

Innovation and Ratcheting in Captive Orangutans

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Dedicated to my parents

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Zusammenfassung

Auffallende geographische Variation von Verhaltensweisen ist Beleg für das Vorhandensein von Kultur in unseren nächsten lebenden Verwandten, den Schimpansen und Orangutans. Kultur entsteht, wenn in einer Population mehrere innovative Verhaltensweisen von Individuum zu Individuum sozial weitergegeben werden. Innovation und soziales Lernen sind die Grundlage für Tradition und Kultur. Aber im Vergleich zu den Mechanismen sozialen Lernens und wie diese ermöglichen, dass sich eine von einem Individuum neu erfundene Verhaltensweise in einer Population verbreitet, hat das eigentliche Auftreten solcher neu gelernter Verhaltensweisen, Innovationen, weit weniger Beachtung gefunden. Dies gründet grösstenteils in den Schwierigkeiten, Innovationen überhaupt zu erkennen. Ramsey & Co. (2007) liessen sich bei ihrer Vorgehensweise zur Erkennung von Innovationen in natürlichen Populationen von Methoden inspirieren, anhand derer sich Kultur implizieren lässt. Da die kulturelle Verbreitung von Innovationen dazu führt, dass es zu geographischen Unterschieden im Repertoire an Verhaltensweisen zwischen Populationen derselben Art kommt, welche sich nicht alleine durch genetische und ökologische Faktoren erklären lassen, kann gefolgert werden, dass es sich bei solchen Verhaltensweisen um Innovationen handelt. Dieser Ansatz wurde von van Schaik & Co. (2006) bei der Erstellung einer Liste von 43 potentiellen Innovationen in wilden Orangutans angewandt. *Der erste Gegenstand der vorliegenden Arbeit war daher die Überprüfung des von Ramsey & Co. (2007) vorgeschlagenen Verfahrens zur Bestimmung von Innovationen im Freiland.*

Zu diesem Zweck wurde der Vergleich der Verhaltensrepertoires auf eine Population Orangutans des Zoos Zürich ausgedehnt. Zuerst erstellten wir ein Inventar der Verhaltensweisen der Gruppe; vier der zehn mutmasslichen Innovationen aus dem Feld die alle auch unter den vorherrschenden Bedingungen im Zoo hätten beobachtet werden können wurden aufgrund ihrer Abwesenheit als Innovationen verifiziert. Als zweites stellten wir die relevanten Bedingungen experimentell her, um den Innovationsstatus fünf weiterer mutmasslicher Innovationen freilebender Orangutans zu evaluieren. Vier davon konnten als Innovationen bestätigt werden und eine weitere als Modifikation einer Innovation. Die Qualifikation basierte in einem Fall auf Abwesenheit, in den anderen Fällen auf der verstrichenen Zeit, bis zu der die verschiedenen Individuen eine Verhaltensweise erstmals zeigten, im Vergleich mit dem Auftreten schon bekannter Verhaltensweisen. 53 % (8 von 15)

der hier untersuchten mutmasslichen Innovationen aus dem Freiland konnten als Innovationen bekräftigt werden, und die Zugabe von drei weiteren Fällen von möglichen Innovationen und dem einem Fall der Modifikation einer Innovation würde diese Zahl gar auf 80 % ansteigen lassen. Daraus folgern wir, dass das Verfahren von Ramsey & Co. (2007) zur Bestimmung von Innovationen im Freiland auch tatsächlich geeignet ist.

Die Verifizierungsstudie zeigte auch ein unerwartetes Resultat, nämlich eine bemerkenswert hohe Innovationsrate der Zoo-Orangutans. Diese Erkenntnis konnte dazu verwendet werden, um Licht ins Dunkle einer der verblüffendsten Beobachtungen über Kultur bei Menschenaffen zu bringen: die einzigartigen kulturellen Errungenschaften des Menschen, gegenüber der bescheidenen Kultur von Schimpanse oder Orangutan. Es wird argumentiert, dass diese Diskrepanz dadurch entstand, dass nur der Mensch kumulative Weiterentwicklung von Techniken betreiben kann. Kulturelle Elemente und Produkte des Menschen ändern sich im Laufe der Zeit, wobei verschiedene Individuen diese kumulativ in Richtung höherer Komplexität modifizieren, was als kumulative kulturelle Evolution oder als „Ratchet Effekt“ bezeichnet wurde (Tomasello & Co., 1993). *Der zweite Gegenstand dieser Dissertation war daher die Fähigkeit für kumulative Weiterentwicklung von Techniken bei Zoo-Orangutans zu evaluieren.*

Es gibt bisher keine Hinweise für kumulative Weiterentwicklung von Techniken bei Orangutans, hingegen von Schimpansen gibt es ein paar Hinweise aus dem Freiland. Kürzlich wurde aber bei Zoo-Schimpansen festgestellt, dass sie eher konservativ sind und an der ihnen bekannten Technik festhalten, selbst nachdem man ihnen effektivere Alternativen vorgezeigt hat. Flexibilität im Problemlösen, im Sinne dass Individuen auch nach dem Ausüben einer ersten Lösungsmöglichkeit weiterhin Bereitschaft zeigen, neue Lösungswege zu akquirieren, sei es durch eigene Innovation oder durch soziales Lernen von einem anderen Individuum in der Gruppe, ist eine zwingende Grundvoraussetzung für kumulative Weiterentwicklung von Techniken und schliesslich auch für kumulative Kultur. Wir untersuchten, ob Zoo-Orangutans, anders als Zoo-Schimpansen, solche Flexibilität im Problemlösen zeigen würden. Dazu schränkten wir die Bedingungen in einem Experiment zweimal ein, indem zuvor bevorzugte Techniken zur Lösung des Problems verunmöglicht wurden.

Unsere Orangutans zeigten tatsächlich grosse Flexibilität; sie gaben bevorzugte aber verunmöglichte Techniken auf und wechselten zu anderen Techniken, welche nicht nur funktional sondern auch effizient waren. Wenn neue Bedingungen auftreten, kann sich Flexibilität ultimativ auch in Innovationen ausdrücken, die kumulativ auf bisherigen

Lösungswegen aufbauen. Und in der Tat erfanden unsere Versuchstiere zwei Techniken, die kumulative Weiterentwicklungen von früheren Techniken darstellten.

Nachdem wir also zeigen konnten, dass Zoo-Orangutans die Fähigkeit für kumulative Weiterentwicklung von Techniken besitzen wenn die Bedingungen der Aufgabe erschwert wurden, untersuchten wir weiter, ob sie das auch bei konstanten Bedingungen noch tun. Wir stellten aber fest, dass das Auftreten von neuen Notwendigkeiten durch das Vereiteln bisheriger Lösungen eine Voraussetzung für die kumulative Weiterentwicklung von Techniken war. Kein Tier war unter sich nicht ändernden Bedingungen in der Lage, eine vorgegebene kumulative Technik zu lernen. Erst nachdem bisherige Lösungen zur Aufgabe vereitelt wurden schaffte es schliesslich ein Tier, die kumulative Technik zu erlernen.

Zusammengefasst zeigten unsere Experimente, dass Zoo-Orangutans nicht nur viel innovativer sind als ihre wilden Artgenossen, sondern auch zu kumulativen Innovationen fähig sind, Innovationen also, welche kumulative Weiterentwicklung auf bisherigen Techniken darstellen. Wir fanden weiter, dass das Auftreten von neuen Notwendigkeiten, kreiert durch das Vereiteln bisheriger Lösungen, ein notwendiger Faktor war für die kumulative Weiterentwicklung von Techniken. Dies deutet darauf hin, dass das Fehlen von kumulativer Kultur bei Orangutans im Freiland nicht in mangelnder Flexibilität gründet wenn bisherige Lösungen nicht mehr taugen, und auch nicht mit einer generellen Unfähigkeit zu kumulativer Weiterentwicklung bestehender Techniken erklärt werden kann. Vielmehr tritt der dafür kritische Faktor, das Auftreten neuer Notwendigkeiten durch das Wegfallen der bisherigen Lösung(en), im Freiland kaum je in dieser Form auf, hingegen spielen andere Faktoren eine Rolle, die für die Objektmanipulation hinderlich sind und auch zu einer geringeren Neigung zu Innovationen bei freilebenden Orangutans führen.

Summary

Striking geographic variation in behavior provides evidence for culture in our closest living relatives, chimpanzees and orangutans. Culture consists of multiple innovations that have been socially transmitted within a population. Hence, innovation and social learning are the raw materials for traditions and culture. But compared to social learning mechanisms and how they allow novel learned behaviors to be transmitted in a group, the very occurrence of such novel learned behaviors, innovations, have received far less scrutiny, largely because of difficulties assessing the innovation status of behaviors. A recent attempt to recognize innovations in natural populations suggested by Ramsey et al. (2007) was inspired by techniques to infer culture from geographic patterns in behavior. The basic idea is that since cultural transmission of innovation results in geographically different behavioral repertoires among populations of the same species that cannot be explained by genetic or ecological factors alone, innovation status can be inferred to such behavior patterns. The approach of Ramsey et al. (2007) has been applied by van Schaik et al. (2006) to generate a list of 43 potential innovations in wild orangutans. Thus, *the first objective was to validate that procedure for recognizing innovations.*

We did so by extending the comparison to a captive population of orangutans from Zoo Zurich. First, we created an inventory of the behavioral repertoire in the zoo populations; four of ten putative innovations recognized in the field and potentially observable in our captive population were verified as innovations based on their absence despite appropriate conditions. Second, we experimentally produced relevant conditions to evaluate the status of another five putative innovations from the wild. Four qualified as innovations and one as modification, based in one case on absence and in the remaining others on latencies of first occurrence across individuals relative to known behaviors. Because 53 % (8 of 15) of those putative innovations recognized in the field we investigated in this analysis were confirmed as innovations, and adding another three assigned possible innovation status and one modification would raise this figure to 80 %, we conclude that our findings largely confirm the assessments of innovations by van Schaik et al. (2006) and hence the geographic method for detecting innovations in the wild (Ramsey et al., 2007) is valid.

One unexpected finding of this validation study was the remarkably high rate of innovation among captive orangutans. This finding could be used to shed light on one of the most striking findings of culture studies on wild great apes, namely the vast discrepancy in

cultural accomplishments between human and great apes. This discrepancy has been argued to be due to cumulative build-up of techniques being a human uniqueness. Human cultural variants tend to change over time, and many seem to accumulate modifications made by different individuals over time in the direction of greater complexity, which has been described as cumulative cultural evolution or the ratchet effect (Tomasello et al., 1993). *The second objective of this thesis was therefore to evaluate captive orangutans' ability for cumulative build-up of techniques.*

So far there has been no indication of cumulative build-up of techniques (ratcheting) in wild orangutans, unlike in chimpanzees where there are some possible examples from the field. But captive chimpanzees were recently found to be rather conservative, sticking to the technique they had mastered, even after more effective alternatives were demonstrated. Behavioral flexibility in problem solving, in the sense of individuals' continued interest in and acquisition of new solutions to a task, through either innovation or social learning, after already having mastered a previous solution, is a vital prerequisite for cumulative build-up of techniques, and eventually for cumulative culture. We investigated whether captive orangutans would, in contrast to chimpanzees, show the behavioral flexibility necessary for cumulative build-up of techniques. We restricted the condition of a task twice, thereby making previously preferred techniques impossible.

Orangutans indeed showed high behavioral flexibility, abandoning preferred techniques that had been made non-functional, and switching to different, functional and efficient techniques. As novel conditions arise, behavioral flexibility may ultimately be expressed by innovations that are solutions cumulatively building up on previous ones. Indeed, subjects eventually came up with two solutions that cumulatively built up on earlier ones.

After having demonstrated that captive orangutans were capable of cumulative build-up on previous techniques as conditions of the task changed, we evaluated whether cumulative build-up of techniques was also possible under constant conditions. But we found that novel exigencies were indeed required for ratcheting. None of the subjects was able to learn a cumulatively built-up technique under unchanging conditions, only after previous solutions to the task had been made ineffective, one individual finally succeeded to learn the ratcheted technique.

In conclusion our results showed that captive orangutans are not only more innovative than their wild conspecifics, but captive orangutans are also capable to make ratcheted innovations (i.e. innovations that are solutions cumulatively building up on previous

solutions). Novel exigencies inhibiting previous solutions to the task were found to be a factor stringently required for such cumulative build-up of techniques. This suggests that the lack of cumulative culture in wild orangutans is not due to a lack of behavioral flexibility when existing solutions to tasks become impossible, or an inability to cumulatively build up on previous solutions. Rather, this critical factor of novel exigencies inhibiting previous feeding techniques is mostly missing in the wild, while at the same time other factors are in place that are impeding object manipulation and also cause the low innovation tendency in wild orangutans.

Chapter 1

General Introduction

Culture and tradition

People in similar environments vary behaviorally in ways that are unlikely to be the result of genetic differences (Alvard, 2003). Much behavioral diversity in humans cannot be explained by genetic or ecological differences, but has been attributed to (the concept of) culture (Guglielmino et al., 1995; Henrich & Boyd, 1998). When people think of culture, what likely comes to mind first will be art museums, opera and play houses, followed maybe by movie theaters, churches, national holidays and many cherished traditions like the Scots' kilt or the Swiss' alphorn. But human culture also contains language and basic subsistence techniques, "simpler" things like people in Switzerland using knife and fork for eating while people in China are using chopsticks. Most importantly, culture affects how things are done in a certain society, including many little things of everyday life, or what values are believed in. Culture thus seems to describe typical human characteristics. It therefore does not come as surprise that culture has long been considered a hallmark of humanity – indeed, culture was considered human by definition (reviewed in McGrew, 1998).

Because culture consists of socially transmitted innovations, it is more dynamic than behavioral systems based on genetic traits subject to some degree of developmental plasticity. Thus, human cultural variants change over time, and many cultures seem to accumulate modifications made by different individuals over time in the direction of greater complexity, which has been described as cumulative cultural evolution or the ratchet effect (Tomasello et al., 1993a). Animals, on the other hand, were then accorded traditions; a tradition representing a behavioral practice that is shared by two or more individuals in a social unit, which persists over time and is acquired by new individuals in part through socially aided learning (Fragaszy, 2003; Frigaszy & Perry, 2003). There are authors that equate culture and tradition, using the terms interchangeably, whereas others do make distinctions between them of various kinds, usually requiring additional criteria to classify a phenomenon as cultural (as noticed by Whiten & van Schaik, 2007).

There is an array of more or less subtly different definitions of culture around (e.g. Rendell & Whitehead, 2001 for an overview), rather than one consensual that is commonly referred to nowadays (McGrew, 2004). But there is consensus that culture is learned from other group members; neither is it transmitted genetically, nor is it reliably induced by particular environmental conditions (Boesch, 2003). Such understanding of culture no longer automatically excludes all non-human species. Whiten and van Schaik (2007) define culture as the possession of multiple traditions, and cultural variants as innovations that have become common in a population through social learning. I also conceive culture to consist of multiple innovations that have been socially transmitted within a population. This can then result in geographically varying behavioral repertoires among populations of the same species, which arose through innovation (Ramsey et al., 2007) and cannot be accounted for by environmental and genetic differences. Such geographic variation can of course be detected more easily in the field than can the processes of social learning or innovation.

Culture in non-human species?

Striking behavioral variations from one site to another have been detected in our closest living relatives, chimpanzees (Boesch, 1996; Whiten et al., 1999), orangutans (van Schaik et al., 2003), bonobos (Hohmann & Fruth, 2003) and gorillas (Cipolletta et al., 2007). Culture could be ascribed at least to chimpanzees (Boesch, 1996; Whiten et al., 1999) and orangutans (van Schaik et al., 2003), after ecological explanations could be discounted. At the same time, there was experimental demonstration of the requisite capacity for social learning (Whiten, 2005). The above claims for culture were based on extensive fieldwork and generated excitement on the one hand (Byrne, 2007), but also hostile reactions on the other hand, as Whiten et al. (2003) stated. Both reactions need not surprise, because for so long culture has been considered a unique human hallmark and culture was even per definition human (reviewed in McGrew, 1998). By now it is widely accepted that culture is no longer exclusively limited to our own species. Convincing reports of cultural variants have come from other animal species than great apes too, e.g. dolphins and whales (Krutzen et al., 2005; Rendell & Whitehead, 2001) and capuchin monkeys (Fragaszy et al., 2004; Perry et al., 2003). But in comparison to most reports in non-ape species where only one or a few cultural behaviors have been identified, the number of cultural variants identified was much larger in chimpanzees (39), including tool usage, grooming and courtship behaviors (Whiten et al.,

2001; Whiten et al., 1999), and in orangutans (26) (van Schaik et al., 2003; van Schaik et al., 2006).

One example of chimpanzee cultures can serve to illustrate the interplay between ecological and cultural forces: ant dipping for army ants. At Bossou (Guinea, West Africa) chimpanzees prey on several species of army ants, applying two ant-dipping techniques: direct mouthing of the tool, removing the ants with the teeth or lips; and swiping the length of the tool to gather the ants in the hand before rapid transfer to the mouth, known as the pull-through technique (Humle & Matsuzawa, 2002). Initially, there was indication for a strong influence of prey (*Dorylus* spp.) species and characteristics on tool length and technique employed by the chimpanzees (Humle & Matsuzawa, 2002). Thus, ecological differences seemed to be responsible for differences in techniques and length of tools used, both within and between communities, which was grist to the mills of the critics of the geographic method for implying culture. However, more recent findings changed the balance of power in favor of a cultural explanation. It is undisputed that some of the geographic variation reflects environmental influences driven by the prey species characteristics, as species with aggressive workers that can cause painful bites are gathered with a long tool by the "pull-through" technique, whereas species with less aggressive workers are gathered with short tools and by the "direct-mouthing" technique. However, several differences in army-ant-eating between Bossou (Guinea) and Tai (Ivory Coast) were not linked to prey characteristics, which were therefore considered cultural (Schoning et al., 2008). Most recently, Humle et al. (2009) demonstrated the important role of mothers and learning opportunities in the acquisition of ant-dipping behavior by offspring. Although ant-dipping behavior does reflect to some extent local behavioral responses to prey characteristics and behavior, it is a good example of culture in chimpanzees, showing that material culture can be a product of a complex interaction between cultural processes and ecological factors (Humle et al., 2009).

Cultural variants do not only exist in the functional context of tool use, but also in artificial and arbitrary ways, e.g. stylized forms of grooming. There is the grooming hand-clasp, a symmetrical, elegant mutual gesture, with a palm-to-palm configuration that maintained the fully extended arms overhead, originally discovered in Mahale chimpanzees (McGrew & Tutin, 1978), later also observed in Kibale and Tai chimpanzees but absent in populations at Gombe, Bossou and Budongo (Whiten et al., 1999). There is also the non-palm-to-palm version in which no clasping occurs at all; instead, wrists of the two chimpanzees make only minimal contact (McGrew, 2004). In orangutans, certain sounds

(“nest smacks”) made during the last phase of nest building are common in some but absent in other places, indicating a cultural variant (van Schaik et al., 2006).

Components of culture: 1) Social transmission

As I have mentioned before, culture consists of multiple innovations that have been socially transmitted within a population. Therefore, studying culture also means studying experimentally its two components: social transmission and innovation. Great effort has been made to understand the social learning processes that underlie diffusion of novel learned behavior through a population (Box & Gibson, 1999; Heyes & Galef, 1996; Laland, 2004; Whiten et al., 2004; Galef & Giraldeau, 2001). Several forms of social learning (learning from other individuals) have been distinguished (for an overview e.g. Heyes & Galef, 1996; Whiten et al., 2004; Whiten et al., 2009a). I only want to state some of the most important ones here: *Local or stimulus enhancement* represents a very simple form of social learning, in which an individual learns nothing from its observations, but is merely drawn to a location or object due to the presence of activities of a conspecific and then engages in independent trial-and-error learning (Tomasello, 1998). By *affordance learning*, a form of emulation learning, an observer learns from its observation (of a model’s actions) about the environment, e.g. properties of objects, but not about the behavior (combination from: Tomasello, 1998; Whiten et al., 2009a). *End-state emulation* refers to copying the product of the model’s action, but re-inventing the way to get there on its own (combination from Tennie et al., 2009; Whiten et al., 2009a). By *imitation* an observer reproduces not only the result, but the model’s actual behavioral strategy toward a goal (Tomasello, 2001). *Teaching* is characterized by the active involvement of experienced individuals in facilitating learning by conspecifics (Caro & Hauser, 1992). Typically such studies of social learning processes have been dyadic, thus establishing what one observer can learn from attending to a model.

But as culture refers to the spread of behaviours through a group, this had to be accounted for in further investigations of social learning. Whiten et al. (2005) therefore recently started using a different approach, the diffusion method. In such experiments, each of two models was first trained to solve a tool use task by applying a different technique; then it was investigated if these two solutions spread differentially in the groups according to the present model, and indeed most chimpanzees adopted the solution seeded in their group, also suggesting the techniques were socially learned (Bonnie et al., 2007; Hopper et al., 2007; Whiten et al., 2005; Whiten et al., 2007). Such diffusion studies do not tell us whether certain

putative cultural variants from the wild, such as the described ant-dipping, have been socially transmitted as well; but this does demonstrate that chimpanzees have the capacity to sustain certain tool use techniques with sufficient fidelity to maintain them across cultural generations (Whiten et al., 2009b).

Components of culture: 2) Innovation

Compared to social learning mechanisms and how they allow novel learned behaviors to be transmitted in a group, the very occurrence of such novel learned behaviors, innovations, have received much less attention. As culture consists of multiple innovations that have been socially transmitted within a population, studying innovations is essential for research of culture. Innovation is the engine of cultural change (de Waal, 2001; Kummer, 1971), and repeated innovation is required for cumulative culture (Henrich & McElreath, 2003).¹

Yet, innovation had largely been neglected, until Reader and Laland's (2003) edited volume opened debate on the topic of animal innovation. They regard innovation as a learned behaviour pattern that was not previously present in the population. Thus to recognize innovations, this requires observing the first occurrence of an innovation and, for the field, long term data. A different operationalization was suggested by Ramsey et al. (2007), which takes advantage of the culture concept. Cultural transmission of innovation results in geographically different behavioral repertoires among populations of the same species. Thus, principally from such geographically different behavioral repertoires that cannot be explained by genetic or ecological factors alone, innovation status can be inferred to these behavior patterns. This geographic method requires comparative data from multiple locations instead of long-term data from a single location. This is the basic idea of the approach by Ramsey et al. (2007). More formally, they set up three criteria for innovations: First, an innovation is a non-universal behavior, i.e. it is either both present in some populations and absent in others, or it is present in all populations but then only shown by a few individuals. Their second criterion concerns the properties and the contexts of the behavior: an innovation must not reflect a particular status of the individual (e.g. age class, reproductive state, social position), because a behavioral pattern might be rare overall, but quite frequent among individuals of a certain status, such as infanticidal behavior of males having taken over a group. A behavior must also

¹ Innovation might also be important to endangered species that are forced to adjust to altered or impoverished environments (Greenberg & Mettke-Hofman, 2001; Sol, 2003). Innovative species would be expected to be at less risk of extinction than less innovative ones. However, current comparative data does not support this idea (Lefebvre et al., 2004).

not be rare because the context in which it occurs arises only rarely. The third criterion, following Reader and Laland (2003), requires that the behavior be performed at least twice to qualify as an innovation, in order to distinguish innovations from accidental behavior. Ramsey et al. (2007) suggested that this procedure allows us to identify innovations.

The approach of Ramsey et al. (2007) has been applied by van Schaik et al. (2006) to a population of wild Bornean orangutans (*Pongo pygmaeus*) at Tuanan, who compared their data with results reported for six other sites. Using this procedure they generated a list of 43 potential innovations in orangutans, henceforth referred to as the *preliminary list*. However, as both Ramsey et al. (2007) and van Schaik et al. (2006) emphasized, this result is preliminary and needs to be validated, because some of the absences of behaviors could be artificial, rather than due to ignorance on the part of the animals, because observers in one place could have failed to recognize particular behaviors or because the conditions under which they can be performed arise only rarely. This uncertainty can be reduced by comparison with an additional population, where conditions are appropriate for investigated behaviors to occur spontaneously and observers could not miss it, or where we can create the required conditions experimentally, which can best be done in captivity.

If we assume for now that the classification of innovations from the preliminary list will be supported experimentally, we then can be quite confident that the procedure suggested by Ramsey et al. (2007) provides us with a new tool to recognize innovations in the wild, and thus with an alternative to the requirement of observing the first occurrence of novel learned behaviors. This could possibly boost further research on innovation, as reliable results can be expected to be obtained faster. Furthermore, and more important in the present context, validation of innovations in orangutans would also support the claims made for culture in the species. Yet the role of social learning in the cultures of orangutans (van Schaik et al., 2003) and chimpanzees (Whiten et al., 1999) of course remains implied rather than observed. However, the main alternative to such geographically variable behavioral variants representing socially transmitted innovations would be that they were not innovations in the first place, but represent behaviors that develop reliably under certain environmental conditions or the given genetic composition of the population (Laland & Hoppitt, 2003; van Schaik, 2009). Thus, if we select some of these behaviors to experimentally investigate their innovation status, finding that they are indeed innovations, this supports that in the wild they are innovations which were then socially transmitted, resulting in geographically different behavioral repertoires among populations of the same species that then are cultures.

Cumulative culture: one cause of human uniqueness?

If both humans and great apes have culture, what then causes the big gap that indisputably exists, allowing only humans to ride cars or fly into space? Humans use behavioral strategies and technologies that are definitely much more complex than those of great apes. This vast discrepancy in technological accomplishments between human and great apes is doubtless due to cumulative culture. Human cultural variants change over time, and many seem to accumulate modifications made by different individuals over time in the direction of greater complexity, which has been described as cumulative cultural evolution or the ratchet effect (Tomasello et al., 1993a). By greater complexity, Boesch and Tomasello (1998) meant that a wider range of functions is encompassed. Some have argued then that cumulative culture is indeed uniquely human (Henrich & McElreath, 2003; Tomasello, 2001; Tomasello, 1999b; Tomasello et al., 1993a). However, the increasing complexity of hominid culture, first noticeable as the Acheulian lithic industry superseded Oldowan ones, was very slow and gradual until much more recent times (Whiten et al., 2003). McGrew (2004) pointed out that there are at least two major problems with the “space shuttle” argument, because by these criteria many human societies nowadays still lack cumulative culture, as many of them are non-literate, and because even in modern industrialized cultures with near-universal literacy, technology and higher education, there are only few among us that ever invented or composed anything, so most of us would fail on the “space shuttle” criterion. Thus we should also think of products of cumulative culture that are less fancy than a space shuttle. Taking all these considerations into account, this leads to the question whether such cumulative build-up of techniques could not also be present in great apes, expressed in of course relatively simple forms.

There are several authors who think that cumulative build-up of techniques and cumulative culture is not necessarily limited to humans (e.g. Boesch, 2003; Boyd & Richerson, 1996; Hunt & Gray, 2003; Whiten et al., 2003). New Caledonian crows from various parts of the island cut leaves to different designs of distinct step shapes, ranging from ones with a single step to others with four steps tools; such a multi-step tool is conspicuously wider and tapered, making it both stiff at the base but also pointed at the working end, both features combined likely facilitating controlled manipulation and reducing buckling when the tool is held near the base and inserted into sites to search for prey (Hunt & Gray, 2003). Hunt and Gray (2003) suggested that this diversification of *Pandanus* tool designs they found in New Caledonian crows are the first indication that a non-human species may have evolved

techniques that built up on previous versions and were passed on through social learning. However, some doubt about this interpretation has arisen because naive captive crows of this species have been shown to spontaneously cut and use *Pandanus* tools on first contact with leaves of the plant, although these did not resemble the distinct stepped tools produced in the wild (Kenward et al., 2005).

Whiten et al. (2003) and Boesch (2003) argued that there are examples which show that chimpanzees have some modest power for cumulative build-up of techniques. For instance, many chimpanzee populations crack nuts by hitting them directly with the hand against tree trunks or are using stone hammers on stone anvils to break nuts that are harder and smaller. But in one population they use an additional stone to increase the stability of the stone or to level the stone anvil (Matsuzawa & Yamakoshi, 1996). The modification to prop up the anvil with a small stone represents a cumulative build-up on the customary anvil use already in place; however it has not been observed to really spread in the population and therefore does not meet this criterion of cumulative culture (Whiten et al., 2003). Thus, it remains to be investigated whether there is cumulative build-up of techniques and cumulative culture in non-human species.

Aims, organization and study species of thesis:

Culture, following Whiten and van Schaik (2007), consists of multiple innovations that have been socially transmitted within a population. Thus both innovation and social learning are the preconditions for culture. This of course also holds true for cumulative culture; but additionally it has been proposed that only certain types of social learning allow accumulation (Tennie et al., 2009; Tomasello et al., 1993a). Tomasello et al. (1993a) state that cumulative cultural evolution critically depends on innovation and imitation, and perhaps teaching, and that it can not arise through other forms of social learning such as emulation, nor by any form of individual learning alone.

However, Mithen (1999) argued that in early hominid culture, Acheulian artifacts could be produced only through a complex sequence of actions that must have been transmitted culturally by a process no less sophisticated than imitation, while at this stage there was only minimal accumulation and Acheulian artifacts showed no considerable change over many millennia. He concluded that imitation has existed without evidence of significant cumulative build-up of techniques. Thus, the emergence of cumulative culture is not caused by imitation, which was available (at a high level of sophistication) much earlier (Whiten et

al., 2003). Furthermore, the capacity for imitation in chimpanzees has been demonstrated more adequately since then (Hopper et al., 2007; Horner & Whiten, 2005; Whiten, 2005; Whiten et al., 2003; Whiten et al., 2009a). It has been proposed that perhaps “the really significant change during hominid evolution was not so much in social learning mechanisms themselves, but rather in the kinds of behavior patterns that were invented” (Whiten et al., 2003). For this reason, in my studies on cumulative culture I put my focus on innovations, while largely neglecting whether and how these are then socially transmitted in the group.

The number of cultural variants that have been identified is largest in chimpanzees (Whiten et al., 2001; Whiten et al., 1999) and orangutans (van Schaik et al., 2003; van Schaik et al., 2006). The large number of cultural variants in orangutans is interesting, or actually a bit surprising, given that orangutans are a semi-solitary species living in fission-fusion societies (Delgado & van Schaik, 2000), while culture and thus social learning obviously require some degree of gregariousness (van Schaik et al., 1999). Immature orangutans spend several years in close association with the mother, even after they begin to move independently at around age three (van Noordwijk et al., 2009; van Noordwijk & van Schaik, 2005), their slow life history (Wich et al., 2004) giving them many opportunities to learn vertically by simple forms of social learning such as stimulus enhancement. Diets of immature Bornean orangutans have been found to be essentially identical to their mothers', while not all mothers had the same diet, suggesting vertical transmission of diet by (stimulus or local) enhancement (Jaeggi et al., 2010). Great ape populations vary widely in the proportion of time animals spend together in tolerant proximity, even within chimpanzee and orangutan populations, but on average orangutans are less gregarious than chimpanzees (Whiten & van Schaik, 2007). It has been shown for both chimpanzees and orangutans that inter-population variation of time spent in tolerant proximity is positively correlated with the number of cognitively complex cultural variants, and that the number of such variants is larger in chimpanzees (Whiten & van Schaik, 2007).

Nevertheless, orangutans also have fancy cultural variants, requiring higher forms of social transmission than stimulus enhancement; one example is the technique used to extract seeds from the fruits of the *Neesia* tree. This tree produces woody, five-angled capsules, which are filled with brown seeds the size of lima beans. The fruit's husk is very tough, but when the seeds are ripe, the husk begins to crack open; as the cracks gradually widen, they are exposing neat rows of seeds, which are shielded by a mass of razor-sharp needles that fill the husk. In order to avoid the painful needles, the orangutans in Suaq on Sumatra produce a tool by stripping the bark off short, straight twigs. They then hold this tool with their mouth and

insert it into a crack of the fruit. By moving the tool up and down inside the crack, the ape detaches the seeds without getting injured; afterwards it can drop the seeds straight into its mouth (van Schaik, 2006; van Schaik & Knott, 2001).

