Junior from G1 and Tobias from G2), only one (Knerten) seemed to do it with the intention of obtaining a specific result and did it more than one time; in addition this action did not seem to be facilitated by any other action.

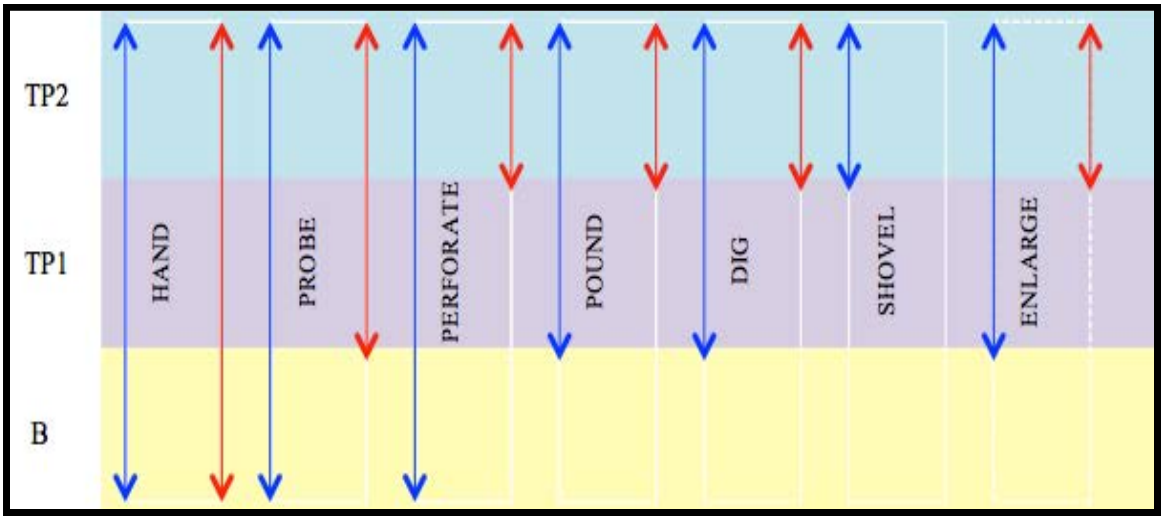

Figure 3.7. Timing of emergence of excavation actions in each study group. The arrows indicate each stage where actions occurred in G1 (blue) and G2 (red). The chimpanzees initiated tool-use by probing the holes and then each action (probe, perforate, pound, dig and shovel) emerged sequentially. Enlarge is shown in the square with broken lines because it is not part of the sequence, see text. Stages: B= Baseline, TP1= First Test Phase, TP2= Second Test Phase.

Table 3.4. Manual and tool-use excavation actions observed for each individual chimpanzee in the two phases of the study, after Baseline. During Baseline Julius and Junior (from G1) performed probing and Junior performed perforating. Phases: TP1 = First Test Phase, TP2 = Second Test Phase; Groups: G1 (Group 1), G2 (Group 2).

		Excavation actions													
		Manual		Tool use											
Group	**Name**	Hand		Probe		Perforate		Pound		Dig		Shovel		Enlarge	
		TP1	TP2	TP1	TP2	TP1	TP2	TP1	TP2	TP1	TP2	TP1	TP2	TP1	TP2
G1	Binni	--	--	Yes	--	--	--	--	--	--	--	--	--	--	--
	Julius	Yes	Yes	--	Yes	Yes	Yes	Yes	Yes	Yes	Yes	--	Yes	--	--
	Junior	Yes	Yes	Yes	Yes	Yes	Yes	Yes	--	Yes	Yes	--	--	--	Yes
	Knerten	Yes	Yes	Yes	Yes	--	--	--	Yes	Yes	Yes	--	--	Yes	Yes
	Miff	Yes	Yes	--	--	--	Yes	--	--	--	Yes	--	--	--	--
G2	Dixi	--	--	--	--	--	--	--	--	--	--	--	--	--	--
	Josefine	Yes	Yes	Yes	Yes	--	Yes	--	Yes	--	Yes	--	--	--	--
	Tobias	Yes	Yes	Yes	Yes	--	Yes	--	Yes	--	Yes	--	--	--	Yes
	Jane	Yes	Yes	--	--	--	--	--	--	--	--	--	--	--	--
	Yr	Yes	Yes	--	--	--	--	--	--	--	--	--	--	--	--

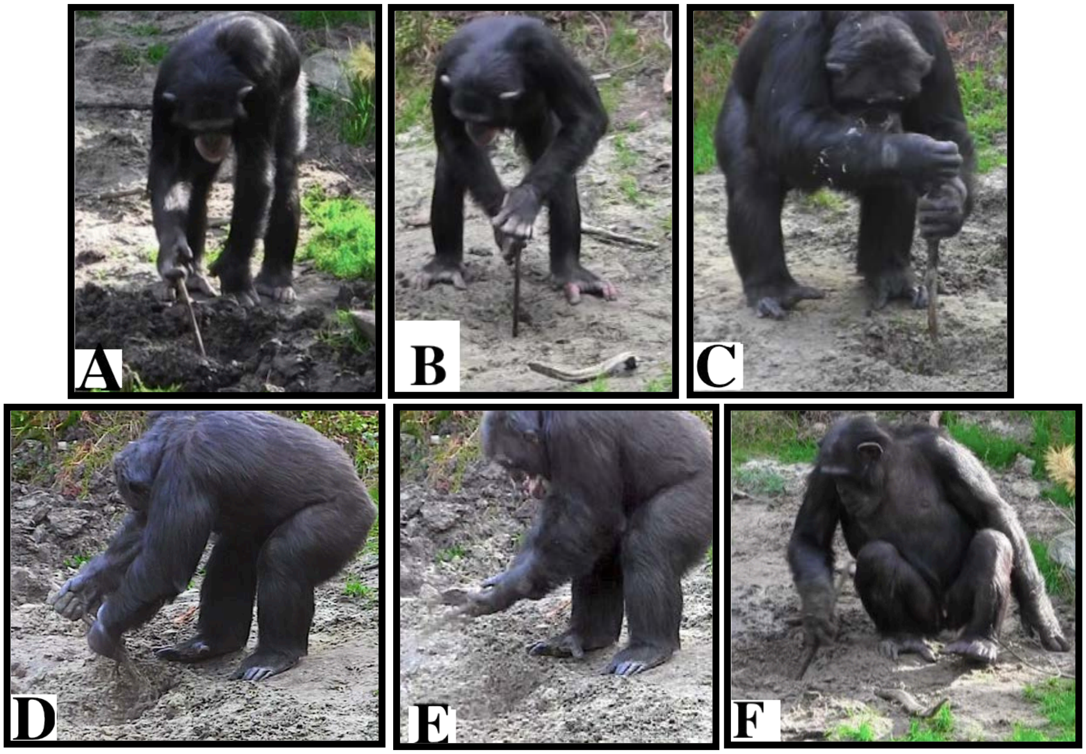

Figure 3.8. Tool-use excavation actions: A) Probe, B) Perforate, C) Pound, D) Dig, E) Shovel, and D) Enlarge.

3.7 Excavation-related behaviors

Out of 690 episodes in which the chimpanzees attempted to excavate the fruits, 177 were successful, meaning they obtained the fruit (26%), and 513 was unsuccessful, failing to obtain the fruit (74%). Out of the successful episodes, food sharing was possible in 86 episodes (49%): other chimpanzees observed the owner and begged for the fruit. The observers begged in three different ways: they reached out an extended hand towards the owner, they positioned themselves in a close face-to-face posture with the owner and gazed intensely at his/her mouth, or they pulled the owner's hands without using aggression (Appendix 6). The owners rejected the beggars 58 times: they sat with their backs to the beggars, or sat far from the beggars. Chimpanzees were also seen to prevent begging before it occurred: soon after they obtained the fruit, they ran away from the study area and sat where no other chimpanzee was present. However, food was shared 11 times: 9 times the owner offered a piece of the fruit to the beggar and 2 times the whole fruit was given. In addition, once, a chimpanzee obtained a fruit by stealing it from the owner: the owner (Josefine) left the fruit on the ground and continued to excavate with her head down, looking at the working hole; the other chimpanzee (Tobias) picked it up and ran away. The chimpanzees scrounged the fruits that were abandoned by other chimpanzees in the study area 14 times. Finally, once an individual gently took a tool that another individual was using, this individual allowed the first one to take the tool without aggression.

