2 Ecology and cognition of tool use in chimpanzees

Christophe Boesch
Max Planck Institute for Evolutionary Anthropology

Introduction

Humans, as the most technological species, tend to assume that tool use is a sign of higher intelligence and that, over the course of our evolution, tools conferred a decisive advantage in the struggle to adapt to different environments (Mithen, 1996; Wynn, 2002; Wolpert, 2003; Dietrich *et al.*, 2008). As such, animal species that use tools are considered more intelligent, while those that do not are judged as being less intelligent. This amounts to an anthropocentric judgment whereby humans adopt a human criterion to judge the adaptive skills of other species (Barrett *et al.*, 2007; Goodrich & Allen, 2007). However, both *phylogeny* and *ecology* must be taken into account before one makes judgments about when and where we might expect tools to be used (Bluff *et al.*, 2007; Hansell & Ruxton, 2008).

Tool use as an adaptation

Physical adaptations

If one remembers that, in most cases, tools are an extension of one's body that allow an individual to solve tasks that cannot be solved with the body alone (Goodall, 1970; Beck, 1980; Boesch & Boesch, 1990), we must acknowledge that some primate species possess more efficient physical specializations than humans. For example, baboons have very hard, sharp teeth, which allow them to break open hard-shelled fruits that humans would be unable to open without the help of a tool (Kummer, 1968). Similarly, orangutans and gorillas, which are clearly physically stronger than humans, have been seen accessing food resources using sheer force in situations where humans would need to rely on tools (Schaik & Knott, 1996; Cipolletta *et al.*, 2007). In addition to sheer force, it has been argued that hands help in tool use and this would then explain some of the distribution of tool use in the animal kingdom, although we should not forget that birds hold tools with their beaks and some otters use tools as well. Therefore, independent of the cognitive capacities required to use tools, tool use by animals should not be expected to occur in all situations where humans might use them. Our natural tendency to anthropomorphize

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

hinders us from reaching a better understanding of the evolution of tool use, and it is imperative that we look directly to animals for answers about when tools might be beneficial.

Challenges imposed by ecological niche

Furthermore, each individual animal lives in a specific ecological niche, where they encounter daily challenges that must be solved, and some of these challenges might be more efficiently solved with the help of tools. Moreover, such challenges will vary according to the species and the specific population studied. For example, a capuchin monkey living in the dry open areas of northeast Brazil only faces a limited number of challenges similar to those encountered by a capuchin monkey in wetter regions of Brazil (Moura & Lee, 2004; Visalberghi *et al.*, 2007; Canale *et al.*, 2009; Souto *et al.*, 2011; Spagnoletti *et al.*, 2011). Moreover, both face totally different conditions than capuchin individuals living in captivity. In addition, each species possesses different physical adaptations, which might directly affect the possibility of using tools. The result might be that, within each population, an individual's development of causal understanding – the understanding of the relationship between a set of factors (causes) and a phenomenon (the effect) – will be promoted by being exposed to situations where such understanding confers a competitive advantage. In turn, this will increase the exposure of juveniles to specific object–object interactions that promote the development of folk physics and select adaptive population-specific cognitive traits responsible for their specific tool-use abilities (Fragaszy & Visalberghi, 2004; Boesch, 2007; Bluff *et al.*, 2010).

So the question should really be, what is the best way to solve a challenge faced by an individual within his ecological niche, rather than, why doesn't a particular species/individual use tools? Such an ecological approach toward tool use avoids the anthropocentric assumption that it is better to use tools in most situations and allows us to look at the ecological and morphological factors that affect tool use. It is important to note that, in the real world, there is a constant interaction between brain, body and world (Barrett *et al.*, 2007; Boesch, 2007, 2010), and that we need to put ourselves into the situation of the animals as much as possible if we want to understand the solutions they adopt.

Macaques, a widely distributed genus, have not been observed to be particularly adept tool users; however, whenever facing the appropriate conditions, such as those of the Piak Nam Yai Island in the Andaman Sea, they have been observed to become skilled tool users and develop customary forms of tool use to extract food items in the intertidal zones of the coastal habitats and select tools based on the food being processed (Gumert *et al.*, 2009). "Appropriate conditions" are going to be species-specific, making any claims about limitation in tool-using abilities hazardous, before we have gained an in-depth knowledge of the species-wide population variations.

Some have argued that mental reasoning and understanding of the technical aspects of tool use can only be demonstrated in "new situations on the first trial" (Tomasello & Call, 1997; Bluff *et al.*, 2007; Penn & Povinelli, 2007). However, such a criterion cannot apply to natural situations, and thus, by definition, would seem to thwart any claims about reasoning and understanding from natural observations. If such a biased approach to the study of animal behavior could be adhered to for the few animal species that can be maintained in ethically and ecologically valid captive conditions, it would prevent any understanding of higher cognition for all species in which captive conditions cannot be implemented with ecologically valid environment. Besides this, below we will see that some tool techniques result from very specialized ecological challenges that cannot be fully mimicked in captive conditions. Nevertheless, some birds have proven to be the ideal subjects and careful experimentation has allowed for much progress in detailing some of the cognitive requirements of tool use (see reviews by Emery & Clayton, 2004; Hunt *et al.*, 2006; Bluff *et al.*, 2007; Seed *et al.*, 2009a).

In the present review, I propose to concentrate on natural observations of tool use in capuchins and chimpanzees in an attempt to understand causal understanding in primates. This will allow me to illustrate the central role ecology plays in tool use, especially for complex tool use aimed at retrieving food embedded in natural substrate. For many complex real-world situations, experiments are not possible and only natural observations will guide our thinking about animal reasoning and produce hypotheses about the way animals might understand and alter their environments.

Tool use and anthropomorphism

Anthropomorphism, the attribution of human feelings and intention to other species, is an inherent tendency of each human observer (Keeley, 2004; Goodrich & Allen, 2007; Wynne, 2007). This is potentially dangerous as such an attribution can be purely a consequence of our own way of thinking and have nothing to do with the way an animal is thinking. At the same time, without an intimate understanding of the real challenges an animal faces and the way it can arrive at solutions, there is no way we can make progress in understanding the ways animals react in their environment. By definition, we can only achieve that in an anthropomorphic way as we are humans. The nut-cracking behavior in Taï forest chimpanzees or the underground termite fishing in Goualougo forest chimpanzees has to be solved within the technical constraints of those forests and only human experiments can give us a feeling of what the real challenges are. So, basically, it is our anthropomorphic understanding of the technical components of a tool-oriented task that forms our basis for evaluating the appropriate solutions and estimating the cognitive challenges.

Having said that, no observer thinks animals have to solve the task in a human way, and we do consider the specificity of the animal's way of addressing the technical challenges, but this remains a challenge for us as we are humans and cannot really make judgments about the perceptions, understanding, previous experiences or alternatives that another species brings with them when solving a task. This problem is especially acute in captive experimental situations where all dimensions of the settings and the solutions are an enforced human design, often with very limited ecological validity (Allen, 2002; Boesch, 2007, 2010), and it becomes particularly difficult to untangle what animals have brought in apart from the human impositions.

The importance of ecology, cognition and culture

The "eco-cultural model" was originally proposed to explain the differences in cognitive development observed between humans belonging to different cultures (Segall *et al.*, 1999; Carpendale & Lewis, 2004), and I proposed to expand it to include all large-brain animal species capable of learning (Boesch, 2007). This model stresses that behavior and cognition are not purely driven by genetics, but result from the year-long ontogenetic interactions of the individual with his social group and his ecological niche. The eco-cultural model predicts that tool-use frequency should vary according to the ecological challenges faced by different species. The more ecological niches are encountered by a species, the more diverse technological solutions should be observed in that species, when all other factors would remain constant. In other words, with the same level of learning ability and the same physical ability, more tool uses should be observed in the species with larger diversity of ecological niche (Boesch, 2007). Such a model would concur with the "technical intelligence hypothesis," which was proposed to relate the technical and cognitive demands of using tools and thereby explain the origin of the ape/monkey grade-shift in intelligence (Byrne, 1997, 2004). The classic example of the influence of ecology and culture is nut cracking with hammers, which has been observed in chimpanzees and capuchin monkeys (Boesch *et al.*, 1994; Visalberghi *et al.*, 2007; Spagnoletti *et al.*, 2011); to be able to crack the nuts, those nuts must be present and large proportions of chimpanzee and capuchin monkey populations do not live in forests where the nuts are available, and therefore were not seen to use hammers to crack them. On the other hand, many populations of chimpanzees live in forest where the nuts are present, but they do not crack those (Boesch *et al.*, 1994; Boesch, 2003).

Tool use as complex behavior

A tool is defined as an external object detached from its substrate use to attain a goal (Goodall, 1970; Beck, 1980). In a sense, a tool is perceived as an extension of the body that is used to achieve a goal that cannot be directly achieved with the use of only hands or teeth. To be able to achieve such a task, an individual needs to have a certain level of causal understanding about the effect of one's own body on objects as well as on the body's actions on external objects (Greenfield, 1991; Visalberghi & Tomasello, 1998; Boesch & Boesch-Achermann, 2000; Fragaszy & Visalberghi, 2004; Visalberghi & Fragaszy, 2006; Fragaszy, 2007; Hansell & Ruxton, 2008; Wimpenny *et al.*, 2009; Bluff *et al.*, 2010). As the latter functions only through the force exerted on the tool to achieve a certain goal, it was proposed that this requires some more complex forms of causal understanding. While new examples of tool use have been uncovered from wild animals, causal-understanding abilities were suggested to be very limited in primates but at the center of the evolution of human intelligence (Mithen, 1996; Wolpert, 2003). While the causal understanding in each species must indeed be critically considered, it is only with a detailed and precise consideration of all field evidence that we will be able to comprehend what level of causal understanding and technical expertise animals have acquired.