So far there has been no indication for cumulative build-up of techniques in orangutans, unlike in chimpanzees where there are some possible examples. Nevertheless, it is promising to investigate the capability for cumulative build-up of techniques in both chimpanzees and orangutans. Most researchers are studying culture in chimpanzees. However, since the only formal study of innovations in great apes had been on orangutans (van Schaik et al., 2006), I chose to do my studies with orangutans. My overall goals were to recognize innovations and the orangutans' ability for cumulative build-up of techniques. Specifically, I had the following two goals:

1) The first objective was to validate the procedure suggested by Ramsey et al. (2007) for recognizing innovations. I did so by using a captive population from Zoo Zurich to test the preliminary list of 43 potential innovations that van Schaik et al. (2006) generated for orangutans by applying that procedure. First, I examined which of those putative innovations from the wild that were potentially observable in the zoo population occurred spontaneously. Those behaviors that are on the list but absent in the zoo population would then be supported as innovations. Second, I selected those potential innovations from the preliminary list for which we could feasibly create the required physical conditions needed for their occurrence. Those that could not be elicited or that would be shown following a period of clear attention to the stimuli by a first animal but afterwards repeatedly by that individual would qualify as innovations. Within the same context, e.g. a specific experiment, I expected innovative behaviors to be distinguishable from known behaviors based on longer latencies between exposure to the relevant stimuli and first occurrence of the behavior, provided I could demonstrate that the longer latency is not due to lack of interest on the part of the animal. This validation of innovations from the preliminary list is treated in chapter 2.

2) The second objective was to evaluate captive orangutans' ability for cumulative build-up of techniques. As mentioned earlier, so far there has been no indication for cumulative build-up of techniques in wild or captive orangutans. Cumulative culture requires from a species (1) the ability to produce superior innovations in the first place, (2) the ability to recognize alternatives as superior and thus flexibly switch to them, and (3) the ability to

faithfully acquire novel alternatives through social learning. I will concentrate on the first two requirements.

In chapter 3, I investigate orangutans' behavioral flexibility, i.e. their tendency to switch to other techniques when this is advantageous or necessary. I use and define behavioral flexibility as individuals' continued interest in and acquisition of new solutions to a task, through either innovation or social learning, after already having mastered a previous solution. This behavioral flexibility is a vital precondition for cumulative build-up of techniques, and eventually for cumulative culture. Furthermore, orangutans' ability to show cumulative build-up of techniques as conditions are changing is investigated in chapter 3.

In chapter 4, I evaluate whether cumulative build-up of techniques is possible under constant conditions or strictly depends on novel exigencies. Tomasello et al. (1993a) recognize cumulative cultural evolution when members of a cultural group acquire a practice begun by others relatively faithfully, and then modify it as needed to deal with novel exigencies, which is again acquired by others. Novel exigencies, or changing conditions, are thus part of their description of cumulative culture, suggesting that without such novel exigencies there would be no cumulative build-up of techniques. A more demanding level of cumulative culture could potentially be based on cumulative change under constant conditions, which is therefore addressed in chapter 4.

Chapters 2 to 4 constitute the core of this thesis and each of these chapters stands on its own. In chapter 5, I discuss some of the results and implications of ratcheting for the understanding of human evolution.

Chapter 2

An evaluation of the geographic method for recognizing innovations in nature, using zoo orangutans

Innovation and social learning are the raw materials for traditions and culture. Of these two, innovation has received far less scrutiny, largely due to difficulties of assessing the innovation status of behaviors. A recent attempt proposes to recognize innovations in natural populations based on assessment of the behavior's properties and its geographic and local prevalence. Here we examine the validity of this approach and the list of 43 potential innovations it generated for wild orangutans by extending the comparison to zoo orangutans. First, we created an inventory of the behavioral repertoire in the zoo population. Four of ten putative innovations recognized in the field and potentially present in captivity did not occur despite appropriate conditions, suggesting they are indeed innovations. Second, we experimentally produced relevant conditions to evaluate whether another five potential innovations could be elicited. Based on their continued absence or on their latencies relative to known behaviors, four of them could be assessed as innovations and one as a modification. Because 53 % of relevant innovations recognized in the field could be confirmed in this analysis, and another 27 % assigned possible innovation status, we conclude that the geographic method for detecting innovation in the wild is valid. However, the experiments also yielded up to 13 additional innovations, suggesting that zoo orangutans are far more innovative than wild ones. We discuss the implications of this latter finding with regard to limiting factors for the expansion of cultural repertoires in wild orangutans.

Introduction

Animal cultures and traditions (Fragaszy & Perry, 2003) refer to learned behaviors that are maintained in a population through socially mediated learning. Ever since the first reports of animal traditions appeared (Kawai, 1965), great effort has been made to understand the social learning processes that underlie their diffusion and maintenance (Box & Gibson, 1999; e.g. Heyes & Galef, 1996; Laland, 2004; Whiten et al., 2004; Caldwell & Whiten, 2006; Galef & Giraldeau, 2001). In contrast, although innovation is a key component of most definitions of culture (McGrew, 1998; Rendell & Whitehead, 2001) and the ultimate source of all cultural change (de Waal, 2001; Kummer, 1971), it was largely ignored until Reader and Laland's (2003) edited volume recently rekindled interest in it (Boogert et al., 2008; Bouchard et al., 2007; Day et al., 2003; Kendal et al., 2005; Lefebvre et al., 2004; e.g. Reader & Laland, 2002; Sol et al., 2005; Whiten & van Schaik, 2007).

This neglect of innovation can be explained at least partly by conceptual difficulties. First, innovation is always relative to some standard. The most commonly used definitions (Kummer & Goodall, 1985; Reader & Laland, 2003) regard an innovation as a learned behavior pattern that was not previously present in the population. However, this inevitably means that what is considered an innovation depends on the size of the population and the duration of study. Thus, one can recognize a gradient from weak to strong innovation to invention (cf. Ramsey et al., 2007), although there are no objective criteria to demarcate discrete regions on this gradient. Experimentally, the degree of innovativeness can be operationalized by estimating the average latency among a set of individuals until the first occurrence of the innovative behavior in the appropriate conditions, but this criterion cannot be applied in field conditions. Second, a related problem is that of delineation: when is a behavioral action a new innovation rather than a slight variation or modification of a routine action or an existing innovation? Ramsey et al. (2007) suggested various criteria, dependent on the extent to which their functional use by individuals is different, but in practice there may often be insufficient data to apply these criteria. Third, and most pressing, is the problem of operationally recognizing innovation. It is rarely practicable to use the first occurrence in a population as the operational criterion, because this requires very long-term study (but see Nishida et al., 2009). An approach that may be more feasible for use in natural populations is to focus on specific characteristics of the innovative behaviors, such as an incomplete geographic distribution or low prevalence within a population.

These considerations led Ramsey et al. (2007) to suggest a new approach to assessing innovations in nature. Basically, an innovation is a behavior shown in some populations or individuals, but not in others, where its absence is due to a lack of knowledge rather than different physical or social conditions or different genetic backgrounds. More precisely they set up three criteria for innovations: First, an innovation is a non-universal behavior, i.e. it is either present in some populations and absent in others, or it is present in all populations but then only shown by a few individuals. Their second criterion concerns the properties and the contexts of the behavior: an innovation must not reflect a particular status of the individual (e.g. age class, reproductive state, social position), because a behavioral pattern might be rare overall, but quite frequent among individuals of a certain status, such as infanticidal behavior of males having taken over a group. A behavior must also not be rare because the context in which it occurs arises only rarely. The third criterion, following Reader and Laland (2003), requires that the behavior be performed at least twice to qualify as an innovation, in order to distinguish innovations from accidental behavior. Ramsey et al. (2007) suggested that this procedure allows us to identify innovations.

Applying the approach of Ramsey et al. (2007), van Schaik et al. (2006) compared the data collected in an intensive field study of Bornean orangutans (*Pongo pygmaeus*) with results reported for six other sites, four on Bornean and two on Sumatran orangutans (*Pongo abelii*). Using this procedure they generated a list of 43 potential innovations in orangutans, henceforth referred to as the *preliminary list*. However, as both Ramsey et al. (2007) and van Schaik et al. (2006) emphasized, this result needs to be validated, because some of the absences of behaviors could be artificial (rather than due to ignorance on the part of the animals), because observers in one place could have failed to recognize particular behaviors or because the conditions under which they can be performed arise only rarely. This uncertainty can be reduced by comparison with an additional population, where conditions are appropriate for investigated behaviors to occur spontaneously and observers could not miss it, or where we can create the required conditions experimentally, which can best be done in captivity.

The aim of this study, therefore, is to validate the geographic method for recognizing innovations, using a captive population to test the preliminary list in two ways. First, the captive population adds another population to the comparison, which is likely to be independent of the others investigated in the field so far. Because the founders of the zoo population were almost certainly captured as infants, even if they hailed from a population where some of these 43 innovations were later observed, the chances they could have already

learned any of them are negligible. Thus, the zoo population qualifies to a large extent as an independent new data point. We therefore attempted to validate the innovation status of the putative innovations from the preliminary list by examining which of those that were potentially observable in the zoo population occurred spontaneously. This comparison would indicate that behavior patterns that are on the list but absent in the zoo population are innovations.

Second, and more importantly, we can perform experiments to reveal whether the absence of a particular putative innovation is due to actual lack of knowledge of how to perform it, or rather due to unsuitable physical or social conditions. We therefore selected those potential innovations from the preliminary list for which we could feasibly create the required physical conditions in captivity needed for their occurrence. We then recorded which of those behaviors actually occurred under these conditions and if so, after which latencies, investigating their innovation status by considering the following three possible outcomes. First, all or most animals would immediately respond to the new condition and stimuli by performing the particular behavior from the preliminary list (or any other behavior from that list). In that case, this behavior would not represent an innovation, but rather a common response to the new condition, and its absence in some populations in the wild is likely to be due to the absence of the proper eliciting conditions, or perhaps recording error. For example, Morand-Ferron et al. (2004) could easily elicit dunking of food pieces in an experiment with wild-caught Carib grackles, *Quiscalus lugubris*, despite its absence in field observations, by offering different social conditions. Second, the behavior could not be elicited within a reasonable period of time. This suggests that it is not part of the zoo population's behavioral repertoire and thus an innovation in the wild. (We assume that a lack of time to invent it cannot account for its absences in some wild populations.) Third, following a period of clear orientation and attention to the condition or stimuli, the putative innovation would be shown after some time by a first animal and subsequently be shown repeatedly by that individual. In this third case, the behavior would also qualify as an innovation, because it is not part of the individual's spontaneous behavioral repertoire. The behavior obviously remains an innovation if it is later learned by other group-members through individual or social learning.

Behaviors belonging to individuals' spontaneous repertoire are therefore likely to be distinguishable from innovative responses due to their different latencies of first occurrence. Within the same context (e.g. a specific experiment) we expect these latencies to be shorter for known behaviors relative to latencies of innovative behaviors, provided we can demonstrate that the latency between exposure to the relevant stimuli and the first occurrence

of the behavior is not due to lack of interest on the part of the animals. Furthermore, the longer this latency across individuals, the higher the degree of innovativeness we ascribe to the behavior in question.

Methods

Animals and living conditions

The study was conducted in Zurich Zoo. Subjects were neither food- nor water-deprived. The zoo population consisted of Sumatran orangutans, 7 females (ages: Lea 40; Timor 32; Selatan 24; Oceh 19; Tuah 14; Xirah 10; Cahaya 5) and 2 males (ages: Djarius 13; Dahulu 4 [excluded from experiments due to young age]). They were socially housed in one main indoor cage (480 m³), an adjacent smaller indoor cage (192 m³) and an outdoor cage (188 m³). In addition, they had the opportunity to retreat into boxes formerly used as sleeping boxes, out of sight of the visitors. The cages were equipped with tree trunks and ropes, which allowed the animals to show their natural locomotion, and a water source; an environmental enrichment program was provided almost daily.

Directly observable behaviors

Baseline data were taken to assess the population's behavioral repertoire, but also to record which of the potentially observable behaviors from the preliminary list compiled by van Schaik et al. (2006) occurred spontaneously in our captive population (Table 2.1). Behaviors recorded were those from the preliminary list, and any others compiled for the field study but not found to be innovations, the orangutan ethogram (Rijksen, 1978; see also www.aim.uzh.ch/orangutannetwork.html), and any other noteworthy behaviors (involving unusual actions or action-object combinations). In total, 95 hours of baseline observations were collected in the indoor cages of the orangutans from the zoo's visitor room, with observations made between 10 a.m. and 5 p.m. during nearly three months. At the time, the orangutans were only rarely outside, and the outside cage did not contain physical elements not found in the indoor cages. Baseline data were collected by 1-hour focal samples, systematically alternating between subjects to ensure equal coverage of all individuals. At the same time, additional data were recorded by *ad libitum* sampling (Altmann, 1974), in order to

record rarely appearing behaviors that otherwise would have been missed. Because no sounds of the orangutans were audible in the visitor's room where the baseline observations were taken, the behavioral repertoire recorded does not include vocalizations.

In order to assess the completeness of the behavioral repertoire of the population, and thus also the extent to which we sampled the directly observable behaviors from the preliminary list from the wild, a cumulative record of first appearances (a so-called collector's curve) was constructed (Tomasello & Stahl, 2004). To estimate the repertoire size of the group, we fitted an arctangent function to the cumulative number of first appearances of behaviors per observation hour. This was done by repeatedly applying tangent-transformations with different asymptotes to the data in order to linearize it, and then fitting a line with least-squares regression (DMK, 2006). The linearization with the best fit (highest R^2) was then selected. The function of the corresponding tangent transformation yields the value of the asymptote of the original, untransformed data, and this asymptote represents the estimated size of the group's behavioral repertoire.

Furthermore, we wanted to compare the behavioral repertoire of our zoo population with a wild one. We therefore also constructed a corresponding collector's curve for the wild population of orangutans from Tuanan (Borneo), using the same criteria as above. These data were solely based on focal animal sampling, whereas in the zoo we also relied on additional *ad libitum* sampling. However, because the zoo records were almost certainly largely complete, we decided to make the collectors' curves of the zoo and the wild population comparable by assuming we conducted 9 parallel focal samples in the zoo. Although some behaviors may have been missed, the resulting underestimation of the zoo curve is conservative because the zoo curve rises more steeply than the wild curve. This procedure allowed us to compare after how many observation hours 95 % of the behavioral repertoire had been observed in zoo and wild population.

Experimental elicitation of behaviors

For the experimental part we selected those behaviors from the preliminary list for which we could feasibly provide the required conditions in captivity, giving the animals the opportunity to show them. Experiments were carried out at the group's main indoor cage, where subjects could put their forearms through the grid and sounds were audible. Because we tested subjects as a group, only the first individual to show a certain new behavior would be considered its innovator. Briefly, with a blow-pipe experiment, we attempted to elicit kiss-

squeaks on leaves. Further experiments involved smearing hot sauce to make “Leaf-body scrub” and “Leaf napkin” possible; and offering syrup in a vertical tube to elicit “Branch scoop” and “Sponging”. These behaviors are listed below, along with their definition and a description of the corresponding experiment we performed:

- “Kiss squeak with leaves”: Using leaves on mouth to amplify sound. They are performed towards other orangutans, human observers, or predators to intimidate or scare them away.

Blow pipe experiment: We simulated a dangerous condition as a person with a blow tube was presented that occasionally aimed with the blow tube at the animals during seven minutes. The animals were familiar with the blow pipe in connection with medical treatment by a veterinarian and they were known to respond strongly with distress signals. But on those previous occasions no leaves had been available, whereas in these experimental conditions leaves were now provided. Data were gathered continuously by behavior sampling.

- “Leaf body scrub”: Using a leaf to clean body surface (remove dirt from the fur). In captivity, instead of leaves, wood wool or paper could also be used.

Smearing experiment: In three sessions of approximately 30 minutes on different days a zoo keeper was smearing hot sauce (a mixture of Tabasco and Sambal Oelek) with a long brush onto their body. Ideally, each individual was hit at least once in a session; however, this was not always possible. Data were collected continuously by behavior sampling.

- “Leaf napkin”: Using handful of leaves to wipe latex off the chin after eating some fruits. This behavior was also investigated in the “Smearing experiment”, but hot sauce was smeared under the subjects’ chins instead.
- “Branch scoop”: Drinking water from deep tree hole using a leafy branch.

Syrup tube experiment: In seven sessions of 90 minutes on different days, two transparent tubes that were filled with syrup to about a quarter were fixed to the outside of the cage. Animals were able to reach with their arms through the grid of the cage. The tube used was 35 cm in height and 10 cm in inner diameter, which allowed the orangutans to reach about 20 cm inside the tube with their hands (except for the male adult, who could not reach inside the tube). Sticks, twigs (with leaves), wood wool, and paper were provided. Two video cameras were directed at either one of the tubes and recorded continuously. Continuous behavior sampling was done from video tapes. At the same time this experiment was run to provide the proper conditions for “Sponging” to be possible.

- “Sponging”: Using crumpled leaves to absorb water from a tree hole, then drink the water from the leaves.

Results

Assessing the completeness of the behavioral repertoire

During 95 hours of baseline observations, 129 distinct behavior patterns were recorded using focal sampling, and an additional nine through *ad libitum* sampling, for a total of 138 (see Appendix 2.1). Figure 2.1 shows the cumulative number of recorded behaviors obtained through focal sampling as a function of observation time (a so-called collector’s curve), as well as the best fitting function.

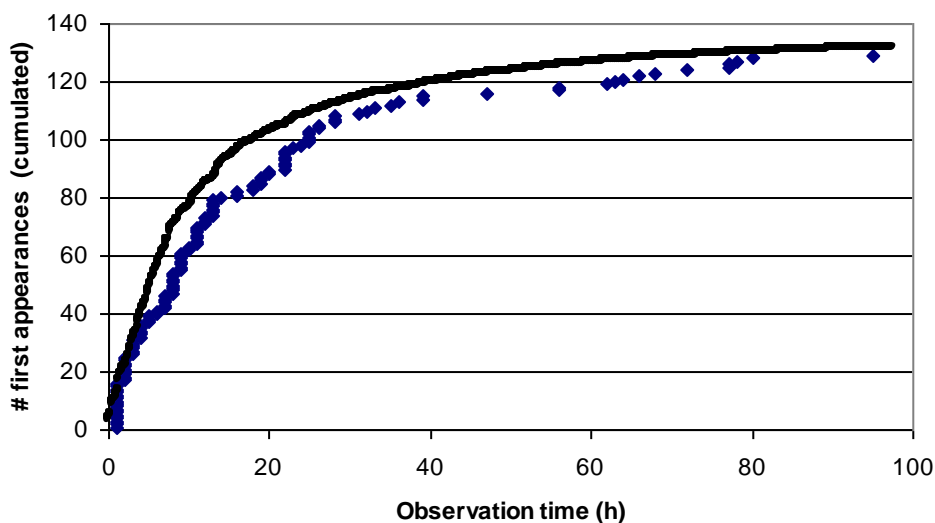


Figure 2.1: Cumulative collector’s curve: The cumulated number (freq.) of first appearances of behaviors per observation hour by focal subjects ($N = 9$). The continuous line represents the function $y = (282/\pi) \cdot \arctan(x)$, with an asymptote value of 141 yielding the best fit to the data.

After 68 hours of observation, 95% (123) of all observed behaviors had been recorded, which means that in the following 27 hours of observation, there were only 6 more behaviors that had been performed for the first time. The function that best fitted our data (Figure 2.1) $y = (282/\pi) \cdot \arctan(x)$ yielded an expected repertoire size of 141 behaviors (asymptote, $R^2 = 0.983$), only marginally exceeding the observed 138. Thus our record of the local behavioral

repertoire was largely complete, and we can be confident that behaviors that had not been recorded were not part of the population's behavioral repertoire at the time. It was therefore valid to compare the present sample with that from the wild populations and to assign behaviors from the preliminary list that could potentially be directly observable in captivity but that did not occur within our observation time as innovations.

Comparison of our captive and the natural populations: Directly observable behaviors

Table 2.1 furnishes a detailed overview of the assessments of the innovation status of all ten behaviors. Six out of ten behaviors from the preliminary list that were potentially directly observable (Table 2.1) occurred spontaneously in our captive population. Thus the remaining four that did not occur were not part of the captive population's behavioral repertoire and could therefore be validated as innovations. Those six that did occur would still represent innovations if they had originated as an individual's innovation that subsequently spread through our zoo population (in which case comparisons with other captive populations would show that they are missing in other captive populations). Here we have the same problem as field workers, and in order to be conservative, none of the behaviors on the preliminary list that had been observed were considered innovations until further investigation suggested otherwise.

The first three of the following six behaviors that did occur could possibly be earlier innovations, because they were rare and apparently did not depend on a particular status of the individuals showing them: (1) "Symmetric scratch" was shown by two different animals once each (Ti 1x, Tu 1x), despite abundant opportunities; (2) "Branch cushion" was shown at slightly higher individual rate by three of nine individuals (Sel 3x, Dj 2x, Tu 1x); and (3) "Leaf gloves" was shown by only two individuals, although all subjects had been handling nettles to eat them.

"Tree-hole tool use" was shown by 8 of 9 subjects, but is rare in the wild (see Table 2.1), leaving us in this case with an unclear innovation status. Another behavior (females rubbing genitals together) was regularly performed by 5-year old female Cahaya (6x), and thus more likely to be an example of status-dependence and not an innovation. "Autoplay with water" was shown only once (by Ca) and might be accidental or state-dependent.

In sum, four of the ten behaviors classified as innovations through the geographic approach were assessed as innovations by our zoo study. Moreover, three of the remaining six are possible innovations, but the remaining ones probably not.

Table 2.1: Potentially directly observable behaviors from the preliminary list, i.e. all behaviors from the preliminary list that could occur spontaneously in the zoo, given the captive conditions

Behavior^a	Zoo N	Tuanan	N wild pops	Conclusion
Auto-erotic tool (c10)	0	A	2/7	I
Scratch with stick (c9)	0	R	3/7	I
Twig biting (c13)	0	H	1/3	I
Branch dragging (i9)	0	A	1/6	I
Branch cushion (c27)	3	H	1/3	pI
Symmetric scratch (c12)	2	A	2/7	pI
Leaf gloves (c16)	2	E	2/5	pI
Tree-hole tool-use (c17)	8	A	1/7	I?
Female rubbing genitals together (i1)	1	R	4/7	N
Autoplay with water (i17)	1	R	1/1	acc

^a Numbers in parantheses correspond to the numbering of van Schaik et al. (2006)

The column “Zoo N” states how many of our nine subjects in Zoo Zurich have shown a certain behavior

In column “Tuanan” we present the cultural status of the same behaviors at Tuanan (van Schaik et al., 2006), categorized as follows: Absent (A), rare (R), habitual (H: several individuals), customary (C: most individuals), absent for ecological reason (E)

The column “N wild pops” states the number of wild populations where the behavior has been found (van Schaik et al., 2006), out of the number of populations where (i) ecological conditions allowed for the behavior to be shown and where (ii) its absence or presence is reported

The column “Conclusion” briefly explains which conclusion we draw for each candidate behavior concerning its innovation-status: I: Behavior was absent in zoo population and therefore is an innovation in nature. pI: Behavior was rarely shown by few individuals, not depending on an individual’s certain status, thus is a possible innovation. I?: Unclear if this is an earlier innovation that spread successfully. N: Behavior was regularly shown, but only by individual(s) of a particular status, thus it is not an innovation. acc: Behavior occurred only once, maybe accidentally, thus not qualifying as an innovation

Table 2.2: Experimental elicitation of behaviors: Lists those behaviors from the preliminary list we tried to elicit experimentally in captivity through offering the required conditions

Behavior	Zoo N	Tuanan	N wild pops	Conclusion
Kiss-squeak with leaves (c2)	0	C	3/7	I
Leaf body scrub (i2)	6	A	1/7	I (lat)*
Leaf napkin (c14)	6	A	1/7	I (lat)
Branch scoop (c19)	4	A	1/7	I (lat)
Sponging (i11)	5	A	1/7	I (lat)

One animal was not considered for experiments (Dahulu). Otherwise the same explanations as provided in Table 2.1 apply

The column “Conclusion” consists of an additional explanation: I (lat): Behavior qualifies as an innovation, based on the relative latencies of behaviors occurring within this experiment

* Modifications of previous innovations

Table 2.3: Description of the potential innovations and their modifications that occurred during experiments, stating the respective innovator, as well as the latency (hh:mm:ss) from the beginning of an experiment till the innovation occurred, sorted by experiment and latency

	Behavior	Experiment	Description	Innovator	Latency
1	Leaf napkin	Smearing	Using a leaf, wood wool or paper to wipe off the sauce of the chin	Tu	00:01:02
2	Leaf body scrub*	Smearing	Using a leaf, wood wool or paper to wipe off the sauce of the body surface	Dj	00:14:30
3	Shield	Smearing	Using a respectable amount of paper or wood wool in front of the body as a protection shield to prevent being smeared	Tu	00:20:50
4	Rub off	Smearing	Clean self from the pasted sauce by rubbing it off to the ground or a tree	Dj	00:32:25
5	Clean somebody with napkin	Smearing	Clean somebody from the pasted sauce, by wiping it off with a napkin (i.e. leaf, wood wool, or paper)	Ca	01:08:00
6	Fish	Syrup tube	Fishing in the tube with a stick to get out leaves, paper or wood wool that have accrued in the tube by previous action of subjects	Tu	00:11:17
7	Branch scoop ⁺	Syrup tube	Use a twig with leaves like a rod, so hand is only little or not at all put inside the tube; pull twig out, then suck syrup out by gently chewing the leaves	Sel	00:12:30
8	Paper squash ⁺	Syrup tube	Force paper directly with hand into the tube, pull paper out, take it in mouth and suck it out	Tu	00:39:15
9	Wood wool squash*	Syrup tube	Push wood wool down into the syrup, pull it out, take it in mouth and suck it out	Ti	00:40:15
10	Sponging	Syrup tube	Paper or wood wool chewed to a ball is dropped inside the tube; then reach with hand down into the syrup, take it out by hand, take the whole piece into the mouth, chew and suck it out (like a chewing gum)	Ca	01:44:00
11	Vegetable rod*	Syrup tube	Using vegetables like leek or chard as a rod by holding it down into the syrup, taking it out and sucking it out	Sel	02:46:00
12	Twig squash*	Syrup tube	Squash twig into the tube with hand reaching inside the tube, then pull and suck it out	Tu	04:33:00
13	Twisted paper rod (TPR)	Syrup tube	Twist paper and use it as a rod by holding one end down into the syrup, pulling it out and sucking it out	Sel	09:59:00

Omitted are “Dip stick” (Dip a bare stick into the tube, then lick the syrup from the stick; latency: 00:00:50) and “Clean with hand” (Wipe off sauce with hand; latency: 00:00:05), which also occurred during experiments, because they were not considered innovations

* Modifications of previous innovations

⁺ Picture available in Appendix 2.3

Comparison of captive and natural populations: Experimental elicitation of behaviors

In the experimental part, we selected those five behaviors from the preliminary list that could potentially be elicited in captivity through offering appropriate conditions. Four could be classified as innovations, one as modification, as shown below.

The “blow pipe” experiment was aimed at eliciting “Kiss squeaks on leaves”, but only ordinary kiss squeaks were performed, and not the *kiss squeak on leaves*, despite the availability of leaves. Thus, the latter was assessed as an innovation. In the other experiments, the remaining four appropriate behaviors were indeed elicited (see Table 2.2). This result might suggest that the majority of putative innovations described in the field were not in fact innovations, but the pattern in the latencies suggests otherwise, as elaborated below.

In addition to behaviors on the preliminary list, however, several others accrued, resulting in a total of 13 potential innovations that occurred during experimentation, nine alone in the experiment “syrup tube”. All these potential innovations are listed and described in Table 2.3, along with the identity of the innovator and the latency from the beginning of an experiment until the novel behavior occurred. Only five of 13 were shown more than one hour after the conditions had been offered, the slowest after ten hours. The majority of them occurred within one hour (often being performed by more than one subject), suggesting that they do not qualify as innovations, following the criteria of Ramsey et al (2007).

In order to determine whether these behaviors of the experiments “syrup tube” and “smearing” were part of the population’s repertoire, or whether they were invented during experimentation and thus represented innovations, we analyzed their latencies in more detail across individuals. Complete information about the latencies after which subjects successfully performed a particular behavior for the first time can be found in the Appendix 2.2. Because we do not expect an absolute threshold for latency to indicate innovations, we examined the relative latencies of behaviors within each experiment separately. For the experiments “syrup tube” and “smearing” we analyzed the latencies after which subjects used distinct techniques for the first time. Lea was excluded from the “syrup tube” experiment, because she never manipulated the syrup tubes. A Friedman Test revealed that techniques of the “syrup tube” experiment varied highly significantly in the latency until first performance among the seven individuals (Friedman Test: $\chi^2 = 17.294$, $N = 7$, $k = 6$, $p = 0.004$; techniques where the same behavior was applied to different materials were lumped for this analysis). A follow-up procedure (Sachs, 1999), where a sum of ranks difference threshold between two behaviors is calculated, showed that significant differences only arose between a pair of techniques if one

of them was “Dip stick”. The behavior “Dip stick” differed from the rest in latency of occurrence in being shown by several individuals within much shorter latencies than the other techniques, as illustrated by Figure 2.2a. “Dip stick” is thus an example of a behavior that was already part of the population’s repertoire, a suggestion confirmed by observations of tool use with sticks applied to environmental enrichment tasks during the baseline period.

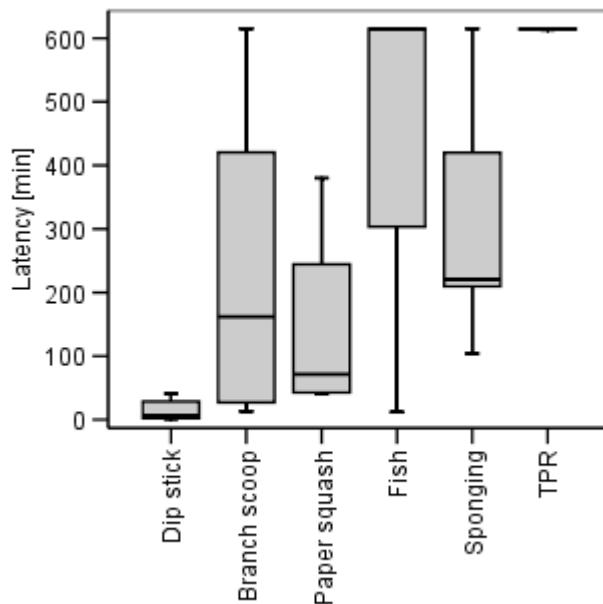


Figure 2.2a: Latencies (min) until individuals’ ($N = 7$) first successful performance of a technique in the experiment “syrup tube”. For individuals that never showed a particular behavior, the latency was set coinciding to the duration of the experiment (615 minutes). Medians and quartiles are shown.

All the other eight techniques used in the experiment “syrup tube” were not shown by most individuals after such a short latency, suggesting that they were indeed invented during the experiment, representing anything between strong innovations, weak innovations, or modifications. As stated earlier, the average latency across individuals until the first occurrence of (innovative) behaviors in the appropriate conditions may be the best way to operationalize degree of innovativeness. Thus, a rather low average latency as in “Branch Scoop” would suggest a weaker innovation, as opposed to the high latency of “Twisted paper rod” indicating a stronger innovation (Figure 2.2a).