4 Discussion

Wild chimpanzees exhibit a wide diversity of complex extractive foraging behaviors, some of these to access underground sources: social insects and their products, water, and USOs (Appendix 7). One type of extractive foraging believed to have been key in human evolution is the excavation of USOs (Hatley and Kappelman 1980; Wrangham *et al*., 1999), which is also present in wild chimpanzees, sometimes involving the use of tools (Hernandez-Aguilar *et al.*, 2007; Gaspersik and Pruetz, 2011). Despite the enormous importance of studying this behavior in chimpanzees to model how early hominins may have used tools in the context of USO excavation, it has yet to be directly observed due to the chimpanzees' lack of habituation in the two study sites that yielded evidence of this behavior. Consequently, the present experiment was designed to present captive chimpanzees with a task that resembled the excavation of USOs in wild chimpanzees with the aims of investigating how this behavior could emerge and the specific actions involved in extracting underground food. The experiment was successful: the chimpanzees achieved excavation, eight out of ten excavated manually the buried food and six of these (and one that did not excavate manually) used tools in the task (Table 3.4).

4.1 Characteristics of the tools used

The analysis showed that chimpanzees in the present study were selective in their choice of materials and their source: the materials used as tools were longer and heavier than those unselected and they preferred tree to shrub or bark materials. In line with this, the tools they gathered had similar physical characteristic to the tools they selected and were also from trees. Selectivity of tool materials for a specific task and even of individual tools has been reported for wild chimpanzees (Carvalho *et al*., 2008, 2009; Sanz *et al*., 2010, Wynn *et al*., 2011), and may indicate preference or even possessiveness (Matsuzawa, 1999). In the present study, the tools that chimpanzees selected and obtained shared physical characteristics that seemed to make them more functional for the excavation task, suggesting that the chimpanzees were able to discriminate among materials and physical characteristics, and further illustrates the existence of non-random tool choice by chimpanzees. In short, "A tool is not an object but a mental program which can interrelate that object with others to implement anticipated external effects. Tools, in other words, are as much mental as material, and their description is not a photograph of the material object itself but an empirically verifiable characterization of the mental knowledge and behavioral program which allow the object to be produced and used." (Reynolds, 1982:377). In the present study tools were heavier and had thicker ends compared to the tools found in Ugalla (see Table 3.1 and 3.2 and Figure 2 in Hernandez-Aguilar et *al*., 2007), possible reasons for this difference are discussed below.

4.2 Tool reuse

In the present study, some tools remained in the study area and were reused in different days. Wild chimpanzees reuse both wooded (Sanz *et al*., 2004) and lithic (Carvalho *et al*., 2009) tools, and transport favorite individual stone tools around nut-cracking sites (Matsuzawa, 1999). Wild capuchins also reuse their excavating stone tools (Moura and Lee, 2004). But why were tools reused in the present study? In wild chimpanzees selectivity towards particular tools may result in the reuse of those tools (Carvalho *et al*., 2009) and this may also hold for the present study, as the chimpanzees were selective in their choice of tools (see above). It is also possible that other tool characteristics besides the ones analyzed here (e.g. durability) resulted in reuse. In addition, the competitive nature of this study may have influenced the reuse of tools: searching for appropriate tool materials or raw materials to make tools and transporting them to the study area would have been costly for an individual as other chimpanzees were working to gain the fruits and thus it may have been a better strategy to reuse tools already present in the study area or close by. In Westergaard and Suomi (1995) experiment, captive capuchins only used digging tools once, making new tools when needed, but conditions were different since the monkeys were in a cage and the chimpanzees in the present experiment were in an outdoor enclosure with natural vegetation.

4.3 Tool modification

Over the study, only one instance of tool modification was witnessed: a chimpanzee removed the bark from a tool. Tool modification is common in wild chimpanzees (e.g. Goodall 1986; Sanz *et al*., 2004, 2009) and it is believed to enhance tool-using performance (Sugiyama, 1985; Sanz *et al*., 2009), for example making a brush end on a fishing probe makes more termites cling to it in comparison with plain-tipped sticks (Sanz *et al.*, 2009). Even though the only modification observed in the present study was clearly intentional, it was not clear whether the goal was to make the tool more efficient in the task. In the experiment by Westergaard and Suomi (1995) capuchins modified their tools by breaking the sticks and removing bark and leaves, producing sharp points on the broken ends that seemed to increase the tools' efficiency; however, the authors were not certain that efficiency was the monkeys' intention. The characteristics of the materials provided to the chimpanzees in the present study may have influenced the almost lack of modification: they were all dead sticks and branches that did not have leaves or side branches to remove. However, when the chimpanzees gathered their own tools from the enclosure they could have chosen to take branches from trees as they do for other types of tool-use, but the sticks and branches they gathered were also dead. Whether dead branches are better tools for excavation compared to fresh materials requires further investigation.

4.4 Tool transport

During the present study the chimpanzees were observed to manufacture tools for different purposes (e.g. reaching food floating in water) but despite their tool-making abilities they were never seen to make tools for excavation. However, the chimpanzees obtained their own tools in advance of use by gathering materials lying on the ground and transporting them several meters to the study area. In the wild, chimpanzees pick up materials or manufacture tools in advance, transporting them up to hundreds of meters to the place where they will be used (Goodall, 1964, 1986; McGrew, 1974; Boesch and Boesch, 1984; Sanz *et al*., 2004). The transport of tools by the study chimpanzees before they needed them indicates that they were able to plan ahead, a capacity that exists in wild chimpanzees (Goodall, 1986). Sometimes, the chimpanzees in this study fetched materials and transported them to the holes to use them as tools, even if they could use tools that were close to the holes. The tools that were reused more were transported more. The chimpanzees' reason in spending extra time and energy to obtain specific tools may be answered by their preference for these tools, which may be related to the tools' appropriateness for the excavation task. The most reused tools by event and day were tools 102 and 108 and these were also the ones that were transported more times and showed the longest total transport distance.

4.5 Excavation-related techniques and actions

Wild chimpanzees obtain USOs manually: at Tongo they excavate sandy soil to reach water-rich tubers (Lanjouw, 2002); at Bossou, instead of excavating, they pull the above-ground stem of cassava (*Manihot esculenta*) until the tubers are uprooted from the soil (Hockings *et al*., 2010); at Ugalla evidence suggested that chimpanzees were also excavating USOs by hand (Hernandez-Aguilar *et al*., 2007). Chimpanzees manually excavate underground ant nests to obtain the eggs, larvae and pupae of safari ants (*Dorylus* spp.) (McGrew 1974; Boesch and Boesch, 1990). They also excavate sandy or damp riverbeds to obtain drinking water with or without tools (Galat-Luong and Galat 2000; Hunt and McGrew, 2002; McGrew *et al*., 2007; Galat *et al*., 2008, Nishida *et al*., 2009), but no direct observation of this behavior has been achieved. The exception being in Mahale, where in two separate instances researchers directly observed one individual each time using a stick for this task (Nishida *et al*., 2009).

The manual excavation techniques used by the chimpanzees during the present study depended on the hardness of the soil. When they excavated regular soil (compacted or not compacted) only one hand was used, but when they excavated clay they alternated the use of both hands presumably because clay was harder to excavate and alternating hands could reduce exhaustion. Similarly, whether chimpanzees used tools mostly depended on the hardness of the soil: they predominantly used tools to excavate naturally compacted soil (below the depth where the fruits were placed) and to excavate clay. In general, tool-use increased in the excavation of harder soil. These results are consistent with the findings of Roffman *et al*. (2012): captive bonobos excavated to access buried food manually in soft sand, using wooden materials (e.g. branches) in muddy soil, and with stone and antlers in hard soil.