Flexible tool use, the use of different types of tools in different contexts and to reach different types of rewards, has been observed more frequently in chimpanzees and humans than in any other animal species (see below; Boesch & Boesch-Achermann, 2000). This distribution of flexible tool use in primates suggest that an elaborate understanding of causal relationships between different external objects favors the development of tool use to new and different contexts, and this might be an important prerequisite for the evolution of flexible tool use (Boesch & Boesch-Achermann, 2000).

More categorical definitions of tool use have become important due to the growing evidence that tool-use skills could be found in many different animal species, including birds and the increasing evidence of flexible tool use, both in captive and wild animals (Goodall, 1970; Beck, 1980; Fragaszy, 2007; Hansell & Ruxton, 2008; Wimpenny *et al.*, 2009). In an attempt to single out some of the cognitive demands of tool use, some authors have proposed a "tree model" of tool use using a sequential hierarchical approach concentrating on the number of spatial relations produced by the actor as well as the order in which they occur (Greenfield, 1991; Matsuzawa, 2001). Developing on this and focusing on capuchin monkey tool use, a "spatial relation model" was proposed that identifies four specific aspects of tool use, with a special emphasis on the spatial relations necessary to master how to place and manipulate the tool correctly in connection with the food reward (Visalberghi & Fragaszy, 2006; Fragaszy, 2007). Such spatial relations are qualified depending on if they are performed concurrently or sequentially, and in a dynamic fashion or not (see Table 2.1). Recently, a new taxonomy of tools has been proposed based on the number of tools used or combined, stressing the importance of metatools that were suggested to included all secondary tools as well as combined tools (Wimpenny *et al.*, 2009). This new taxonomic approach tends to underestimate the complexity of the decisions made when using tools, as revealed by a chaîne opératoire approach (Bar-Yousef *et al.*, 1992; Carvalho *et al.*, 2008; Bar-Yousef & van Peer, 2009; Boesch *et al.*, 2009). Furthermore, since I am mainly interested in the ecological challenges solved with tools, I want to categorize them according to the technical challenges addressed. Therefore, I will discuss tools within a framework that attempts to distinguish four levels of increasing complexity in the decision process and come back to the spatial relation model approach when discussing the effect of cognition on tool use.

Simple tool use

Simple tool use includes all instances where a single tool is used to perform all the actions necessary to obtain the reward. Examples of simple tool use are: an Egyptian vulture breaking an egg with a stone held in its beak; a Californian otter pounding an oyster on a stone placed on its belly; a chimpanzee fishing termites with a twig; and a human cutting a piece of meat with a knife (see review by Goodall, 1970; Beck, 1980). The actions performed with the tool can be numerous, but they are all performed with that single tool, and therefore the causal understanding remains rather straightforward and the delay to obtain the reward is limited as the connection between the body and the reward is direct via the tool.

Table 2.1 Cognitive aspects of tool use based on my definitions of the different types of tool use (adapted and expanded from Visalberghi & Fragaszy, 2006; Fragaszy, 2007).

Type of tool use	Numbers of relationships	Temporal actions	Static/dynamic	Permissive/ specific	Direct/indirect
Simple tool use					
a-Probe a hole	1	N/A	Static	Permissive	Direct
b-Break through resin	1	N/A	Static	Permissive	Direct
c-Fish for termite	1	N/A	Static	Specific	Direct
d-Dip for ants	1	N/A	Static	Permissive	Direct
e-Push food in trap-tube	2	Concurrent	Dynamic	Specific	Direct
Combined tool use					
a-Pound nut/surface	1	Sequential	Static/dynamic	Permissive	Direct
b-Pound held nut/surface	2	Concurrent	Dynamic	Permissive	Direct
Sequential tool use					
a-Tree honey	≥3–5	Sequential	Dynamic	Specific	Indirect/indirect/direct
b-Underground termite	2	Sequential	Static	Specific	Indirect/direct
c-Underground honey	2–3	Sequential	Dynamic	Specific	Indirect/indirect/direct
d-Secondary tool	2–3	Sequential	Static	Specific	Indirect/direct
Composite tool use	≥3	Concurrent	Static	Specific	Indirect/direct

Tool-use examples are as follows:
Simple tool use: (a) The use of a stick to inspect inside a hole, as seen in many animal species; (b) The use of a heavy stick to break open the resin blocking the nest entrance of a bee hive, as seen in different chimpanzee populations; (c) The classic example of the Gombe chimpanzees using small twigs, bark or herbs to fish for termites by inserting it in holes of the termite mound; (d) The use of a stick or wands placed in a driver nest entrance to let soldiers bite and climb on it; (e) The classic tube test in which an animal has to push food out of a tube with a stick while at the same time avoiding making the food fall into a trap.
Combined tool use: (a) The classic nut cracking in chimpanzees, in which a nut is placed on a hard surface and then pounded with a hammer; (b) The same sequence but in a tree, where the tool user must stabilize the nut with its free hand at the same time, in order to prevent it from falling down.
Sequential tool use: (a) The use of a set of up to five different tools to open, access and extract honey from bee hives located in trees; (b) The use of two types of tools to locate and fish termites out of underground mounds; (c) The use of up to three different tools to locate, access and extract honey from underground bee hives; (d) The use of a tool to produce a tool that will be used, for example, to cut meat.
Composite tool use: The production of a spear with a sharp-edge stone attached to a straight branch with binding material.

Body → Tool → Reward

Hence, such simple tool use has been labeled as a first-order problem by Visalberghi and Fragaszy (2006), as they imply a single relationship between the body and a tool producing a single dynamic spatial relation (Table 2.1). Simple tool use is a widely observed ability in the animal kingdom, but one striking difference is that, in most species, a single or very few different types of simple tool use have been seen (Beck, 1980; Schaik & Knott, 2001). On the other hand, the flexible use of simple tools is limited to only a couple of species, which suggests that flexibility in tool use is a demanding aspect (Beck, 1980; Byrne, 1995). As simple as they may be, such tool use still requires an understanding of the relationship between tool rigidity and function, on the one hand, and an understanding between tool orientation and position of food reward as well as the relationship between trajectory and substrate on which tools move, on the other (Santos *et al.*, 2006).

As in dense and rich habitats, where opportunities to access embedded resources with tools are high, flexible tool use could rapidly result in an adaptive advantage, and it is intriguing that such flexibility is so rarely seen in the wild (Beck, 1980; Boesch & Boesch-Achermann, 2000; Visalberghi *et al.*, 2007; Hansell & Ruxton, 2008; Spagnoletti *et al.*, 2011). However, each simple tool use requires the understanding of and control over a specific causal and spatial relationship. It is therefore conceivable that the mastery of multiple relationships such as this rapidly becomes quite demanding, both in terms of cognitive understanding and flexibility. All chimpanzee and human populations have been seen to use a variety of simple tools so regularly that we can identify where individuals originate from on the basis of their specific tool repertoire. As would be expected from the predictions of the eco-cultural model, these two species face the largest number of different ecological niches within the primate family (Wolfheim, 1983) and, therefore, face the most diverse sets of ecological challenges.

Combined tool use

In some specific ecological contexts, such simple tool use might not be efficient to solve a given technical challenge and some innovations can then become necessary. Although a single tool can successfully extract ants or termites from their nests, it will not successfully crack hard-shelled fruits, like nuts. In that case, the nut must be placed on a hard surface and pounded with a hammer in order to be successful (Boesch & Boesch, 1984; Visalberghi *et al.*, 2007). An infant who has forgotten to place the nut on a hard surface will quickly notice that the nut will become encased in the soil and will never break open, no matter how hard one pounds (Boesch & Boesch-Achermann, 2000). Therefore, in this situation, the nut must not only be placed in relation to the hammer but, at the same time, must also be placed on a hard anvil in order for the pounding to be successful. Chimpanzees and capuchin monkeys are able to flexibly do this, as they select the hardness of both the anvil and the hammer in accordance with the hardness of the nut they intend to crack (Boesch & Boesch, 1984; Visalberghi *et al.*, 2009; Spagnoletti *et al.*, 2011). This combination of two types of relationships requires a precise understanding of causal relationships and this results in further delay in achieving success as the tool user needs to bring the two objects together before being able to act (Boesch & Boesch, 1984; Inoue-Nakamura & Matsuzawa, 1997).

Body → Hammer + Anvil → Reward

Combined tool use, which has also been termed a "second-order problem" as individuals are required to manage two spatial relationships between objects concurrently (Visalberghi & Fragaszy, 2006), has also been observed in primates, although clearly less frequently than simple tool use (e.g., nut cracking [see above] or honey extraction [see below]). Wild capuchin monkeys have been seen to efficiently master both the spatial relationships between positioning the nut on the anvil as well as the pounding of the nut with a hard hammer.

Sequential tool use

In addition to combined tools that are used at the same time, animals have been observed to use tools one after the other before reaching the reward. Two types of sequential tools can be distinguished. True sequential tools that are used one after the other in a sequence before reaching the goal, and secondary tools where one tool is used to make a tool, that can then be used to reach the goal (see Watanabe, 1972 in Sumita, 1985).

Such sequential tool use is observed when important food resources are not always directly accessible with a single tool in nature, as they are either too well protected from predators or are too distantly located to be reached directly with only one tool. Two major classes of resources are concerned here. The first, honey, is a very attractive food resource for many animal species, and therefore bees construct well-protected hives as they rely on them for their survival and reproduction. Many hives are located in small openings high up in trees and accessing them is a real challenge, even for honey badgers, which are armed with specialized morphological tools such as powerful claws and teeth. Some hives are impressively large; for example, some stingless bees in the forests of Gabon produce hives that are up to 100 cm deep, making it mandatory to use tools to reach the honey for animals that are physically too large to enter the nest. The second class of resources includes underground foods such as tubers, termites, ants and honey. For all of these, the resource must first be located, then accessed and, finally, the food must be extracted. Often many tools are necessary for consumption to be successful.