There are three reasons to assign these eight behaviors at least some innovation status. First, individuals were engaged with the apparatus before finding a first alternative solution to “Dip stick”. Thus, we can exclude that animals simply have been inactive in the meantime and therefore all other solutions were not invented either but simply remembered later

(although this argument should equally apply to “Dip stick”). We measured subjects’ active engagement by means of the frequency of one-minute intervals they were either observing the apparatus or an individual manipulating it from close distance (less than 20 cm), or touching the tube with their hands, manipulating it unsuccessfully, or using the technique “Dip stick”.

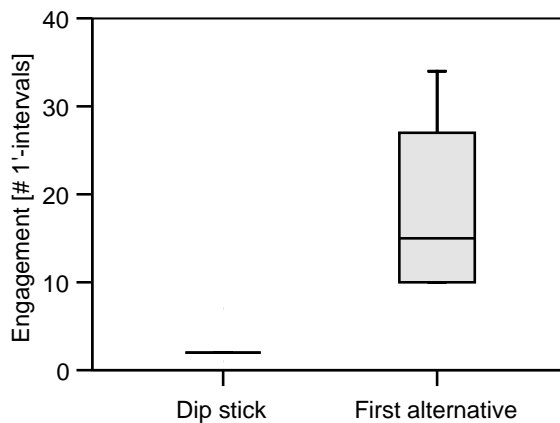


Figure 2.2b: Frequency of 1-minute intervals in which individuals ($N = 5$) were actively engaged with the task, before showing the technique “Dip stick” for the first time, and before a first solution other than “Dip stick”. Medians and quartiles are shown.

Indeed, as Figure 2.2b illustrates, subjects were much more engaged with the task before showing a first alternative solution to “Dip stick” compared to before applying “Dip stick” for the first time (Wilcoxon signed-ranks test: $Z = -2.032$, $N = 5$, $p = 0.042$). Therefore we conclude that the behavior “Dip stick” was already in the population’s repertoire, whereas the other eight solutions were invented during the experiment (including the two behaviors from the preliminary list: “Branch scoop” and “Sponging”), and therefore represent innovations.

The second argument is that longer latencies until first occurrence do not simply indicate that these are non-preferred techniques already known to the animals. Thus, after its first occurrence an innovative behavior was performed more often (within shorter time), which would not make sense if they were non-preferred, known behaviors. We analyzed the time intervals until first occurrence of an innovative technique and between the seven subsequent occurrences in the experiment “syrup tube”. A Friedman Test showed that these time intervals were significantly different (Friedman Test: $\chi^2 = 17.537$, $N = 8$, $k = 8$, $p = 0.014$). The same follow-up procedure as described above (Sachs, 1999) showed that

significant differences only arose between two time intervals if one of the two was the time lag until the first performance of a behavior. This first time interval differs from the following seven, which were all shorter, as illustrated in Figure 2.3. Page's L Trend Test (Page, 1963) was used to test for a successive decrease of these eight time intervals. It revealed that there is a highly significant trend for time intervals to become shorter (Page's L Trend Test: $L = 1452$; $k = 8$; $N = 8$; $p < 0.001$). Therefore we can also exclude the possibility that these behaviors had been non-preferred, known techniques.

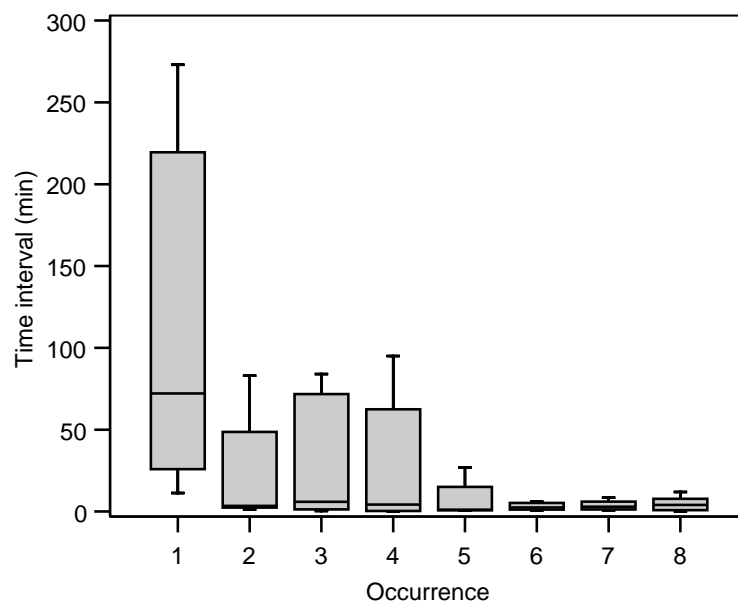


Figure 2.3: Time intervals (min) until first occurrence of behaviors ($N = 8$) and between the seven following occurrences in the experiment “syrup tube”. The time lag until the first performance of behaviors (occurrence 1) is higher than between the other occurrences. Medians and quartiles are shown.

The third argument is that even apparently similar techniques seem to be functionally different from the orangutan's perspective. Where the same behavior pattern is applied to a different material, but animals do not use the materials randomly and interchangeably, we regard them as modifications of an innovation (Table 2.3). In case of “Wood wool squash”, “Paper squash” and “Twig squash” the same behavior pattern is applied to different materials. However, our subjects discriminated between these three forms. Although these materials were all continuously available, only two of six animals using any of the three materials used all of them; two animals used two of the three materials, and two animals used only a single

material (see Appendix 2.2). Furthermore different subjects preferred different materials: three animals preferred wood wool over paper (19min vs. 5min; 1h 27min vs. 36min; 11min vs. 2min), whereas another animal used paper two times more often than wood wool (1h 13min as opposed to 38min), and only one animal used paper and wood wool equally much (9min; 8min), while both materials were always equally abundant. Thus, animals clearly distinguished between the three techniques. Therefore, “Wood wool squash” and “Twig squash” are assessed as modifications of the innovation “Paper squash”, as the latter occurred first. On the other hand, the behavior pattern of “Sponging”, where paper is chewed to a ball and then dropped, is clearly different from “Paper squash”, where a large amount of paper is directly forced into the tube. Finally, “Branch scoop” involves another behavior pattern than “Dip stick” (gently sucking syrup out of leaves as opposed to licking it from a bare stick), whereas “Vegetable rod” is a modification of “Branch scoop”, and “Twisted paper rod” again involves another behavior than “Vegetable rod”.

For the “smearing” experiment, a Friedman Test revealed that the techniques also had highly significantly different latencies until first performance among the eight individuals (Friedman Test: $\chi^2 = 17.602$, $N = 8$, $k = 6$, $p = 0.003$). The follow-up procedure (Sachs, 1999) showed that significant differences between two techniques were only found if one of the two was “Cleaning with hand”. This simple cleaning with the hand differed from the other techniques in latency of occurrence, as several individuals showed it sooner than the other techniques, as illustrated in Figure 2.4.

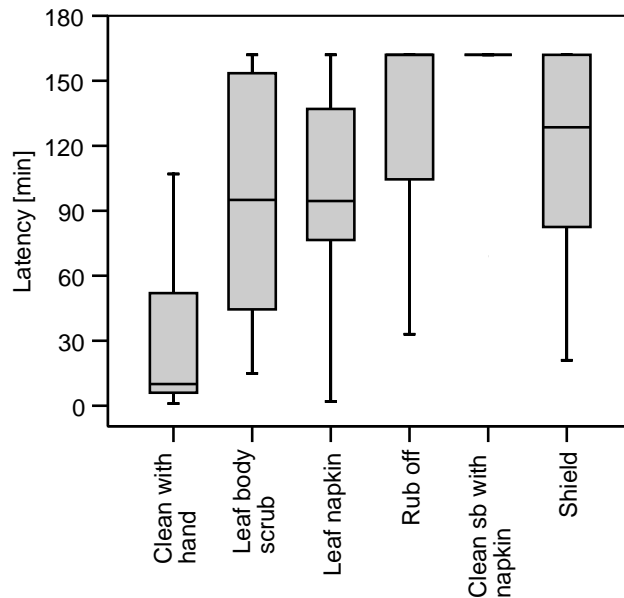
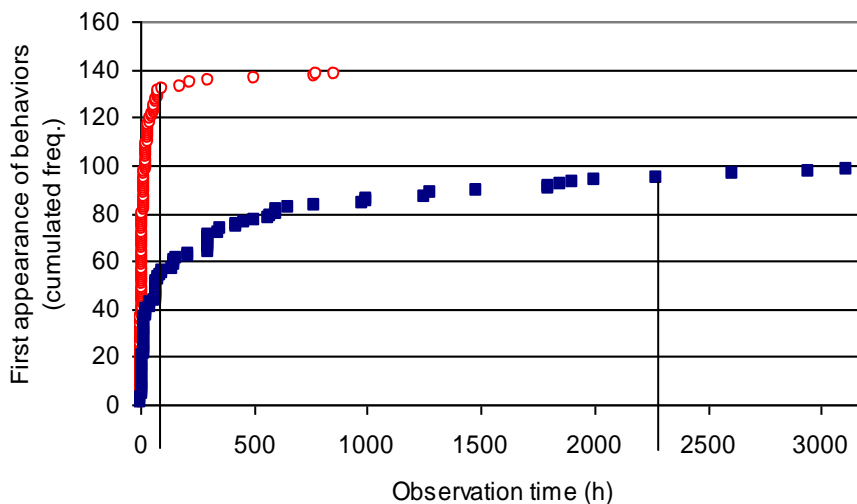


Figure 2.4: Latencies (min) until individuals' ($N = 8$) first successful performance of a technique in the experiment "smearing". For individuals that never showed a particular behavior, the latency was set coinciding to the duration of the experiment (162 minutes). Medians and quartiles are shown.

We thus conclude that whereas "Cleaning with the hand" was already part of the subjects' repertoires, the other five techniques (see Table 2.3) were invented during the "smearing" experiment and qualify as innovations, including the two behaviors from the preliminary list ("Leaf body scrub", "Leaf napkin") that inspired the experiment. The latter are very similar, but subjects apparently made a distinction: four animals showed both of them, but another four animals only showed either one or the other (see Appendix 2.2). "Leaf body scrub" is therefore considered a modification of the earlier occurring "Leaf napkin". Subjects clearly disliked being smeared, as indicated by their attempts to avoid it and their facial expression when they had been hit; therefore there was no need to quantify their motivation for solving this task.

Comparison of the corresponding behaviors with a natural population (Tuanan)

Comparison of collector's curve of captive and wild population (Figure 2.5) showed that the captive population had a larger behavioral repertoire. Moreover, zoo subjects showed their full repertoire within a much shorter time than the wild population, suggesting that they showed the elements in their repertoire more frequently. Within 80 hours of observation time zoo animals showed 95 % of their behavioral repertoire, whereas the wild ones took over 2,000 hours to show the corresponding proportion. Although the habitats are not directly comparable, these differences suggest a larger innovation repertoire in the zoo, i.e. that zoo animals were more innovative, and that each element is shown more frequently.



F Collector's curve) for wild (filled squares) and zoo (open circles) orangutans. To make them comparable, the zoo data were treated as 9 parallel focal samples (because the additional *ad libitum* sampling was considered nearly complete). Vertical lines indicate the time at which animals in the wild or the zoo reached 95% of their repertoire.

Discussion

The validity of the geographic method

We found that of the ten potential innovations from the wild (van Schaik et al., 2006) we could potentially expect to observe directly in zoo conditions, four did not occur in the zoo, even though we could be confident we had collected an adequate sample of the zoo

population's repertoire. These four were therefore considered innovations. Of the other six, three may be possible innovations, because they were rare and apparently not depending on a certain status of individuals showing them (Table 2.1).

The experiments allowed us to qualify this conclusion. Of the five behaviors from the preliminary list that we could potentially elicit in captivity by experimentally offering the relevant conditions, only one did not emerge (Table 2.2). "Kiss squeaks with leaves" was not performed in the "blow pipe" experiment. Although this experiment was very short and conducted only once in order to minimize stress, it successfully established the appropriate conditions, as subjects did respond with regular kiss squeaks. "Kiss squeak with leaves" is thus neither part of our subjects' behavioral repertoire, nor was it invented during the experiment; its occurrence in the wild can therefore be classified as an innovation.

Although those that were actually elicited in the experiments might seem unlikely to be innovations or modifications, they nonetheless were. Based on latencies across individuals we confirmed the innovation status of "Branch scoop", "Sponging" and "Leaf napkin", while "Leaf body scrub" was assessed as a modification. This was possible because in the experiments several other behaviors occurred too, allowing us to distinguish between solutions that were already part of the population's repertoire and techniques that were invented during the experiment. Latencies of "Dip stick" in the "syrup tube" experiment and simple cleaning with bare hand in the "smearing" experiment were significantly shorter relative to latencies of other techniques in the specific experiments; this suggests that the former were already in the population's repertoire, whereas the latter were invented during the experiments. Subjects were not inactive in the meantime but in fact clearly engaged with the syrup tube before showing a first alternative solution to "Dip stick." Furthermore we could rule out the possibility that the longer latencies of techniques other than "Dip stick" in the experiment "syrup tube" indicated non-preferred, known behaviors, rather than innovations. We demonstrated that time intervals between consecutive occurrences of innovative behaviors were significantly smaller after the first occurrences, which would not have been found if these had simply been non-preferred but known techniques. There is no explanation for why time intervals between two subsequent occurrences of non-preferred techniques should decrease; but it makes well sense in case of innovations that are more frequently performed by the inventor after their initial occurrence, and eventually also by some group-members having learned the new technique either socially or on their own. Finally we showed that orangutans discriminate among similar techniques, which were therefore distinguished as modifications.

In conclusion, our attempt to validate the geographic approach for identifying innovations in wild populations by comparison with a captive population suggested that at least eight of the 15 investigated behaviors from the preliminary list (putative innovations recorded for wild orangutans) could indeed be classified as innovations, and one additional behavior as a modification (Tables 2.1 and 2.2). First, at least four of the ten behaviors from the preliminary list we could expect to observe directly were verified innovations in our captive population based on their absence (Table 2.1). Second, attempts to experimentally elicit five additional behaviors from the preliminary list showed that four qualified as innovations and one as modification, based in one case on absence and in the remaining others on latencies of first occurrence across individuals (Table 2.2). Thus, in total at least 53 % (8 of 15) of the putative innovations recorded for wild orangutans were assessed as innovations. If we add the three possible innovations and the modification (Table 2.1), this figure becomes 80 %. Therefore our findings largely confirm the assessments on the preliminary list by van Schaik et al. (2006) and thus the approach of Ramsey et al. (2007).

The geographic method largely relies on patterns of presence and absence to assess a behavior's innovation status, making it difficult to assess its degree of innovativeness. The experimental approach, by measuring latencies, allows for a quantification of the strength of the innovations hitherto unavailable. Future work could use this quantification to test hypotheses about differential degree of the strength of various innovations.

Innovativeness in the zoo and in the wild

The data also revealed a phenomenon that was not part of the original aim of this study. The zoo environment seems to be conducive for the emergence of innovations. Several observations support this conclusion. First, the repertoire comparison (Figure 2.5) suggests a far larger innovation repertoire in the zoo population. Although temporal variability in habituation, ecological conditions and climate and poorer visibility in the wild may play a role in this difference, the recent origin of the zoo population compared to the wild ones would have suggested a much smaller repertoire in zoos. Second, the appropriate experimental conditions elicited many more innovative responses in captivity than had been observed in the wild, and moreover did so in a remarkably short time frame. In the "syrup tube" experiment alone, which represented an imitation of a tree hole filled with water, the subjects of a single zoo population came up with five innovative solutions and three modifications, as opposed to the mere two innovations recorded in a total of seven wild populations. The data suggest the

existence of a gradient of innovations, with a rather low average latency as in “Branch Scoop,” suggesting a rather weak innovation, and a long latency of “Twisted paper rod” in the same task, indicating a stronger innovation. Third, we also observed several other behaviors in our captive population under regular conditions not reported from the wild. Two of these should be possible in the wild, and were therefore potential innovations: (1) “Bag use”: putting small, loose food items on a piece of paper, grab its corners to form a bag and carry it somewhere else for eating (in nature big leaves could be used for this); (2) “Foot in mouth”: climbing while having several digits of one foot in its mouth. Finally, “Tree-hole tool-use” was frequently shown. Indeed, zoo orangutans commonly use sticks to poke in holes and crevices (Jantschke, 1972; p. 196), whereas stick use is strikingly absent in most orangutan populations in the wild (Table 2.1). Similarly, in one wild chimpanzee community where sticks were occasionally used, animals readily applied sticks in a given task, whereas in a second community that did not use sticks, the animals did not (Gruber et al., 2009). Thus we may have been overly conservative not to assign innovative status to “Tree-hole tool-use.”

All these differences indicate that captive orangutans are far more innovative than wild ones. Russon et al. (2009) similarly found that ex-captive rehabilitants who were released onto an island with natural habitat but continued to be provisioned, developed an innovation repertoire in their natural habitat enclosures that was far richer than that found in natural populations. Kummer and Kurt (1965) found that captive hamadryas baboons had added new social behavior patterns not found in the wild populations studied by them. Although Kummer (1995; 1992) suggested that captivity especially promotes social behaviors, the orangutan findings indicate that technical innovations are also more numerous in captivity compared to the wild.

In the wild, infant orangutans rely heavily on what their mother eats and does, and largely eschew independent exploration of the environment (Jaeggi et al., 2010). Even independent orangutans show remarkably little sampling of potentially novel foods (Zweifel, 2008). In a simple but pioneering experiment, Menzel (1968) found that wild Japanese Monkeys, *Macaca fuscata*, ceased coming to a previously frequently visited spot after a set of innocuous toys had been placed there, suggesting that they actively avoided the area because of these unfamiliar objects.

Overall, then, there are enough findings to suggest that wild orangutans may have a very low innovation tendency, whereas being in captivity unblocks the innovation tendencies of individual primates. What causes this contrast? The most likely explanation is that wild primates associate unfamiliar, novel objects with danger (be it through poisoning, lack of

vigilance, or simply opportunity costs; Halsey et al., 2006) and thus largely avoid them (cf. Menzel 1968), whereas captive conspecifics associate them with a food reward or other positive reinforcement. As a result, captive individuals are more likely to approach and explore novel objects and to do so more quickly than do wild animals. Kummer's (1995) explanation for social life growing luxuriantly in captivity compared to its reduction under food shortage in the field (Morrison & Menzel, 1972) may also apply to our findings. Kummer (1995) explained his findings with a separation of an individual's gratification value and the survival value for its genes. The alienation from the environment experienced by zoo animals provided them with more spare time and spare energy (than their conspecifics ever had in the wild), allowing them to play with their gratification system, as a human does. An animal released from the pressure to survive can choose more freely than a wild animal how much exertion, excitement, novelty or uncertainty it wants to experience. The zoo baboons at that time only had their conspecifics to maximize gratification, resulting in a luxuriant social life. Kummer's explanation (1995) of the emancipated gratification system may also apply to our zoo orangutan population. Released from danger avoidance and the intensive subsistence lifestyle of the natural world, zoo orangutans could overcome neophobia and invest their larger amount of spare time and spare energy in manipulation of novel objects and tasks to maximize gratification. This could then yield the higher (technical) innovativeness in zoo orangutans we observed, compared to wild ones.

Furthermore, captive orangutans recognize a task as such probably faster than their conspecifics in the wild. Using a stick as a tool to gain honey is present in some wild populations, but not in most others (van Schaik et al. 2006). In the latter sites, tree holes filled with honey are less abundant, leaving orangutans with a lower probability of inventing a tool-based solution (Fox et al., 2004). In the case of the "Branch scoop" innovation, the wild innovator first had to stumble upon a tree hole filled with water out of arm's reach, in combination with being motivated to get some water. This latency largely ceases to apply in captivity, where a new opportunity is often immediately recognized as such by subjects.

These two factors together (positive association with novelty and easy recognition of something novel as potentially rewarding) add up to innovations appearing in captivity much faster and, given excellent conditions for social transmission, to be retained better in the population, leading to larger population-specific innovation repertoires. (We do not know whether the mean duration of retention in the population differs between zoos and the wild, but 'fashions' are certainly not limited to captive populations: Nishida et al. 2009).

A possible alternative, but not mutually exclusive explanation for the wild-zoo contrast is that the increased innovativeness in captivity is an enculturation effect (Call & Tomasello, 1996; Tomasello et al., 1993b). However, in this zoo population of orangutans, only one animal (Lea) is human-reared, and she did not contribute any of the experimentally induced innovations (see Table 2.3). Tomasello & Call (2004) later changed the enculturation hypothesis to a weaker socialization hypothesis, saying that “in growing up with humans who control their world totally and who interact with them in ways that other apes do not, apes acquire a different set of social skills than their wild conspecifics for interacting with humans” (p. 214). However, as we saw, it is not only in the social domain that innovations are increased. Thus, neither enculturation, nor socialization can account for the contrast we found.

Finally, the greater innovativeness of captive orangutans compared to wild ones may be relevant to the main issue of this paper: using the captive population to validate the innovation status of behaviors classified as innovations in the wild. Due to the higher innovativeness of the zoo orangutans, the method we used is actually very conservative: if a behavior that qualified as an innovation in captivity is present in the less innovative wild animals, its assessment as an innovation of the wild conspecifics can hardly be false. At the same time we may not succeed in assessing a behavior as an innovation in captivity despite it actually being one in the wild.

Appendix

Appendix 2.1: Behaviors (138) recorded during observational phase of study and components of the zoo collector's curve in Figure 2.5. Some of the definitions are from the ethogram of Rijksen (1978).

Behavior	Explanation of behavior
Angel	Lying on its back, moving arms up and down (arms are always in contact with the ground).
Avoid	Actor leaves his place (e.g. nest) because another subject is approaching him but apparently not stopping. If the "avoider" lingers, waits and looks back, it is called "hesitant avoidance".
Awry lips	Animal warps its mouth and makes awry lips.
Backdance	Lying on its back and circling.
Balance on rope	Walk a few steps bipedally and erect on a rope without hands grasping another rope, grid or anything else for support.
Bared-teeth scream	By animals who were attacked and bitten: Loud, high-pitched, drawn-out hoarse screams, each of which may end with a choking sound. Mouth is wide open with the teeth and gums exposed. Thus also recognizable only visually.
Bark biting	Biting into the bark of a tree, sometimes followed by tearing off long strips of bark and then dropping it immediately.
Biting	When biting, the actor closes his jaws abruptly, usually on a victim's hand or foot.
Brachiate	Body is hanging, arms are extended, feet are in the air or are only partly supportive, the animal is moving by clinging with one hand alternately to branches/roots (e.g.).
Branch cushion	Cushion a big branch, a wire-nest, or a rope with wood-wool to sit or lie on it.
Brusque charge	Actor suddenly rushes towards his opponent, silently and in a straight line. The head is withdrawn between the shoulders, actor often shows piloerection of shoulder- and upper-arm region, accompanied by "frowning" and "tense-mouth". When catching up with the partner, actor may grasp an extremity and bite. Partner is typically fleeing when seeing the actor rushing towards him.
Butt-head	Actor presses its bottom in the face of a partner.
Call on someone to groom him/her	Actor calls on someone to groom him/her. Actor sits with ostentation in front of a partner, typically showing him his back.
Chew	Actor is chewing on something (typically on a stick, or cardboard) but apparently not for feeding reasons.
Climb	Using all 4 extremities to move on branch, rope or grid, up or down.
Climb on someone	Youngster climbing around on another orangutan.
Climb with foot in mouth	Actor climbs with some fingers of one foot in the mouth, thus using only 2 or 3 extremities to climb.
Clinging	Prolonged embracing or clinging to the partner. Hanging/holding on to the partner, potentially hindering the partner's movement: usually by infants.
Cushion ground	Cushion the hard ground with wood-wool to sit or lie on it.
Direct smell	Smelling directly at the partner's face or shoulder, may result in nose to nose contact.
Dive	Dropping the upper part of the body, head down and arms extended, holding on with feet. Results in an extended upside down hanging position.
Dragging	Rather fierce grasping or pulling of a partner and dragging him along for some distance.
Drink bowl hl/nhl	Drink water out of a bowl (a) either humanlike (hl) by tilting the bowl and letting the water pour into the mouth, or (b) by holding the head into the bowl (nhl).
Drink directly	Drink water directly with mouth from the fountain.
Drink milk	Drink milk from Mum.
Drink pee	Drink the pee from someone else that is peeing.
Drive away someone	Actor is moving towards another animal, but unlike in "join" the actor is not stopping and the partner is leaving (when the actor is coming within a distance of approx. 0 - 3 m).

Drop	Drop an object the subject was carrying around before for some time.
Feed	Animal takes in food or is chewing food. Animal may move while feeding. Several variant of feeding on small loose food (e.g. pellets, kernels, grains) are further distinguished: - Pick-feeding: Picking grains with fingers from the ground and putting them in the mouth. - Grazing: Feeding directly with mouth on the ground, supporting the body with 1 or 2 arms or both hands that remain in contact with the ground, or supporting the body by clasping a rope with one hand. - Hand-feeding: Feeding grains directly with mouth out of a heap in the hand. - Box-feeding: Feeding grains directly with mouth out of a heap in a box/paper bag. - Box-pick-feeding: Picking grains with fingers out of a heap in a box.
Fill bowl	Fill water in a bowl by (a) holding the bowl under the water jet or (b) by putting it on the floor in the right place.
Fill box	Actor puts sawdust including grains and/or little food pellets in a box or bowl.
Fix paper	Fix paper (typically a paper bag) to the grid, to a branch or a rope by bending the paper over one of these objects, then twining the ends together.
Flap lip	Flap upper lip up, so teeth and upper gum are visible.
Flee	Actor moves as fast as possible, thereby seems to lose its normal caution.
Follow	Animal coordinates his movements with his partner, often moving closely behind the partner in the same direction (or leaving e.g. the same nest shortly (< 5s) after the partner did).
Gathering	Mother pulling infant towards her. "Hold out hand" is often followed by "gathering".
Genital inspection	Actor brings his face close to the genital region of a partner or touches it with a finger.
Genital self-inspect	Touching vulva or penis with finger(s) or foot and then sniffing at it. Or rubbing genitals to an object and then sniffing the contact place.
Gnaw wrestle	2 orangutans rolling over one another, pushing, hitting, tugging each other by the hairs of the neck (e.g.). Gnawing consists of pushing the bared teeth onto a hand or a foot (e.g.; face, throat and breast are seldom touched).
Grab	Grab objects (e.g. wood wool, paper bag, food, stick) with hand, foot or mouth. In context of food "grab" is only stated, if animals doesn't immediately start feeding but is moving around with the grabbed food instead.
Grasp	Grasp partner by the hair or limb and holding on so.
Gymnastics	Various activities (giving the impression of being non-functional) and locomotor patterns that are not oriented in a particular way with respect to a partner (could also be termed self-play).
Hand wrestle	Two individuals are lying next to each other, one extends a hand/foot to touch the other's hand/foot, the other grasps the partner's foot/hand and both try (without much force) to release the other's grip.
Hang	Hanging without moving, on grid or rope, with 1 to 4 extremities grasping the grid or rope. If actor is hanging, supported by both arms with limbs fully extended, this is "posturing hanging". Special and distinct forms of hanging are also "hang exposed" and "dive".
Hang exposed	Actor is hanging with legs sideways up and both feet grasping to the grid above, sometimes with one hand also grasping to the grid above. The genital region is exposed.
Head jerk	Fast jerky movement with the head towards a partner.
Hit object	Strike fist quickly downwards from above onto an object.
Hitting	A single stroke with the extended hand, brought downwards from above and landing on the head or on the shoulder of a partner.
Hold out hand	Actor extends his arm in the direction of a partner and maintains that position for some time. When the juvenile screams, the mother holds out her hand preliminary to "gathering" it.
Horizontal bared-teeth face	Strong retraction of the mouth corners and lips, thus exposing the teeth and gums, while the jaws remain closed.
Join	Animal moving towards another one and stopping within an arm's reach distance; the other animal does not leave, they are staying together for some time. Joining a partner also means remaining (sitting or lying) next to it. If animals simply comes close to another one e.g. while they are feeding, grabbing food, this is not "join". "Join" ends if one of the animals moves away, or if both are involved in an active behavior.
Knock	Knock on glass with a finger (typically with the pad of the forefinger) 2 or 3 times quickly in a row, usually when a visitor is there.
Knock self	Knock with a finger several times in a row against own head/ear.

Leaf gloves	Using leaves as gloves to handle nettles or other spiny food.
Leave	Animal leaves the immediate surrounding of the partner at a normal, smooth pace.
Lie	Lie on back or on belly, in nest or on ground. Animal may either watch the surroundings or sleep. The majority of the animal's weight is supported by its torso, and the animal is in a horizontal position, its body reclining somewhere.
Lift	Lift e.g. wood wool, paper bag, and then drop it shortly afterwards, then usually looking (for food) at the place where the lifted object used to be, or looking at the object in some cases.
Lift cover of so	Lift cover (e.g. paper bag) of someone else to see who is beneath it.
Load and fold paper	Put sawdust containing little food items (e.g. pellets or grains) on a piece of paper, and then fold paper so it can be carried away like a bag.
Look at mouth	While holding the face very close to that of the partner, the actor looks intently at the other's chewing mouth. The actor's under lip is often slightly protruding and he may hold an open hand under the partner's chin, without touching it.
Look at partner	While holding the face very close to that of the partner, the actor looks intently at the partner: in contrast to "look at mouth" the partner's mouth is not chewing, and the actor does not look at the partner's mouth only.
Look at tool-user	While holding the face very close to the partner that is manipulating an apparatus with a tool, the actor looks intently at the partner or the tool or the apparatus.
Look up-around	Animal looks up from what it is doing (e.g. feed) and is looking around.
Manipulate apparatus	Manipulate an apparatus (enrichment task). Note type of apparatus and tool (typically a stick) used, and whether actor is successful (s) and provides himself with the bait (s+), another animal takes it (s-), or actor is not successful (ns).
Mold	Molding paper or cardboard in bowl that has been filled with water before, then bring the molding mass to the mouth from time to time, chew it.
Mouth-mouth	Mouth-to-mouth contact: Press the (slightly opened) mouth on that of the partner.
Nest-building with paper and wood wool	Actor is building a nest without branches, usually on the ground or a platform. Actor uses wood wool and uses pieces of paper (which it typically produces before: "Rip paper"). On tree/rope no nest building is possible (only cushioning), whereas on ground/platform nest building and cushioning is possible.
Nest-building with twigs	Consists of breaking and bending twigs and roughly interlacing these to form a platform.
Nest-building with wood wool only	Actor is building a nest with wood wool only (without branches or paper), usually on the ground or on a platform. If animal only quickly uses wood wool, then the behavior is called "nest cushion", nest building must last at least 10s to be defined as such.
Nod	Nod with head up and down with a regular rhythm and quite fast.
Open paper bag	Actor opens a paper bag and holds its head inside.
Open-mouth bared-teeth face	Lips and mouth corners are drawn back, exposing the teeth, but in this element the mouth is widely opened.
Paper forehead	Push paper on forehead, followed by taking paper in mouth.
Pick nose	Elaborately picking own nose.
Pick teeth	Elaborately picking own teeth.
Pick with mouth	Actor is gently picking with its mouth the fur of another animal.
Pirouette	While standing, actor is turning around its own axis (like a pirouette of a figure skater).
Play with object	Animal is handling an object (e.g. paper), doing various activities with that object that are giving the impression of being non-functional.
Play with someone	Various activities, giving the impression of being non-functional, (as for "gymnastics"), but another individual is involved and follows.
Play with water	Actor is splashing or otherwise playing with water.
Pluck lip	Actor is plucking at its lip with a finger.
Poke hole	Actor pokes in small hole with finger, and then licks the finger.
Posturing standing	Body is exhibited at maximal size: Actor stands erect, bipedally with extended arms and legs. Actor typically stands on a rope with both legs while his arms are hanging from another rope

	or the grid above.
Press to self	Actor presses the child to her body. May follow after “gathering”.
Prolonged Pulling	Two animals are pulling on the same object against each other, e.g. pulling a twined paper bag, for a prolonged time (more than 5s).
Push away	Push a partner away with hand or foot.
Reel lips in	Actor reels lips in with closed mouth.
Rip paper	Animal rips paper: Actor holds paper to the mouth and makes a small crack with the mouth, and then the paper is ripped in two pieces with the hands afterwards. Occurs in context with nest building.
Rolling object	Actor is rolling/pushing an object/heap (e.g. wood wool) in front of him, or dragging it behind him (likely because it is too much to carry), object is in contact with the ground.
Rolling sideways	Rolling sideways (not over head like in “somersault”).
Roundabout	Riding “roundabout” on a big bowl or around a post.
Rub own genitals to other’s	Actor is rubbing its genitals against the genitals of another animal.
Rush after someone	Actor is rushing after a partner who is fleeing. This behavior is performed at very fast speed, in contrast to “follow”.
Scratch	Fast movement of fingertips over some part of the body. Actor doesn’t look at body part where it is scratching, unlike in “grooming”.
Self-covering	Actor covers itself, typically with a paper bag, using it like a blanket. Animal is sitting or mostly lying under it.
Self-decorating	Pieces of vegetation or objects like paper or wood wool are draped around the neck or put on the head, or held in an extended arm above the head.
Self-grooming	Animal runs his fingers or the back of his hand through his hair against the direction of growth; also picks things with his fingers or mouth, looks in direction of the treated region.
Shake	Shake an object (e.g. rope).
Shake hand	While letting the arm hang, animal shakes hand and wrist (seems to occur when animal is impatient, e.g. during or before manipulation of an apparatus, or when awaiting feeding).
Share food	Actor is apparently offering the food and willing to share it. This “food-offering” is indicated by the actor not making a movement away, but having the hand that is holding the food in a posture not hidden by the body, but instead making a movement with the hand towards the partner so it can easily bite or pull a piece of food off.
Silent-pout face	The lips are pushed forwards while they are pressed together at the mouth corners, but slightly opened in the middle, to form a small round aperture.
Sit	Sit on ground, rope, tree or in nest. Animal may either watch the surroundings or sleep. The majority of the animal’s weight is supported by its rear end, and the upper body is in a quite upright (> 45°) position.
Sit big	Sit with 1 or 2 arms extended vertically above and hands grasp to the grid above. Arm(s) are stretched, the underarm is extended in an angle of 90° or more from the body, the upper body is thus quite stretched as well and the animal looks big.
Sit folded arms	Animal is sitting with folded arms: hands clasp opposite arms above the elbow.
Sit folded hands	Sit with folded hands: individual grasps with one palm of its hand the other palm of the other hand.
Slide	Sliding down the rope by hands loosely clasping the rope.
Social-grooming	Grooming a partner. (For further details on grooming see “self-grooming”)
Somersault	Turning somersaults forwards or backwards.
Stand	Animal is standing still, not moving, either erect or quadrupedally: a) Stand erect: The majority of the animal’s weight is on its legs, it may hold on to a tree/rope/grid with one or both of its hands. b) Stand quadrupedally: The animal is standing on all its extremities, the weight is distributed equally.
Steal food	Opposed taking, owner tries to prevent the theft. But actor grabs food from another animal with his hand, or bites off a piece with the teeth, while the owner is turning away trying to protect the food and clearly not willing to give food away.
Steal wood wool	Grab the majority of wood wool from a platform where another animal is sitting or lying.