More detailed descriptions on the excavation techniques and actions are not provided by studies that directly observed the behavior (Lanjouw, 2002; Roffman *et al*., 2012; Nishida *et al*., 2009) and thus a more comprehensive comparison with these studies is not possible. The only more detailed description available for chimpanzees excavating underground food is for the obtention of safari ants and their products: the chimpanzees scratch loose soil with separated and flexed fingers of both hands fast and vigorously until they make a hole to access the insects (McGrew 1974; Boesch and Boesch, 1990). In contrast, during this study, the chimpanzees were never observed to excavate using both hands at the same time. When the chimpanzees excavated manually, they used one hand to excavate soil but both hands (alternating left and right) to excavate clay. But this difference in techniques may be due to the different food sources: chimpanzees excavating ant nests are dealing with defensive insects, while chimpanzees excavating fruits are not.

The present study did not aim to investigate behavioral laterality of hand use in chimpanzees (e.g. whether they show left or right-sided bias at the individual or group level), but it seems that chimpanzees were lateralized (preferred to use either the left or right hand) when excavating regular soil but not clay. Even tough which hand(s) the chimpanzees used in excavation is recorded on video, these data have not been analyzed yet and this hypothesis cannot be tested at the present. Until now, most studies of behavioral laterality of hand use (handedness) in wild chimpanzees have found no population level laterality and captive studies showed a mixed picture (reviewed in McGrew *et al*., 2007).

4.6 Sequence for the emergence of tool actions

Chimpanzees in both groups achieved tool-use but G1 began using tools earlier (from the beginning of the experiment, in Baseline) and all tool-use actions emerged earlier in G1 than in G2 (see Figure 3.7). Throughout the study, the two groups were kept in different enclosures (inside or outside), it was not possible for one group to see the other, and thus it is remarkable that all tool actions emerged in a similar sequence in both groups (except for shoveling, which only emerged in G1), see Figure 3.7. Both groups initiated tool use by investigatory probing (basis of the sequence), acquiring the other actions sequentially one after another (perforate, pound, dig and shovel). Each new action seemed to have been facilitated by executing and becoming skilled in the preceding action. To probe during excavation may have emerged based on the chimpanzees' tool-use knowledge (they used tools before and during this study in different contexts, see Appendix 1) and perhaps due to the chimpanzees' known inclination to investigate unknown objects with probes, as this is a behavior known in all long term study sites (Whiten *et al*., 2001). Shoveling was the last action to emerge, done only by Julius; however, since he was raised in a human household it cannot be discarded that he may remember this action from seeing humans shoveling. Wild chimpanzees perform different tool actions to reach a single goal. For example, they extract honey by performing several tools actions (pound the hive, enlarge entrance of hive, dip honey, lever hive entrance, "spoon" honey), but can also use a single tool for different functions in the same sequence (Sanz and Morgan, 2009; Boesch *et al*., 2009). This supports the hypothesis that the different tool-use actions involved in the excavation of underground fruits are likely to be linked and may have evolved from one another in the present study.

4.7 Excavation-related behaviors

In the present study, after each fruit was obtained, the owner mainly ate it him/herself. However, less frequently, they were observed to share it with others. Three factors may explain the low frequency of sharing: 1) the non-cooperative nature of the task, 2) the size of the obtained fruit, and 3) the fact that fruits constituted a treat. Excavation was an individual action rather than social. In Tai, most monkey meat is shared between chimpanzees who contribute to the hunt (Boesch, 2002). In Fongoli, females and juveniles hunt bushbabies (*Galago sengalensis*) alone and meat sharing seldom occurs; in addition, bushbabies are small in comparison with other prey obtained by chimpanzees and thus not really "shareable" (Pruetz and Bertolani, 2007). When chimpanzees share fruits, these are large such as papaya in Bossou (Hockings *et al*., 2007) or exist in medium to large sized patches relative to average chimpanzee party size, such as baobab in Fongoli (Pruetz and Lindshield, 2012). In the present study, the excavated fruits were few (5 each day), small and hardly dividable. Hence, sharing was expensive for the donor: excavating was a time and energy-consuming solo activity. Sometimes a chimpanzee was assisted indirectly when different individuals excavated on a hole but left before obtaining the fruit, leaving the partially excavated hole more easy to work for this last chimpanzee who succeeded in obtaining the fruit; but the chimpanzee seemed unaware of this and thus it is unlikely to have influenced sharing decisions. At Tongo tubers are a valuable source of water and sharing was confirmed only once (Lanjouw, 2002). Fruits in the present study were also valuable, a treat for the chimpanzees since the majority of their diet is composed of vegetables. Tongo chimpanzees sometimes gather several tubers and sit away from other individuals (Lanjouw, 2002). The same form of food protection was observed in the current study and was considered a strategy to reduce beggars' harassment.

4.8 Implications of this study for the behavior of wild chimpanzees

From the observations in the present study, it became clear that excavating was not just one action, but a series of different actions performed (manually or with tools) with a single goal: to extract the underground food. Excavating was thus a more complex and flexible behavior than it had been anticipated. Wild chimpanzees excavate soil to extract different sources (insects and their products, USOs and water) using different techniques according to the type of soil and the physical characteristics of each source. However, detailed descriptions of the actions involved in excavation by wild chimpanzees are largely lacking either because the chimpanzees have not been directly observed (Ugalla, Fongoli) or because the behavior has been only partially described (e.g. Tongo).

Based on indirect evidence, McGrew *et al*. (2007) hypothesized that chimpanzees in Semliki were manually bilateral (or ambidextrous) when excavating sandy riverbeds. Their hypothesis was based on the fact that the volume of excavated piles (or tailings) was symmetrical at both sides of the hole, suggesting that the chimpanzees did not have a hand preference in the task. During the present study, when the chimpanzees excavated with one hand the soil was deposited on any side of the hole (Appendix 4), opening the possibility that McGrew *et al*. (2007) hypothesis may not be accurate. This demonstrates the relevance of conducting experiments with captive chimpanzees to inform about the possible behaviors that their non-habituated wild counterparts could exhibit.

The following factors may be involved in the difference between tools found in Ugalla (Hernandez-Aguilar et *al*., 2007) and those used in the present study: the depth where food was buried, the experience in the task, and the type of tool-actions performed. Similarly to what was found in Ugalla (Hernandez-Aguilar et *al*., 2007), the chimpanzees in the present study predominantly excavated the buried fruits manually. The chimpanzees used tools to excavate further than the depth where fruits were placed (30 cm), in trying to look for more fruits. In contrast, in the wild, holes were in average less deep, suggesting that the chimpanzees did not need to excavate as further from the surface as the chimpanzees in the present study. Based on the physical characteristics of the tools and their wear patterns, Hernandez-Aguilar et *al*. (2007) suggested that tool-use in the excavation of USOs in Ugalla was an incipient behavior, meaning that chimpanzees were yet to become proficient in the task. In support of this interpretation, in the beginning of the present study the chimpanzees selected tools that were more flimsy, and later, when they seemed to be more experienced in excavating, used tools that were longer and heavier. Hernandez-Aguilar *et al*. (2007) suggested a short working life for the tools they found and thus the most probable tool actions during excavation, based on the results of the present study, were probe and perforate, as well as brief dig and pound events.

We already know that wild chimpanzees are able to: associate the above-the-ground plants' parts with presence of USOs, excavate (by hand and sometimes with the aid of tools) to the right depth where USOs are present, apply the required amount of force with tools to break through the surface ground, and excavate several USOs in a specific day or over several days in the same area. Based on the results from the present study it is hypothesized that in the wild: chimpanzees may alternate both hands to excavate USOs in hard soil; may perform several tool actions during a single episode of USOs excavation; may share this food, although most likely infrequently; and the most probable tool actions in excavation are: probe, perforate, dig and pound.

4.9 Implications of this study for captive chimpanzees

Even though the goal of this study was not to provide enrichment for the chimpanzees, the experiment was a stimulating activity (they showed high interest in the task) that increased the time they spent gathering food and so it was considered beneficial. In addition, it was an entertaining form of informing zoo visitors about the tool-use abilities of chimpanzees. Replication of this study, or the implementation of other experiments that simulate the extractive foraging contexts present in wild chimpanzees, is recommended to enrich the lives of captive chimpanzees.