The technical challenges of accessing such resources may discourage some animal species, who will then simply neglect them, while others may acquire morphological adaptations in order to specialize for them. This is the case with honey badgers in African forests, which specialize on honey, and with pangolins, which specialize on termites. However, in other habitats, food availability might make such resources highly prized, and sequential tool use will be the logical consequence.

In the past, the cognitive challenges of attaining such underground resources were proposed to be too demanding for non-human primates and to therefore be a uniquely human specialty (Hatley & Kappelman, 1980; Laden & Wrangham, 2005). Recent observations have shown that the exploitation of such protected food resources is well within the ability of chimpanzees and that they do so regularly, using complex tool sets (Sanz *et al.*, 2004; Hernandez-Aguilar *et al.*, 2007; Boesch *et al.*, 2009; Sanz & Morgan, 2009). Tool set use, which is the use of different tools one after the other in order to reach a reward, is in fact a sequential tool use as the order in which each tool is used is not independent from the others.

Sequential tool use adds a layer of complexity, as the likelihood of randomly finding the correct sequence to use the tools decreases proportionally with the number of different tools used and, at the same time, requires a longer delay in obtaining the reward. That each tool is of a different type and fulfills a different function implies that individuals must keep track of different causal relationships in a sequential order, of which only the last step allows access to the reward. Continuing with the example of honey extraction in chimpanzees, tool 1, called the pounder, is used to forcefully hit the wax covering the entrance to the bee hive until it is broken, which is sub-goal 1. Once this is achieved, tool 2, the enlarger, is used to open the honey chambers within the nest, which is sub-goal 2. Finally, a collector, tool 3, is used to extract the honey, which is the reward (Boesch *et al.*, 2009; Sanz & Morgan, 2009; see Figure 2.1). As such nests are very large, an individual might have to reuse an enlarger (tool 2) to access a new honey chamber (sub-goal 2) to be able to extract more honey with a collector (tool 3). Therefore, tool users must differentiate between the spatial relationships of "tool 1," with its specific action to object

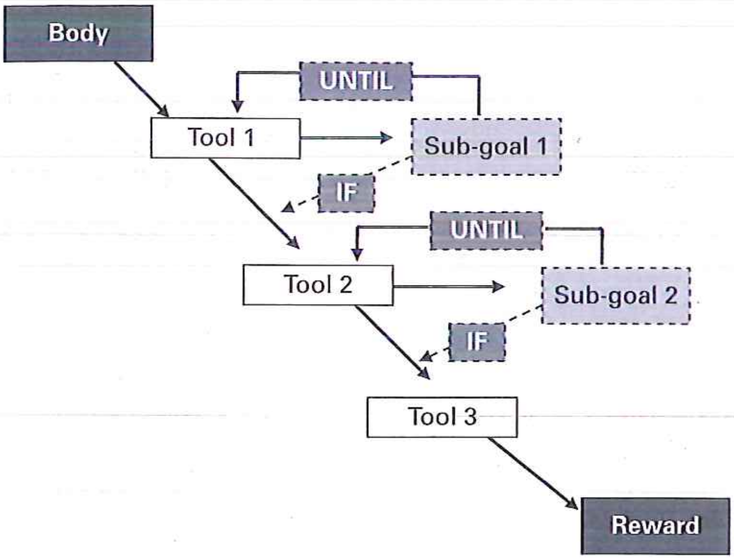

Figure 2.1 General diagram of sequential tool use based on the complex situations seen in chimpanzees. "Tool 1" will be reused *until* "sub-goal 1" is reached. Only *if* "sub-goal 1" is reached will "tool 2" be used, and then *until* "sub-goal 2" is reached. This can go on for up to five different tools until the reward is reached (Boesch *et al.*, 2009; Sanz & Morgan, 2009). If only one tool is used, this diagram reduces itself to the simple tool use presented above.

1 – intact bee hive entrance – from the spatial relationship of "tool 2," with its other specific action to object 2 – chamber walls within the broken bee hive entrance – from the spatial relationship of "tool 3" – collecting honey from deep inside the hive. Tool size, weight and hardness is selected and modified by tool users in accordance with such specific actions and functions (see Boesch *et al.*, 2009; Sanz & Morgan, 2009). Thus, the memorizing of different steps within a specific sequence and the hierarchical differentiation between them is what makes sequential tool use challenging.

Furthermore, the same tool is often used repeatedly until the sub-goal is reached, at which point the individual will shift to using a second type of tool (see Boesch *et al.*, 2009; Sanz & Morgan, 2009; Figure 2.1). In some sequential tool use, this requires quite extensive use of the tool and the time delay before the use of the second tool can be quite considerable. For example, when using a pounder (tool 1) to break open the bee hive, a Goualougo chimpanzee could perform the action over 280 times before attaining sub-goal 1 and switching to tool 2 (Sanz & Morgan, 2009). Furthermore, quite often the sequential tool use needed to reach a bee hive is challenging and chimpanzees are regularly unsuccessful, as bee hives are often well protected. Underground hives, in particular, are very hard to locate (Boesch *et al.*, 2009; Sanz & Morgan, 2009). Thus, sequential tool use imposes not only an important time delay before getting at the reward, but requires that an individual apply a "conditional recurrent hierarchical sequence" as each tool is inserted within a sequence and each has to achieve a certain function that is dependent upon the functions performed by previous tools and that will be performed by subsequent ones.

The puzzling observation that Central African chimpanzees employ sequential tool use regularly but West African chimpanzees have been observed to do so only very rarely begs the question of why some populations seem to use sequential tools much more often than others. Taï chimpanzees have been seen to use sequential tools only in the context of nut cracking, when they use sticks to extract the pieces of kernel out of nut shells after breaking them open with hammers, while in 30 years of observations, we saw them using simple tools only to extract honey from honeybee hives (Boesch & Boesch-Achermann, 2000). At the same time, chimpanzees in Central Africa have been seen to employ sequential tool use extensively for honey extraction from both honeybee and stingless bee hives. Therefore, it does not seem to be a cognitive limitation, but more likely an ecological one, in the sense that the density of bee hives could be lower in Taï forest compared to Central African forests. In addition, honeybee hives seem to be constructed in larger holes in trees in the Taï forest, permitting its exploitation directly with the hand, while this has not been seen in Central African populations, where honeybees may face higher predation pressure and select tree holes that are narrower and therefore more difficult to reach. Similarly, differences in the presence of stingless bees between West and Central African forests, as well as differences in the amount of honey found in those nests, could contribute to the fact that Central African chimpanzee populations seem to raid them more often and with more tools. It is still premature to make any firm conclusions, but ecology might be largely responsible for the differences we see in sequential tool use between chimpanzee populations.

Secondary tools that are produced with the help of another tool, as is so typical in stone knapping, rests on a similar technical process, where tool 1 is used to reach sub-goal

1, which produces tool 2, which is the tool that will reach the reward (McPherron, 2000; Ambrose, 2001; Sharon, 2009). Up to now, using one tool to make another tool has not been observed in chimpanzees, but the sequential dimension is very similar, and planning to transform either the tool or the object has many striking similarities. Making secondary tools is still, by nature, the imposition of form on the raw material resulting from detailed planning and a balance with the technical constraints of the raw material and the function of the tool (e.g., Wynn, 1993; McPherron, 2000). The essential difference, however, lies in the additional complexity of concurrently mastering the external causal relationships between two objects external to the actor, by which the first external object transforms the second one, while previous tool transformations seen in other animal species were always directly done by the actor. Before concluding about the inability of chimpanzees or other animal species to master secondary tools, we must first see them face an ecological challenge that would require them to shape one tool with another tool, such as cutting the meat of large dead prey, or perforating a hole in a hard-to-reach solid surface that would require a pointed end on a large branch (see also a captive bonobo successfully making a secondary tool: Toth & Schick, 1993).

Composite tool use

Composite tools are tools that are made of at least two different material elements that are kept together so as to function as one tool (Ambrose, 2001). This type of tool use, which has been proposed to be unique to humans as it has not yet been seen in non-human animals (Goodall, 1970; Beck, 1980; Boesch & Boesch, 1990), appeared in the course of our evolution when we entered the Middle Stone Age (Ambrose, 2001, 2010). Analysis of such composite tools suggests that they were mainly used to produce spears, knives and scrapers involving at least three tool components, such as a handle or shaft, a stone insert and a binding material (Ambrose, 2001). They seem to have developed as an adaptation to the hunting of large prey species for which long-distance weapons and increased cutting technology would have conferred an adaptive advantage to the tool users. Chimpanzees have not yet been seen to hunt large mammals, and therefore have not yet been seen to face the challenges that would make composite tools beneficial. It is clear that the technical challenges of making such tools are important and novel, and require an essential planning component and hierarchical sets of actions. However, the sequential hierarchical actions discovered recently in Central Africa suggest that the differences might be smaller than was previously thought and more observations of wild chimpanzee tool use should help to clarify the differences in such a domain between human Middle Stone Age technology and chimpanzees (see Mercader *et al.*, 2007).

A special ecological challenge: non-visible food resources

To illustrate the cognitive demands that ecological challenges may represent, I discuss here the special situation of non-visible food resources before moving to the general question of tool use as a cognitive challenge (see below).