Strangulate	Twining paper around the neck, as if strangulating self.
Struggle	Animal attempts to free himself from the grip or restraint exerted by a partner.
Symmetric scratch	Exaggerated, long, slow, symmetric scratching movements with both arms at the same time.
Take food	Grab food from another animal with hand or bite off a piece with the teeth, while the other animal does not do anything to prevent it and is apparently tolerating the theft.
Take in mouth partner's limb	Actor takes an arm or foot of a partner in its mouth, very gently. It does not result in gnaw wrestling.
Take object from somebody away	Actor takes the object (e.g. a stick, bowl) from another animal away.
Throat pouch inflation	Orangutans (both m and f) may inflate the large cavernous pouch that lies anterior to their throat (it is suggested to represent a state of general arousal).
Throw object	Actor is throwing objects around, apparently not aiming for anyone or anything, but quite forceful.
Tongue play	Consists of fast movements with the tongue backwards and forwards, the mouth is slightly opened. Usually performed in front of the glass pane or even in contact with it.
Tool preparation	Prepare an object to use as a tool afterwards: making a tool.
Touch	Touch another orangutan with hand, finger or foot; or touch an object without grabbing the object.
Tree-hole tool-use	Using tool to poke into small holes to extract honey.
Under lip forwarding	Actor is pushing under lip and under chaw forward.
Urinate on someone	While urinating another animal is hit.
Vibrating lips	Animal's lips are vibrating.
Walk bipedally	Walking erect on ground, with hands not holding on somewhere.
Walk hand-in-hand	Walking with someone and holding on to the other one's hand.
Walk on rope	Walking erect on rope, with the feet moving on the rope and the hands clasping to another rope above.
Walk quadrupedally	Walking on ground quadrupedally, thus all hands and feet contacting the ground, or only the feet contacting the ground but the hands holding on somewhere to balance or to swing the body forwards.
Watch	Actor stops what he was doing, sits down and attentively watches another orangutan, or watches in a particular direction for some time.
Wipe	Make wiping-movement with the forearm on the ground, wiping sawdust to a line and investigate it for food (usually kernels or grains).
Wrestling	Resembles "gnaw wrestle", but it is distinguished on the basis of a passive or clearly uncooperative attitude by the recipient.
Yawning	Usually starts with an extreme pouting of the lips, changing to an opening of the mouth, and ends with a widely opened mouth exposing the gums and teeth.

Appendix 2.2: First successful performance of a behavior for every subject

Behavior	Ca	Dj	Lea	Oc	Sel	Ti	Tu	Xi
Dip stick	00:01:40	00:40:40		00:15:10	00:05:26		00:00:50	00:01:52
Branch scoop				02:42:00	00:12:30		00:32:25	00:20:15
Vegetable rod					02:46:00			
Twisted paper rod				10:13:00	09:59:00			
Paper squash	01:48:40			01:37:20	06:20:00	00:46:50	00:39:15	
Wood wool squash	03:46:00			00:43:40		00:40:15	00:42:50	01:10:30
Twig squash				08:10:00			04:33:00	
Fish				04:49:00		05:18:00	00:11:17	
Sponging	01:44:00			03:45:00		03:32:00	03:41:00	03:27:00
Clean with hand	00:06:02	00:00:05	00:10:05	00:04:10	01:46:15	00:08:00	01:00:20	00:42:05
Leaf napkin	01:16:00	01:15:12	01:40:00			01:27:39	00:01:02	01:51:10
Leaf body scrub	02:16:25	00:14:30		02:24:00	00:39:27	00:52:30		00:48:05
Rub off	00:46:15	00:32:25						
Clean sb with leaf	02:14:00							
Shield	01:24:40				01:19:15	01:34:35	00:20:50	

The latency (hh:mm:ss) from the beginning of an experiment till an individual's first successful performance of the potential innovations occurring in the experiments, with the innovator's latency in bold letters.

“Dip stick” and “Clean with hand” are not assessed as innovations.

Appendix 2.3: Pictures of (a) “Branch scoop” and (b) “Paper squash”



a



b

Chapter 3

Can captive orangutans be coaxed into cumulative build-up of techniques?

While striking cultural variation in behavior from one site to another has been described in chimpanzees and orangutans, cumulative culture seems to be far more pronounced in humans. Captive chimpanzees were recently found to be rather conservative, sticking to the technique they had mastered, even after more effective alternatives were demonstrated. Behavioral flexibility in problem solving, in the sense of acquiring new solutions after having learned another one earlier, is a vital prerequisite for cumulative build-up of techniques. Here, we experimentally investigate whether captive orangutans show such flexibility, and if so, whether they show techniques that cumulatively build up (ratchet) on previous ones after conditions of the task are changed. We provided nine Sumatran orangutans with two types of transparent tubes partly filled with syrup, along with potential tools such as sticks, twigs, wood wool and paper. In the first phase, the orangutans could reach inside the tubes with their hands (regular condition), but in the following phase, tubes had been made too narrow for their hands to fit in (restricted condition 1), or in addition lacked their favorite materials (restricted condition 2). The orangutans showed high behavioral flexibility, applying nine different techniques under the regular condition, abandoning preferred techniques and switching to different techniques under restricted conditions when this was advantageous. Two of these techniques cumulatively built up on earlier ones. This suggests that the near-absence of cumulative culture in wild orangutans is not due to a lack of flexibility when existing solutions to tasks are made impossible.

Introduction

For a long time, culture was considered unique to our own species and therefore inaccessible to analysis by the comparative method (Byrne, 2007). But recently, based on extensive fieldwork, striking behavioral variations from one site to another have been described to constitute culture in our closest living relatives, chimpanzees (Boesch, 1996; Whiten et al., 1999) and orangutans (van Schaik et al., 2003).

Human cultural traditions change over time, and many seem to accumulate modifications made by different individuals over time in the direction of greater complexity, a phenomenon called cumulative cultural evolution or ratcheting (Tomasello et al., 1993a). Greater complexity means that a wider range of functions is encompassed (Boesch & Tomasello, 1998). Such modifications have often been understood to represent improvements (Tennie et al., 2009; Marshall-Pescini & Whiten, 2008), be more efficient or productive (Laland, 2004; Marshall-Pescini & Whiten, 2008), or be an elaboration of a previous one (Marshall-Pescini & Whiten, 2008). Some have argued that cumulative cultural evolution is limited to humans (Henrich & McElreath, 2003; Tomasello, 1999b; Tomasello, 2001; Tomasello et al., 1993a). Others think it is limited to humans, song birds, and perhaps chimpanzees (Boyd & Richerson, 1996). Indeed, Whiten et al. (2003) and Boesch (2003) argued that there are examples which show that chimpanzees do have some modest power for cumulative build-up of techniques. For instance, many chimpanzee populations crack nuts by hitting them directly with the hand against tree trunks or are using stone hammers on stone anvils to break nuts that are harder and smaller. However, in one population they use an additional stone to increase the stability of the stone or to level the stone anvil (Matsuzawa & Yamakoshi, 1996). Similarly, Hunt and Gray (2003) hypothesized that the diversification of *Pandanus* tool designs they found in New Caledonian crows evolved from cumulative changes to earlier versions and hence was the first indication of rudimentary cumulative cultural evolution in a non-human species. Thus, whether cumulative culture is unique to humans is therefore debated, but it is nonetheless clear that humans use many more technologies or behavioral strategies that are beyond the innovation reach of individuals of great apes, and have done so for at least 1.6 million years, with the onset of the Acheulean tool cultures (Klein, 1999).

Possible, non-mutually exclusive explanations for a lack of cumulative culture are (1) the absence of the ability to faithfully acquire novel alternatives, (2) the inability to recognize

alternatives as superior and thus flexibly switch to them, and (3) the absence of the ability to produce such superior innovations in the first place. First, Tomasello et al. (1993a) stated that cumulative cultural evolution critically depends on innovation and imitation, and perhaps teaching, and that it can not arise by other forms of social learning such as emulation, nor by any form of individual learning alone. Tomasello et al. (1993) reasoned that if one individual would come up with a more efficient technique, for example of fishing termites, observers would only be able to adopt this improved variant if they were capable of imitation, i.e. faithful copying of the actions involved, because in the absence of the imitation ability other individuals would basically have to invent the novel technique independently. At that time, the consensus was that great apes did not have this ability (cf. Tomasello, 2001). However, the capacity for imitation in chimpanzees has been demonstrated more adequately since then (Hopper et al., 2007; Horner & Whiten, 2005; Whiten, 2005; Whiten et al., 2003; Whiten et al., 2009a). There are experimental data on orangutans suggesting they can imitate too (Bering et al., 2000; Bjorklund et al., 2000; Stoinski & Whiten, 2003; Whiten et al., 2004). An inability of faithful copying thus no longer qualifies as a valid reason for a lack of cumulative culture in apes.

Teaching, the second form of social learning Tomasello et al. (1993a) considered to allow cumulative cultural evolution, is not a uniquely human faculty. There is indeed only scant evidence for teaching in great apes (Whiten, 1989). Teaching is clearly present in other taxa (Hoppitt et al., 2008), but is unlikely to represent intentional teaching, *sensu* Caro and Hauser (1992), and cumulative culture almost inevitably requires intentional teaching. However, teaching may not have been as prominent in pre-agricultural human life, as only little overt teaching was found to occur in a traditional African society (Whiten & Milner, 1984) and among hunter-gatherer societies (Hewlett & Cavalli-Sforza, 1986) who nonetheless clearly do have cumulative forms of culture. Regardless, teaching is only relevant to the spread of cumulatively built-up innovations, not to their origin. Thus, at present there is no consensus about the importance of imitation and teaching as a prerequisite for cumulative cultural evolution (Boyd & Richerson, 1996; Caldwell & Millen, 2008b; Heyes, 1993; Laland, 2004; Laland & Hoppitt, 2003; Tomasello et al., 1993a).

As to the second reason, Laland (2004) suggested that cumulative culture is made possible by the ability to assess whether a novel solution to a problem yields a higher return than does an established behavior. In essence, this criterion amounts to whether an animal can recognize an innovation and the relative effectiveness of behavioral alternatives, and then switch to the better variant. In an experiment with chimpanzees, Marshall-Pescini & Whiten

(2008) found that chimpanzees having learned a first solution did not switch to a more productive alternative that was demonstrated to them. In another experiment, chimpanzees similarly did not even switch to a more productive alternative used by others in the same group when their own technique was made impossible (Hrubesch et al., 2009). Thus, a lack of recognizing superior alternatives and/or of flexibility to switch to them seems to be a promising candidate for explaining the lack of cumulative build-up of techniques in chimpanzees.

The third possible reason for the absence of cumulative culture is that, if observers have trouble recognizing the utility of an innovation, the same may hold true for the inventors themselves. Numerous innovations have been documented for great apes (van Schaik et al., 2006; Whiten et al., 1999), but few of them actually represent superior alternatives to a habitual behavior pattern found elsewhere, or if they do, they have been argued to represent innovations roughly all individuals could have invented on their own if all of the external and internal conditions were right (Tennie et al., 2009). Therefore the ability to produce superior alternatives might be limited in apes, at least as documented in wild populations to date.

The second and third obstacles both refer to a cognitive deficit pointing to a lack of flexibility. Flexibility is considered the hallmark of complex cognitive adaptations for tool use (Chappell & Kacelnik, 2002). In the tool-use context, flexibility is expressed in the ability to select an appropriate tool for a task. For instance, Chappell & Kacelnik (2002) showed that New Caledonian crows were able to select a stick matching the distance to the target. Similarly, Fox et al. (1999) showed that Sumatran orangutans selected tools of varying dimensions depending on detailed features of the task. But flexibility is more often expressed as producing an appropriate response when conditions have changed (e.g. Lefebvre et al., 1997; Piersma & Drent, 2003; Sol & Lefebvre, 2000; Sol et al., 2005). Behavioral flexibility (sometimes also called behavioral plasticity) has been described as the tendency to use novel means to adjust to environmental change (Lefebvre et al., 1997), or as the ability of individuals to express “distinct behaviors in different contexts through innovation and learning processes” (Sol et al., 2005). Species and populations with high behavioral flexibility are expected to be characterized by a high innovation frequency (Reader & Macdonald, 2003). Innovation is one component of behavioral flexibility, but the tendency for social learning and to use tools have also been considered components of behavioral flexibility (Reader & Laland, 2002). The concept of flexibility comes very close to that of intelligence (Byrne, 1995).

In sum, behavioral flexibility includes both the ability to innovate, as well as the ability to switch to another solution if appropriate (and thus recognizing its utility). We therefore use and define behavioral flexibility as individuals' continued interest in and acquisition of new solutions to a task, through either innovation or social learning, after already having mastered a previous solution. This behavioral flexibility is a vital precondition for cumulative build-up of techniques, and eventually for cumulative culture. As novel conditions arise, behavioral flexibility may be expressed as innovations that represent solutions that cumulatively build upon ("ratchet") previous ones.

Accordingly, the objectives of this study of captive orangutans were to investigate (1) their behavioral flexibility, i.e. their tendency to switch to other techniques when advantageous or necessary, and (2) their ability to show cumulative build-up of techniques as conditions are changing.

The first objective was to investigate whether captive orangutans satisfy the vital prerequisite for cumulative culture of behavioral flexibility by showing sustained acquisition of new solutions to a problem-solving task. We examined whether subjects would switch techniques, and thus relinquish established techniques, if this was advantageous to them, either because another technique was more efficient, or because the established technique has been made impossible by changing conditions of the task; or whether they would instead be conservative in the techniques they apply and would stick to an initially learned or established technique, as has been found for chimpanzees (Hrubesch et al., 2009; Marshall-Pescini & Whiten, 2008). We therefore initially provided a task under the regular condition that gave rise to potentially more solutions than were later possible under restricted conditions. If subjects behave flexibly, we expect them to switch techniques once their original technique was no longer possible. We also examined whether subjects improved gradually in selecting techniques that were not merely appropriate to solve the task, but also more efficient.

The second objective was to investigate whether the captive orangutans show cumulative build-up of techniques, as conditions of the task changed. The experimental setup to test for the subjects' behavioral flexibility was also designed to potentially lead to solutions cumulatively building up on previous ones. Tomasello et al. (1993a) recognize cumulative cultural evolution when members of a cultural group acquire a practice begun by others relatively faithfully, and then modify it as needed to deal with novel exigencies, which is again acquired by others. Novel exigencies, or changing conditions, are thus part of this description of cumulative culture, suggesting that without such novel exigencies there would be no cumulative build-up of techniques. (Note, however, that a more demanding level of

cumulative culture could potentially be based on cumulative change under constant conditions).

Methods

Animals and living conditions

The study was conducted in Zurich Zoo. Subjects were not deprived of food or water. The zoo population consisted of 9 Sumatran orangutans, 7 females (ages: Lea 40 (did not participate); Timor 32; Selatan 24; Oceh 19; Tuah 14; Xirah 10; Cahaya 5) and 2 males (ages: Djarius 13; Dahulu 4 (the latter excluded from examination due to young age)). For examination we could therefore use seven subjects. The orangutans were socially housed in one main indoor cage (480 m³), an adjacent smaller indoor cage (192 m³) and an outdoor cage (188 m³). They also had the possibility to retreat in boxes formerly used as sleeping boxes. The cages were equipped with tree trunks and ropes, which allowed the animals to show their natural locomotion, and a water source; an environmental enrichment program was provided almost daily.

Apparatus

The task was inspired by the challenge of acquiring water from a deep tree hole in the wild. Wild orangutans have been observed to use two innovative behaviors to get to water in this context: “Branch scoop” (using leafy branch to dip in water) and “Sponging” (absorb water with crumpled leaflets) (van Schaik et al., 2006). To transfer this task into an experimental setup in captivity, we used two transparent tubes that were maximally one quarter full with syrup. Two types of tubes were used: Both were 35 cm in height, but they differed in their inner diameter, which was either 10 cm or 5 cm. The wide tube allowed all animals to reach about 20 cm into the tube with their hands, except for the adult male (whose hands were too large). In contrast, the narrower tube did not allow subjects to reach inside with their hand (except for the 4 year old youngster who was excluded from the analyses).

Procedure

Experiments were performed at the main indoor cage and orangutans were tested as a group. Two tubes of the same type were attached to the outside of the main cage, at a distance of approximately 2 meters from each other. Subjects could reach with their arms through the grid of the cage to interact with the tubes. Experimental sessions usually lasted 90 minutes; maximally two sessions were run per week. For an overview of the experimental procedure see Table 3.1. The experiment consisted of the following three phases:

1) Regular condition (REG): First, under the regular condition we used the wide tubes where animals could reach inside with their hands. We expected some of the orangutans' solutions to take advantage of the possibility to reach about halfway inside the tube with the hand. Subjects were provisioned with sticks, leafy twigs, wood wool and paper. Seven sessions of 90 minutes each were performed.

2) Restricted condition 1 (RC1): Second, under the "restricted condition 1" we used the narrower tubes, where animals could no longer reach inside with their hands, to test subjects' behavioral flexibility (objective 1). Hence, the number of possible techniques was restricted to techniques that did not involve reaching partly inside the tube with the hand. Seven sessions under the restricted condition were performed following the last session under the regular condition, the first one lasting only 40 minutes (due to problems with fixing the tubes to the cage), the other six 90 minutes each. We investigated the behavioral response of subjects whose preferred techniques of the regular condition were inhibited under the "restricted condition 1". We aimed at examining whether they would quickly reduce the application of those techniques that no longer yielded a return and switch to different, functional and efficient techniques.

3) Restricted condition 2 (RC2): To test for cumulative build-up of techniques under changing conditions (objective 2), the experiment under the restricted condition was continued, but at the 8th session we added a further restriction by removing the supply of leafy twigs, inhibiting the "Branch scoop" behavior known from the wild. This new condition served to suppress the hitherto favorite techniques. Another seven sessions of 90 minutes each were performed, for a total of 14 sessions with the narrower tube. By inhibiting preferred efficient techniques we intended to keep subjects' motivation high to acquire new solutions, which might potentially lead to cumulative build-up of techniques.

Table 3.1: Experimental setup

Task	Regular condition	Restricted condition 1	Restricted condition 2
Tube diameter	10 cm	5 cm	5 cm
Sticks, wood wool, paper	Yes	Yes	Yes
Leafy twigs	Yes	Yes	No
Duration	7 sessions of 90 min	1 session of 40 min, 6 sessions of 90 min	7 sessions of 90 min
Techniques	Regular condition	Restricted condition 1	Restricted condition 2
Efficient techniques shown	Branch Scoop, Fish, Twisted paper rod, Vegetable rod, Paper squash, Wood wool squash, Twig squash, Sponging	Branch Scoop, Fish, Twisted paper rod, Vegetable rod, Squash- and-fish	Fish, Twisted paper rod, Vegetable rod, Squash- and-fish, Drop-and-fish
Non-efficient techniques	Dip stick	Dip stick	Dip stick
Impossible techniques		Paper squash, Wood wool squash, Twig squash, Sponging	Branch scoop, Paper squash, Wood wool squash, Twig squash, Sponging

The experiment consisted of three phases: (1) Regular condition, (2) restricted condition 1, where the tube was narrowed, and (3) restricted condition 2, where the supply with leafy twigs was stopped

Table explicitly states for every phase of the experiment which of the shown techniques were efficient, inefficient, or made impossible

Criteria of cumulatively built-up techniques

We used the following criteria for innovative techniques to qualify as cumulatively building up on previous techniques, and thus allow cumulative culture. First, the new technique is more complex (Boesch & Tomasello, 1998; Tomasello et al., 1993a), i.e. its range of application is larger (Boesch & Tomasello, 1998), the number of physically distinct constituent components (also called “technounits”) is higher (Oswalt, 1976), or the number of behavioral steps involved is higher. Second, the new technique is an elaboration of a previous one, i.e. includes a variation or a behavioral element of a previous one, as suggested by Marshall-Pescini & Whiten (2008). Therefore we only expect individuals that have used the specific component technique(s) to master the corresponding built-up technique. Otherwise the technique does not qualify as cumulatively built-up.

Behavioral coding

Techniques were categorized based on their efficiency to gain syrup and on the range of conditions under which they worked. Efficiency of a technique depended on the absorptivity of the material used. Techniques that yielded only a low return because the material used absorbs very little fluid (here a bare stick) were assigned as non-efficient techniques. Efficient techniques involved materials that soak up fluids (e.g. paper, wood wool, leaves of a leafy twig). There were techniques that were efficient to acquire syrup in all phases of the experiment; several others were efficient under the regular condition but not possible under restricted conditions 1 and 2; and one technique (Branch scoop) was efficient in REG and RC1 but was made impossible in RC2. An overview of the suitability of the different techniques under the three conditions is provided in Table 3.1.

Data coding and analyses

The experiments were all recorded with two video cameras, each directed at one tube. Continuous behavior sampling was done from video records. Statistics were calculated in SPSS 14.0. Page's L Trend Test (Page, 1963) was used to test for successive improvement in the use of techniques over the seven sessions under REG and RC1.

Results

All individuals, except the oldest female, participated in the task and actively manipulated the syrup-tubes in all the three conditions for varying, but always substantial, amounts of time. The duration of the three conditions were similar, ranging from 10 to 10.5 hours; given that two tubes were provided this allowed interaction times with a tube summed over all subjects of 20 to 21 hours under all three conditions. The tubes were used by subjects for the majority of the time, but because they remained unoccupied for a sufficiently long part, roughly 7 hours for each of the three conditions, individual access to the task was not limited (Table 3.2).

Table 3.2: Individuals' participation in the task under the three different conditions

Individual	Regular condition	Restricted condition 1	Restricted condition 2
Ca	00:55:12	01:22:06	02:07:34
Dj	00:08:44	00:07:00	00:02:47
Oc	04:12:55	03:35:14	04:48:31
Sel	03:35:09	03:06:59	02:46:49
Ti	00:31:59	00:27:25	00:19:12
Tu	02:34:22	03:19:45	04:00:40
Xi	00:42:01	00:46:52	00:15:08
None ^a	07:08:30	07:01:00	07:14:30

Participation is presented as duration (hh:mm:ss) of active manipulation with the tubes for each subject and condition

^a Indicates for how long either of the two tubes was not used by any subject

Regular Condition: Baseline

Under the regular condition (REG), the first solution to the task for six of seven test subjects was the use of a stick to dip into the syrup-tube and then licking syrup from the stick (“Dip stick”). Five subjects used this technique within the first 15 minutes. It did not yield a high return as sticks hardly absorbed any syrup; hence it was appraised as a non-efficient technique. But already within the first session, the subjects came up with four innovative and efficient techniques, using twigs, paper and wood wool, materials that all soaked up more syrup, and therefore these techniques were more efficient (see Table 3.3 for a detailed description of all techniques and the latency to first occurrence). Over time, subjects increasingly solved the task by applying efficient techniques (see Table 3.1 for an overview which techniques were efficient in which phase of the experiment), rather than by the simple but inefficient “Dip stick”. Page’s L Trend Test (Page, 1963) revealed that there was a highly significant trend for subjects to gradually increase their successful use of efficient techniques, expressed as a proportion of their total manipulation time ($L = 873.5$; $k = 7$; $n = 7$; $p < 0.01$).

Table 3.3: Techniques used to solve the syrup-tube task

Behavior	Description	Latency
Dip stick	Dip a bare stick into the tube, then lick the syrup from the stick	00:00:50
Paper squash	Force paper directly with hand into the tube, pull paper out, take it in mouth and suck it	00:39:15
Wood wool squash	Force wood wool directly with hand down into the tube, pull wood wool out, take it in mouth and suck it	00:40:15
Twig squash	Squash twig into the tube with hand reaching inside the tube, then pull twig out and suck it	04:33:00
Sponging	Paper or wood wool chewed to a ball is dropped inside the tube; then reach with hand down into the syrup, take it out by hand, take the whole piece into the mouth, chew and suck it (like chewing gum)	01:44:00
Branch scoop	Use a twig with leaves like a rod, so hand is only slightly or not at all inside the tube; pull twig out, then suck syrup out by gently chewing the leaves	00:12:30
Fish	Use a stick to get out leaves, paper or wood wool that have accrued in the tube by simultaneously pushing such an item with the stick against the inner wall of the tube and lifting the stick upwards	00:11:17
Twisted paper rod (TPR)	Twist paper and use it as a rod by holding one end down in the syrup, pulling it out, and sucking it	09:59:00
Vegetable rod	Use vegetables like leek or chard as a rod by holding it down in the syrup, pulling it out, and sucking it	02:46:00
Squash-and-fish	Use a stick to force paper down into the syrup; get paper out by simultaneously pushing the paper with the stick against the inner wall of the tube and pulling the stick upwards	19:21:00
Drop-and-fish	Paper or wood wool chewed to a ball is dropped inside the tube; get it out by simultaneously pushing the paper ball with a stick against the inner wall of the tube and pulling the stick upwards	20:23:25

Descriptions are given of all techniques the subjects used to solve the syrup-tube task

Additionally, the latency (hh:mm:ss) from the beginning of the experiment till the first occurrence of each technique is given

What kind of techniques did subjects use in phase REG? We determined subjects' most preferred techniques by analyzing their manipulation activities in the last two sessions (in REG) they were actively engaged with the task. Subjects showed substantial variation in their most preferred techniques, with the four most commonly used techniques distributed across seven different individuals (Table 3.4). One subject (Sel) preferred to use efficient

techniques that would still be possible under the “restricted condition 1” (RC1, the next experimental phase) for most of its manipulation time (Table 3.4): “Branch scoop” (74.5%), “Twisted paper rod” (21.4%) and “Vegetable rod” (4.1%). Five individuals (Ca, Oc, Ti, Tu, Xi) faced the problem that they almost exclusively preferred to use efficient techniques that had been efficient so far in phase REG but that would no longer be possible in the next experimental phase RC1 (“Paper squash”, “Wood wool squash”, “Twig squash”, “Sponging”) with the narrower tube (Table 3.4). All five animals had used those efficient techniques that would still be possible in phase RC1 (see Table 3.1) only for less than 3% of their total manipulation time in REG; one had never performed any such technique. These five animals were therefore the focus of the next experimental phase RC1. Would they quickly reduce the application of techniques that no longer work and flexibly switch to other solutions that are efficient?

Table 3.4: Subjects’ two favorite techniques used under the regular condition (REG)

Individual	Preferred Technique^a	% used	2nd preferred Technique^a	% used
Ca	Wood wool squash (REG)	65.4	Paper squash (REG)	20.3
Dj	Dip stick (inefficient)	100		
Oc	Wood wool squash (REG)	56.4	Paper squash (REG)	19.8
Sel	Branch scoop (REG & RC1)	74.5	Twisted paper rod (REG & RC1)	21.4
Ti	Paper squash (REG)	51.3	Sponging (REG)	43.6
Tu	Paper squash (REG)	74.1	Wood wool squash (REG)	14.5
Xi	Wood wool squash (REG)	59.9	Paper squash (REG)	24.1

Subject’s preferred techniques are indicated as percentage of their successful manipulation time in the last two sessions of the regular condition

^a In parentheses it is stated whether a technique was inefficient, efficient in the regular condition only (REG), or if the technique was efficient in the regular condition as well as in the following experimental phase, the restricted condition 1 (REG & RC1)

Objective 1: Flexibility to abandon a non-functional technique and switch to a functional technique

a) Switch 1: Regular condition – restricted condition 1:

During RC1 (restricted condition 1), the tubes were made 5 cm narrower. One subject (Selatan) under REG exclusively preferred efficient techniques that would still work with the narrower tube, and she kept on applying these techniques in RC1. Five subjects (Ca, Oc, Ti,

Tu, Xi) had preferentially used efficient techniques during REG that were no longer possible in RC1, with the narrower tube (Figure 3.1a: left half: dashed line). These five subjects largely still tried to apply them in vain in the first RC1 session, but then gradually reduced the proportion of their manipulation time dedicated to these now ineffective techniques, and after the fourth session these techniques had almost completely been abandoned (Figure 3.1a: right half: dashed line). Page's L Trend Test revealed that subjects highly significantly reduced applying these techniques over the seven sessions under the "restricted condition 1" ($L = 660$; $k = 7$; $n = 5$; $p < 0.001$).