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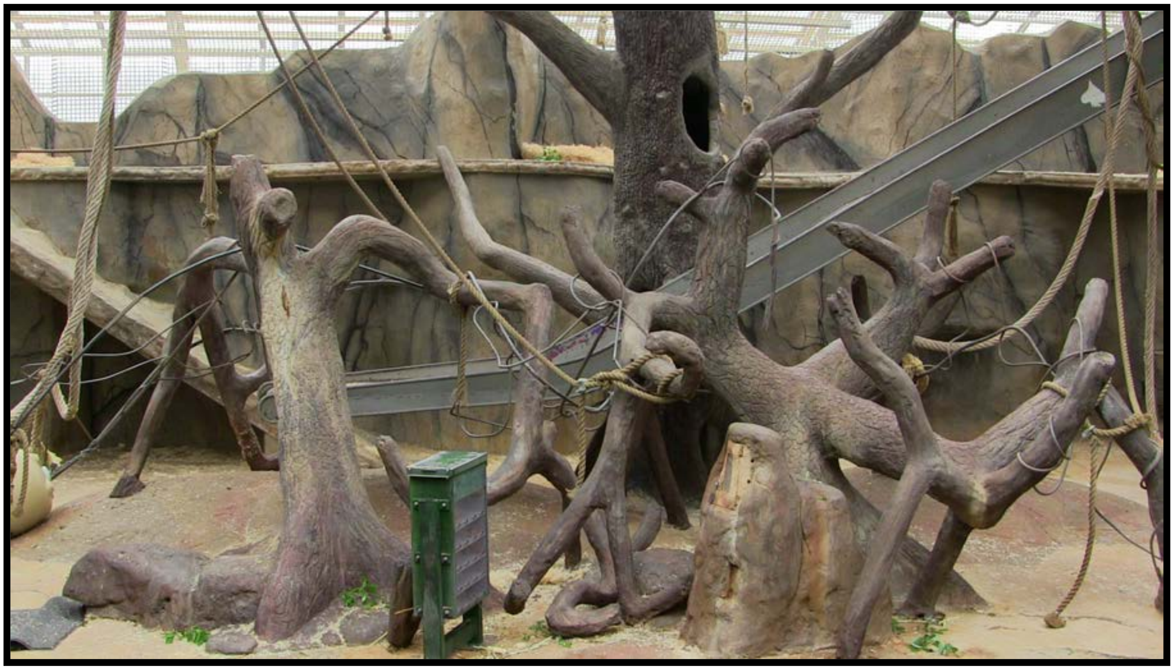
Appendices

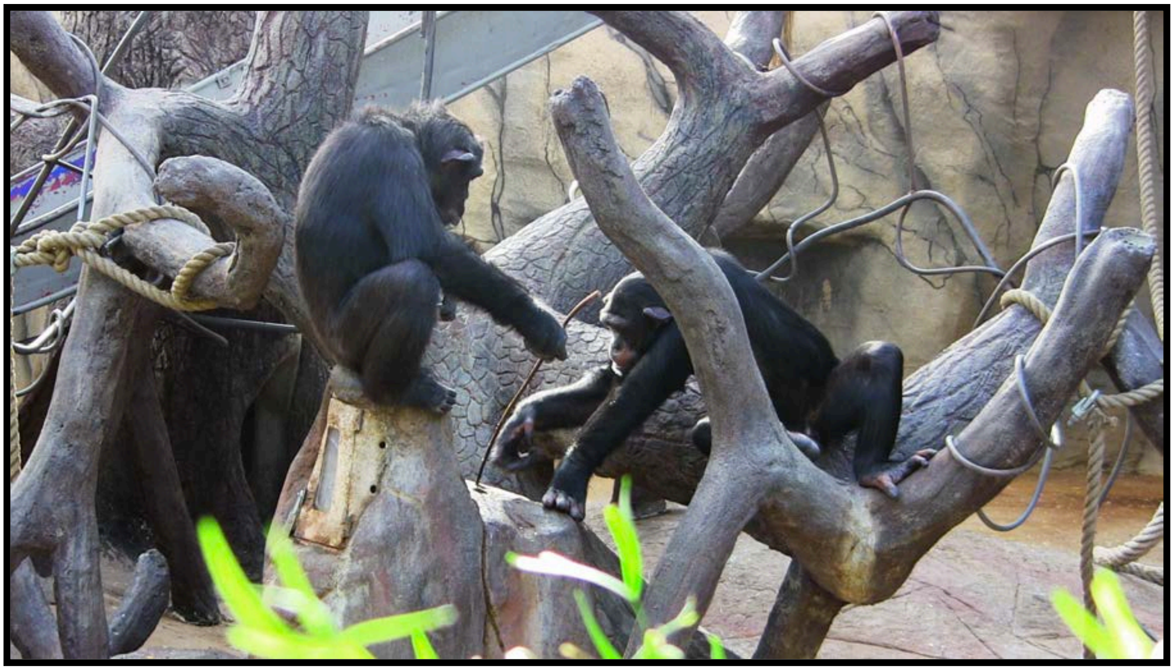
Appendix 1

Enclosures

The exhibit part of the indoor enclosure



The green box is a puzzle feeder. The chimpanzees use a flexible stick to take peanuts out of the box through the window's holes.



The artificial termite mound filled with honey. The chimpanzees use a long stick to extract honey from the reservoir.