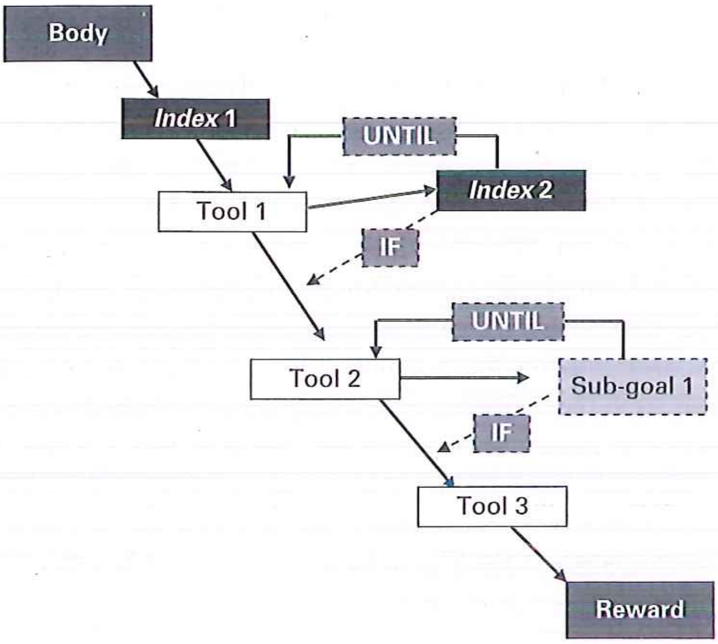

Figure 2.2 Schematic diagram of sequential tool use for non-visible resource, as used by chimpanzees in Goualougo Triangle, Congo, or in Loango National Park, Gabon. First, an individual searches for an indirect index of the presence of the resource, like a termite mound elevation, and once found, "tool 1" is used to locate another indirect index, index 2, which indicates the precise underground location of the termite chamber. "Tool 2" is then used to fish for termites by Goualougo chimpanzees. In Loango, chimpanzees must first find the opening of the nest marked by a small wax tube, index 1, and then tool 1 is used to perforate the ground until the nest is located, normally by smell, which is index 2. Then tool 2 can be used to dig a tunnel to reach the honey in the nest, which is sub-goal 1. Thereafter, and depending on the depth of the nest, tool 3 can be used to help extract the honey.

Animals may face situations that are difficult even for human researchers to understand, and for that I would like to turn my attention to the extraordinary case of sequential tool use aimed at underground non-visible food resources. When chimpanzees in the Goualougo forest intend to feed on underground termites, they first need to locate them. To do so, they use sticks to puncture the ground until they find the termite mound chamber (Sanz *et al.*, 2004).

Similarly, when Loango chimpanzees feed on honey from underground stingless bee hives, they must first locate the invisible honey chamber below the ground (Boesch *et al.*, 2009). The particular challenge of such an endeavor is that the reward – termite soldiers or honey – is not directly visible, so its location must first be inferred with the help of indices that suggest the presence of the reward – such as a small elevation increase on the ground surface or a tiny opening of a wax tube. Nevertheless, such indices constitute only a very rough indication of the reward's location ("index 1" in Figure 2.2). This is very different from ant-dipping or classic termite fishing, where the location of the nest is directly visible and determining whether the ants or termites are present can be done with a simple scratch on the surface of the nest entrance (Goodall, 1968; Boesch & Boesch, 1990).

Index 1 is only a rough indicator of the location of the food resource, because the prey species – termites and bees – do their best to hide the resource from the many

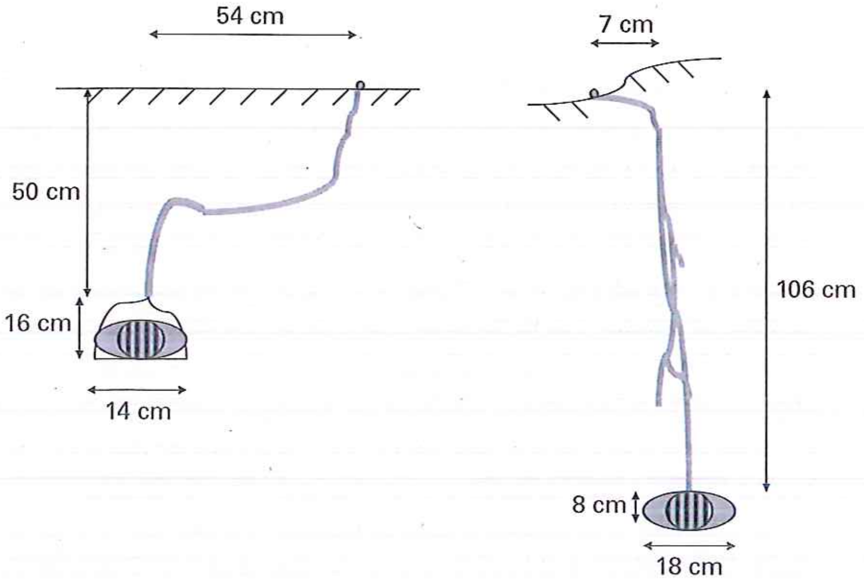

Figure 2.3 A vertical schematic illustration of the structure of two Melipone underground bee nests of the species predated by chimpanzees in Loango National Park, Gabon. We extracted those nests that were intact and active ourselves, as otherwise there was no way we could understand the technical challenges the chimpanzees face when trying to access honey in underground nests. The honey chamber within the nest is located underground, anywhere from 20 cm to over 100 cm from the surface, and, as illustrated, can be located laterally quite far away from the tube exit at the surface. The very thin wax tube made by the bees can follow either a relatively straight path or a very convoluted path to the chamber, which nothing on the surface would allow an individual to predict.

predators present in the forest. In the case of underground bee honey, the nest can be up to 100 cm under the surface of the ground, and sometimes up to 70 cm laterally from the only visible sign of a nest, the 3 mm wide wax tube marking the entrance of the nest (see two examples of underground bee nests in Figure 2.3). After finding "index 1," chimpanzees will select a tool to puncture/perforate the ground, in order to better locate the resource. By doing this, they are looking for a second indirect sign of the reward location, "index 2." From personal trials and by looking at the actions of the other chimpanzees, index 2 can remain indirect in the sense that it can be a change in the physical property of the ground that a chimpanzee has to then relate to the food (Figure 2.2). For example, a chimpanzee must relate the perceived change in the resistance of the soil as it forcefully pushes the stick through the ground trying to detect the honey chamber or termite mound. Sometimes a chimpanzee will then smell the end of the stick, as if confirming the localization of the resource. Index 2 will then be used to direct the subsequent actions of the individual (Figure 2.2), and additional tools might be needed before an individual gets to eat the food. Without such indices, the actions would be performed purely at random and with very low success rates. Indices are a cognitive challenge as they are not the reward but *stand for the reward* and guide the chimpanzee. Furthermore, they are not visual cues, but instead involve other sensory modes, as lower soil resistance implies the presence of a termite mound or honey chamber.

After finding index 2, chimpanzees often dig tunnels that are barely large enough to let a human hand enter, indicating that they know exactly where they are aiming at. They cannot do that by simply following the bee tube, as this is much too fragile to resist the tool-assisted digging process. Personal testing at locating the nest proved to be extremely difficult as the soil can be so hard that I was unable to perforate the ground beyond 30–40 cm. In fact, local pygmy trackers told me that the elderly in their village advised them not to try to search for the honey of this species of bee as it "is too deep." When successful, it took me up to 40 minutes just to locate the honey chamber (Figure 2.3). At the time of writing, Luisa Rabanal, the student working on this technique, and myself are still unclear about how the chimpanzees are able to locate the nest so precisely and how often they are successful in reaching the honey. Luckily, the chimpanzees are habituated to the presence of camera traps and we are presently in the process of filming chimpanzees as they try undisturbed to solve this technical challenge.

Thus, an elaborate understanding of unseen nest structure, combined with a clear appreciation that tools permit the location of unseen resources and a precise three-dimensional sense of geometry to reach the honey chamber from the correct angle is demonstrated by the chimpanzees when extracting underground honey. In addition, due to the important variation in nest structure and the impossibility of predicting it from visible cues, chimpanzees have to demonstrate a high sense of flexibility in implementing the sequence shown in Figure 2.2, as angles, depth, direction and size of the nest, as well as hardness and type of soil vary for each nest, requiring a permanent adaptation to the local situation in the selection and the number of tools, as well as the modification to do to them (Figure 2.3) (Boesch *et al.*, 2009). Finally, the tool users' techniques also vary, as they may use one or both hands or use both their hands and their feet to perforate the ground with the tool.

Tool use as a cognitive challenge

Different aspects of tool use can represent a cognitive challenge and different authors have tried to address them and place them within a coherent framework so that different types of tool use can be compared. Tool selection has been considered as an important cognitive challenge as it requires a flexible adaptation to the technical constraints (e.g., Boesch & Boesch, 1990; Bluff *et al.*, 2007). Tool selection has been studied with some captive monkeys and apes in different artificial experiments and results have shown that, after training, some limited understanding of the functional property of tools could be demonstrated (Povinelli, 2000; Santos *et al.*, 2003, 2006; Herrmann *et al.*, 2008). Intriguingly, all species seem to give more importance to proximity – when a tool touches an object – rather than to connectivity – when a tool is attached or supports the object – leading to a lot of surprising and mysterious mistakes. In the real world, confusing proximity with connectivity would not be very adaptive, and neither nut cracking nor ant dipping would be successful and might even be deadly when it comes to jumping between branches high up in trees.

In order to get a grip on all these different aspects of tool use and, therefore, make comparisons between the different tool-use possibilities, I suggest adapting and expanding the relation spatial model in order to describe the cognitive challenges of tool use. This model was initially proposed to address the tool-using skills of capuchin monkeys (Visalberghi & Fragaszy, 2006; Fragaszy, 2007), and studies found that, in its more complex forms, capuchins were able to concurrently master two different spatial relationships when using tools with a dynamic dimension (see Table 2.1 under combined tool use (b)). I have expanded on this by adding one more dimension than was originally proposed and have used my four levels of different tool-use types (see above). In this model, each tool use is classified with respect to four orthogonal properties; the number of spatial relationships that need to be mastered for the tool use to be accurate (1) if such spatial relationships have to be managed successively or concurrently; (2) if the relationships are static in time or needed to be dynamically adapted during the course of actions; (3) if the tools needed to be used in a specific manner or could be used in a more permissive manner (for example, whether or not both sides of a stick could be used); and (4) if direct body contact is involved or not.