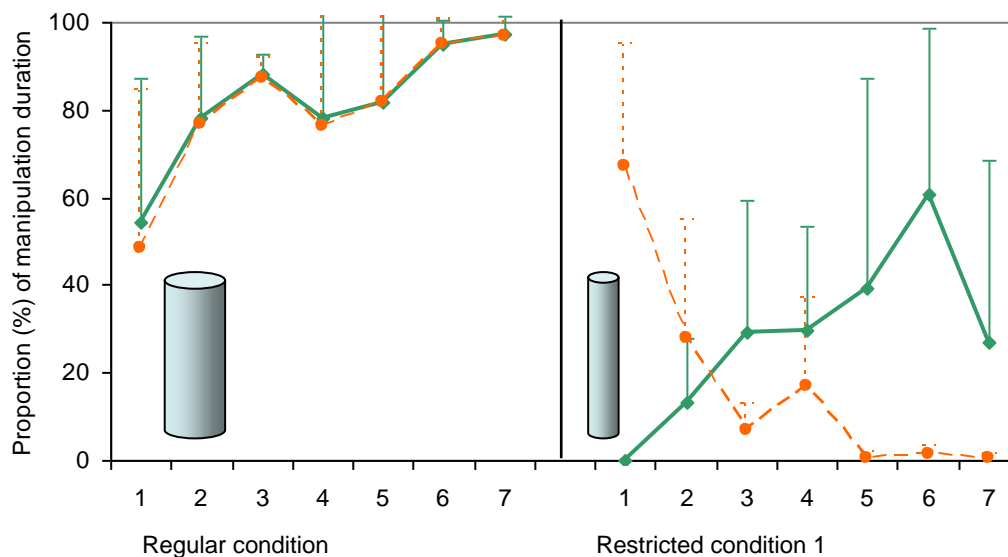


Figure 3.1a: Behavioral flexibility 1: Regular condition – restricted condition 1:

Bold line: Average proportion of total manipulation time used by subjects ($N = 5$: Ca, Oc, Ti, Tu, Xi) for performing efficient techniques in the seven sessions under regular condition (REG) and, after novel exigencies had been created by providing a narrower tube, in the seven sessions under restricted condition 1 (RC1).

Dashed line: Average proportion of techniques that were efficient in REG but that had been made impossible in RC1, thus in RC1 indicating how much subjects in vain still tried to apply them.

Means and SD are shown. Flexibility demonstrated by those five subjects forced to abandon their preferred techniques and to switch to different techniques.

As they reduced applying previously efficient techniques, they could either have gone back using the non-efficient technique "Dip stick" all but one of them had used initially under the regular condition (which would still work), or they could have switched to efficient techniques they had used only very rarely in REG (totaling 0-3% of their manipulation time) or had not learned yet at all. Indeed, initially they all relied on the non-efficient technique

“Dip stick” to gain syrup, averaging 77.4 % of their successful manipulation time in the first two sessions of RC1, but they more and more started using techniques that were efficient in RC1 (Figure 3.1a: right half: bold line; see Table 3.1 for efficient techniques in RC1). Page’s L Trend Test revealed a highly significant trend of subjects gradually increasing successful use of techniques efficient in RC1 as a proportion of their total manipulation time ($L = 622.5$; $k = 7$; $n = 5$; $p < 0.01$). So finally, all five animals that had been forced to abandon their hitherto preferred techniques successfully did so and switched to techniques that were functional and efficient under RC1 (Figure 3.1a). For the whole study group the preference for these efficient techniques was significantly greater in RC1 than in REG (Wilcoxon signed-ranks test: $Z = -2.023$; $N = 7$; $p = 0.043$). Thus, despite some initial reluctance, the orangutans in this study were able to switch to new techniques when their preferred old technique was made impossible.

b) Switch 2: Restricted condition 1 – restricted condition 2:

In the last two sessions of RC1, four subjects (Sel, Ti, Tu, Xi) used the “Branch Scoop” technique for an average of 75.2% of their manipulation time (Figure 3.1b: left half: dashed line). Under RC2 (restricted condition 2), the supply with leafy twigs was terminated to inhibit the “Branch Scoop” technique. These four individuals had to abandon their preferred technique, three of them (Ti, Tu, Xi) for the second time. They were forced to use techniques in RC2 (see Table 3.1 for efficient techniques in RC2) they had not used much in RC1 (totaling 3-21% of their manipulation time), or not learned yet at all. Subjects again demonstrated high behavioral flexibility by abandoning a preferred technique (Branch scoop) and successfully switching to different efficient techniques (Figure 3.1b). For the whole study group the preference for efficient techniques other than “Branch Scoop” was significantly greater in RC2 than RC1 (Wilcoxon signed-ranks test: $Z = -2.023$; $N = 7$; $p = 0.043$).

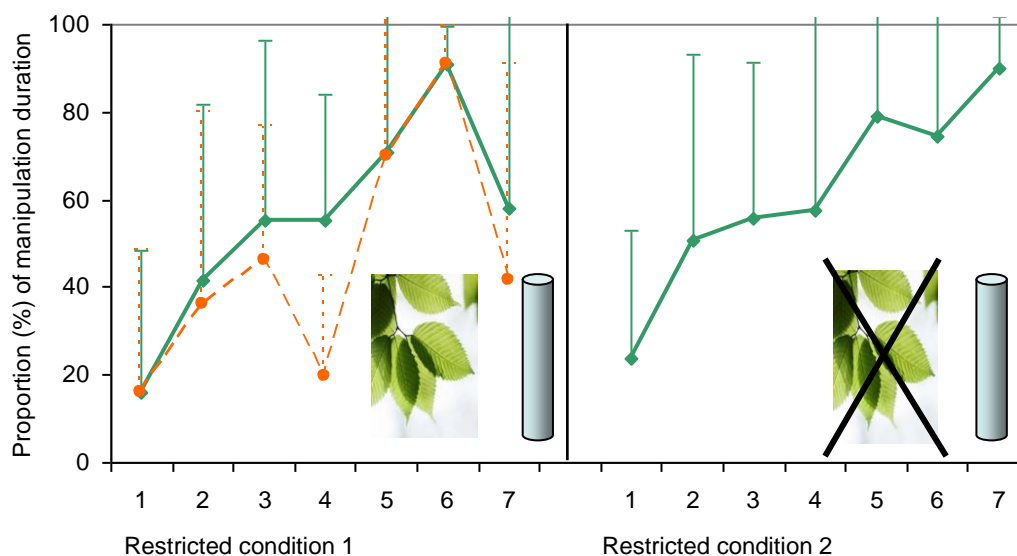


Figure 3.1b: Behavioral flexibility 2: Restricted condition 1 – restricted condition 2:

Bold line: Average proportion of total manipulation time used by subjects ($N = 4$: Sel, Ti, Tu, Xi) for performing efficient techniques in the seven sessions under restricted condition 1 (RC1) and, after novel exigencies had been created by terminating the supply with twigs, in the seven sessions under restricted condition 2 (RC2).

Dashed line: Average proportion of technique “Branch scoop” that was efficient in RC1 but impossible in RC2.

Means and SD are shown. Flexibility demonstrated by those four subjects forced to abandon their preferred technique “Branch scoop” and to switch to different techniques.

Objective 2: Cumulative build-up of techniques?

During restricted conditions, two solutions eventually emerged that fulfilled the criteria of a cumulatively built-up (ratcheted) technique: the “Squash-and-fish” technique and the “Drop-and-fish” technique.

The “Squash-and-fish” technique builds up on the techniques “Paper-squash” and “Fish” (see Table 3.3 for definitions) and was first invented by one animal (Ti) in the last session of RC1, i.e. after more than 19 hours of experimentation. In “Squash-and-fish” a subject uses a stick to push some paper down the tube into the syrup. After the paper had soaked up syrup, the subject removed it by simultaneously pushing the paper with the stick against the inner wall of the tube and pulling the stick upwards. The “Squash-and-fish” technique fully meets our two criteria for a ratcheted technique. First, it is more complex than “Paper-squash” for two reasons: it involves an additional component (the stick), and it can be applied in a greater number of situations, namely with both the wide and the narrow tube. Second, it represents an elaboration of the previous technique “Paper-squash”, as the stick

substitutes for hand and arm. The progress on the technique “Fish” is also obvious. When applying the technique “Fish,” a subject took out any objects that had happened to fall into the syrup before through somebody’s actions. In contrast, with “Squash-and-fish” a piece of paper or wood wool was put into the syrup and then immediately afterwards taken out again by the same single individual. The techniques “Paper-squash” and “Fish” are both clearly pre-stage techniques of “Squash-and-fish”, as only subjects that first used both these component techniques (Ca, Ti, Tu) later performed the final ratcheted technique “Squash-and-fish” (Figure 3.2a; Fisher exact test: $N = 7$; $p = 0.029$). No subject directly learned the technique “Squash-and-fish” without having learned “Paper-squash” and “Fish” before (more detailed information about the latencies after which subjects successfully performed these three techniques is illustrated in Appendix 3.1).

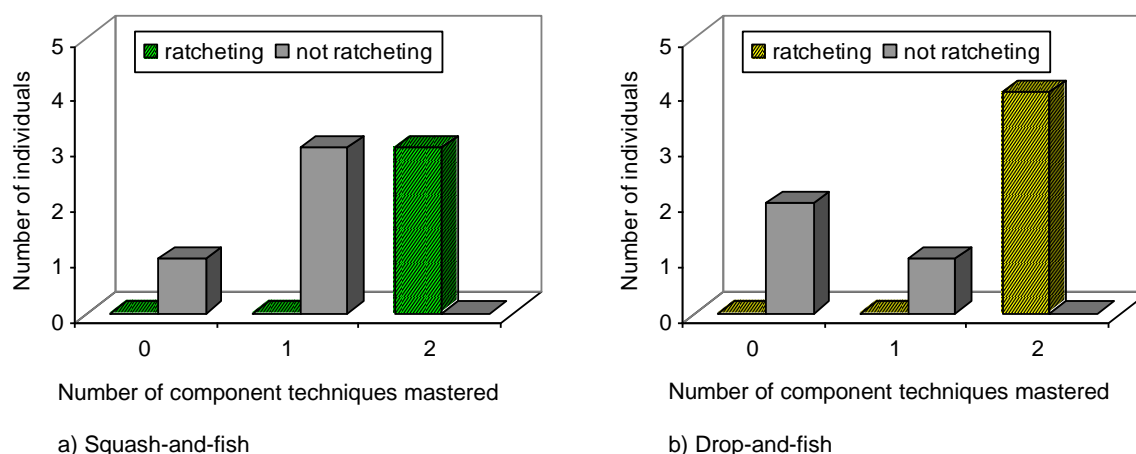


Figure 3.2: Cumulative build-up of techniques: Shows how many individuals succeeded to perform the ratcheted techniques (ratcheting: hatched) and how many failed (not ratcheting: gray), depending on whether they had previously mastered 0, 1, or both its component techniques, for (a) the technique “Squash-and-fish” and (b) the technique “Drop-and-fish”.

The second ratcheted technique they invented is “Drop-and-fish”. It builds up on the techniques “Sponging” and “Fish” (see Table 3.3 for definitions) and was first discovered by a subject (Tu) in the first session of RC2, i.e. after more than 20 hours of experimentation. In “Drop-and-fish”, paper or wood wool chewed to a ball is dropped into the syrup; after that ball had soaked up syrup the subject would take it out by simultaneously pushing the paper with the stick against the inner wall of the tube and pulling the stick upwards. “Sponging” and “Fish” are obviously pre-stage techniques of “Drop-and-fish”, as only subjects that first used

both these component techniques (Ca, Ti, Tu, Xi) later performed the final ratcheted technique “Drop-and-fish” (Figure 3.2b; Fisher exact test: $N = 7$; $p = 0.029$). Subjects had to know both component techniques to master the ratcheted technique (more detailed information about the latencies after which subjects successfully performed these three techniques is illustrated in Appendix 3.2).

Discussion

Behavioral flexibility (objective 1)

This study first demonstrated that captive orangutans of Zurich Zoo complied with the vital prerequisite for cumulative culture of behavioral flexibility by showing continued interest in acquiring new solutions to a problem-solving task, and furthermore by switching to other techniques and relinquishing established techniques when this was advantageous.

Even under the regular condition, subjects kept exploring the problem and acquiring new solutions despite having mastered an initial technique. Most subjects started with a non-efficient technique (“Dip stick”), but then spontaneously came up with innovative and more efficient solutions, and eventually largely switched to these and preferentially used them. Minimally, this indicates that they recognized which of two techniques yields a higher return, which has been suggested as a prerequisite for cumulative culture (Marshall-Pescini & Whiten, 2008; Laland, 2004). At the same time, most individuals kept on using a variety of techniques under the regular condition, predicting they would show high flexibility to abandon preferred techniques and switch to different techniques as the condition was changed. Moreover, subjects showed great diversity in their most preferred techniques (with the four different most preferred techniques distributed across seven different individuals) which would not be expected if subjects followed rules of conformity (Henrich & Boyd, 1998), where they had ended up with one technique being preferred in the group. We return to this topic below.

As the condition was restricted a first time by narrowing the tube, those five subjects whose preferred efficient techniques had thereby been made impossible, initially still unsuccessfully tried to apply them. Conservative subjects (cf. Hrubesch et al., 2009) would continue to do so for a long time. But the orangutans in this study gradually reduced the

proportion of manipulation time dedicated to vainly apply their preferred techniques that no longer yielded a return. Instead, they first switched back to the non-efficient technique “Dip stick” that all but one of them had used initially under the regular condition, but eventually they began to switch to more efficient techniques. We found that these subjects in the “restricted condition 1” (RC1) significantly increased the use of different techniques that were functional and efficient but that they had hardly ever used before (in the regular condition less than 3% of their total manipulation time) or not known at all, revealing a high level of behavioral flexibility.

As the condition was restricted a second time by removing all leafy twigs, the “Branch scoop” technique that had become the preferred technique of four individuals was made impossible. Subjects again demonstrated a high flexibility to abandon a preferred technique that had been made non-functional and to switch successfully to different, functional and efficient techniques.

Such flexible switching of techniques contrasts with the findings of chimpanzees in similar situations, where several studies report them to show a bias of conformity or conservatism (Bonnie et al., 2007; Hrubesch et al., 2009; Marshall-Pescini & Whiten, 2008; Whiten et al., 2005). Conformity implies that individuals possess a propensity to preferentially adopt the solution being most common in the population, thus eventually leading to the same solution to a problem in the whole population (Henrich & Boyd, 1998). In a task where two different techniques were possible solutions, a substantial number of chimpanzees able to use both methods adopted the group’s norm, thus perhaps showing a conformity bias (Whiten et al., 2005). For the present purpose, it is irrelevant whether the chimpanzees showed true conformity in the sense of positive, frequency-dependent social learning where the probability of acquiring a trait increases disproportionately with the number of demonstrators performing it (Boyd & Richerson, 1985).

Alternatively, conservatism implies that individuals that had become proficient with a first technique did not switch to the second one that was considered more efficient, not even after the first technique had been made ineffective (Hrubesch et al., 2009). Thus, having learned a particular solution suppresses further exploration of the task and thus prevents the emergence of other solutions (Boyd & Richerson, 1985). Interestingly, Marshall-Pescini & Whiten (2008) also found that chimpanzees who had acquired a first solution to a task did not learn a second, more complex and productive solution that incorporated the core actions of the first technique. They concluded their chimpanzees to have become “stuck” on a technique

they had learned initially, inhibiting cumulative social learning and possibly constraining the species' capacity for cumulative cultural evolution.

Whether these chimpanzees showed conservatism or conformity, they showed very limited behavioral flexibility. However, for a proper comparison of the behavioral flexibility of orangutans and chimpanzees, the same experiments would have to be conducted in multiple groups of both.

Cumulative build-up of techniques (objective 2)

Second, this study demonstrated that captive orangutans were capable of cumulative build-up on previous techniques as conditions of the task changed. These ratcheted techniques were then also adopted by some other group members, suggesting that modest cumulative culture could actually be possible in captive orangutans, at least if they have to deal with novel conditions.

As we restricted conditions of the task, first by using a narrower tube, and second by ceasing to supply the animals with leafy twigs, we inhibited most of the efficient techniques used preferentially under the regular condition. This kept subjects' motivation high to invent and acquire new solutions, as they were very eager to get syrup. Indeed, they eventually came up with two solutions that fulfilled the criteria of a ratcheted technique (and that would allow cumulative culture). These techniques were more complex and they were performed only by subjects that had mastered the pre-stage techniques previously.

Finally, although it was not within the scope of this study to study social learning, to amount to cumulative culture the ratcheted techniques would have to be adopted by other group members (Boesch & Tomasello, 1998). Indeed, in our group the two ratcheted techniques "Squash-and-fish" and "Drop-and-fish" were performed by three and four subjects, respectively. Subjects that acquired such a technique, after a first individual invented them, previously observed the performance of the new technique, suggesting they used this social information to adopt the ratcheted techniques by socially mediated learning, establishing a cumulative tradition.

Novel exigencies, or changing conditions, are part of Tomasello et al.'s (1993a) description of cumulative culture, which suggests that without such novel exigencies there would be no cumulative build-up of techniques. In our present study, we created novel exigencies by changing conditions of the task. Indeed, this was probably crucial for the invention of the two ratcheted techniques. Although subjects showed exploration during the

regular condition, the invention of these ratcheted techniques was clearly stimulated by the inhibition of previous solutions. This could explain why cumulative build-up of techniques was possible in this set-up and a cumulative tradition was established in the present group of captive orangutans.

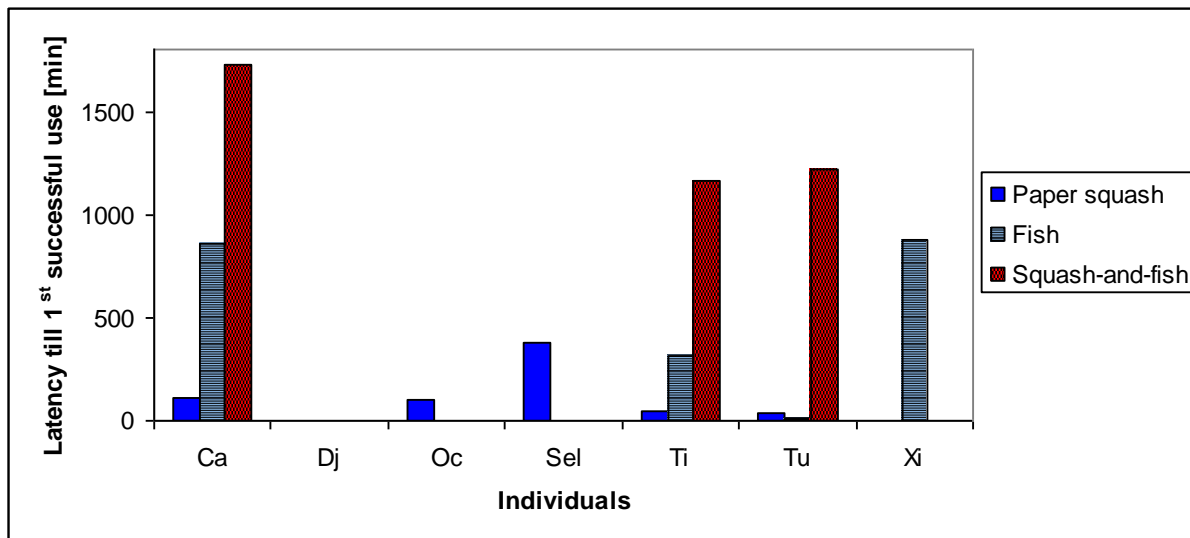
From the wild, there are no similar observations of cumulative build-up of techniques in orangutans up to date. They largely seem to fail to produce superior innovations in the first place. Indeed, captive and ex-captive rehabilitant orangutans have been found to be far more innovative than wild ones (Lehner et al., 2010; Russon et al., 2010; Russon et al., 2009). Lehner et al. (2010) suggested that captive orangutans associate novelty with the presence of food rewards, thus favoring the appearance of innovations and, given excellent conditions for social transmission, their retention. This leads to larger innovation repertoires in captive populations compared to wild ones. Consequently, cumulative build-up of techniques can be expected to occur in captive orangutans more likely than in wild conspecifics as well.

Given this contrast between captive and wild subjects, it would be interesting to introduce our present experiment into a wild population of orangutans. We would first choose a population where orangutans have been observed by van Schaik et al. (2006) to use the techniques “Branch scoop” (in Suaq Balimbing on Sumatra) or “Sponging” (Ketambe, Sumatra) to collect water from a deep tree hole. Supposing they would voluntarily approach and engage with the set-up we could eventually compare their performance with the captive subjects. Potentially, this might lead to the foundation of the same cumulative tradition in wild orangutans too.

Our findings suggested that creating novel exigencies by inhibiting preferred techniques was crucial to motivate subjects to modify and improve on present solutions. We will address this possible influence of novel exigencies in a subsequent experiment with our group of captive orangutans of Zurich Zoo. A more stringent test for a population’s potential for cumulative culture would be to investigate the ability for cumulative build-up of techniques under constant conditions. Nevertheless the results presented here showed that cumulative build-up of techniques is not per se a uniquely human characteristic, because two ratcheted techniques were invented by the orangutans of Zurich Zoo. This suggests that modest cumulative culture could be possible in captive orangutans, at least when they have to deal with novel exigencies.

Appendix

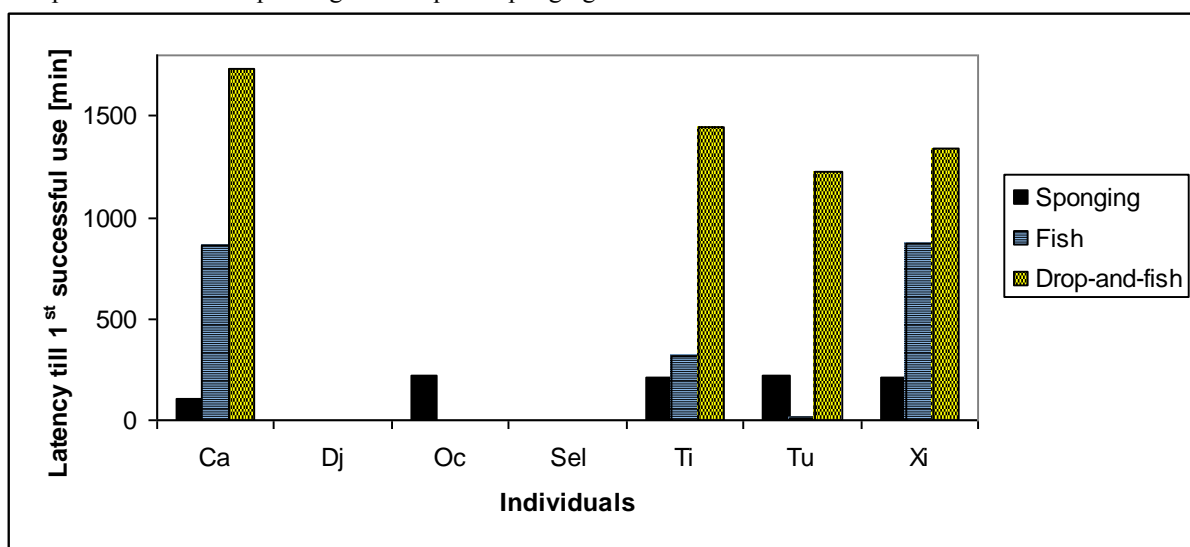
Appendix 3.1: Latencies (min) till individuals' (N = 7) first successful performance of the ratcheted technique "Squash-and-fish" and its pre-stage techniques "Paper squash" and "Fish"



The total duration of the syrup-tube experiment was 1860 minutes, whereof the first 615 minutes were conducted under the regular condition, the rest under restricted conditions.

One individual's (Tu) latency for "Fish" was only 11 minutes, which is not well visible in this figure.

Appendix 3.2: Latencies (min) till individuals' (N = 7) first successful performance of the ratcheted technique "Drop-and-fish" and its pre-stage techniques "Sponging" and "Fish"



The total duration of the syrup-tube experiment was 1860 minutes, whereof the first 615 minutes were conducted under the regular condition, the rest under restricted conditions.

One individual's (Tu) latency for "Fish" was only 11 minutes, which is not well visible in this figure.

Chapter 4

Cumulative build-up of techniques in captive orangutans: the role of novel exigencies

Striking geographic variation in behavior provides evidence for culture in our close relatives, chimpanzees and orangutans. However there is a vast discrepancy in cultural accomplishments between human and great apes, arguably due to cumulative build-up of techniques being a human uniqueness. Cumulative cultural evolution refers to cultural traditions that have changed over time and accumulated modifications made by different individuals in the direction of greater complexity. Indeed, in recent experiments, captive chimpanzees were found to conservatively stick to a technique they had learned earlier, thus preventing cumulative social learning. Orangutans, however, demonstrated high behavioral flexibility, modifying preferred techniques when this became necessary. Our main objective here therefore was to investigate in orangutans whether ratcheting of techniques requires novel exigencies or whether they can also arise spontaneously under constant conditions; and second, and if not, whether orangutans can learn ratcheted techniques through socially mediated learning if they are demonstrated to them. We presented nine Sumatran orangutans a foraging box similar to one used for chimpanzees. The task could be solved in roughly two different ways, one of which cumulatively built upon the other one. We found that novel exigencies were indeed required for the emergence of the cumulatively built-up technique. These results showed that captive orangutans could learn something by social mediation they previously failed to learn on their own. We discuss these results in the light of a recently suggested concept called “the zone of latent solutions” that we suggest can be expanded by social learning.

Introduction

Striking behavioral variations among long-term study sites in our closest relatives, chimpanzees (Boesch, 1996; McGrew, 1992; Whiten et al., 1999) and orangutans (van Schaik et al., 2003), have been regarded as evidence of culture in these species, depending on one's definition. In comparison to most reports in non-primate species where only one or a few cultural behaviors have been identified, the number of such traditions identified in chimpanzees (Whiten et al., 2001; Whiten et al., 1999) and orangutans (van Schaik et al., 2003; van Schaik et al., 2006) was much larger (≥ 39 and ≥ 24 , respectively). Moreover, the assessment of innovations in the wild was largely confirmed experimentally in case of the orangutans (Lehner et al., 2010). Thus the strongest arguments for culture in non-human species can be made in our closest relatives, chimpanzees and orangutans. This would then also hint at a more ancient ancestry in the phenomena of culture, as explored in Whiten et al. (2009b).

Nevertheless there is no doubt that human cultures are maintaining many more traditions than the chimpanzee and orangutan cultures do. The difference in traditions is not only quantitative, but also qualitative, as humans use behavioral strategies and technologies that are much more complex. This vast discrepancy in cultural accomplishments between human and great apes could be due to cumulative culture. Indeed, human cultural traditions change over time, and many of them seem to accumulate modifications made by different individuals over time in the direction of greater complexity, which has been defined as cumulative cultural evolution or ratcheting (Tomasello et al., 1993a). By greater complexity Boesch and Tomasello (1998) meant that a wider range of functions is encompassed. Another way to recognize cumulative culture is whether it is likely that naïve individuals can invent the ratcheted technique on their own (Boyd & Richerson, 1996).

Arguably, cumulative culture is uniquely human (Henrich & McElreath, 2003; Tomasello, 2001; Tomasello, 1999b; Tomasello et al., 1993a). The first traceable archeological indication of cumulative build-up of technology is seen in the replacement of the Oldowan by the Acheulian stone industry (Mithen, 1999). The main question is to what extent great apes are capable of such cumulative build-up, or can be coaxed into inventing or adopting ratcheted techniques.

Whiten et al. (2003) and Boesch (2003) suggested that there are examples which could indicate that chimpanzees do have some power for cumulative build-up of techniques, at least in qualitative, modest terms. For instance, several chimpanzee populations crack nuts by

hitting them directly with the hand against tree trunks or use stone hammers to break harder and smaller nuts on stone anvils, but only at Bossou have some individuals been observed to occasionally use an additional stone to prop up the stone anvil, thus leveling it or increasing its stability (Matsuzawa & Yamakoshi, 1996; Sugiyama, 1997). However, because the technique did not reach customary status, one could doubt its interpretation as cumulative culture.

Recent reports of evidence for cumulative material culture in chimpanzees are more convincing. Chimpanzees in the Congo Basin have been found to use two or more different tools in one functional sequence in termite extraction or during honey gathering. In the latter case, they use a large club-like stick to pound open a beehive and then extract honey by dipping into the hive, using a smaller stick (Sanz & Morgan, 2009). While using a probe to dip into a beehive to extract honey is a widespread tactic used by chimpanzees in honey-gathering, pounding of beehives with a large club seems exclusive to populations of the Congo Basin (Sanz & Morgan, 2009). The “pound-and-dip” technique probably allows the chimpanzees to forage at many more sites than if they only possessed the dipping technique, makes additional beehives accessible and includes behavioral elements of the previous one. Thus, it is reasonable to consider the “pound-and-dip” technique as cumulatively building up on the dipping technique. Nonetheless, it is remarkable how rare such built-up techniques are, and explaining this rarity remains a priority if we are to explain the ape-human contrast in culture.

This question can be addressed experimentally with captive great apes. In a first experiment on cumulative culture in great apes Marshall-Pescini and Whiten (2008) investigated chimpanzees’ capacity for cumulative social learning by designing an apparatus whose food content could be extracted in two different ways. Both solutions were demonstrated to the subjects by a familiar human. The second technique incorporated the core actions of the first technique and was both more complex and more productive. Subjects that had previously learned the first technique did not learn the second more complex one, thus proving incapable of acquiring a cumulatively built-up technique through socially mediated learning. The authors concluded their chimpanzees had become “stuck” on a technique they had learned initially, which inhibited cumulative social learning and possibly constrains the species’ capacity for cumulative culture (Marshall-Pescini & Whiten, 2008). On the other hand, captive orangutans in a different experiment demonstrated a high flexibility to abandon a preferred technique that had been made non-functional for solving the task and to switch successfully to different, functional techniques (Chapter 3). More importantly, they invented

two techniques that cumulatively built up on previous ones; these built-up techniques were acquired by other group members, indicating that modest cumulative culture is possible in captive orangutans. Creating novel exigencies by inhibiting preferred techniques was probably crucial for subjects to modify and improve on present solutions, finally resulting in ratcheted techniques. Novel exigencies are part of Tomasello et al.'s (1993a) description of cumulative culture, which suggests that without such novel exigencies there would be no cumulative build-up of techniques.

The positive findings regarding cumulative build-up of techniques in orangutans (Chapter 3), as opposed to the negative findings in chimpanzees (Marshall-Pescini & Whiten, 2008), ask for further tests of orangutans' potential for cumulative culture by investigating their ability for cumulative build-up of techniques under *unchanging* conditions, as well as for comparable experiments. There is a variety of potential reasons why chimpanzees stuck to their first solution (Hrubesch et al., 2009) and failed to cumulatively build up on it (Marshall-Pescini & Whiten, 2008), whereas orangutans flexibly abandoned a preferred technique and switched to different techniques that were eventually cumulatively built-up on previous solutions (Chapter 3), apart from a species difference in behavioral flexibility in the application of techniques to a task. The studies differed in experimental designs regarding (i) the task used, (ii) changing conditions and novel exigencies, as well as presumably (iii) the cognitive demands of the tasks (possibly the ratcheted technique in the task of Marshall-Pescini and Whiten (2008) is beyond apes' cognitive capabilities).

The main objective of this study with captive orangutans was therefore to investigate whether novel exigencies further prove to be indispensable for cumulative build-up of techniques, or whether this is also possible under constant conditions. A secondary objective was to investigate whether orangutans could socially learn something they previously failed to invent by themselves. According to Tennie et al. (2009) chimpanzees only socially learn what they (i.e. some individuals) could learn for themselves, although one may doubt whether the Congo Basin chimpanzees could have independently invented their tool sets.

We performed an experiment using an apparatus functionally similar to the one used by Marshall-Pescini and Whiten (2008) to be able to compare results of orangutans and chimpanzees to a better extent than before. We first examined if under constant conditions subjects would spontaneously find both the simple solution first, and then also the second more complex solution that cumulatively builds up on the simple technique. Second, because subjects failed to find the ratcheted technique on their own, we investigated whether they could learn it from a familiar human demonstrator (by socially mediated learning). Third,

because subjects still did not succeed, a third phase of the experiment followed, where we created novel exigencies by making the first technique nonproductive, while demonstrations of the built-up technique were continued. Thus, we examined whether subjects could adopt a cumulatively built-up technique that was demonstrated to them (but they previously had not been able to invent on their own) if conditions of the task were changed and novel exigencies created. In this phase, an individual finally succeeded to learn the ratcheted technique.