The outdoor enclosure

East view

North view of the outdoor enclosure

Appendix 2
Samples of the selected tools and gathered tools

Selected tools

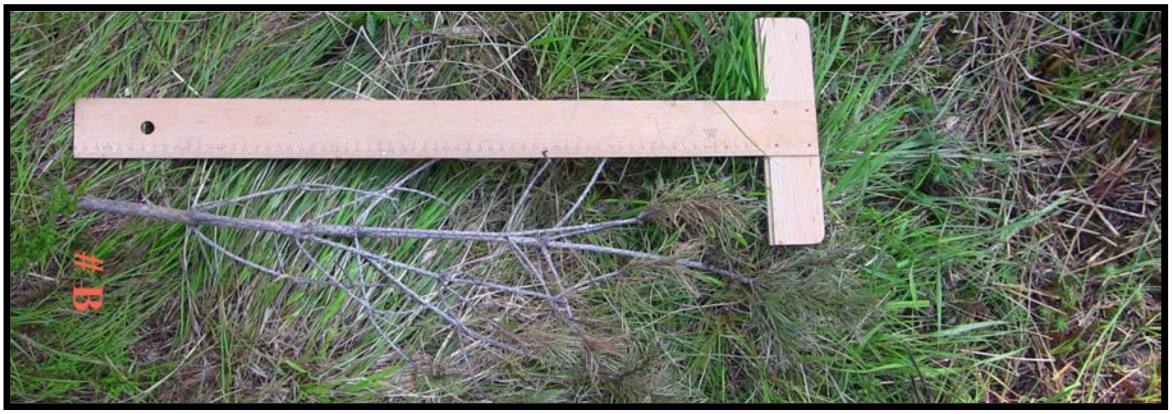
***Tool 84**: non-reused*

***Tool 102**: reused*

***Tool 108**: reused*

Gathered tools

Tool B: *non-reused*



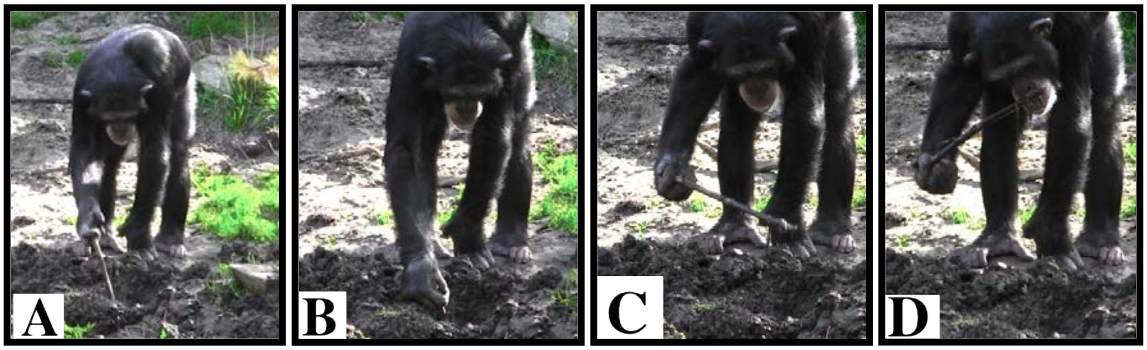
Tool C: *reused*

Tool K: *Plastic tube*

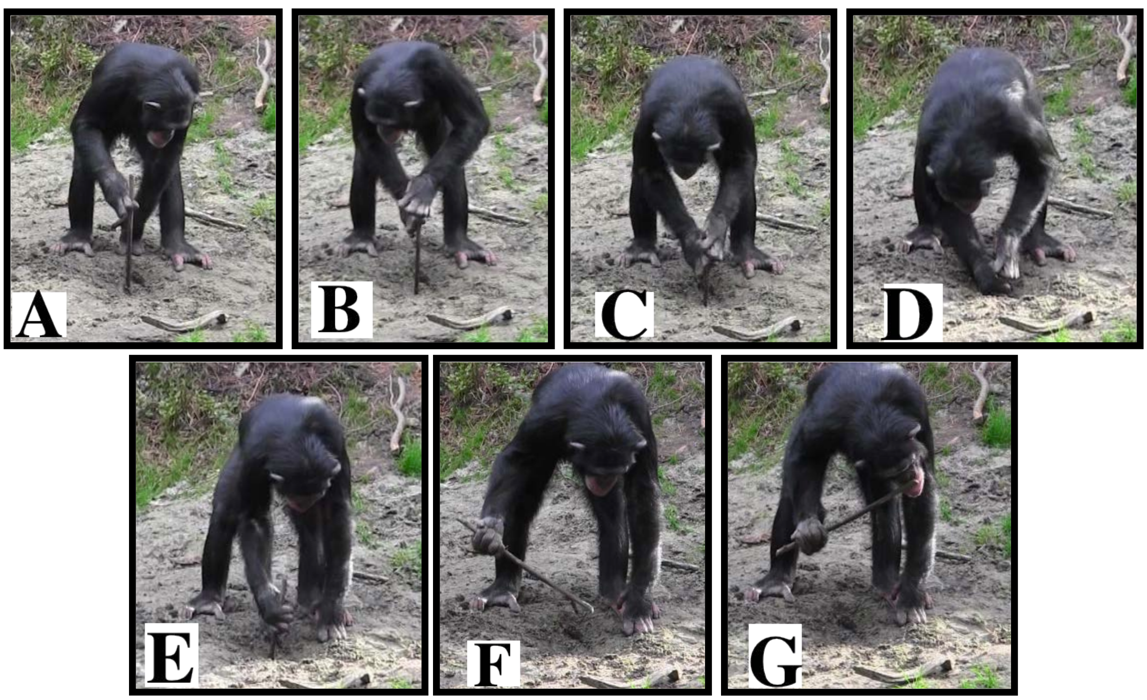
(Tobias used the same tube that Knerten is holding in this picture)

Appendix 3

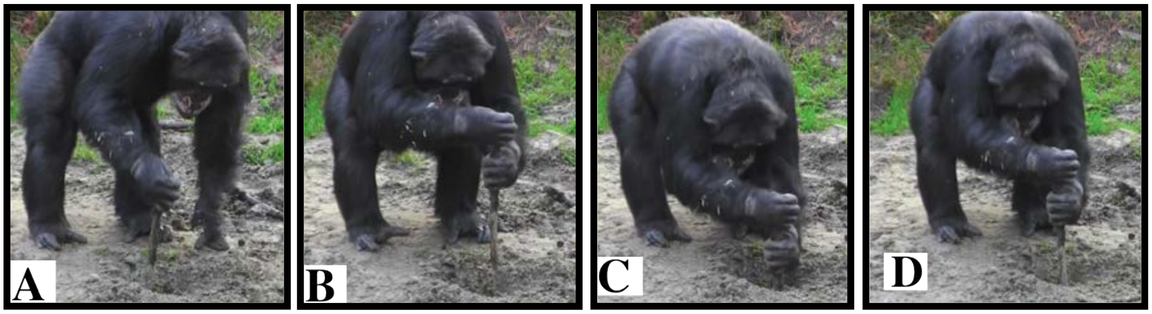
Tool-use actions



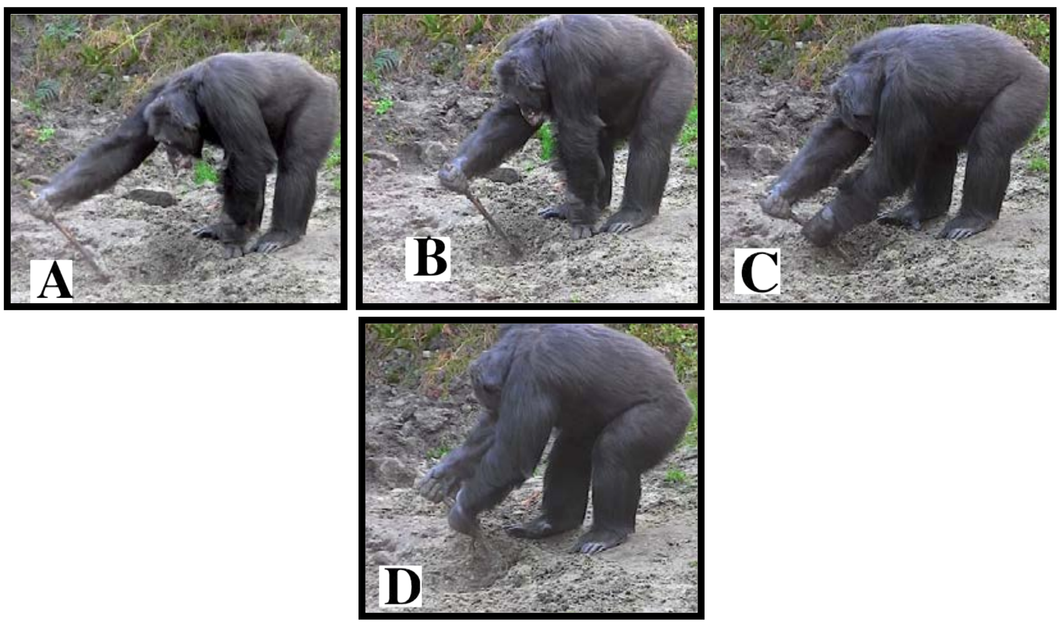
Probe: A) a male chimpanzee (Junior) held one end of the tool and enters the other end in the hole, B) the inserted end reached the holes' bottom; no force was applied here, C) the chimpanzee withdrew the tool, D) the inserted end was visually and olfactorily examined.



Perforate: A) a male chimpanzee (Junior) held the end section of the tool and inserted the other end on the ground above where food is placed, B) he used both hands to hold the tool, C, D) he pushed the tool forcefully in the ground. E) The chimpanzee withdrew the tools using one hand, while used the other hand to keep his balance, F) the tools was visually and G) olfactorily examined.