The concurrent mastering of two spatial relationships has recently been suggested to be crucially important in explaining some of the difficulties observed when captive chimpanzees attempt to solve the tube-trap problem (Visalberghi & Limongelli, 1994; Povinelli, 2000; Mulcahy & Call, 2006; Seed *et al.*, 2009b), as it requires an additional load on the subject's attention system, cross-modal matching if different sensorial modes are used, and increased response variability. The hierarchic sequential mastering of more than one spatial relationship might similarly represent a cognitive challenge, as cross-modality, attention and response variability with two spatial relationships is equally required. Furthermore, since actions are not concurrent, the more tools an individual uses, the more demands there will be on remembering them and placing them in the appropriate sequential order. Tool use has been suggested to be the outcome of coordinated multiple cognitive processes, each of which can respond differently to experience and to immediate circumstances (e.g., Spencer *et al.*, 2001; Fragaszy *et al.*, 2009).

Of special relevance here are the works comparing the performance of capuchin monkeys versus chimpanzees, our two best primate tool users. Comparative approaches using exactly the same procedure showed that capuchin monkeys fail a causal reasoning task that chimpanzees could solve (Visalberghi & Limongelli, 1994), and children and chimpanzees viewing similar films fare comparably well in another comparative causal reasoning test (O'Connell & Dunbar, 2005). More directly related to tool-use reasoning, capuchin monkeys and chimpanzees were able to maintain focus on moving a cursor toward a goal and monitoring the effect of each choice, but only chimpanzees could master the notion of detour to reach a goal and plan the continuity of the path to that goal, which made them more able to redirect their behavior when faced with multiple possibilities (Fragaszy *et al.*, 2009). In addition, the performance of chimpanzees, but not capuchin monkeys, increased with experience. Both are relevant to our understanding of the differences in the tool-use skills of capuchin monkeys and chimpanzees, as monitoring the effect to reach a goal is important for simple tool-use efficiency, while planning a path to a goal with distinct detours and incorporating different tools is at the base of performing sequential tool use, and reaches a higher level of complexity than does simple tool use. Capuchin monkeys have been observed to use simple and combined, but not yet sequential, tools.

Tool use in the wild imposes an additional need for flexibility on tool users, as in all tool-use contexts, variations are found in the shape, structure, location and hardness of the food, as well as in the size, hardness, weight and color of the tools. This requires additional flexibility in the individuals using the tools, as this will increase with the number of different tool-use contexts. This might contribute to the observations that tool use in birds is limited to clearly defined contexts, normally that of extracting insects and grubs from holes in branches, and the time delay to solution is relatively short. By contrast, chimpanzees use tools in a wide variety of contexts, such as during social play, to attain food, for defense and hygienic purposes and as a means of communication (Goodall, 1970; Boesch & Boesch, 1990). The more tools that are made from different materials and used in different contexts, the more the individuals will have to make decisions specific to each situation. Nut cracking, for example, is not only about hitting a nut with a hard hammer, but the hardness, the weight and the color of each hammer is different, while the placement of the nut on the anvil, and therefore its stability and accessibility (the angle to hit it), will vary as well. In reality this makes each situation different from the previous ones and represents a new challenge each time.

As can be seen in Table 2.1, the cognitive demands of sequential tool use have reached a challenging level of complexity, and it is not surprising that such an ability was previously thought to be restricted to humans; this also used to be thought of the ability to extract underground food resources (Hatley & Kappelman, 1980; Laden & Wrangham, 2005). Interestingly, following reviews of cognitive achievements such as those demonstrated from comparative experiments with captive monkeys and apes, the "unobservability hypothesis" states that only humans, but none of the non-human primates, are able to reason and understand causality about unobservable entities (Povinelli, 2000; Penn & Povinelli, 2007; Penn *et al.*, 2008; Vonk & Subiaul, 2009). If true, this would match nicely with the proposed dichotomy in the ability to extract unseen resources with sequential tool techniques. However, if this hypothesis might apply to some captive individuals that have experienced only very deprived ecological conditions throughout their lives, it seems totally at odds with the new discoveries of underground resource exploitation by chimpanzees in Central Africa, as well as some Tanzanian chimpanzees who have been observed to extract underground tubers (Sanz *et al.*, 2004; Hernandez-Aguilar, 2007; Boesch *et al.*, 2009; Sanz & Morgan, 2009). This is not the only hypothesis constructed from captive experimental works that is hard to reconcile with new evidence of sequential tool use in wild chimpanzees; for example, some have suggested that captive chimpanzees show strong limitations in causal reasoning compared to humans (Premack, 2007), while others have argued that great apes are unable to flexibly generalize from one task to another equivalent one (Martin-Ordas *et al.*, 2008). In particular, the flexibility of wild chimpanzees in applying sequential tool solutions to such different but equivalent tasks as the extraction of kernels from nuts, honey from both tree and underground bee hives, soldiers from underground termite mounds and soldiers from deep driver ant nests seems impossible to reconcile with such cognitive limitations.

An attempt to experimentally identify the cognitive requirements for sequential tool use has been tried with Caledonian crows (Taylor *et al.*, 2007; Wimpenny *et al.*, 2009). However, due to the limitations of captivity, the procedures developed did not faithfully mimic natural conditions, but instead forced the subjects to adopt a sequential approach not by nature of the challenge, but simply by making them physically unable to directly reach "tool 2," which would have allowed them to directly get at the food reward. The experimental setup forced the birds to select first tool 1 to extract tool 2 from a tube before being able to use tool 2 to reach the food. Therefore, the experimental procedure not only imposed an artificial sequential sequence, but also imposed the order in which the tools could be used, so that the sequence was imposed by the procedure rather than being a decision made by the subject when facing a demanding ecological challenge. Such experiments did not really test the ability of crows to spontaneously understand sequential tool use. In the real world, it is the subject itself that has to decide about the sequence and order of use of the different tools. Second, in the real world, the sequence is often more complex due to the fact that it is not length alone that is important, but rather a combination of length, width and weight. When underground termite fishing, the Goualougo chimpanzees insert a thin fishing probe into a tunnel made with a wider, stout puncturing tool (Sanz & Morgan, 2009). Similarly, when gathering tree honey, a thinner and longer collector or fluid dip is used only after a short, heavy, thick pounder has broken open the bee hive (Boesch *et al.*, 2009; Sanz & Morgan, 2009). The striking feature of natural sequential tool use is that chimpanzees perform them with a clear structure in mind as they follow a precise sequence, despite encountering numerous and important difficulties in attaining sub-goals; different types of branches can be used as pounders in Central African forests, and when the first pounder does not succeed in opening the nest, the chimpanzees continue selecting only branches that could function as pounders until the opening is made (often keeping unsuccessful pounders for later reuse; Sanz & Morgan, 2009). Similarly, chimpanzees in Mahale National Park, Tanzania, have been observed to regularly arrive at ant fishing sites carrying up to three manufactured fishing probes with them, as the probes wear out rapidly when used, which the chimpanzees were anticipating (Nishida & Hiraiwa, 1982; personal observation). From video recordings, Goualougo chimpanzees arrived sometimes at termite nests carrying two readily prepared types of sticks (Sanz *et al.*, 2004), demonstrating that they correctly anticipated the future need of sequential tools.

Viewing tool use as a problem-solving task and considering that the problems are set by the ecological niche of each population predicts a less rigid relationship between tool-use skills and phylogeny, as illustrated by the extraordinary observations of New Caledonian crows manufacturing and using complex tools (Hunt, 1996; Kenward *et al.*, 2005; Hunt *et al.*, 2006). Similarly, we should expect that some ecological challenges in nature might require similar causal understanding without requiring a tool and, therefore, the observations that some tool-use abilities have already evolved in non-tool-using primates is not totally unexpected (Santos *et al.*, 2003, 2006). Furthermore, the evolution of a complex causal understanding of external objects in chimpanzees has been proposed to be selected by hunting, as this requires thinking, anticipating and reacting to the movements of the prey species (Boesch & Boesch-Achermann, 2000). In particular, the transfer of hunting skills to tool-use situations that are perceptually quite different but conceptually quite similar would favor the development of the type of flexibility that might be important for acquisition of flexible tool use as well as the sophisticated sequential tool use seen in chimpanzees.

Tool use as a cultural expression

According to the "eco-cultural model" (Segall *et al.*, 1999; Carpendale & Lewis, 2004; Boesch, 2007), we should expect not only the ecology to be fundamental in explaining the tool use observed within a species, but also the cultural environment to shape tool use. The best-studied example of such a cultural tool use is the nut-cracking behavior observed in chimpanzees (Sugiyama & Koman, 1979; Boesch & Boesch, 1984, 1990; Boesch *et al.*, 1994; Boesch, 2003). The chimpanzees of the Taï forest crack five species of nuts and the chimpanzees of Bossou, Guinea, crack an additional species. All of these species of nuts have a large distribution range within the tropical forests of West and Central Africa, going from Sierra Leone–Liberia to Gabon– Congo. *Coula edulis* is one of the most abundant canopy trees in these forests and also has one of the least hard nuts of those that the chimpanzees crack. Furthermore, observations in the Taï forest have shown that adolescent individuals have enough strength to crack them open directly with their teeth (e.g., Tina, an adolescent female with handicapped hands was seen to crack them successful for many months; Boesch & Boesch-Achermann, 2000). Despite this, no evidence of nut cracking has been found in *Coula*-rich forests east of the Sassandra River in Côte d'Ivoire, where chimpanzees live (see Figure 2.4), or in many forested regions of Gabon, Tanzania, Uganda and Congo. Only in the Ebo forest in southern Cameroon were a handful of observations of nut cracking reported (Morgan & Abwe, 2006). These observations made nut cracking one of the most cited cultural tool-using behaviors (Boesch, 2003).