Methods

Animals and living conditions

The study was conducted in Zurich Zoo. Subjects were not deprived of food or water. The zoo population consisted of 9 Sumatran orangutans, 6 females (ages: Timor 33; Selatan 26; Okeh 21; Tuah 16; Xirah 12; Cahaya 7) and 3 males (ages: Djarius 14; Dahulu 5; Hadia 1 [excluded from examination due to young age]). For examination we could therefore use eight orangutans. They were socially housed in one main indoor cage (480 m³) and an outdoor cage (188 m³). In addition they had the possibility to retreat in boxes formerly used as sleeping boxes, out of sight of the visitors. The cages were equipped with tree trunks and ropes, which allowed the animals to show their natural locomotion, and a water source; an environmental enrichment program was provided almost daily. Experiments were performed in the main indoor cage with the whole group.

Apparatus

Subjects were presented with a foraging box (l = 25cm, w = 15cm, h = 15cm) originally containing syrup and peanuts. A transparent window (9 x 9 cm) in the front allowed animals to look into the wooden box. In the front of the box there was a tunnel with a recessed bolt inside that locked the lid at the top of the box. This lid had a hole (d = 1cm) that was covered by a transparent trap door; the hole led to the box's content. The size of the hole did not allow zoo orangutans to insert a finger, as we absolutely did not want to give subjects the possibility to lever open the lid by any other means than inserting a stick in the hole, because this is crucial for the "Poke and Lever" technique to qualify as a ratcheted technique (explanation to follow where describing the "Poke and Lever" technique). This is an

important and intentional difference to the box used by Marshall-Pescini and Whiten (2008) where the hole happened to be wide enough for chimpanzees to insert a finger and to lever the lid open with the finger. In its home position the box's lid was locked by the recessed bolt and the trap door covered the lid's hole (Figure 4.1a).

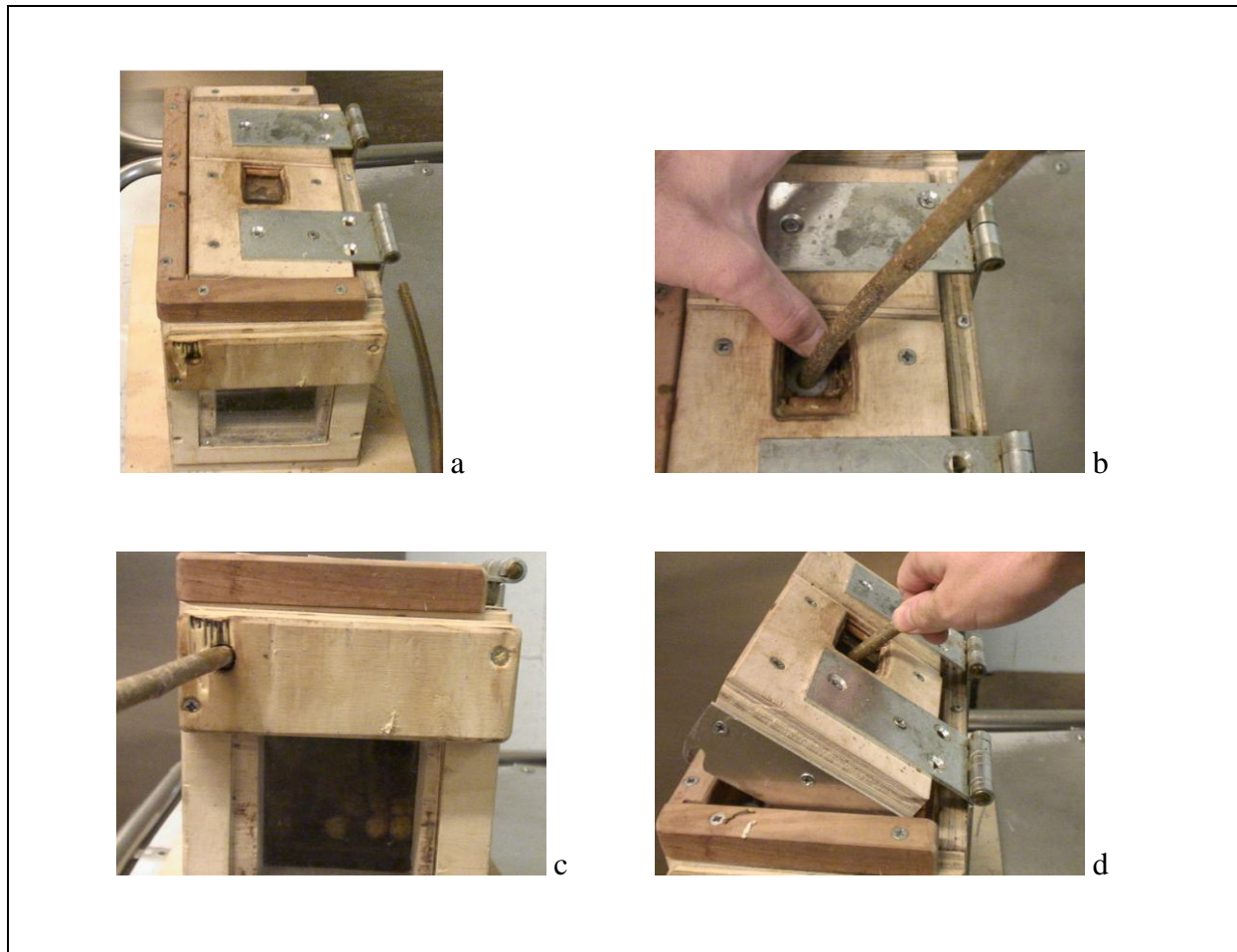


Figure 4.1: Foraging box and its techniques. a) Overview of box in its home position. b) “Dipping” technique. c) “Poke and Lever” technique: Poke. d) “Poke and Lever” technique: Lever.

The foraging box was constructed so it could be solved in two different ways, by either “Dipping” or “Poke and Lever”.

(1) “Dipping” technique: Sliding open the trap door by pushing it back with a finger, thereby exposing the hole of the lid, and whilst holding on, use other hand to dip a stick into the revealed hole down into the syrup (Figure 4.1b), pull stick out and lick syrup from stick. In addition to this “intended” dipping technique we distinguished two slight variations of dipping techniques where the trap door was let go before pulling the stick out or where the

same stick was used to both open the trap door and dip in the revealed hole, as described in more detail in Table 4.1.

(2) “Poke and Lever” technique: Using a stick to poke the recessed bolt inwards, thereby unlocking the lid at the top (Figure 4.1c). Slide open the trap door with a finger and use the other hand to insert a stick into the hole (as in the “Dipping” technique), let trap door go, lever open the lid, making all the contents available (Figure 4.1d). Within the latter technique a variation of the first technique is contained, and while the “Dipping” technique makes only little amounts of syrup accessible (and no peanuts), the second one allows rapid access to both syrup and peanuts, making the “Poke and Lever” technique a solution cumulatively building up on the “Dipping” technique. Holding the trap door open and dipping a stick in and out of the hole in the “Dipping” technique is modified to letting the trap door go after having put the stick in the hole, so the stick is blocked in the hole and the lid can be levered open in the “Poke and Lever” technique. Thus, broadly summarized, the components of “Poke and Lever” are “Poke” and a modification of “Dipping” (see also Figure 4.2). Therefore subjects are expected to first show both “Poke” and “Dipping” before mastering “Poke and Lever”.

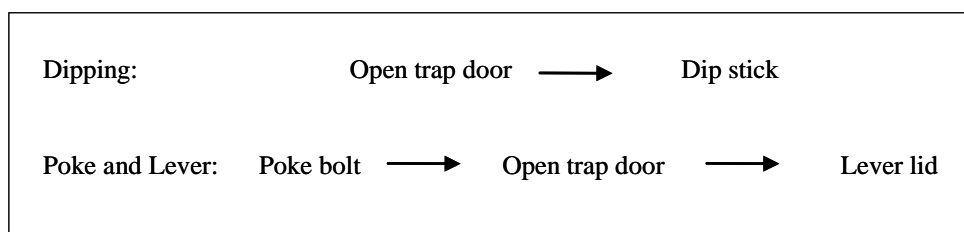


Figure 4.2: The task could be solved by two techniques: 1) Dipping, 2) Poke and Lever.

For a detailed description of the techniques see Table 4.1.

The “Poke and Lever” technique stringently must include a variation of the “Dipping” technique, in order to be a ratcheted technique. Therefore we prohibited subjects to lever the lid open in any other way than putting a stick in the lid’s hole, e.g. by inserting a finger into the hole instead of a stick, or by inserting fingernails along the lid; such forms of “Poke and Lever” would not qualify as cumulatively building up on “Dipping”. See Table 4.1 for an overview of the main behaviors that were recorded along with their descriptions.

Table 4.1: Descriptions of the main behaviors that were distinguished in context with the foraging box

Behavior	Description
Open trap door finger	Open trap door by pushing it back with finger
Open trap door stick	Open trap door by pushing it back with a stick
Dipping a	Open trap door by pushing it back with finger, whilst holding on followed by dipping a stick in and out the revealed hole, then licking syrup off the stick (the exactly intended first technique)
Dipping b	Slight variation from Dipping a: Open trap door by pushing it back with a stick, then dipping the same stick in and out the revealed hole and licking syrup off the stick
Dipping c	Slight variation from Dipping a: Open trap door by pushing it back with finger, holding on to dip in a stick, then letting trap door go and rap the stick out, and lick syrup off the stick
Tap	Tap with stick or finger on closed trap door
Poke	Poke bolt back with stick, thereby unlocking the lid of the apparatus
Lever	Lever the lid open by inserting the stick in the hole, then bringing the stick at an angle so it is blocked in the hole; then the lid can be opened by pushing the stick to one side
Poke and Lever	Poke bolt with stick, followed by opening the trap door, levering the lid open with a stick that is inserted in the hole so the stick is blocked in the hole and then pushing the stick to one side the lid can be opened (intended 2 nd technique, cumulatively building upon dipping technique)
Lever in vain	Trying in vain to lever open the lid of a locked box (but with the correct lever technique)
Lever in gaps	Unsuccessfully attempting to lever the lid open by inserting a stick or fingernails in gaps along the opening
Touch apparatus	Touching apparatus with hand or mouth
Look at apparatus	Look at window of apparatus at very close distance (< 10cm)
Look at demonstrator	Look from close distance (< 2m) at human demonstrator (or later a subject in group) performing the “Poke and Lever” technique

Experimental procedure

The experiment was carried out at the group’s main indoor cage, where subjects could put their forearms through the grid. The apparatus was fixed to the outside of the cage, allowing subjects to watch through the box’s transparent window and see the content. The content originally consisted of syrup and peanuts (or occasionally walnuts), all highly appreciated food items. Several sticks were provided that were adequate to perform the two techniques.

Table 4.2: Experimental setup

Task	Innovation phase	Demonstration phase	Novel exigencies and demonstration phase
Syrup	Yes	Yes	No
Peanuts	Yes	Yes	Yes
Duration	7 sessions of 90 min	7 sessions of 90 min	10 sessions of 90 min
Demonstrations	No	1 session box with lid opened; 6 sessions “Poke and Lever”	10 sessions “Poke and Lever”
Techniques	Innovation phase	Demonstration phase	Novel exigencies and demonstration phase
Dipping: Food accessed:	Syrup	Syrup	No food reward
Poke and Lever: Food accessed:	Syrup and Peanuts	Syrup and Peanuts	Peanuts

The experiment consisted of three phases: (1) The innovation phase, followed by (2) the demonstration phase, and (3) the novel-exigencies-and-demonstration phase

Table explicitly states for every phase of the experiment the presented task and which techniques were productive to acquire syrup or peanuts

The experiment consisted of 3 phases (Table 4.2): (1) an innovation phase; (2) a demonstration phase; and (3) a novel-exigencies-and-demonstration phase. Subjects were tested as a group. Experimental sessions usually lasted 90 to 100 minutes each and were performed on different days. There were maximally two experimental sessions per week. (Continuous behavior sampling was done from video records of experimental sessions.)

(1) In the innovation phase, seven experimental sessions were run to investigate how successfully subjects would handle the foraging box that was attached to the outside of the cage. Because subjects did not innovate the “Poke and Lever” technique by the end of the seventh session, the next phase followed.

(2) In the demonstration phase, first one session was run where one box was presented in its home position as before, but a second box was also present, which was empty but had the lid opened, to ensure that subjects knew the lid could be opened. If subjects had learned the “Poke and Lever” technique at this stage this would have implied a form of emulation learning, product copying (end-state emulation) or affordance learning (cf. Whiten et al., 2009a; Tomasello, 1996; Tomasello, 1998; Wood, 1989). Then in the next six sessions the complete process of the “Poke and Lever” technique was demonstrated to the orangutans by a

familiar human (S.L.). Demonstrations were carried out at a distance of about 1m, in front of the whole group. For the first 20 minutes of a session, demonstrations were repeatedly carried out. After that, the box used by the demonstrator was put in its home position and was fixed to the cage for subjects to interact with for the following 70-80 minutes, whereas the demonstrator now used a second box to demonstrate the technique “Poke and Lever” whenever a subject was watching the human demonstrator or this box. Since at the end of this second phase no subject acquired the “Poke and Lever” technique, a third phase was added.

(3) In the novel-exigencies-and-demonstration phase, demonstrations were paired with changed conditions. Subjects were exposed to the foraging box, which now no longer contained syrup but only peanuts. This made the “Dipping” technique (that had so far made the syrup accessible) ineffective, leaving subjects only the “Poke and Lever” technique to access the reward. Demonstrations were carried out the same way as described for the demonstration phase. We expected that with the novel conditions subjects would be more attentive to the demonstrations of the “Poke and Lever” technique by the human demonstrator than in the demonstration phase, and furthermore that subjects would show greater effort to lever open the lid. Seven sessions were scheduled, but three more were added.

Data coding and analyses

The experiments were all video-recorded. Continuous behavior sampling was done from the video records. Statistics were calculated in SPSS 14.0. Page’s L Trend Test (Page, 1963) was used to test for successive increase in successful application of the “Dipping” technique over the seven sessions of the innovation phase.

Results

Innovation phase

In the seven sessions of the innovation phase (lasting 10 hours 14 minutes), 6 out of 8 orangutans discovered at least one of the three forms of the “Dipping” techniques that could be distinguished, while two subjects did not get beyond opening the trap door with either finger or stick yet (complete information about latencies after which subjects successfully performed a particular behavior for the first time can be found in Appendix 4.1). During the course of the innovation phase subjects increasingly performed the “Dipping” techniques in a successful way to gain access to the syrup (Figure 4.3). Page’s L Trend Test (Page, 1963) revealed that there is a highly significant trend for subjects gradually increasing their successful use of any of the three forms of “Dipping” proportionally to their total manipulation time ($L = 975.5$; $k = 7$; $n = 8$; $p < 0.01$).

Two of the subjects that had used “Dipping” also discovered “Poke”, but no individual came up with the technique “Poke and Lever” in this phase. As orangutans failed to innovate the cumulatively built-up technique “Poke and Lever” under constant conditions, we followed up with a demonstration phase (of this technique).

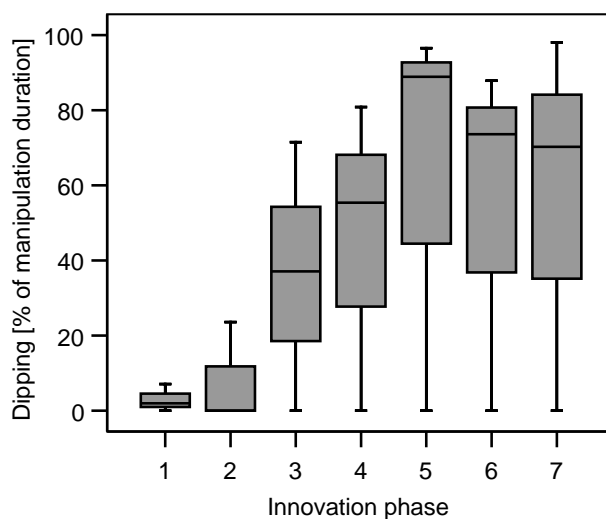


Figure 4.3: Successful performance of the “Dipping” techniques as proportion of subjects’ ($N = 8$) total manipulation durations in the seven sessions of the innovation phase. Medians and quartiles are shown.

Demonstration phase

In the demonstration phase, the technique “Poke and Lever” that cumulatively builds up on the “Dipping” techniques was still not performed by any subject. Rather, their interest in the task declined, as indicated by a lower participation with the task than in the innovation phase, measured as individuals’ active manipulation with the apparatus proportionate to the time the apparatus was fixed to the cage in the corresponding phase (Wilcoxon signed-ranks test: $Z = -1.960$, $N = 8$, $p = 0.05$; Figure 4.4). The six individuals that had learned “Dipping” techniques still applied them in the demonstration phase to extract some syrup from the apparatus.

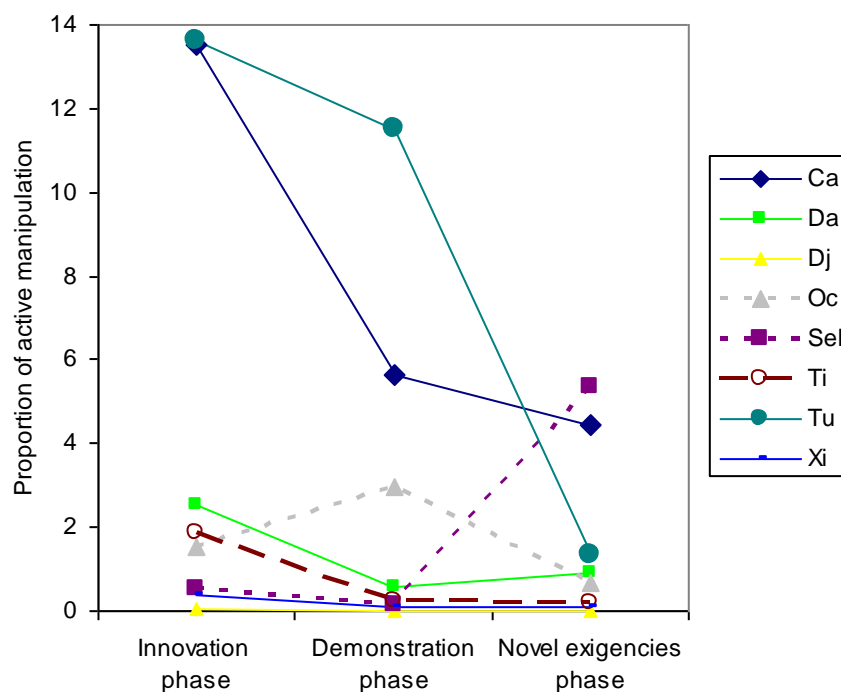


Figure 4.4: Individuals’ participation in the three phases of the experiment, the innovation phase, the demonstration phase, and the novel-exigencies-and-demonstration phase, presented as duration of active manipulation with the apparatus proportionate to the time the apparatus was fixed to the cage in the corresponding phase.

Novel-exigencies-and-demonstration phase

In the subsequent novel-exigencies-and-demonstration phase, demonstrations of “Poke and Lever” were continued the same way, but in addition the foraging box now only contained peanuts and no syrup. This change made the “Dipping” techniques (that had so far made the syrup accessible) ineffective. One subject, Sel, finally succeeded in performing the technique “Poke and Lever”, in the end totaling six correct performances over four consecutive sessions. The first time was in the fifth session, hence the 19th session overall, or after a latency of more than 27 hours. As expected, this individual had previously acquired both “Poke” and “Dipping” (Figure 4.5). In the remaining sessions, amounting to 10 in this novel-exigencies phase, and 24 overall, no other subject learned the “Poke and Lever” technique. Sel did not perform the “Poke and Lever” technique during the last two sessions, despite some attempts.

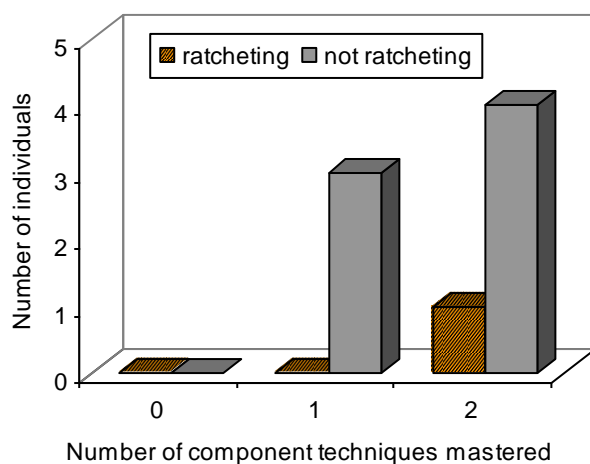


Figure 4.5: Cumulative build-up of techniques: Shows how many individuals succeeded to perform the ratcheted technique “Poke and Lever” (ratcheting: hatched) and how many failed (not ratcheting: gray), depending on whether they had previously mastered 0, 1, or both its component techniques.

Evaluation of most subjects' failure to acquire the ratcheted technique

We then investigated why most animals failed to acquire the “Poke and Lever” technique. Subjects mainly seemed to fail because they largely neglected to “Poke”. Broadly, the components of “Poke and Lever” are “Poke” and a modification of “Dipping”, thus subjects were expected to first show both “Poke” and “Dipping” before mastering “Poke and Lever”. First, we therefore analyzed subjects' latencies till discovering “Poke” and “Dipping”.

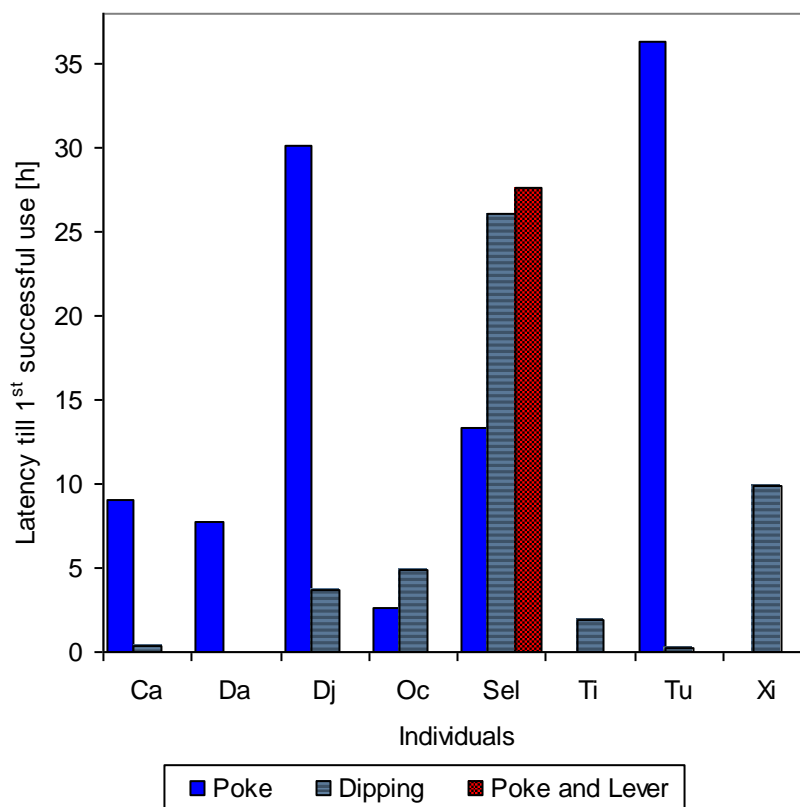


Figure 4.6: Latencies (h) till individuals' (N = 8) first successful performance of a “Dipping” technique, the first successful “Poke”, and the first correct cumulative build-up on these two resulting in the ratcheted technique “Poke and Lever”.

Figure 4.6 shows that most subjects' latencies till the first correct performance of “Poke” were longer than for “Dipping”. Five animals learned both “Poke” and “Dipping”; but of these only one succeeded to combine and modify them into the effective “Poke and Lever” technique, while three of these animals had discovered “Poke” much later than “Dipping”. Two other subjects had learned one of the “Dipping” techniques but never acquired “Poke”. Only one subject (Da: male youngster) acquired “Poke” but not “Dipping”.

Second, we examined whether at some point “Poke” became common by analyzing its frequency in the three phases of the experiment. “Poke” was very rarely shown in the innovation and demonstration phases, but more often under the novel conditions of the last phase (Figure 4.7). We corrected the frequencies of “Poke” for the different time the apparatus was attached to the cage in the three phases (by calculating all frequencies relative to the time the foraging box was available in the demonstration phase). In the novel-exigencies-and-demonstration phase subjects showed significantly more correct “Poke” than in both the demonstration phase (Wilcoxon signed-ranks test: $Z = -2.207$, $N = 8$, $p = 0.027$) and the innovation phase (Wilcoxon signed-ranks test: $Z = -2.207$, $N = 8$, $p = 0.027$). Although “Poke” was most frequent in the novel-exigencies-and-demonstration phase, its occurrence did not become common there either; except for the individual that learned the ratcheted technique “Poke and Lever” no individual “poked” more than eight times in the 10 sessions of the novel exigencies phase.

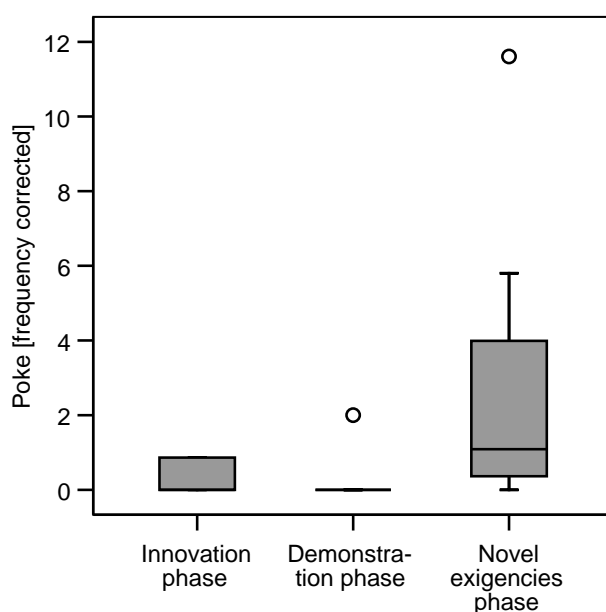


Figure 4.7: Subjects' ($N = 8$) successful performance of “Poke” in the innovation phase, the demonstration phase, and the novel-exigencies-and-demonstration phase. Frequency corrected for different durations of the three phases. The positive outliers represent the performance of the only individual (Sel) that mastered the “Poke and Lever” technique. (“Poke” that occurred within “Poke and Lever” are included.) Medians and quartiles are shown.

Thus, these analyses both support the idea that most subjects failed to acquire the “Poke and Lever” technique because they largely neglected to “Poke”. But several other potential factors why most animals failed to acquire the “Poke and Lever” technique also have to be excluded, namely (1) subjects did not pay attention to the human’s demonstration of the “Poke and Lever” technique, (2) subjects lacked motivation to lever open the lid (because they did not understand its need), and (3) limited access to the task.

First, analyzing subjects’ attentiveness to the demonstrations of the “Poke and Lever” technique we could exclude the possibility that most subjects failed to acquire this technique because they did not watch demonstrations. All subjects paid attention to the demonstrations of the “Poke and Lever” technique by the human demonstrator (Figure 4.8). A seven-year old female (Ca) was the most attentive individual, completely watching 92 demonstrations, followed by a 16-year old female (Tu) that watched 39 demonstrations, but both did not manage to reproduce the exact observed pattern. The individual (Sel) that did acquire the “Poke and Lever” technique in session 19 watched a total of 21 demonstrations before its first successful performance.

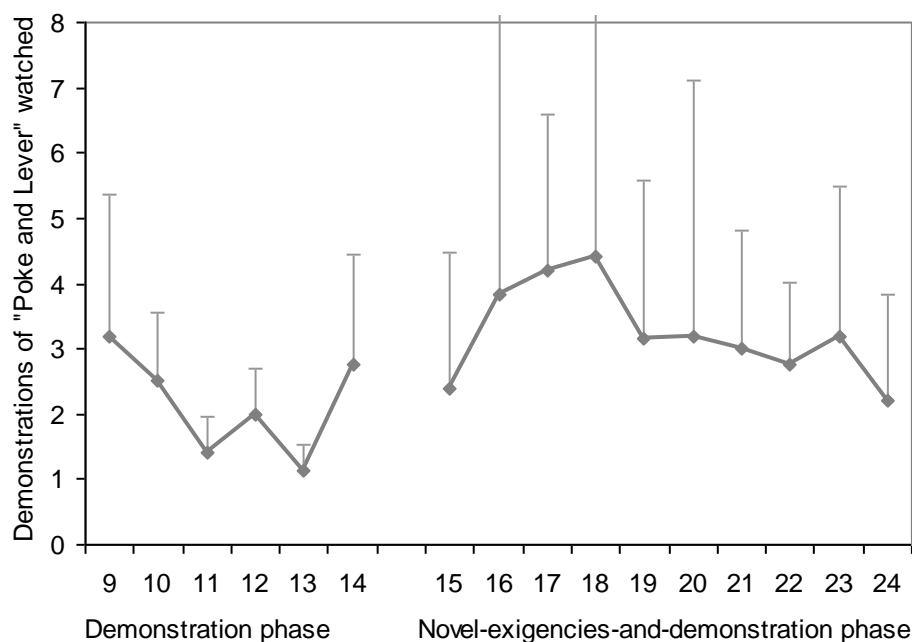


Figure 4.8: Frequency of “Poke and Lever” demonstrations watched by individuals (N = 8) per sessions in the demonstration phase and the novel-exigencies-and-demonstration phase. The “Poke and Lever” technique was demonstrated by the human model. Means and SD are shown.

Second, a simple lack of motivation (and of understanding the need to open the lid) could also be excluded as possible explanation for most animals' failure to show the "Poke and Lever" technique in the novel-exigencies-and-demonstration phase. As with the novel conditions only the "Poke and Lever" technique was effective to gain a reward, we expected subjects to increase their efforts to somehow lever open the lid in the novel-exigencies-and-demonstration phase. Therefore we measured individuals' time spent attempting to lever open the lid without succeeding (sum of: Lever non-successful, Lever in vain, Lever in gaps) and calculated its proportion of the time during which subjects could manipulate the foraging box in the corresponding phase to correct for different such durations in the three phases of the experiment. Indeed, subjects' effort to lever open the lid was greatest when the novel exigencies prevailed (Figure 4.9), and this effort to lever open the lid was significantly greater in the novel-exigencies-and-demonstration phase than before in the demonstration phase (Wilcoxon signed-ranks test: $Z = -2.197$, $N = 8$, $p = 0.028$). This indicates that subjects indeed recognized the need to open the lid due to the novel conditions in the novel-exigencies-and-demonstration phase and that they were motivated to do so.

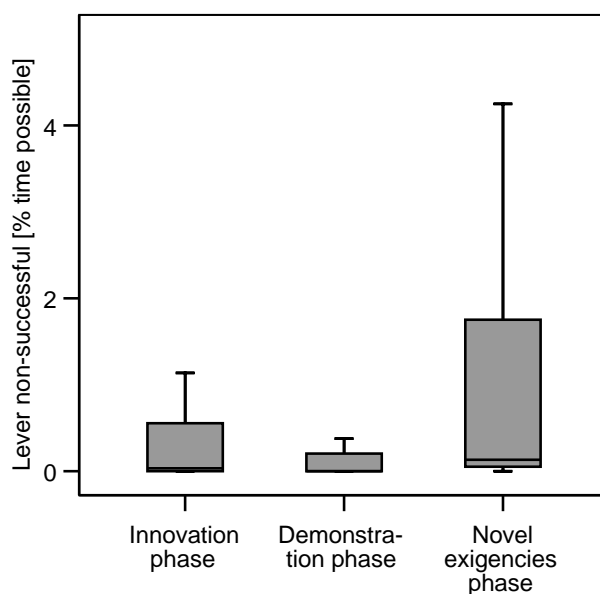


Figure 4.9: Effort to lever open the lid without succeeding as proportion of the time during which subjects ($N = 8$) could interact with the apparatus for the innovation phase, the demonstration phase, and the novel-exigencies-and-demonstration phase. Medians and quartiles are shown.