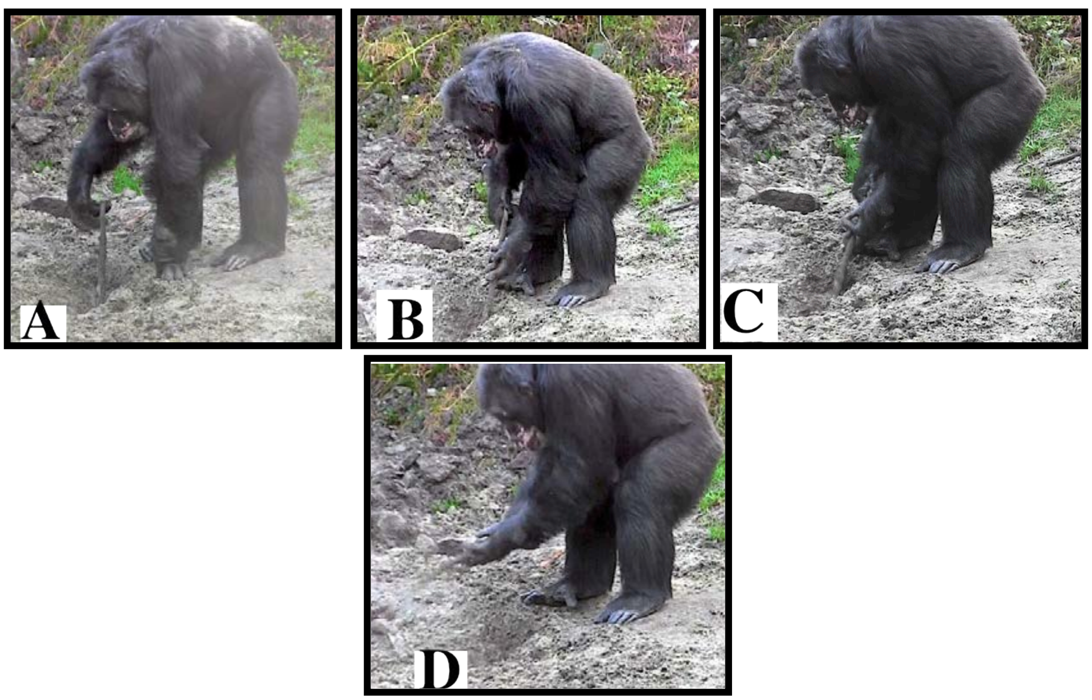


Pound: A male chimpanzee (Julius) insert the tool in the partially excavated hole, B) he held the tool with both hands and brought it higher from the ground surface and C) he hit the ground above where the fruit was placed with back and D) forth movements of the tool. The action was repeated several times.

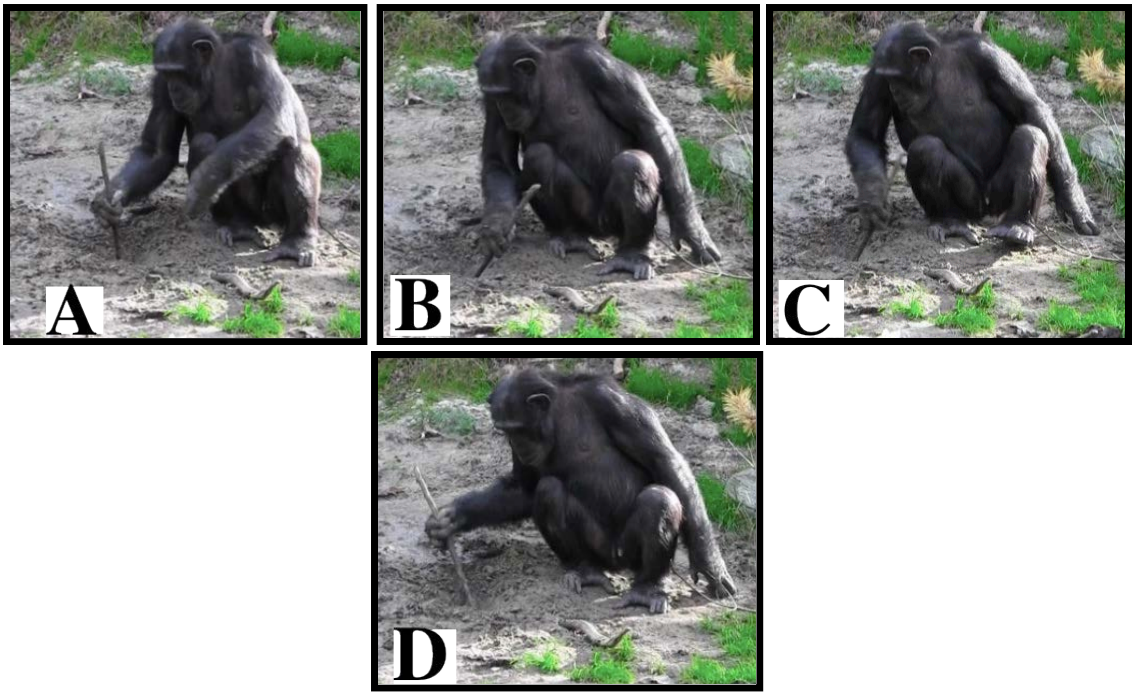


Dig: A) a male chimpanzee (Julius) placed a tool far from where he stood above the partially excavated hole, using only one hand, B) he moved the tool inward while pushing it into the ground with force, using the same hand, C, D) he used the other hand and held the midsection of the tool to continue his action to remove the soil. The action was repeated several times.

Shovel, using hand and foot: A) a male chimpanzee (Julius) held one end of the tool with a foot and the midsection with the opposite hand and placed it on the ground above the area with buried fruit, B) he inserted the tool in the ground (the displacement of the hand in the picture A and B shows the depth of penetration), C) he withdrew the tool inward, pushing the tool with the hand upward and with the foot inward; a pile of clay was removed from the surface. The action was repeated several times.



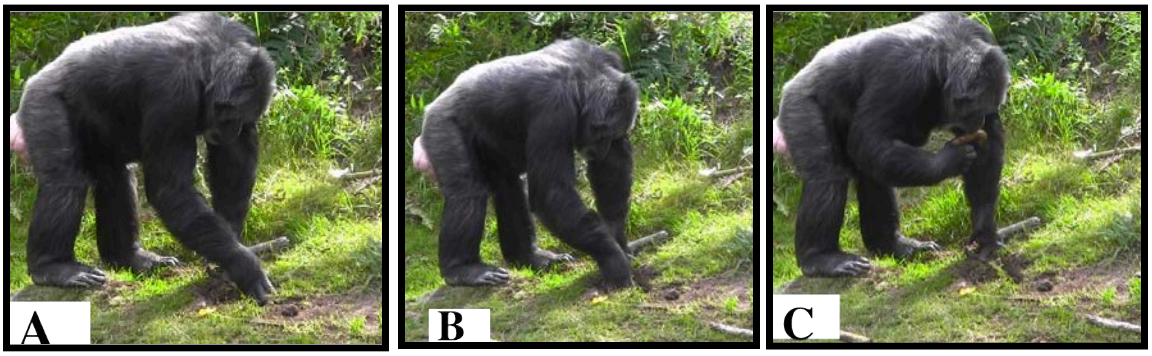
Shovel, using both hands: A) a male chimpanzee (Julius) placed a tool on the ground close to where he stood B) he held the end of the tool with one hand and the midsection of the tool with the other hand C), he pushed the tool in the ground using force D) with an inward movement of the hand the tool was withdrew and a pile of clay was deposited out of the hole. The action was repeated several times.



Enlarge: A) a male chimpanzee (Knerten) inserted a tool into a hole above where the fruit was placed. He moved the tool with sweeping, circular motions, B) 90 degree to the west, C) 90 degree to the south, D) 90 degree to the east.