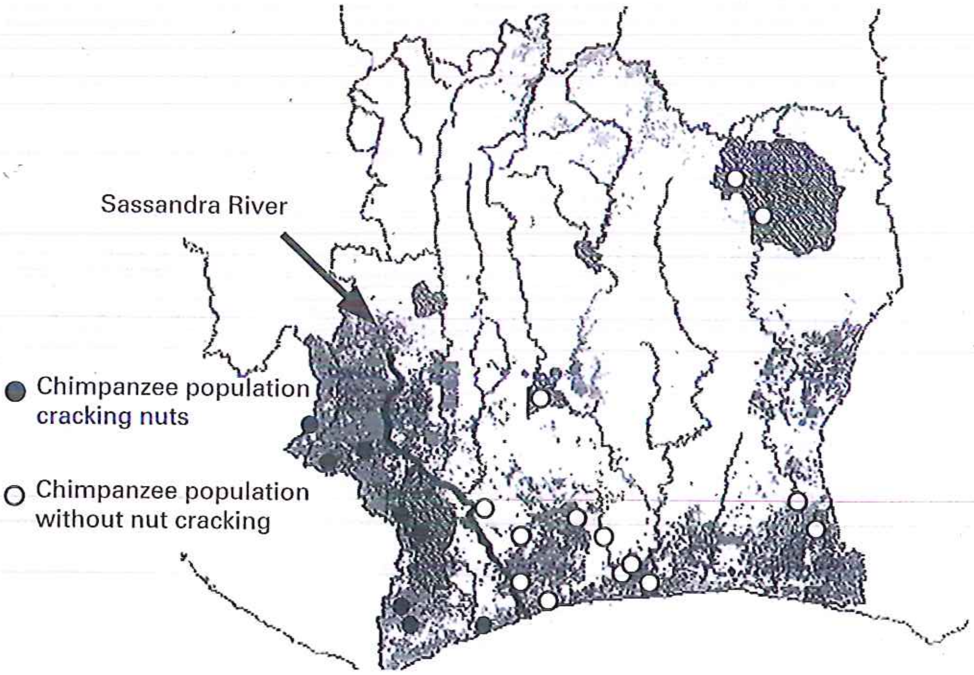

Figure 2.4 Nut cracking has been found in wild chimpanzees of Côte d'Ivoire only on the western side of the Sassandra River, despite the fact that *Coula edulis* and *Panda oleosa* nuts are found in all forests in the south of the country. Twenty-two locations in the country with the confirmed presence of chimpanzees have been visited for signs of nut-cracking sites in 1994–1995 (Boesch *et al.*, 1994).

Ant dipping in chimpanzees has also been shown to be significantly affected by cultural preferences when this behavior is compared between different populations. Two main ant-dipping techniques have been identified. First, the chimpanzees of Gombe National Park in Tanzania have been described to use relatively long wands to dip for the soldiers or driver ants directly from the nest entrance and then use their two hands to bring the ants into their mouths (Goodall, 1968, 1970; McGrew, 1974). This technique is very efficient as it allows individuals to capture about 700 ants per minute (Boesch & Boesch, 1990). Second, the chimpanzees of Taï National Park in Côte d'Ivoire have been described to use much shorter sticks to dip the soldiers out of the nest entrance and then put the end of the stick directly into their mouth to remove the ants with their teeth (Boesch & Boesch, 1990). This technique is proven to be much less efficient, as only about 125 ants are captured per minute, but this method is nevertheless systematically used by all group members of four chimpanzee communities observed in Taï forest.

A precise comparison of the techniques used by chimpanzees in the Taï forest and in Bossou, Guinea, has confirmed that some aspects of the way the chimpanzees in Bossou dip for ants are influenced by the species of ants they dipped for, as well as the location they dipped for them (Möbius *et al.*, 2008). However, most of the differences observed between the Bossou and Taï populations were not explained by ecological differences (Möbius *et al.*, 2008). A larger review of chimpanzee populations has supported that conclusion in the sense that we see a mixture of ecological effects as well as important cultural effects in the presence of the ant-dipping behavior (Schöning *et al.*, 2008). Therefore, in agreement with the prediction of the eco-cultural model, tool use in chimpanzees is affected by both the ecology experienced by group members as well as by the specific cultural environment they face (Boesch, 2007, 2010).

Cumulative cultural evolution in tool use

Complex cultural tool use as observed in nut cracking and honey extraction strongly suggest a cumulative cultural process. Let me take here the example of nut cracking, and include the observations of tool technology from different chimpanzee populations. We can see that flailing insects, conspecifics or snakes with branches or saplings has been reported from all chimpanzee populations, as has clubbing playmates or social competitors with wooden sticks (named as "universal " in Figure 2.5). One innovation was added to this universal in Gombe and Taï chimpanzees when they used tree trunks or roots to pound hard fruit against; this is similar to clubbing, but in this case, the club was a different sort of object and served a different purpose, namely to access food (Figure 2.5). A second innovation was seen in West Africa, where hammers were used to pound on food that had been placed on a hard surface. From this last innovation, two possible further novelties, both examples of sequential tool use, were incorporated: the Taï chimpanzees added a stick in order to extract nut remains from cracked shells; and the Bossou chimpanzees used mobile anvils on which they placed nuts. A final innovation that was observed a few times in the

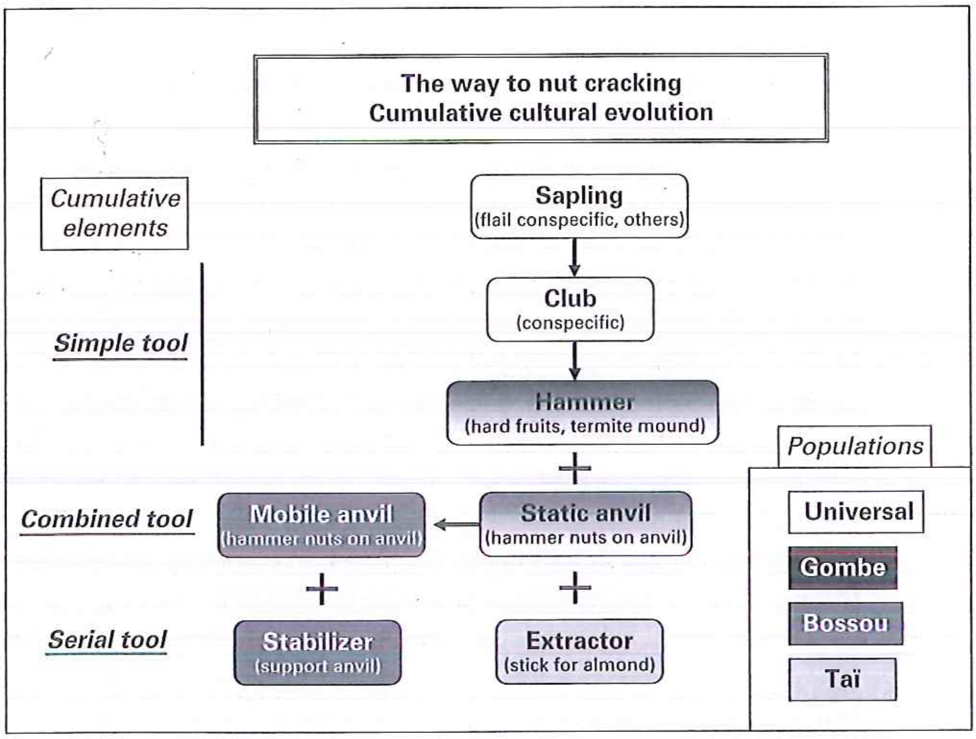

Figure 2.5 Cumulative cultural evolution leading to nut-cracking technique, whereby a behavior seen in all chimpanzee populations is elaborated through successive additions of new, different elements. First, a simple tool is integrated into the pounding movements, as seen in Gombe, Bossou and Taï chimpanzees. Then, the introduction of a second tool led to the invention of a combined tool use as seen in Taï and Bossou chimpanzees. For each step of the accumulation process seen in a given population, I have listed the different resources gained or involved.

Bossou chimpanzees was the placement of a stone under the mobile anvil to stabilize it before hitting the nut with the hammer (Figure 2.5). For each step in the cumulative process, the tool technique was efficient to improve the access to a given food resource and is still used effectively in at least one chimpanzee population, but it was later elaborated for a new food source. Thus, nut cracking in chimpanzees resulted from a cumulative cultural process developing from a universal, simple chimpanzee technique.

The cumulative innovations were most likely not due to one single individual using them, for the different techniques are all still in use in different populations. As the Taï chimpanzees are separated from these other groups by about 3000 km and several major rivers, it would be unreasonable to assume one inventor for all these innovations. Thus, this might be a very good example of what has been labeled a "collective cast of mind" in the human literature, whereby the invention of one group member that has disseminated to the whole group could be improved by another invention from another individual, and that collective product would then disseminate again to the whole group before being improved once again (Boesch, 2012). This accumulation of innovations, which improves the product at each step, is what has been labeled a "cumulative cultural evolution."

Conclusion

The observations of sequential tool use that have recently been observed in Central African chimpanzees could become the flagship example of how much can be missed about the behavioral and cognitive abilities of a species when important ecological niches of an animal species' range are not studied. After over four decades of field studies on wild chimpanzees, new studies following chimpanzees in the Congo basin regions have uncovered such sophisticated tool-use skills. Following the "eco-cultural model," we must expect that the greater number of different ecological niches a species experiences, the greater number of different solutions they will develop. Thus, we must expect more new discoveries about chimpanzees, as they are one of the primate species with the largest distribution ranges in Africa, ranging from dry savannah regions, like in Senegal and Mali, to the deepest rainforests in Côte d'Ivoire, Congo, Gabon and the DRC.

The tool-use framework discussed here has, in conjunction with some careful captive experiments, allowed us to pinpoint some important technical skills that require cognitive skills that, at present, seem to explain some species differences. The number of spatial relationships that must be controlled during tool use seems to place important cognitive demands on the individual performing it and could explain why, at present, no sequential tool use has been observed in wild capuchin monkeys. Similarly, the flexibility demands of natural ecological challenges in terms of synchronicity of actions, the dynamic dimension of the actions itself, as well as the specificity of the actions requiring more flexibility are all important demands on the individuals that need to be solved for tool use to be successful. The discoveries of sequential tool use and cumulative culture evolution in wild chimpanzees have shed new light on their tool-use abilities. Further new discoveries on chimpanzee skills are overdue and will help us to understand about their abilities and the influence of ecology on such technical behavior.