Third, limited access to the foraging box also needs to be excluded as possible explanation for most animals' failure to show the "Poke and Lever" technique. Access to the foraging box was clearly not limited: Although all subjects participated in the task in all phases of the experiment the apparatus remained unoccupied for most of the time. The only individual that acquired the "Poke and Lever" technique showed most interaction with the task in the novel exigencies phase but by no means monopolized the apparatus (Figure 4.4).

Discussion

Our original aim here was to investigate whether captive orangutans (after having learned a simple technique) would be able to invent a cumulatively built-up technique under constant conditions. We also examined whether orangutans, having previously failed to invent the built-up technique by themselves, could learn it after observing demonstrations by a human model: first still under constant conditions, second under novel exigencies where the simpler "Dipping" techniques were ineffective. Our experiment therefore consisted of an initial innovation phase, followed by a demonstration phase, and finally by a novel-exigencies-and-demonstration phase.

Cumulative build-up of techniques: novel exigencies required

We found that orangutans did not learn the cumulatively built-up technique by themselves under the constant conditions of the innovation phase during the time available. Six subjects learned at least one of the three forms of "Dipping" techniques, and two of those six also discovered "Poke", but none combined and built up on these two techniques to invent the ratcheted technique "Poke and Lever". In the demonstration phase, the "Poke and Lever" technique was demonstrated to the subjects, but none acquired it. Rather, they continued using "Dipping" techniques. Thus, orangutans did not learn the ratcheted technique "Poke and Lever" under constant conditions, neither individually in the "innovation phase", nor socially mediated in the "demonstration phase". These findings suggest that captive orangutans do not show cumulative build-up of techniques as long as conditions remain unchanged and applying their existing, but less efficient "Dipping" techniques provided them with some syrup. This is in accordance with the experiment of Marshall-Pescini and Whiten (2008) that used a similar

foraging box: Chimpanzees that learned the simple dipping technique did not learn the cumulatively built-up technique, although both techniques had been demonstrated to them.

Novel exigencies indeed proved to be indispensable in this experiment for captive orangutans to learn the cumulatively built-up technique. In the novel-exigencies-and-demonstration phase we created novel exigencies by loading the foraging box with peanuts exclusively rather than both syrup and peanuts, while demonstrations of the “Poke and Lever” technique were continued. Thereby we made the “Dipping” techniques nonproductive. In order to extract any food reward from the foraging box subjects now had to apply the “Poke and Lever” technique. One individual finally succeeded to learn this cumulatively built-up technique in this phase. Despite extensive demonstrations all other subjects failed, although four of them had learned both one of the “Dipping” techniques and “Poke”. If “Dipping” is modified (instead of dipping the stick in and out the hole whilst holding the trap door open, now putting the stick in the hole, letting the trap door go so the stick is blocked and pushing the stick to one side to lever the lid open) and additionally “Poke” is preceded, these are the two components that form “Poke and Lever”. But these four subjects failed to do so and therefore to learn the ratcheted technique “Poke and Lever”.

These results have several implications. First and foremost, this study showed that cumulative build-up of techniques is possible in captive orangutans and not exclusive to humans, as also demonstrated in Chapter 3. Second, there was no cumulative build-up of techniques under constant conditions. Cumulative build-up of techniques required novel exigencies that inhibited previous solutions to the task. This corroborates our findings of Chapter 3, using the same subjects, that creating novel exigencies by inhibiting preferred techniques was likely crucial for subjects to modify and improve on present solutions to finally result in cumulative built-up of techniques. At the same time the present study agrees with the findings of Marshall-Pescini and Whiten (2008) in chimpanzees in that in both cases there was no cumulative build-up of techniques as long as dipping techniques were effective and this condition remained unchanged. Additionally, they presented the task without syrup from the beginning on to three naïve subjects, making only the “Poke and Lever” technique effective from the start. Two of these subjects actually discovered both the dipping technique and a poke and lever technique by themselves, leading the authors to conclude that the poke and lever technique was not too difficult for chimpanzees. However, the box used by Marshall-Pescini and Whiten (2008) allowed chimpanzees to lever the lid open with a finger, which was not possible in our case. As a consequence, the results of the two studies are not directly comparable, because the definition for the poke and lever technique was then also less

restrictive in the study of Marshall-Pescini and Whiten (2008). We would argue that such a form of poke and lever that included inserting a finger instead of a stick into the lid's hole to lever the lid open is not really a ratcheted technique. At best it might be justifiable to suggest that such poke and lever represents a technique cumulatively building up on "Dipping" to a much weaker degree, if at all. In order for the "Poke and Lever" technique to qualify as cumulatively building up on the "Dipping" technique, it stringently must include a variation of the "Dipping" technique; therefore we constructed our box in a way that prohibited levering the lid open in any other way than putting a stick in the lid's hole. Thus, our "Poke and Lever" clearly was a ratcheted technique, whereas in the study with the chimpanzees behavioral patterns that arguably did not qualify as ratcheted were also ascribed to the poke and lever technique.

Third, the data strongly suggest that captive orangutans can learn something by social mediation that they previously failed to learn on their own. Innovation was the main limiting factor for cumulative build-up of techniques in this task, but social learning was also a limiting factor as the only subject that succeeded to acquire the "Poke and Lever" technique did so after observing demonstrations by the human model. Individuals were given an extensive amount of time to learn the "Poke and Lever" technique by themselves, as our innovation phase lasted more than 10 hours, but no orangutan invented the "Poke and Lever" technique, suggesting that they could not learn it on their own. The single individual (Sel) that acquired the technique in the novel-exigencies-and-demonstration phase watched a total of 21 demonstrations previously to the first successful performance and was most attentive in the two sessions right before. It seems plausible that as this information was apparently gained it was then also used (in the process) to learn this technique (see Appendix 4.2 for some speculation on which form of social learning could have been at work).

Application of the "zone of latent solutions" concept

According to Tennie et al. (2009) chimpanzees only socially learn something that they (i.e. at least some individuals) could in principle learn by themselves (see also Galef, 1992). They suggested the "zone of latent solutions" (ZLS) concept, a species' potential behavioral repertoire, which encompasses everything the species could learn, both individually and socially. It includes both solutions that every individual could learn on its own, as well as rarely invented behaviors (innovations), solutions that only few particularly gifted individuals are able to invent if all conditions (e.g. physiological or motivational) are right, which other

individuals might then copy. Solutions to tasks that are outside the species' ZLS are suggested to not be copied by chimpanzees (Tennie et al., 2009). Although this concept is impossible to operationalize due to its use of an absolute criterion ("never"), it is likely to be useful in a modified form.

If we apply the ZLS concept to our present study with captive orangutans, then there are two ways to interpret the fact that no individual invented the "Poke and Lever" technique during the ten hours in the innovation phase, while one individual acquired the solution in the novel-exigencies-and-demonstration phase after having observed numerous demonstrations of the solution, which we assume (as argued above) to be acquired by socially mediated learning. First, either the orangutans can learn something socially they could not invent on their own, thus socially learn a solution that was so far outside their ZLS. Or second, the individual that acquired that ratcheted technique by socially mediated learning would have been able to invent it on its own and would actually have done so if the "innovation phase" had lasted even longer than the actual ten hours, thus the "Poke and Lever" technique be within orangutans' ZLS. We do not dismiss this second explanation, but ten hours is a long time subjects were given to find out the solution by themselves, whereas for example Tennie et al. (2009) allowed chimpanzees only five minutes to figure out the "loop technique" before concluding that subjects could not invent it on their own (although they did in fact allow some orangutans to try much longer to figure out the solution, but they also failed (C. Tennie pers. comm.)). For many practical reasons, due to e.g. complexity of tasks, we may not always know for sure whether or not any behavior truly is an innovation or truly lies outside (or inside) the ZLS. We suggest the ZLS be conceived as probabilistic rather than as absolute, just as are innovations (Lehner et al., 2010), which means that it is a matter of probability whether a solution occurs in a group or not, and whether absence of the solution reflects true absence, depending on how much subjects there are and the time subjects are given to find the solution. Thus, the longer a group of subjects fails to invent the solution to a task, the lower the probability they can invent the solution on their own and thus the higher the probability that the solution lies outside their ZLS. Within a short time, subjects can be expected to show solutions to a task that are part of their current behavioral repertoire, whereas to investigate what innovative solutions to the task subjects can find (much) more time needs to be given (Lehner et al., 2010). If the ZLS is to encompass all innovations subjects are capable of, as the description of Tennie et al. (2009) suggests, rather than only solutions from within their current behavioral repertoire, subjects should be given ample time, at least multiple hours, to demonstrate their capabilities (see also Chapter 3).

The first explanation, i.e. that an orangutan could socially learn a technique that was previously outside its “zone of latent solutions”, represents a more useful interpretation of the ZLS than the alternative that orangutans can only socially learn something that is within their ZLS and that this individual that acquired the ratcheted technique by socially mediated learning would eventually have invented it on its own. In common marmosets, only subjects to whom the solution of a task was demonstrated were able to solve the task, suggesting that common marmosets also can learn something socially they are not able to learn on their own (Burkart et al., 2009b), or at least would take very much longer. Thus, one should modify Tennie et al.’s (2009) suggestion that only humans can copy something outside their ZLS, whereas chimpanzees do not, to mean a major difference in likelihoods.

Assuming subjects of various species can socially learn a solution that has so far been outside their ZLS, we suggest social learning expands the ZLS. Thus, we also suggest the ZLS to be more dynamic in its breadth than was claimed by Tennie et al. (2009), in other words, the ZLS may not be fixed in great apes (and possibly some other primates) either. For further future experiments we could then set up the hypothesis that more sophisticated forms of social learning expand the “zone of latent solutions” even more. Or alternatively, one could also suggest that only by imitation (process copying), among all forms of social learning, the ZLS can be expanded, allowing cumulative build-up of techniques. Tennie et al. (2009) also state that process copying (but also other factors) may be responsible for this expansion of the ZLS. However, they claim this exclusively for humans.

Social learning can expand the ZLS of individuals, as well as of a species, if this species socially learns something from another species that was so far outside the species’ ZLS. Great apes have shown impressive cognitive capabilities learning from humans: they were successfully trained by humans to use sign language (e.g. Gardner & Gardner, 1969), lexigrams (geometric symbols representing linguistic units) (e.g. Beran et al., 2000; Rumbaugh, 1977; Savage-Rumbaugh, 1986), the knowledge of which they retained for more than 20 years (Beran et al., 2000), or to count objects by using Arabic numbers (Boysen & Berntson, 1989).

Because Sel did not perform the ratcheted technique during the last two sessions, despite trying, it is possible that what is learned at the edge or outside the ZLS is more likely to be forgotten again. Thus, we have suggested four adjustments to the concept of ZLS: (1) it is probabilistic rather than absolute, (2) it is dynamic rather than fixed, i.e. its breadth can shrink and expand, (3) it is expandable by social learning and (4) what is learned at the edge or outside the ZLS is more likely to be forgotten again.

Whiten and colleagues suggested a concept (Hopper et al., 2007; Whiten et al., 2009a), comparable to the one by Tennie et al. (2009), consisting of three zones: in “zone 1” the task is easy enough for most individuals to learn it individually; in “zone 2” there is still at least one innovator to solve the task from whom others can learn socially (the tradition zone); in “zone 3” the task is beyond the species’ capability, too difficult for any subject to learn, neither individually nor socially. The ZLS by Tennie et al. (2009) includes both solutions that fairly every individual could learn on its own, as well as rare innovations, thus their ZLS seems to correspond to “zones 1 and 2” of Whiten and colleagues – note also that Tennie et al. (2009) propose that within these two zones apes learn mostly via product copying, whereas Whiten and colleagues claim that often process copying underlies the spread – at least in their “zone 2” (Hopper et al., 2007; Whiten et al., 2009a).

The struggle with the ratcheted technique “Poke and Lever”

We now turn to the question why only one of our subjects succeeded to learn the ratcheted technique. Broadly, “Poke” and a modification of “Dipping” are the components of “Poke and Lever”, thus subjects having mastered both these components could be expected to learn the cumulatively built-up technique. There were five animals that learned both “Poke” and “Dipping” but all but one did not succeed to build from these two the “Poke and Lever” technique. In the comparable experiment of Marshall-Pescini and Whiten (2008) chimpanzees that learned a dipping technique (which was demonstrated as first solution to them) all failed to learn the poke and lever technique (which was demonstrated second to them), thus the authors concluded their chimpanzees to have become “stuck” on a technique they had learned initially. This explanation does not fit our findings, because our subjects previously had demonstrated high behavioral flexibility by showing continued interest in acquiring new solutions to a task and by switching to other techniques and relinquishing established techniques when this was advantageous (Chapter 3). “Poke” was crucial for the acquirement of the ratcheted technique, and subjects mainly failed to acquire the “Poke and Lever” technique because they were mostly reluctant to “poke”; although being shown more frequently in the novel-exigencies-and-demonstration phase, “Poke” never became common.

We showed that all subjects paid attention to the demonstrations of the “Poke and Lever” technique, that subjects’ effort to lever open the lid was greatest in the last phase, when the novel exigencies were in place, and that access to the foraging box was not limiting. However, though paying attention to complete demonstrations of “Poke and Lever”, subjects

possibly focused much more on the levering part, then failing to copy the complete action pattern of the ratcheted technique in the correct sequence, thus failing to learn the technique by action copying (imitation). At the same time subjects seemed not to understand how “Poke” contributed to levering open the lid of the box, as this locking mechanism was not visible and seemed arbitrary, which makes the task hard (or even impossible) to be learned by product copying or affordance learning (emulation) but must therefore be learned by imitation. Chimpanzees are capable of socially learning action sequences (Bonnie et al., 2007; Whiten, 1998). Furthermore “Poke” alone was never rewarded. This could explain why subjects rarely “poked” and failed to learn the “Poke and Lever” technique, except for one individual.

Finally, we return to the question whether the “Poke and Lever” technique is outside apes’ ZLS. Our findings with captive orangutans indeed indicate that this ratcheted technique was outside subjects’ ZLS and could only be acquired by socially mediated learning. Because it was not evident why one step (“Poke”) was necessary, which was rather an arbitrary sequence, imitation rather than emulation might be essential. We cannot appraise whether the task was also outside chimpanzees’ ZLS in the experiment of Marshall-Pescini and Whiten (2008), which would support our claim that the task was outside orangutans’ ZLS. Two of their control chimpanzees individually figured out how to lever open the lid by means of poking and levering. However, as mentioned earlier, the tasks differed in that their apparatus also allowed subjects to lever open the lid with a finger, making two different forms of poke and lever possible, whereas in our case the lid could only be opened by inserting a stick into the lid’s hole (the original “Poke and Lever” technique).

In sum we conclude this study supports earlier results (Chapter 3) that cumulative build-up of techniques is possible in captive orangutans and not limited to humans, at least if they have to deal with novel conditions. Second, under constant conditions subjects failed to acquire the ratcheted technique, which corroborates the suggestion that cumulative build-up of techniques requires novel exigencies, so that previous solutions to the task are inhibited. Third, our results indicate captive orangutans can learn (or at least learn it much faster) by social mediation something they previously failed to learn on their own. Applying Tennie et al.’s (2009) concept of “the zone of latent solutions” (ZLS) to this finding that a subject socially learned a technique it previously failed to learn individually, we suggest that orangutans can socially learn a solution that was previously outside their ZLS. These findings

therefore support the Cultural Intelligence Hypothesis (van Schaik & Burkart, in review) and they suggest that social learning can expand the ZLS, a topic to be explored in future studies.

Appendix

Appendix 4.1: Latencies till individuals' first correct performance of selected behaviors regarding the foraging box. For descriptions of behaviors see Table 4.1.

Behavior	Ca	Da	Dj	Oc	Sel	Ti	Tu	Xi
Open trap door finger	17'	2h 56'	2h 41'		28'	1h 11'	5'	1h 23'
Open trap door stick	5'	3h 26'	3h 30'	4h 52'	26h 07'	3h 18'	3'	
Dipping a	6h 21'		9h 08'			1h 52'	2h 44'	9h 51'
Dipping b	5'		3h 41'	4h 52'	26h 07'	3h 18'	3'	
Dipping c	5h 25'		3h 47'			8h 47'	2h 29'	9h 52'
Poke	9h 05'	7h 43'	30h 07'	2h 38'	13h 20'		36h 20'	
Lever (in vain)	22h 53'				27h 31'	34h 20'	26h 26'	
Poke and Lever					27h 41'			

Appendix 4.2: Some speculation on form of social learning by which the successful individual (Sel) acquired the technique “Poke and Lever”.

In the first session of the demonstration phase we presented a foraging box with the lid open, both to show subjects that the lid could be opened and to do a rough control for product copying and affordance learning. If subjects had been able to readily learn the “Poke and Lever” technique by learning about the environment, i.e. the task affordances (affordance learning) or the product of the behavior (end-state emulation, rather than about the actions (Tomasello et al., 1993a; Tomasello, 1998; Tomasello, 1996; Whiten et al., 2009a; Whiten et al., 2004), they would have been expected to do so at this stage of the experiment. Such emulation learning was originally distinguished from imitation in that copiers reach the product in their own way (Wood, 1989). However no one did. The individual (Sel) that finally learned the “Poke and Lever” technique did so only after having closely observed numerous demonstrations of the complete action pattern of the technique. This suggests that observing and copying only the product (end-state emulation) or learning about the properties of the apparatus (affordance learning) was not sufficient to acquire the technique, but that copying the complete behavioral pattern was necessary, and that thus the successful individual learned the technique by imitation. Likewise Bering et al. (2000) concluded that matching behaviors observed after demonstrations of the target behaviors could be attributed to imitation because of the inclusion of an innovation phase first. By means of imitation an observer reproduces not only the result, but the model’s actual behavioral action toward a goal (Tomasello, 2001). Indeed, product copying (end-state emulation) seems not suitable for learning the “Poke and Lever” technique, because the outcome of the action, the opened lid of the box, might rather easily be associated with “somehow levering open the lid”, but the necessary first sequence of “poking” in a hole at some distance to the lid is less obviously associated with the opened lid, and thus the end state; indeed the first sequence is rather an arbitrary contribution to the end state. If subjects only copy the end state of the action, the foraging box will remain locked. Furthermore, this locking mechanism is not easily visible and very difficult to be understood, thus affordance learning about the properties of the food box is not likely to lead to the “Poke and Lever” technique either. Thus, mainly because of the arbitrariness of the first sequence (“Poke”), we suggest learning of this technique by imitation to be more plausible than by emulation in the first place, which was then supported by our findings in the experiment. However, this is of course highly speculative and must only be recognized as such. As later the “Poke and Lever” technique was demonstrated, affordance learning had become even less likely, because the lid of the food box used for demonstrations was closed most of the time and this box was not attached to the cage but in a distance of about one meter, giving subjects fewer and worse chances to study its mechanism. Still, there are also other possible forms of social learning we cannot exclude, for example stimulus enhancement, i.e. that the only successful individual was simply drawn to the apparatus and then blindly engaged in trial-and-error learning (Tomasello, 1998); however, it is only important to recognize that social mediation was necessary, but by which form of social learning the individual learned the ratcheted technique is insignificant here.

Chapter 5

General discussion

Overview of the results

The first objective was to validate the procedure suggested by Ramsey et al. (2007) for recognizing innovations. I did so by using a captive population from Zoo Zurich to test the preliminary list of 43 potential innovations that van Schaik et al. (2006) generated for orangutans by applying that procedure. At least eight of the 15 investigated behaviors from the preliminary list could indeed be classified as innovations, and one additional behavior as a modification. First, at least four of the ten behaviors from the preliminary list we could expect to observe directly were verified innovations in our captive population based on their absence. Second, attempts to experimentally elicit five additional behaviors from the preliminary list showed that four qualified as innovations and one as modification, based in one case on absence and in the remaining others on latencies of first occurrence across individuals. Thus, in total at least 53 % (8 of 15) of those putative innovations recognized in the field we investigated in this analysis were confirmed as innovations. If we add the three possible innovations and the modification, this figure becomes 80 %. Therefore our findings largely confirm the assessments on the preliminary list by van Schaik et al. (2006) and thus the approach of Ramsey et al. (2007).

The second objective was to evaluate captive orangutans' ability for cumulative build-up of techniques. There has been no indication for cumulative build-up of techniques (ratcheting) in orangutans previously. Cumulative build-up of techniques demands of a species (1) the ability to produce superior innovations and (2) the ability to recognize alternatives as superior and flexibly switch to them.

Thus, first we investigated whether subjects showed the behavioral flexibility necessary for ratcheting, expressed by showing sustained acquisition of new solutions to a problem-solving task. We twice restricted the conditions of the task, thereby making previously preferred techniques impossible. Orangutans indeed showed behavioral flexibility, abandoning a preferred technique that had been made non-functional, and switching to different, functional and efficient techniques (syrup tube experiment, Chapter 3). Such flexible switching of techniques contrasts with the findings of chimpanzees in similar

situations, where several studies report them to show a bias of conformity or conservatism (cf. Bonnie et al., 2007; Hrubesch et al., 2009; Marshall-Pescini & Whiten, 2008; Whiten et al., 2005).

As novel conditions arise, behavioral flexibility may ultimately be expressed by innovations that are solutions that cumulatively build up (“ratchet”) on previous ones. However, it is important to emphasize that whereas cumulative build-up of techniques stringently requires behavioral flexibility, behavioral flexibility does not automatically result in cumulative build-up of techniques; subjects having demonstrated high behavioral flexibility do not necessarily also show cumulative build-up of techniques. But in our syrup tube experiment behavioral flexibility was indeed ultimately expressed by ratcheting, i.e. by innovations that cumulatively built up on previous techniques. Subjects eventually came up with two solutions that fulfilled the criteria of a ratcheted technique. These techniques were more complex and they were performed only by subjects that had mastered the component techniques previously. These findings (Chapter 3) demonstrated that captive orangutans were capable of cumulative build-up on previous techniques as conditions of the task changed. These ratcheted techniques were then also adopted by some other group members, indicating that modest cumulative culture could actually be possible in captive orangutans, at least if they have to deal with novel conditions.

The next experiment (Chapter 4) then showed that novel exigencies were indeed indispensable for ratcheting, as the same captive orangutans were not able to learn a cumulatively built-up technique under unchanging conditions. Only after previous solutions (“Dipping” techniques) to the task had been made ineffective, one individual finally succeeded to learn the ratcheted technique (“Poke and Lever”). This in accordance with the experiment of Marshall-Pescini and Whiten (2008) using a similar task in chimpanzees; in both cases there was no cumulative build-up of techniques as long as dipping techniques were effective.

Thus, we found that captive orangutans are capable of cumulative build-up of techniques. Our results also showed that ratcheting required novel exigencies inhibiting previous solutions to the task.

Ratcheting in wild orangutans? Constraints, selective factors and perspectives

There are no similar observations of cumulative build-up of techniques in orangutans from the wild as yet. They largely seem to fail to produce superior innovations in the first

place. Indeed, captive and ex-captive rehabilitant orangutans have been found to be far more innovative than wild ones (Lehner et al., 2010; Russon et al., 2010; Russon et al., 2009). We suggested that captive orangutans have positive associations with novelty, e.g. through the presence of food rewards, thus favoring the appearance of innovations which are then also well retained, due to the excellent conditions for social transmission in the zoo. On the other hand, wild primates rather associate unfamiliar, novel objects with danger, be it through poisoning or injury, or through competition with other activities such as vigilance, i.e. opportunity costs (Halsey et al., 2006), and thus largely avoid them (cf. Menzel, 1968). Released from danger avoidance and the intensive subsistence lifecycle of the natural world, zoo orangutans could overcome neophobia and invest the spare time and spare energy they gained in manipulation of novel objects. This may have led to larger innovation repertoires in captive populations compared to wild ones (Chapter 2). Consequently, cumulative build-up of techniques is also less likely in wild orangutans than in captive conspecifics.

These explanations could actually be tested by future research. The syrup tube experiment (Chapter 3) could well be presented to a wild population. We would first choose a population where orangutans have been observed by van Schaik et al. (2006) to use the techniques “Branch scoop” (in Suaq Balimbing on Sumatra) or “Sponging” (Ketambe, Sumatra) to collect water from a deep tree hole. Supposing they would voluntarily approach and engage with the set-up we could eventually compare their performance with the captive subjects.

However, so far primatologists have largely refrained from conducting experiments in wild great ape populations, both for ethical and scientific reasons, as experimental tasks might have a lasting impact on their behavior, with its attendant consequences. Where indeed field experiments have been performed so far they included natural components like stone tools (Matsuzawa, 1994) or unfamiliar species of nuts (Biro et al., 2003). More recently, experiments with artificial devices and experimental apparatuses have also been conducted (Halsey et al., 2006; Laidre, 2008). Wild common marmosets (*Callithrix jacchus*) were tested in their natural environment whether they were able to successfully complete the simplest form of the patterned string task, parallel strings; although most marmosets succeeded, they made more errors than their captive conspecifics or any other primate species tested in previous studies in captivity (Halsey et al., 2006). Wild baboons were tested on three food-access tasks, but they failed on two of them, even when tools had been appropriately positioned in advance and in spite of their showing a high motivation to access the food (Laidre, 2008). One of these tasks actually involved a tube filled with syrup, but baboons

failed to dip in the sticks provided for them. The wild baboons' weak performance in this study have been suggested to be explained by them having been less familiar with the general properties of objects and the potential function than their captive conspecifics (Laidre, 2008).

Several different selective pressures in wild and captive environments may explain such findings of captive animals performing more impressively with regard to tool use and innovation than their wild counterparts. Unlike wild animals, their captive conspecifics are released from having to attend to possible danger and the intensive subsistence lifestyle of the natural world, which leaves the zoo animals with substantial free time and energy they can use e.g. to intensify their social life (Kummer, 1995) or, what is more relevant here, to explore and manipulate objects (cf. Huber & Gajdon, 2006).

The shielded zoo environment allows orangutans to follow developmental trajectories predisposing them to make more innovations and even be capable to come up with ratcheted techniques. For cumulative build-up of techniques we found evidence that novel exigencies, making present solutions impossible or ineffective, are a critical selective force. This factor of novel exigencies inhibiting previous solutions, which promotes ratcheting of techniques, is missing in the wild, while at the same time forces are in place that are impeding object manipulation (lack of spare time and spare energy due to danger avoidance and intensive subsistence, as explained above). Consequently, conditions for wild orangutans to ratchet must be considered to be suboptimal. Thus, if we conduct the syrup tube experiment in the field, we would not expect wild orangutans to come up with one of the two ratcheted techniques their captive conspecifics invented in Zoo Zurich, nor any other one.

In contrast to orangutans, chimpanzees seem to be able to overcome these tribulations for ratcheting in the wild, as suggested by the few likely examples of cumulative build-up of techniques in wild chimpanzee populations (Boesch, 2003; Matsuzawa & Yamakoshi, 1996; Sanz & Morgan, 2009; Sugiyama, 1997; Whiten et al., 2003). Consequently, additional selective forces have to be at work there. Definitely, more research is needed on ratcheting in orangutans and chimpanzees, both in captivity and in the wild, shedding more light on the promoting and impeding factors of ratcheting. Also, it would be most obvious to conduct the syrup tube experiment with captive chimpanzees, investigating whether chimpanzees are as successful as orangutans were. Furthermore, future research is needed to explore whether and by which form of social learning ratcheted techniques spread in a captive population of orangutans or chimpanzees.

Ratcheting reconsidered

We used the following criteria for innovative techniques to qualify as ratcheted techniques. First, the new technique is more complex (Boesch & Tomasello, 1998; Tomasello et al., 1993a), i.e. its range of application is larger (Boesch & Tomasello, 1998), the number of physically distinct constituent components (also called “technounits”) is higher (Oswalt, 1976), or the number of behavioral steps involved is higher. Second, the new technique is an elaboration of a previous one, i.e. includes a variation or a behavioral element of a previous one, as suggested by Marshall-Pescini & Whiten (2008). Therefore, only individuals that have used the specific component technique(s) master the corresponding built-up technique. Otherwise the technique does not qualify as ratcheted. There are two other interpretations of ratcheting that have been suggested but they are less useful for operationalizing ratcheting in apes.

First, ratcheted techniques are more complex, and as a consequence they often are more efficient. It has been implied (Laland, 2004) that both higher complexity or higher efficiency independently can be used as criteria for ratcheted techniques². However, higher complexity is valid as criterion for ratcheted techniques, but higher efficiency cannot be regarded a criterion for ratcheted techniques; higher efficiency is merely a *consequence* of the more complex technique. Thus, although a more complex technique is often more efficient as a result, a more efficient technique need not necessarily be more complex; it can instead be less complex, thus clearly not representing a ratcheted technique. Therefore we propose not to use higher efficiency as criterion for ratcheted techniques.

Second, Boyd and Richerson (1996) suggested that cumulative culture results in behaviors that no individual could invent on its own. While this illustrates the ratcheting end product, it does not define ratcheting. It is evident that cumulative culture will eventually result in techniques a single individual cannot invent on its own, albeit mainly after a longer process including several cumulative modifications to the technique. But if we do want to investigate the beginning of such a process, i.e. to recognize the first cumulative modification to a technique making it a ratcheted technique, this technique may very well still be learned by an individual on its own, because such a ratcheted technique has not yet developed so far beyond the previous form. Thus, it is not useful to define a ratcheted technique based on the

² ”Recent human culture is characterized by the ratchet effect, or an increase in the complexity or efficiency of technology over time.” (Laland, 2004, p. 10)

inability of single individuals to invent it, first and foremost because we would then miss the early stages of ratcheting. Furthermore, Boyd and Richerson's (1996) operationalization is not testable because a test would require the availability of unlimited time and subjects. Therefore we suggest not using this approach when (experimentally) investigating a species' potential for cumulative build-up of techniques, because it focuses the attention onto the final product of the ratcheting process rather than onto this process itself.

A slight but critical adjustment to the suggestion of Boyd and Richerson (1996) can make it into the same criterion as used in this study: a ratcheted technique should be much more learnable by individuals that have already mastered the corresponding component technique(s) it built upon than by naïve individuals. This approach does not exclude the possibility that a ratcheted technique can be invented by a *single* individual; instead it excludes the possibility that a ratcheted technique is learned by *naïve* individuals, naïve in the sense they do not know the pre-stage or component technique(s) upon which the ratcheted technique has accumulated. Thus, this morphs into a criterion we have actually successfully applied (see Chapter 3: criteria of cumulatively built-up techniques): a specific ratcheted technique can only be mastered by individuals that have used the corresponding component technique(s). In Chapter 3, this criterion was deduced from Marshall-Pescini and Whiten (2008) proposing that since a ratcheted technique is an elaboration of a previous technique, a ratcheted technique must include a variation or a behavioral element of this previous technique.

Finally, I want to discuss an implication of the term “ratcheting” that had been coined by Tomasello et al. (1993a) to be used for illustrating cumulative culture. Cumulative culture requires not only creative invention, but also faithful social transmission that can work as a ratchet to prevent slippage backward (Tomasello, 1999a). I have also used ratcheting interchangeably and synonymously with cumulative culture and cumulative build-up of techniques, especially to name techniques that have cumulatively built-up on previous ones simply as ratcheted techniques rather than always as cumulatively built-up techniques. Like a ratchet, cumulative build-up of techniques turns into one direction, the direction of improvement. However, although the general trend is into this one direction, the ratchet can not be expected to be perfect, i.e. to never slip. Sometimes a big step forward can only be made after having made a small step back before. Ratcheting must be able to cope with some (backward or on the spot) slipping.