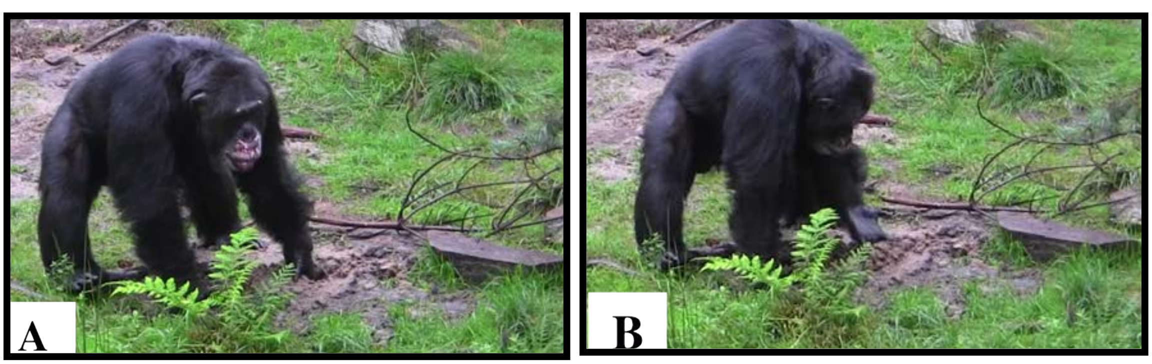
Appendix 4

Manual excavation

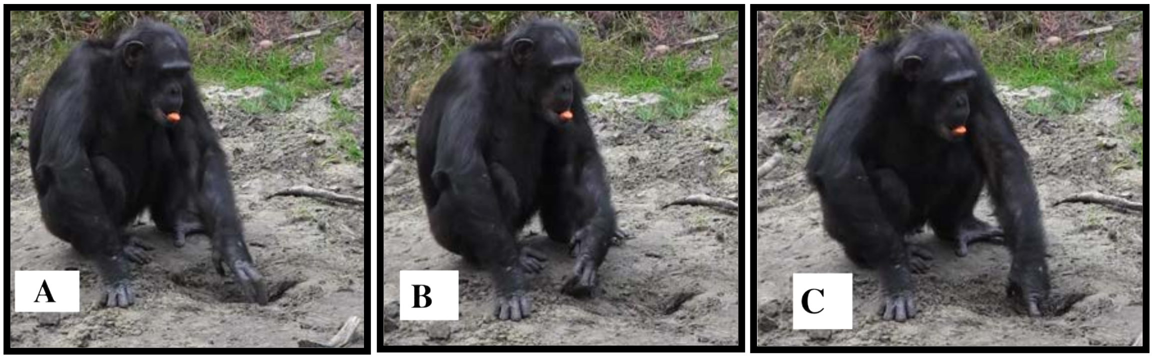


Search: A) a female chimpanzee (Josefine) was searching for the buried fruit in a hole filled with regular (non-compacted) soil, B) The fruit is found, and C) she took it out (note around the hole that no soil was deposited).

Dig: A) a male chimpanzee (Julius) digging manually, B) a pile of soil first was deposited in front and the following time c) to the right side of the hole. The action was repeated several times.



Initiation of clay excavation using four fingers: A) a male chimpanzee (Julius) inserted four fingers in the clay above where the fruit was placed, B) with a circular movement of the hand he took out a pile of clay.

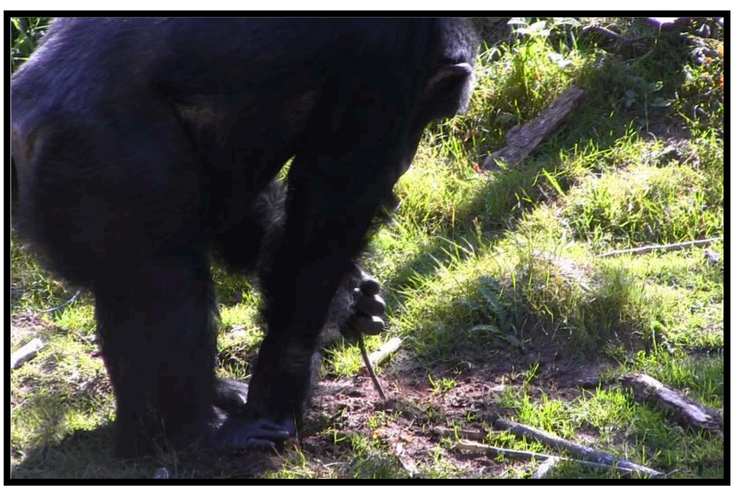


Initiation of clay excavation using index finger: A, B) a male chimpanzee (Knerten) scratching surface clay before C) inserting his index finger in the ground above where food was placed.

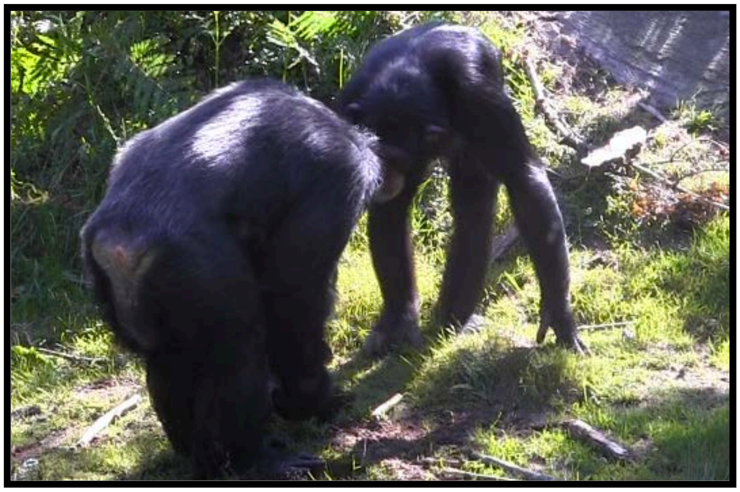
Appendix 5

Observational learning example

On the 10th July at 10:27:56, Julius, after examining the excavated hole (H3) visually, obtained a stick (#98) from about 0.5 m from the hole and started to dig 20 cm away from the hole. He continuously pushed the soil towards him, moving the tool perpendicular to the line of his belly and expanded the area by using the stick to remove obstacles on top of the ground (grass, plant material). Another male member of the group, Junior, came to the work site and started to watch him carefully at close range. Julius then moved the tool to the empty hole and started to scrape the soil at the bottom of the hole for 27 seconds. Julius dropped the tool and moved to a nearby hole (H4) and took a thicker stick (#107), smelled it, inserted it in the hole, and started to dig with intense force. Junior moved closer to Julius in order to watch him at close range again. The digging episode terminated after the observer (Junior) prevented the digger (Julius) from continuing by grabbing the hand that Julius was digging with and a foot in a playful mood (see the pictures below). Both abandoned the study area. From the first day, both subjects were repeatedly observed using digging action to excavate the holes. Junior initiated digging with sticks that were similar in size and thickness to the one he had seen Julius used on the first day.

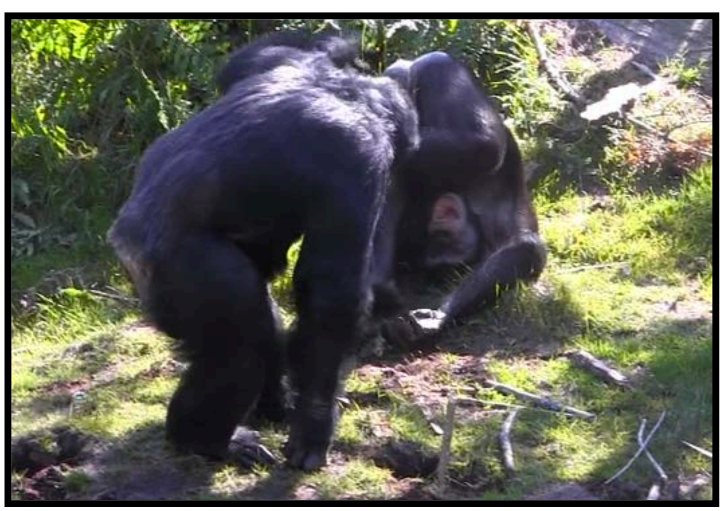


Julius was using a stick to dig near H3.



Junior came to the study area and started to watch him at close range.

Julius moved to H4 and used a thicker stick to dig further down the depth where the fruit was deposited. Junior followed him and looked at his actions again.



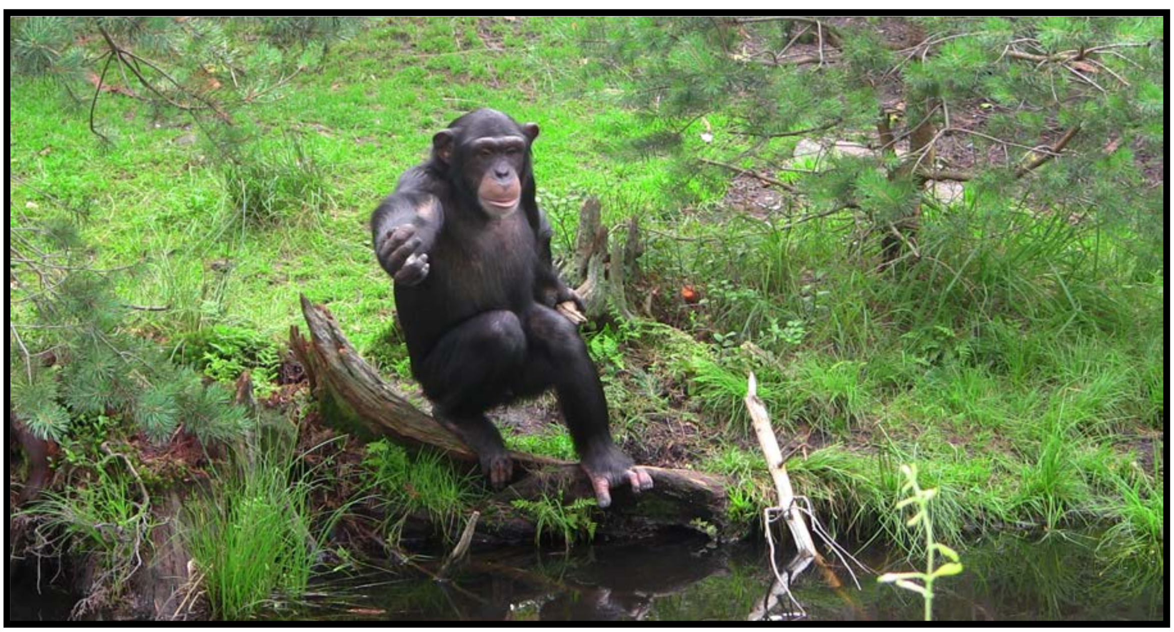
Julius stopped his action to play with Junior.