Viewing tool use as a way to solve natural feeding challenges has proven to have good explanatory power for the distribution of tool-using abilities in the animal kingdom, as it does not relate directly to phylogenetic proximity. Furthermore, the food-storing abilities of certain birds have already pointed to the need to adopt an ecological approach to cognition (Emery & Clayton, 2004), and not stick strictly to a phylogenetic viewpoint based on the anthropocentric belief that, because humans are the best tool users and the most intelligent species, those species most closely related to us must be more elaborate in these dimensions than others. At present, the ecological approach favored by the technical intelligence hypothesis or the eco-cultural model seems much better supported. This also supports the view that we need to be more modest about claiming species differences in such abilities, as long as we have not gained a representative knowledge of ecological cognitive responses of each of those species (see, for example, Boesch, 2010; Heinrich *et al.*, 2010). Such an approach also has the potential future advantage of allowing us to identify those factors that were important to explain the emergence of human technical skills and cognition. The ecological approach suggested here would certainly predict a domain-general view of the evolution of cognition, as is also demonstrated by the presence of tool-use skills in non-tool-using monkeys and birds (Santos *et al.*, 2003, 2006; Huber & Gajdon, 2006).

Tool use as a problem-solving task must be studied and thought about in relation to the ecological challenges a species faces, and the total disconnection of tool-use abilities from the natural challenges make some captive experimental studies difficult to interpret and use to understand real-world animal abilities. I realize that, for birds, the coupling of captive and wild studies is easier because of the increased possibility of producing ecologically valid settings, and that this is more difficult for large mammal species like the great apes. In addition, it may be impossible in captive conditions to mimic the complex technical challenges encountered in the wild. In that light, discussing causal cognition by focusing solely on work done with laboratory animals will, in essence, totally underestimate what animals are capable of (Tomasello *et al.*, 2005; Penn & Povinelli, 2007; Penn *et al.*, 2008), and, therefore, face the risk of being restricted to understand the detrimental effect of captivity on animal cognition (Bard *et al.*, 2005; Leavens *et al.*, 2005; Boesch, 2007, 2010; Ijzendoorn *et al.*, 2009; Lyn *et al.*, 2010). Some species differences could potentially be understood if the experimental designs were exactly the same (e.g., Santos *et al.*, 2006; Fragaszy *et al.*, 2009), but this would only be the case if we assume that the species being compared will react similarly to captive conditions, an assumption that has yet to be proven. Too often, the methods used in the experiments diverge in some ways and this leads to very contradictory results (see, for example, Leavens *et al.*, 2005; Boesch, 2007; Seed *et al.*, 2009b; Lyn *et al.*, 2010) and never-ending discussions about which methods reveal the essence of the animal skills. An enlightening example is the 21-year-old famous trap-tube test developed to study causality understanding in different animal species, by presenting them with a food bait that needed to be pushed out with a tool from a transparent tube while avoiding a trap in which the food would fall (Visalberghi & Trinca, 1989; Visalberghi & Limongelli, 1994). This tube test was very successful and used in many studies with many species, but with hugely contradictory results (e.g., Povinelli, 2000; Martin-Ordas & Call, 2009; Seed *et al.*, 2009b), so that readers reach total confusion as each minimal change in the experimental procedures can lead to major changes in the performance of the animals. In careful experiments done with humans, it could be shown that gratuitous and unsupported assumptions about how humans' folk physics knowledge works was at the base of the imprecision in the experiments (where too many variables were intervening at the same time and could be perceived with different importance), as well as of the errors in the interpretations (as we should expect different responses when following different rules) (Silva *et al.*, 2005; Silva & Silva, 2006).

New observations and discoveries of tool use in macaques, capuchin monkeys, orangutans and chimpanzees will continue to emerge as we study an increasing number of different populations of those species, and they will make us alter our view of species differences in cognition as well as for tool use. This is a very exciting perspective and we hope that human destruction of nature will not prevent this from happening!

References

Allen, C. (2002). A skeptic's progress. *Biology and Philosophy*, **17**, 695–702.

Ambrose, S. (2001). Paleolithic technology and human evolution. *Science*, **291**, 1748–1753.

Ambrose, S. (2010). Coevolution of composite-tool technology, constructive memory and language: implications for the evolution of modern human behavior. *Current Anthropology*, **51**(1), S135–S149.

Bar-Yousef, O. & van Peer P. (2009). The chaîne opératoire approach in middle Paleolithic archeology. *Current Anthropology*, **50**(1), 103–117.

Bar-Yousef, O., Vandermeersch, B., Arensburg, B., *et al.* (1992). The excavations in Kebara Cave, Mt. Carmel. *Current Anthropology*, **33**, 497–534.

Bard, K., Myowa-Yamakoshi, M., Tomonaga, M., *et al.* (2005). Group differences in the mutual gaze of chimpanzees (*Pan troglodytes*). *Developmental Psychology*, **41**(4), 615–624.

Barrett, L., Henzi, P. & Rendall, D. (2007). Social brains, simple minds: does social complexity really require cognitive complexity. *Philosophical Transcriptions of the Royal Society of London B*, **362**, 561–575.

Beck, B. B. (1980). *Animal Tool Behavior*. New York: Garland Press.

Bluff, L., Weir, A., Rutz, C., Wimpenny, J. & Kalcelnik, A. (2007). Tool-related cognition in New Caledonian crows. *Comparative Cognition and Behavior Reviews*, **2**, 1–25.

Bluff, L., Troscianko, J., Weir, A., Kalcelnik, A. & Rutz, C. (2010). Tool use by wild New Caledonian crows *Corvus moneduloides* at natural foraging sites. *Proceedings of the Royal Society of London B*, **277**, 1377–1385.

Boesch, C. (2003). Is culture a golden barrier between human and chimpanzee? *Evolutionary Anthropology*, **12**, 26–32.

Boesch, C. (2007). What makes us human (*Homo sapiens*)? The challenge of cognitive cross-species comparison. *Journal of Comparative Psychology*, **121**(3), 227–240.

Boesch, C. (2010). Away from ethnocentrism and anthropocentrism: towards a scientific understanding of "what makes us human." *Behavioral and Brain Sciences*, **33**(2/3), 26–27.

Boesch, C. (2012). From material to symbolic cultures: culture in primates. In J. Valsiner (ed.) *The Oxford Handbook of Culture and Psychology*. Oxford: Oxford University Press.

Boesch, C. & Boesch, H. (1984). Mental map in wild chimpanzees: an analysis of hammer transports for nut cracking. *Primates*, **25**, 160–170.

Boesch, C. & Boesch, H. (1990). Tool use and tool making in wild chimpanzees. *Folia Primatologica*, **54**, 86–99.

Boesch, C. & Boesch-Achermann, H. (2000). *The Chimpanzees of the Taï Forest*. Oxford: Oxford University Press.

Boesch, C., Marchesi, P., Marchesi, N., Fruth, B. & Joulian, F. (1994). Is nut cracking in wild chimpanzees a cultural behaviour? *Journal of Human Evolution*, **26**, 325–338.

Boesch, C., Head, J. & Robbins, M. (2009). Complex toolsets for honey extraction among chimpanzees in Loango National Park, Gabon. *Journal of Human Evolution*, **56**, 560–569.

Byrne, R. (1995). *The Thinking Ape*. Oxford: Oxford University Press.

Byrne, R. (1997). The technical intelligence hypothesis: an additional evolutionary stimulus to intelligence? In A. Whiten & W. Byrne (eds.) *Machiavellian Intelligence II: Extensions and Evaluations* (pp. 289–311). Cambridge: Cambridge University Press.

Byrne, R. (2004). The manual skills and cognition that lie behind hominid tool use. In A. Russon & D. Begun (eds.) *The Evolution of Thought: Evolutionary Origin of Great Ape Intelligence* (pp. 31–44). Cambridge: Cambridge University Press.

Canale, G., Guidorizzi, C., Kierulff, M. and Gatto, C. (2009). First record of tool use by wild populations of the yellow-breasted capuchin monkey (*Cebus xanthosternos*) and new records for the bearded capuchin (*Cebus libidinosus*). *American Journal of Primatology*, **71**, 366–372.

Carpendale, J. & Lewis, C. (2004). Constructing an understanding of mind: the development of children's social understanding within social interaction. *Behavioral and Brain Sciences*, **27**, 79–151.

Carvalho, S., Cunha, E., Sousa, C. & Matsuzawa, T. (2008). Chaines opératoires and resource-exploitation strategies in chimpanzee (*Pan troglodytes*) nut cracking. *Journal of Human Evolution*, **55**, 148–163.

Cipolletta, C., Spagnolietti, N., Todd, A., *et al.* (2007). Termite feeding behavior of western gorillas (*Gorilla gorilla gorilla*) at Bai Hokou, Central African Republic. *International Journal of Primatology*, **28**, 457–476.

Dietrich, S., Toth, N., Schick, K. & Chaminade, T. (2008). Neural correlates of early Stone Age toolmaking: technology, language and cognition in human evolution. *Philosophical Transactions of the Royal Society of London B*, **363**, 1939–1949.

Emery, N. & Clayton, N. (2004). Mentality of crows: convergent evolution of intelligence in corvids and apes. *Science*, **306**, 1903–1907.

Fragaszy, D. (2007). Relational spatial reasoning and tool use in capuchin monkeys. *A Primatologia no Brasil*, **10**, 521–546.

Fragaszy, D. & Visalberghi, E. (2004). Socially biased learning in monkeys. *Learning and Behavior*, **32**(1), 24–35.

Fragaszy, D., Kennedy, E., Murnane, A., *et al.* (2009). Navigating two-dimensional mazes: chimpanzees (*Pan troglodytes*) and capuchins (*Cebus apella* sp.) profit from experience differently. *Animal Cognition*, **12**, 491–504.

Goodall, J. (1968). Behaviour of free-living chimpanzees of the Gombe Stream area. *Animal Behaviour Monograph*, **1**, 163–311.

Goodall, J. (1970). Tool-using in primates and other vertebrates. In D. S. Lehrmann, R. A. Hinde & E. Shaw (eds.) *Advances in the Study of Behavior*, Vol. **3** (pp. 195–249). New York: Academic Press.

Goodrich, G. & Allen, C. (2007). Conditioned anti-anthropomorphism. *Comparative Cognition and Behavior Reviews*, **2**, 147–150.

Greenfield, P. M. (1991). Language, tools, and the brain: the ontogeny and phylogeny of hierarchically organized sequential behavior. *Behavioral and Brain Sciences*, **14**, 531–595.

Gumert, M., Kluck, M. & Malaivijitnond, S. (2009). The physical characteristic and usage patterns of stone axe and pounding hammers used by long-tailed macaques in the Andaman Sea region of Thailand. *American Journal of Primatology*, **71**, 594–608.

Hansell, M. & Ruxton, G. (2008). Setting tool use within the context of animal construction behaviour. *Trends in Ecology and Evolution*, **23**(2), 73–78.

Hatley, T. & Kappelman, J. (1980). Bears, pigs, and Plio-Pleistocene hominids: a case for the exploitation of belowground food resources. *Human Ecology*, **8**, 371–387.

Heinrich, J., Heine, S. & Norenzayan, A. (2010). The weirdest people in the world? *Behavioral and Brain Sciences*, **3**, 1–75.

Hernandez-Aguilar, A., Moore, J. & Pickering, T. (2007). Savanna chimpanzees use tools to harvest the underground storage organs of plants. *Proceeding of the National Academy of Sciences USA*, **104**(49), 19210–19213.

Herrmann, E., Wobber, V. & Call, J. (2008). Great apes' (*Pan troglodytes*, *Pan paniscus*, *Gorilla gorilla*, *Pongo pygmaeus*) understanding of tool functional properties after limited experience. *Journal of Comparative Psychology*, **122**(2), 220–230.

Huber, L. & Gajdon, G. (2006). Technical intelligence in animals: the kea model. *Animal Cognition*, **9**, 295–305.

Hunt, G. (1996). Manufacture and use of hook-tools by New Caledonian crows. *Nature*, **379**, 249–251.

Hunt, G., Rutledge, R. & Gray, R. (2006). The right tool for the job: what strategies do wild New Caledonian crows use? *Animal Cognition*, **9**, 307–316.

Ijzendoorn, M. van, Bard, K., Bakermans-Kranenberg, M. & Ivan, K. (2009). Enhancement of attachment and cognitive development of young nursery-reared chimpanzees in responsive versus standard care. *Developmental Psychobiology*, **51**, 173–185.

Inoue-Nakamura, N. & Matsuzawa, T. (1997). Development of stone tool use by wild chimpanzees (*Pan troglodytes*). *Journal of Comparative Psychology*, **111**(2), 159–173.

Keeley, B. (2004). Anthropomorphism, primatomorphism, mammalomorphism: understanding cross-species comparisons. *Biology and Philosophy*, **19**, 521–540.

Kenward, B., Weir, A., Rutz, C. & Kacelnik, A. (2005). Tool manufacture by naive juvenile crows. *Nature*, **433**, 121.

Kummer, H. (1968). *Social Organization of Hamadryas Baboons: A Field Study*. Chicago, IL: University of Chicago Press.

Laden, G. & Wrangham, R. (2005). The rise of the hominids as an adaptive shift in fallback foods: plant underground storage organs (USOs) and australopith origins. *Journal of Human Evolution*, **49**, 482–498.

Leavens, D., Hopkins, W. & Bard, K. (2005). Understanding the point of chimpanzee pointing: epigenesis and ecological validity. *Current Direction in Psychological Science*, **14**(4), 185–189.

Lyn, H., Russell, J. & Hopkins, W. (2010). The impact of environment on the comprehension of declarative communication in apes. *Psychological Science*, **21**(3), 360–365.

Martin-Ordas, G. & Call, J. (2009). Assessing generalization within and between trap tasks in the great apes. *International Journal of Comparative Psychology*, **22**, 43–60.

Martin-Ordas, G., Call, J. & Colmenares, F. (2008). Tubes, tables and traps: great apes solve two functionally equivalent trap tasks but show no evidence of transfer across tasks. *Animal Cognition*, **11**, 423–430.

Matsuzawa, T. (2001). Primate foundations of human intelligence: a view of tool use in nonhuman primates and fossil hominids. In T. Matsuzawa (ed.) *Primate Origins of Human Cognition and Behavior* (pp. 3–25). Tokyo: Springer-Verlag.

McGrew, W. (1974). Tool use by wild chimpanzees in feeding upon driver ants. *Journal of Human Evolution*, **3**, 501–508.

McPherron, S. (2000). Handaxes as a measure of the mental capabilities of early hominids. *Journal of Archaeological Science*, **27**, 655–663.

Mercader, J., Barton, H., Gillespie, J., *et al.* (2007). 4,300-year-old chimpanzee sites and the origins of percussive stone technology. *Proceedings of the National Academy of Sciences USA*, **104**(9), 3043–3048.

Mithen, S. (1996). *The Prehistory of Mind: The Cognitive Origin of Art and Science*. London: Thames and Hudson.

Möbius, Y., Boesch, C., Koops, K., Matsuzawa, T. & Humle, T. (2008). Cultural differences in army ant predation by West African chimpanzees? A comparative study of microecological variables. *Animal Behaviour*, **76**, 37–45.

Morgan, B. & Abwe, E. (2006). Chimpanzees use stone hammers in Cameroon. *Current Biology*, **16**(16), R632–R633.

Moura, A. C. & Lee, P. C. (2004). Capuchin stone tool use in Caatinga dry forest. *Science*, **306**, 1909.

Mulcahy, N. J. & Call, J. (2006). How great apes perform on a modified trap-tube task. *Animal Cognition*, **9**, 193–199.

Nishida, T. & Hiraiwa, M. (1982). Natural history of a tool-using behaviour by wild chimpanzees in feeding upon wood-boring ants. *Journal of Human Evolution*, **11**, 73–99.

O'Connell, S. & Dunbar, R. (2005). The perception of causality in chimpanzees (*Pan spp.*). *Animal Cognition*, **8**, 60–66.

Penn, D. & Povinelli, D. (2007). Causal cognition in human and nonhuman animals: a comparative, critical review. *Annual Review of Psychology*, **58**, 97–118.

Penn, D., Holyoak, K. & Povinelli, D. (2008). Darwin's mistake: explaining the discontinuity between human and nonhuman minds. *Behavioral and Brain Sciences*, **31**, 109–178.

Povinelli, D. (2000). *Folk Physics for Apes: The Chimpanzee's Theory of How the World Works*. Oxford: Oxford University Press.

Premack, D. (2007). Human and animal cognition: continuity and discontinuity. *Proceedings of the National Academy of Sciences USA*, **104**(35), 13861–13867.

Santos, L., Miller, C. & Hauser, M. (2003). Representing tools: how two non-human primate species distinguish between the functionally relevant and irrelevant features of a tool. *Animal Cognition*, **6**, 269–281.

Santos, L., Pearson, H., Spaepen, G., Tsao, F. & Hauser, M. (2006). Probing the limits of tool competence: experiments with two non-tool-using species (*Cercopithecus aethiops* and *Saguinus oedipus*). *Animal Cognition*, **9**, 94–109.

Sanz, C. & Morgan, D. (2009). Flexible and persistent tool-using strategies in honey-gathering by wild chimpanzees. *International Journal of Primatology*, **30**, 411–427.

Sanz, C., Morgan, D. & Gulick, S. (2004). New insights into chimpanzees, tools, and termites from the Congo Basin. *American Naturalist*, **164**(5), 567–581.

Schaik, C. van & Knott, C. (2001). Geographic variation in tool use on *Neesia* fruits in orangutans. *American Journal of Physical Anthropology*, **114**, 331–342.

Schöning, C., Humle, T., Möbius, Y. & McGrew, W. (2008). The nature of culture: technological variation in chimpanzee predation on army ants revisited. *Journal of Human Evolution*, **55**, 48–59.

Seed, A., Emery, N. & Clayton, N. (2009a). Intelligence in corvids and apes: a case of convergent evolution? *Ethology*, **115**, 410–420.

Seed, A., Call, J., Emery, N. & Clayton, N. (2009b). Chimpanzees solve the trap problem when the confound of tool-use is removed. *Journal of Experimental Psychology*, **35**(1), 23–34.

Segall, M., Dasen, P., Berry, J. & Poortinga, Y. (1999). *Human Behavior in Global Perspective: An Introduction to Cross-Cultural Psychology*. 2nd edn. New York: Pergamon Press.

Sharon, G. (2009). Acheulian giant-core technology: a worldwide perspective. *Current Anthropology*, **50**(3), 335–367.

Silva, F. & Silva, K. (2006). Humans' folk physics is not enough to explain variations in their tool-using behavior. *Psychonomic Bulletin and Review*, **13**(4), 689–693.

Silva, F., Page, D. & Silva, K. (2005). Methodological-conceptual problems in the study of chimpanzees' folk physics: how studies with adult humans can help. *Learning and Behaviour*, **53**(1), 47–58.

Souto, A., Bione, C., Bastos, M., *et al.* (2011). Critically endangered blonde capuchins fish for termites and use new techniques to accomplish the task. *Biology Letters*, **7**, 532–535.

Spagnoletti, N., Visalberghi, E., Ottoni, E., Izar, P. & Fragazy, D. (2011). Stone tool use by adult wild bearded capuchin monkeys (*Cebus libidinosus*): frequency, efficiency and tool selectivity. *Journal of Human Evolution*, **61**, 97–107.