Appendix 6

Tool-use related behavior

Begging

Begging by gazing at close hand of the fruit owner.



Begging by extending hand towards others (in this case towards me, after associating the availability of fruits and my presence).

Appendix 7.

Extractive foraging contexts in chimpanzees.

		Techniques		Definition	References
Insect extraction	*Ants*	Dipping	Tool	Chimpanzees insert a wooden stick (“wand”) into an ants’ nest to collect individuals streaming along the tool. There exist two techniques upon dipping ants: the “pull-through” technique and the “direct mounting” technique. In the pull-through technique chimpanzees insert a tool into the ants’ nest and once the insects stream up three-quarter of the tool, withdraw it. Subsequently, with the close fingers of the opposite hand they sweep the tool from the proximal to the distal end and transfer the mass of ants into the mouth for ingestion. In the direct mounting technique chimpanzees hold a tool with one hand and dip it in the ants’ nest. Then they withdraw it to either directly nibble the ants off the tool, or pull the tool sideways through the lips.	McGrew, 1974 Boesch and Boesch, 1990 Sanz and Morgan, 2007 Schöning *et al.*, 2008
		Digging	Manual	Chimpanzees crouch over the nest site and rapidly rake out the lose soil with closed and flexed fingers of both hands until a hole is formed. Subsequently, they insert their arm sometimes up to the shoulder in the hole and extract the mass of insects, i.e. brood and workers.	McGrew, 1974 Boesch and Boesch, 1990
			Tool	Chimpanzee use digging and dipping tools in a serial order to extract insects from the underground nest. The digging tool is made of a wooden sapling and has intact leafy branches. This tool is inserted deep into the ants’ nest to perforate the nest and clear obstructions for the use of a second tool, the dipping probe, which is a slender and flexible herb stalk with detached leaves.	Sanz *et al.*, 2010
	Termites	Fishing	Tool	Chimpanzees insert a tool made of different materials (grass, twig, vine, bark) into the termites’ nest passages to pick up termites clinging to the tool.	Goodall, 1964 Nishida *et al.*, 2000
		Digging	Tool	Occasionally, chimpanzees fail manually to reopen the holes used by termites on the above ground mound surface and hence they use a twig to push through the concealed holes. Then they start fishing termites with a slender probe. Chimpanzees puncture the underground nest by pushing a stout stick using both hands or hands and a foot. However, the puncturing stick alone is not effective to lure termites out from their underground nest. Therefore, the chimpanzees switch the punctuation tool with a fishing probe and start fishing termites.	Sanz *et al., 2004*

		Techniques		Description	References
Insect products extraction	*Honey*	Dipping	Tool	The most widespread tactic for gathering honey is through dipping. It is a similar technique as the one described for ants' extraction above (ant dipping).	Sanz and Morgan, 2009
		Digging	Manual	Chimpanzees, in order to get access to honey of the *Xylocopa* sp. that make nest in dead branches on the ground or in the tree, open the branches on the ground where the nest is situated and eat the honey.	Boesch and Boesch, 1990
			Tool	Chimpanzees use a stick ("perforator") to explore and locate the exact position of the honey chamber that is not visible from the ground surface. After spotting the chamber, the chimpanzees make a narrow angled tunnel with the same perforator tool to reach the chamber without mixing honey with soil. Finally, they dip the honey with a probe.	Boesch *et al*., 2009
Extractive hunting	*Animal prey*	Catching	Tool	Chimpanzees manufacture a hunting weapon. They break a straight branch from a tree, trim the leaves and side branches and sharpen the tip into a spear. They take this weapon in a "power grip" and jab it forcefully into the cavities of hollow branches or tree trunks where bushbabies (*Galago sengalensis*) sleep during the day. Then, they extract the disabled prey and consume it.	Pruetz and Bertolani, 2007
Prey products extraction	*Brain*	Extracting	Tool	Chimpanzees were seen to insert sticks through the foramen magnum to eat brain from an intact skull.	Boesch and Boesch, 1990
	Bone marrow			Chimpanzees, after a hunt, eat the marrow from the prey's bones. They first open the entrance to the inner part of the bone by biting the end off and then use a narrow stick to extract the marrow.	Boesch and Boesch, 1990

		Techniques		Description	References
Water extraction	*Water*	Leaf sponging	Tool	Chimpanzees crumple leaves in their mouth and insert them in the cavity where water has gathered; then they remove the crumbled vegetation and squeeze the water into the mouth.	Goodall, 1986 Sugiyama, 1997
		Leaf folding	Tool	Chimpanzees fold leaves at about 3-centimeter intervals and stuff them in hole full of water. The folded leaves are then removed and water is sucked.	Toonoka, 2001
		Digging	Manual	In sandy riverbeds, chimpanzees dig wells in the sand-zone near stagnant water puddles and drink water from those holes.	Galat-Luong and Galat 2000 Hunt and McGrew, 2002 McGrew *et al.*, 2007 Galat *et al.*, 2008
			Tool	Chimpanzees were observed twice to use a stick and dig for water in a streambed during dry season. Indirect evidence for this behavior has also been found.	Nishida *et al.*, 2009 Galat-Luong and Galat 2000 Galat *et al.*, 2008
Kernel extraction	*Nuts*	Cracking	Tool	Chimpanzees hammer or pound nuts on a hard surface to open the hard shell and reach the nutrient-rich kernel. The pounding tool is termed a "hammer" and the hard surface is the "anvil"; an extra tool, or "wedge," may be used to stabilize the anvil.	Boesch and Boesch, 1983 Matsuzawa, 1991 McGrew *et al.*, 1999

		Techniques		Description	References
Plant extraction	*Palm heart*	Pestle Pounding	Tool	Chimpanzees climb into the crown of an oil palm tree, *Elaeis guineensis*. They spread apart the mature leaves, using hands and feet, to reveal the young, centrally placed shoots. Then they tug out the young shoots with force, forming a vertical cylinder hole to reach the apical meristem or apical bud. The petiole of these spear leaves is then mostly chewed and swallowed. The apes use the hard petiole as a tool to pound into the center of the palm crown where the hole was formed, softening the palm heart. Finally, from the opening, they excavate the palm heart by hand and consume it, using part of the loose fiber as a sponge to suck the liquid.	Yamakoshi and Sugiyama, 1995
	USOs	Digging	Manual	Chimpanzee excavate in sandy soil to obtain water-rich tubers.	Lanjouw, 2002
			Tool	Indirect evidence of the use of tools to excavate several species of USOs was found at excavation sites in Ugalla, Tanzania: vocalizations, feces, knuckle prints, spit-out wadges and abandoned tools. Indirect data for this behavior was found at Banfadassi, Senegal, but no details are given.	Hernandez-Aguilar *et al.*, 2007 Gaspersic and Pruetz, 2011
		Pulling	Manual	Chimpanzees raid cultivated areas or visit abandoned farms to obtain the tuberous root of cassava (*Manihot esculenta*), actively pulling the aboveground stem by hand until the root is uprooted from the soil.	Hockings *et al.*, 2010