In a pioneering experiment with humans on cumulative culture by Caldwell and Millen (2008a), generational succession was simulated by repeated removal and replacement

of participants within experimental groups, in such “microsocieties” participants were instructed to build a paper airplane which flew as far as possible or a spaghetti tower as tall as possible. In both tasks successive improvement was observed, paper airplanes of later “generations” gradually flew a longer distance and towers reached a larger height, suggesting information was accumulated within the groups so that later “microsocieties” constructed more successful products. But this example simultaneously illustrates that ratcheting also includes occasional backward slipping. Although there was a general trend of improvement, in both examples there was a change to the worse in some “generations” too. Thus, even in the human case ratcheting includes occasional slippage on the spot or backwards. We suggest these adjustments are made to the illustration of the ratchet for cumulative culture.

Toward a scheme for ratcheted techniques, based on the examples of this study

Finally, I want to develop a scheme for ratcheted techniques, based on the characteristics and criteria for cumulative build-up of techniques discussed above and our experimental examples of the studies of Chapters 3 and 4. In the syrup tube experiment, subjects invented two solutions that fulfilled the criteria of a ratcheted technique (Chapter 3); in the experiment with the foraging box there was one ratcheted technique that a single individual learned (Chapter 4). These three ratcheted techniques are “Squash-and-fish”, “Drop-and-fish”, “Poke and Lever”.

1) “Squash-and-fish” builds up on the techniques “Paper squash” and “Fish”. In “Fish”, a stick is used to get out leaves, paper or wood wool that are lodged in the tube by simultaneously pushing such an item with the stick against the inner wall of the tube and lifting the stick upwards. In “Paper squash”, paper is forced directly with a hand into the tube and down into the syrup; then the soaked paper is pulled out with the hand, taken in the mouth and sucked. In “Squash-and-fish”, a stick is used to force some paper down the tube into the syrup; then the soaked paper is removed by pushing it against the inner wall with the stick and lifting the stick upwards. Thus, “Paper squash” has been modified (a stick is used to force paper into the tube instead of using a hand) and combined with “Fish” to build the ratcheted technique “Squash-and-fish”. The innovator of “Squash-and-fish” (latency until first performance: 19 h 21 min.) had learned the technique “Paper squash” (latency: 47 min.) previously to “Fish” (latency: 5 h 18 min.), but a different individual was first to come up with these two component techniques. Therefore the scheme for the ratcheted technique is as follows (Figure 5.1): The individual that invented “Squash-and-fish” had first learned

technique “A” (“Paper squash”), after some time (Δt_1) it had learned technique “B” (“Fish”), and after a much longer time (Δt_2) and the occurrence of novel exigencies the individual modified “A” (modifications are indicated by a subscript “m”) and combined it with “B” to build the ratcheted technique “A_mB” (“Squash-and-fish”).

For a more detailed scheme, we divide all three behaviors into sub elements (Figure 5.1): In “Paper squash”, paper is forced directly with hand into the tube (a_1), then the soaked paper is pulled out with the hand (a_2); in “Fish”, a stick is put into the syrup in the tube (b_1), next, material that has accrued in the tube is taken out by pushing it with the stick against the inner wall of the tube and simultaneously lifting the stick upwards (b_2); in “Squash-and-fish”, paper is forced with a stick into the tube (a_{1m} : modification of a_1 where this is done by hand), then that paper is taken out by pushing it with the stick against the inner wall of the tube and lifting the stick upwards (similar to b_2 , but here the paper forced into the tube is taken out rather than random material that has lodged in the tube). Thus, by modifying one sub element of the first component technique (a_1 becomes a_{1m}) and combining it with one sub element of the second technique (b_2) we can build the ratcheted technique ($a_{1m}b_2$).

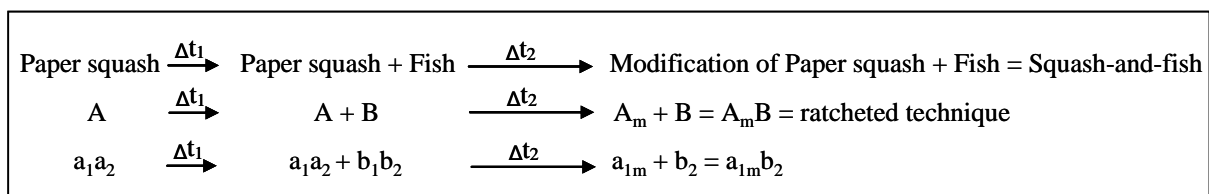


Figure 5.1: Formation of the ratcheted technique “Squash-and-fish” and the corresponding schematic images: a rough one, followed by a more detailed schematic image where behaviors were divided into sub elements. Note that time interval 2 (Δt_2) is larger than time interval 1 (Δt_1), as indicated by the length of the arrows. A modification is indicated by a subscript “m”.

2) “Drop-and-fish” builds up on the techniques “Sponging” and “Fish”. In “Sponging”, paper or wood wool chewed to a ball is dropped inside the tube, followed by reaching down with the hand into the syrup and taking the ball out and into the mouth. In “Drop-and-fish”, paper or wood wool chewed to a ball is dropped inside the tube, but instead of reaching down with the hand as in “Sponging” a stick is used to fish the ball out. The innovator of “Drop-and-fish” (latency until first performance: 20 h 23 min.) had previously also invented “Fish” (latency: 11 min.) and learned “Sponging” (latency: 3 h 41 min.). Therefore the scheme for the ratcheted technique is as follows (Figure 5.2): The individual that invented “Squash-and-fish” had first invented technique “A” (“Fish”), after some time

(Δt_1) it had learned technique “B” (“Sponging”), and after a longer time interval (Δt_2) and the occurrence of a novel condition, the individual reduced “B” and combined it with “A” to build the ratcheted technique “BA” (“Drop-and-fish”).

For a more detailed scheme, we again divide the behaviors into sub elements (Figure 5.2): In “Fish”, a stick is put into the tube (a_1), followed by pushing material with the stick against the inner wall of the tube and simultaneously lifting the stick upwards (a_2); in “Sponging”, paper chewed to a ball is dropped inside the tube (b_1), followed by reaching down with the hand into the syrup and taking the ball out (b_2); in “Drop-and-fish”, paper chewed to a ball is dropped inside the tube (equal to b_1), followed by putting a stick into the tube (equal to a_1), then taking that ball out by pushing it with the stick against the inner wall of the tube and simultaneously lifting the stick upwards (similar to a_2 , but here the same paper dropped inside the tube is taken out rather than random material that has lodged in the tube; however, this sub element could also be considered as a modification of b_2). Thus, reducing component technique “B” to its first sub element (b_1), followed by adding both sub elements of the component technique “A” (a_1 and a_2), we can build the ratcheted technique ($b_1a_1a_2$).

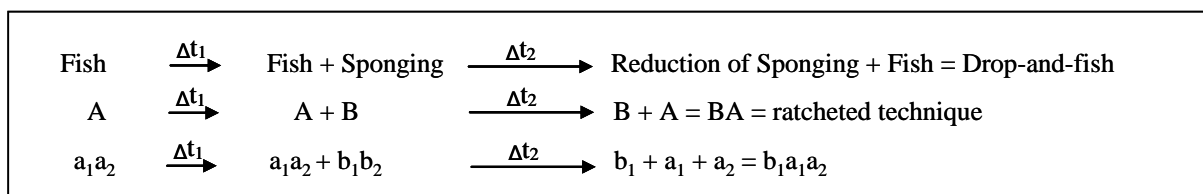


Figure 5.2: Formation of the ratcheted technique “Drop-and-fish” and the corresponding schematic images: a rough one and a more detailed one. Note that time interval 2 (Δt_2) is larger than time interval 1 (Δt_1), as indicated by the length of the arrows.

3) In the experiment with the foraging box the solutions (“Dipping”³, “Poke and Lever”⁴) were completely predetermined by the design of the task. In “Poke and Lever”, first a stick is used to poke the recessed bolt inwards, whereby the lid is unlocked (“Poke”: does

³ “Dipping” technique: Sliding open the trap door by pushing it back with a finger, thereby exposing the hole of the lid, and whilst holding on, use other hand to dip a stick into the revealed hole down into the syrup, pull stick out and lick syrup from stick (see Chapter 4, Figure 4.1).

⁴ “Poke and Lever” technique: Using a stick to poke the recessed bolt inwards, thereby unlocking the lid at the top. Slide open the trap door with a finger and use the other hand to insert a stick into the hole (as in the “Dipping” technique), let trap door go and lever open the lid, making all the contents available (see Chapter 4, Figure 4.1).

not yet lead to any food reward and its functional use to solve the task is not obvious), followed by a modification of the “Dipping” technique: Instead of holding the trap door open and dipping a stick in an out of the hole (as in “Dipping”), this was modified to letting the trap door go after having put the stick in the hole, thus the stick is blocked in the hole and the lid can be levered open. The only individual that acquired “Poke and Lever” (latency till first performance: 27 h 41 min.) had previously learned both “Poke” (latency: 13 h 20 min.) and “Dipping” (latency: 26 h 07 min.). Schematically (Figure 5.3), the individual had first learned element “y” (“Poke”: did not lead to a food reward), after a long time (Δt_1) it had learned technique “A” (“Dipping”), and after some more time (Δt_2) the individual modified “A” and preceded it by element “y” to build the ratcheted technique “yA_m” (“Poke and Lever”).

For a more detailed scheme we divide the behaviors into sub elements (Figure 5.3): “Dipping” means sliding open the trap door by pushing it back with a finger, thereby exposing the hole (a_1), and whilst holding on, use the other hand to dip a stick into that hole, then pull stick out (a_2). In “Poke and Lever”, a stick is used to poke the recessed bolt inwards, thereby unlocking the lid (y), followed by sliding open the trap door (equal to a_1), then letting the trap door go so the stick is blocked and levering open the lid (a_{2m} : modification of a_2 where the trap door was held open and the stick dipped into the hole and pulled out). Thus, preceding technique “A” by element “y” and modifying one sub element of technique “A” (a_2 becomes a_{2m}) we can build the ratcheted technique (ya_1a_{2m}).

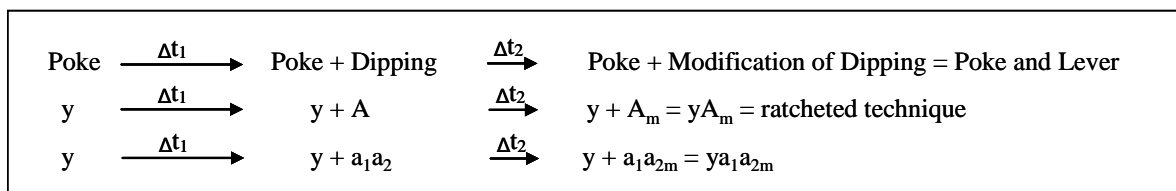


Figure 5.3: Formation of the ratcheted technique “Poke and Lever” and the corresponding schematic images. Note that time interval 2 (Δt_2) here is shorter than time interval 1 (Δt_1). Behavioral element “y” (“Poke”) standing on its own is not a solution to the task (no food reward is made available and its functional use to solve the task is not obvious).

In conclusion, from these three examples we can draw the following two schemes typical for ratcheted techniques (Figure 5.4). An individual first learns a technique “A” (a_1a_2), some time later the individual acquires a second technique “B” (b_1b_2), after some more time the individual modifies a sub element of one of these two techniques (e.g. a_2 becomes a_{2m}) and/or reduces one or both techniques to one of their sub elements (e.g. B is reduced to b_2);

finally, sub elements of the two techniques are combined in a specific order to form the ratcheted technique (e.g. $A_m B = a_{2m} b_2$). In a different case an individual learns a technique “A”, but rather than a second technique the subject additionally has to learn a behavioral element “y”, which on its own does not lead to a reward and the functional significance to solve the task is not obvious; the ratcheted technique is then formed by modifying one technique “A” and combining it with a seemingly useless element “y”. Such a case might be more difficult than one basing on two techniques that had both represented solutions to the task previously.

Therefore, the ratcheted technique “Poke and Lever” may have been much more difficult for the orangutans than the other two examples of ratcheted techniques, because “Poke” never led to a reward in the task and its meaning to solution of the task was not obvious but had to be combined with a modification of the “Dipping” technique. In the other examples two techniques previously being solutions to the task were modified and/or reduced and then combined to form the ratcheted techniques.

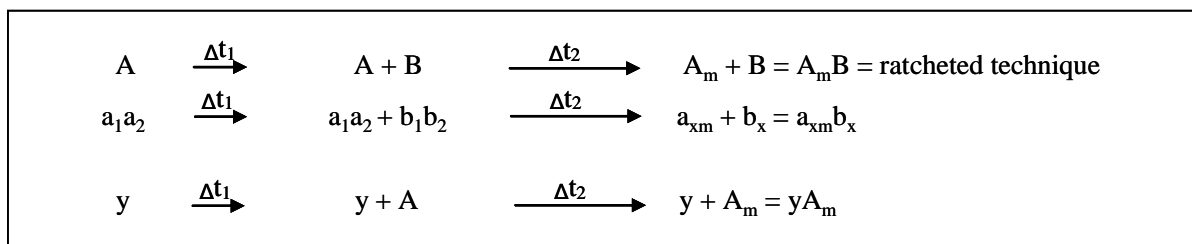


Figure 5.4: Two typical schemes of the formation of ratcheted techniques. One of the two techniques is modified (e.g. A) and/or reduced to one of its sub elements ($a_x = a_1$ or a_2) and combined with sub element(s) of the other one ($b_x = b_1$ or b_2) to form the ratcheted technique. Alternatively one technique “A” is modified and preceded by an element “y” that on its own did not represent a solution to the task.

The three examples showed how the ratcheted technique was formed by the first individual that came up with it. However, basically the same is true for every single individual that learned a ratcheted technique. Only individuals that first had learned both components (A and B; or y and A) later mastered the corresponding ratcheted technique. However, it was not always sufficient for an individual to have the two relevant components in its repertoire in order to master the ratcheted technique. In the experiment with the foraging box four subjects having learned both “Poke” and “Dipping” nonetheless failed to learn the ratcheted technique “Poke and Lever” (Chapter 4).

Individuals differed in which component they had learned first, but this does not imply that they all learned the ratcheted technique individually. It was not within the scope of this thesis to test how individuals learned a ratcheted technique. However, in the experiment with the syrup tube (Chapter 3) the subjects acquiring one of the ratcheted techniques (after they had been invented in the group) first observed the ratcheted technique being performed by a group member, suggesting they likely used this social information to acquire the ratcheted technique. In the experiment with the foraging box (Chapter 4), the single individual succeeding to acquire the ratcheted technique did so only after having observed numerous demonstrations by a human model. As already pointed out by Heyes (1994) and Galef (1995), social learning and individual learning must not be treated as independent processes. Instead, social learning might best be described as socially mediated individual learning (Galef, 1995). Thus, this suggests that captive orangutans can learn something by social mediation they previously failed to learn on their own. But this needs to be supported by future research.

Implications for the understanding of human evolution

As our findings showed that captive orangutans are capable to make cumulative build-up of techniques when novel exigencies inhibited previous solutions, we now briefly add some thoughts what this could mean for human evolution. First, it would suggest that a common human-orangutan ancestor some 14 M years ago had about the same potential as the orangutans; indeed, increasing complexity of hominid culture was only first noticeable when the Acheulean lithic industry superseded the Oldowan, but ratcheting remained very slow until much more recent times (Whiten et al., 2003). Second, we accordingly would expect that ratcheting in humans also started as novel exigencies favored it.

But additionally, there must have been a more fertile ground in the human case than in case of the apes onto which novel exigencies fell. This more fertile ground could be represented by the hominins' cooperative breeding system. Environmental changes some 2 M years ago led them to live on the savannah and hunt in a larger area for larger prey, which resulted in a better supply with nutrients, but this required a more sociable and tolerant life style involving cooperative hunting and sharing of prey. Prey was not only shared among collaborators, but also with collaborators' offspring who could never have gained such resources on their own during childhood and depended on being provisioned, as well as with elderly people, who supported parents in childcare ("grandmothering"). Although there was little evidence for ratcheting until 1.8 M years ago and the onset of Acheulean (Mithen, 1999),

once this new lifestyle with the cooperative breeding system was in place, ratcheting could start. First, this cooperative lifestyle allowed bigger brains, which resulted in higher intelligence (Burkart et al., 2009a), making more fancy innovations possible and techniques cumulatively building up on a previous one become more likely to be invented. Second, in a tolerant and cooperative society transmission of new techniques becomes easier and more reliable (Whiten & van Schaik, 2007), especially after humans started actively to teach, which then allowed transmission of much more complex techniques. Thus, these are conditions where ratcheting could prosper.

Apes on the other hand did not develop a cooperative breeding system which arguably could have promoted ratcheting. However, our results have shown that captive orangutans have some capability for ratcheting, while it is not exhibited in the wild. We attributed this difference to the special conditions of captivity, producing higher innovative tendencies and better opportunities for reliable social transmission.

References

- Altmann, J. 1974. Observational study of behaviour: sampling methods. *Behaviour*, **49**, 227-267.
- Alvard, M. S. 2003. The adaptive nature of culture. *Evolutionary Anthropology*, **12**, 136-149.
- Beran, M. J., Pate, J. L., Richardson, W. K. & Rumbaugh, D. M. 2000. A chimpanzee's (Pan troglodytes) long-term retention of lexigrams. *Animal Learning & Behavior*, **28**, 201-207.
- Bering, J. M., Bjorklund, D. F. & Ragan, P. 2000. Deferred imitation of object-related actions in human-reared juvenile chimpanzees and orangutans. *Developmental Psychobiology*, **36**, 218-232.
- Biro, D., Inoue-Nakamura, N., Tonooka, R., Yamakoshi, G., Sousa, C. & Matsuzawa, T. 2003. Cultural innovation and transmission of tool use in wild chimpanzees: evidence from field experiments. *Animal Cognition*, **6**, 213-223.
- Bjorklund, D. F., Bering, J. M. & Ragan, P. 2000. A two-year longitudinal study of deferred imitation of object manipulation in a juvenile chimpanzee (Pan troglodytes) and orangutan (Pongo pygmaeus). *Developmental Psychobiology*, **37**, 229-237.
- Boesch, C. 1996. The emergence of cultures among wild chimpanzees. In: *Evolution of social behaviour patterns in monkeys and man* (Ed. by Runciman, W. G., Maynard-Smith, J. & Dunbar, R. I. M.), pp. 251-268. London: British Academy.
- Boesch, C. 2003. Is culture a golden barrier between human and chimpanzee? *Evolutionary Anthropology*, **12**, 82-91.
- Boesch, C. & Tomasello, M. 1998. Chimpanzee and human cultures. *Current Anthropology*, **39**, 591-614.
- Bonnie, K. E., Horner, V., Whiten, A. & de Waal, F. B. M. 2007. Spread of arbitrary conventions among chimpanzees: a controlled experiment. *Proceedings of the Royal Society B-Biological Sciences*, **274**, 367-372.
- Boogert, N. J., Reader, S. M., Hoppitt, W. & Laland, K. N. 2008. The origin and spread of innovations in starlings. *Animal Behaviour*, **75**, 1509-1518.
- Bouchard, J., Goodyer, W. & Lefebvre, L. 2007. Social learning and innovation are positively correlated in pigeons (Columba livia). *Animal Cognition*, **10**, 259-266.
- Box, H. O. & Gibson, K. R. 1999. Mammalian social learning: Comparative and ecological perspectives. Cambridge: Cambridge University Press.
- Boyd, R. & Richerson, P. J. 1985. *Culture and the evolutionary process*. Chicago: University of Chicago Press.
- Boyd, R. & Richerson, P. J. 1996. Why culture is common, but cultural evolution is rare. In: *Evolution of social behaviour patterns in monkeys and man* (Ed. by Runciman, W. G., Maynard-Smith, J. & Dunbar, R. I. M.), pp. 77-93. Oxford: Oxford University Press.
- Boysen, S. T. & Berntson, G. G. 1989. Numerical Competence in a Chimpanzee (Pan-Troglodytes). *Journal of Comparative Psychology*, **103**, 23-31.
- Burkart, J. M., Hrdy, S. B. & Van Schaik, C. P. 2009a. Cooperative Breeding and Human Cognitive Evolution. *Evolutionary Anthropology*, **18**, 175-186.
- Burkart, J. M., Strasser, A. & Foglia, M. 2009b. Trade-offs between social learning and individual innovativeness in common marmosets, Callithrix jacchus. *Animal Behaviour*, **77**, 1291-1301.
- Byrne, R. W. 1995. *The thinking ape: Evolutionary origins of intelligence*. Oxford: Oxford University Press.
-

-
- Byrne, R. W. 2007. Culture in great apes: using intricate complexity in feeding skills to trace the evolutionary origin of human technical prowess. *Philosophical Transactions of the Royal Society B-Biological Sciences*, **362**, 577-585.
- Caldwell, C. A. & Millen, A. E. 2008a. Experimental models for testing hypotheses about cumulative cultural evolution. *Evolution and Human Behavior*, **29**, 165-171.
- Caldwell, C. A. & Millen, A. E. 2008b. Studying cumulative cultural evolution in the laboratory. *Philosophical Transactions of the Royal Society B-Biological Sciences*, **363**, 3529-3539.
- Caldwell, C. A. & Whiten, A. 2006. Social learning in monkeys and apes: cultural animals? In: *Primates in Perspective* (Ed. by Campell, C. J., Fuentes, A., MacKinnon, K. C., Panger, M. & Bearder, S. K.), pp. 652-664: Oxford University Press.
- Call, J. & Tomasello, M. 1996. The effect of humans on the cognitive development of apes. In: *Reaching into thought* (Ed. by Russon, A. E., Bard, K. A. & Parker, S. T.), pp. 371-403. New York: Cambridge University Press.
- Caro, T. M. & Hauser, M. D. 1992. Is There Teaching in Nonhuman Animals. *Quarterly Review of Biology*, **67**, 151-174.
- Chappell, J. & Kacelnik, A. 2002. Tool selectivity in a non-primate, the New Caledonian crow (*Corvus moneduloides*). *Animal Cognition*, **5**, 71-78.
- Cipolletta, C., Spagnoletti, N., Todd, A., Robbins, M. M., Cohen, H. & Pacyna, S. 2007. Termite feeding by Gorilla gorilla gorilla at Bai Hokou, Central African Republic. *International Journal of Primatology*, **28**, 457-476.
- Day, R. L., Coe, R. L., Kendal, J. R. & Laland, K. N. 2003. Neophilia, innovation and social learning: a study of intergeneric differences in callitrichid monkeys. *Animal Behaviour*, **65**, 559-571.
- de Waal, F. B. M. 2001. *The ape and the sushi master: cultural reflections of a primatologist*. New York: Basic Books.
- Delgado, R. A. & Van Schaik, C. P. 2000. The behavioral ecology and conservation of the orangutan (*Pongo pygmaeus*): A tale of two islands. *Evolutionary Anthropology*, **9**, 201-218.
- DMK. 2006. *Formeln und Tafeln*. Zürich: Orell Füssli.
- Fox, E. A., Sitompul, A. F. & van Schaik, C. P. 1999. Intelligent tool use in wild Sumatran orangutans. In: *The mentalities of gorillas and orangutans* (Ed. by Parker, S. T., Mitchell, R. W. & Miles, H. L.), pp. 99-116. Cambridge: Cambridge University Press.
- Fox, E. A., van Schaik, C. P., Sitompul, A. & Wright, D. N. 2004. Intra- and interpopulational differences in orangutan (*Pongo pygmaeus*) activity and diet: Implications for the invention of tool use. *American Journal of Physical Anthropology*, **125**, 162-174.
- Fragaszy, D. 2003. Making space for traditions. *Evolutionary Anthropology*, **12**, 61-70.
- Fragaszy, D., Izar, P., Visalberghi, E., Ottoni, E. B. & De Oliveira, M. G. 2004. Wild capuchin monkeys (*Cebus libidinosus*) use anvils and stone pounding tools. *American Journal of Primatology*, **64**, 359-366.
- Fragaszy, D. M. & Perry, S. 2003. *The biology of traditions: models and evidence*. Cambridge, UK: Cambridge University Press.
- Galef, B. G. 1992. The question of animal culture. *Human Nature*, **3**, 157-178.
- Galef, B. G. 1995. Why behavior patterns that animals learn socially are locally adaptive. *Animal Behaviour*, **49**, 1325-1334.
- Galef, B. G. & Giraldeau, L. A. 2001. Social influences on foraging in vertebrates: causal mechanisms and adaptive functions. *Animal Behaviour*, **61**, 3-15.
- Gardner, R. A. & Gardner, B. T. 1969. Teaching Sign Language to a Chimpanzee. *Science*, **165**, 664-672.
- Greenberg, R. & Mettke-Hofman, C. 2001. Ecological aspects of neophobia and exploration in birds. *Current Ornithology*, **16**, 119-178.
-

-
- Gruber, T., Muller, M. N., Strimling, P., Wrangham, R. W. & Zuberbühler, K. 2009. Wild chimpanzees rely on cultural knowledge to solve an experimental honey acquisition task. *Current Biology*, **19**, 1-5.
- Guglielmino, C. R., Viganotti, C., Hewlett, B. & Cavallisforza, L. L. 1995. Cultural Variation in Africa - Role of Mechanisms of Transmission and Adaptation. *Proceedings of the National Academy of Sciences of the United States of America*, **92**, 7585-7589.
- Halsey, L. G., Bezerra, B. M. & Souto, A. S. 2006. Can wild common marmosets (*Callithrix jacchus*) solve the parallel strings task? *Animal Cognition*, **9**, 229-233.
- Henrich, J. & Boyd, R. 1998. The evolution of conformist transmission and the emergence of between-group differences. *Evolution and Human Behavior*, **19**, 215-241.
- Henrich, J. & McElreath, R. 2003. The evolution of cultural evolution. *Evolutionary Anthropology*, **12**, 123-135.
- Hewlett, B. & Cavalli-Sforza, L. L. 1986. Cultural transmission among Aka pygmies. *American Anthropologist*, **88**, 922-934.
- Heyes, C. M. 1993. Imitation, Culture and Cognition. *Animal Behaviour*, **46**, 999-1010.
- Heyes, C. M. 1994. Social-Learning in Animals - Categories and Mechanisms. *Biological Reviews of the Cambridge Philosophical Society*, **69**, 207-231.
- Heyes, C. M. & Galef, B. G. 1996. *Social learning in animals: The roots of culture*. London: Academic Press.
- Hohmann, G. & Fruth, B. 2003. Culture in Bonobos? Between-species and within-species variation in behavior. *Current Anthropology*, **44**, 563-571.
- Hopper, L. M., Spiteri, A., Lambeth, S. P., Schapiro, S. J., Horner, V. & Whiten, A. 2007. Experimental studies of traditions and underlying transmission processes in chimpanzees. *Animal Behaviour*, **73**, 1021-1032.
- Hoppitt, W. J. E., Brown, G. R., Kendal, R., Rendell, L., Thornton, A., Webster, M. M. & Laland, K. N. 2008. Lessons from animal teaching. *Trends in Ecology & Evolution*, **23**, 486-493.
- Horner, V. & Whiten, A. 2005. Causal knowledge and imitation/emulation switching in chimpanzees (*Pan troglodytes*) and children (*Homo sapiens*). *Animal Cognition*, **8**, 164-181.
- Hrubesch, C., Preuschoft, S. & van Schaik, C. 2009. Skill mastery inhibits adoption of observed alternative solutions among chimpanzees (*Pan troglodytes*). *Animal Cognition*, **12**, 209-216.
- Huber, L. & Gajdon, G. K. 2006. Technical intelligence in animals: the kea model. *Animal Cognition*, **9**, 295-305.
- Humle, T. & Matsuzawa, T. 2002. Ant-dipping among the chimpanzees of Bossou, Guinea, and some comparisons with other sites. *American Journal of Primatology*, **58**, 133-148.
- Humle, T., Snowdon, C. T. & Matsuzawa, T. 2009. Social influences on ant-dipping acquisition in the wild chimpanzees (*Pan troglodytes verus*) of Bossou, Guinea, West Africa. *Animal Cognition*, **12**, S37-S48.
- Hunt, G. R. & Gray, R. D. 2003. Diversification and cumulative evolution in New Caledonian crow tool manufacture. *Proceedings of the Royal Society of London Series B-Biological Sciences*, **270**, 867-874.
- Jaeggi, A. V., Dunkel, L. P., Van Noordwijk, M. A., Wich, S. A., Sura, A. A. L. & Van Schaik, C. P. 2010. Social Learning of Diet and Foraging Skills by Wild Immature Bornean Orangutans: Implications for Culture. *American Journal of Primatology*, **72**, 62-71.
- Jantschke, F. 1972. *Orang-Utans in Zoologischen Gärten*. München: R. Ripper & Co. Verlag.
- Kawai, M. 1965. Newly-acquired pre-cultural behavior of the natural troop of Japanese monkeys on Koshima islet. *Primates*, **6**, 1-30.
-

-
- Kendal, R. L., Coe, R. L. & Laland, K. N. 2005. Age differences in neophilia, exploration, and innovation in family groups of callitrichid monkeys. *American Journal of Primatology*, **66**, 167-188.
- Kenward, B., Weir, A. A. S., Rutz, C. & Kacelnik, A. 2005. Tool manufacture by naive juvenile crows. *Nature*, **433**, 121-121.
- Klein, R. G. 1999. *The human career: human biological and cultural origins*. Chicago: University of Chicago Press.
- Krutzen, M., Mann, J., Heithaus, M. R., Connor, R. C., Bejder, L. & Sherwin, W. B. 2005. Cultural transmission of tool use in bottlenose dolphins. *Proceedings of the National Academy of Sciences of the United States of America*, **102**, 8939-8943.
- Kummer, H. 1971. *Primate societies: group techniques of ecological adaptation*. Arlington Heights, IL: AHM Publ. Corp.
- Kummer, H. 1992. *Weisse Affen am Roten Meer: Das soziale Leben der Wüstenpaviane*. München: Piper.
- Kummer, H. 1995. *In quest of the sacred baboon: a scientist's journey*. Princeton: Princeton University Press.
- Kummer, H. & Goodall, J. 1985. Conditions of innovative behaviour in primates. *Philosophical Transactions of the Royal Society of London Series B-Biological Sciences*, **308**, 203-214.
- Kummer, H. & Kurt, F. 1965. A comparison of social behaviour in captive and wild hamadryas baboons. In: *The baboon in medical research* (Ed. by Vagtborg, H.), pp. 1-46. Austin: University of Texas Press.
- Laidre, M. E. 2008. Spontaneous performance of wild baboons on three novel food-access puzzles. *Animal Cognition*, **11**, 223-230.
- Laland, K. N. 2004. Social learning strategies. *Learning & Behavior*, **32**, 4-14.
- Laland, K. N. & Hoppitt, W. 2003. Do animals have culture? *Evolutionary Anthropology*, **12**, 150-159.
- Lefebvre, L., Reader, S. M. & Sol, D. 2004. Brains, innovations and evolution in birds and primates. *Brain Behavior and Evolution*, **63**, 233-246.
- Lefebvre, L., Whittle, P., Lascaris, E. & Finkelstein, A. 1997. Feeding innovations and forebrain size in birds. *Animal Behaviour*, **53**, 549-560.
- Lehner, S. R., Burkart, J. M. & van Schaik, C. P. 2010. An evaluation of the geographic method for recognizing innovations in nature, using zoo orangutans. *Primates*, **51**, 101-118.
- Marshall-Pescini, S. & Whiten, A. 2008. Chimpanzees (*Pan troglodytes*) and the question of cumulative culture: an experimental approach. *Animal Cognition*, **11**, 449-456.
- Matsuzawa, T. 1994. Field experiments on use of stone tools by chimpanzees in the wild. In: *Chimpanzee cultures* (Ed. by Wrangham, R. W., McGrew, W. C., de Waal, F. B. M. & Heltne, P.), pp. 351-370. Cambridge MA: Harvard University Press.
- Matsuzawa, T. & Yamakoshi, G. 1996. Comparison of chimpanzee material culture between Bossou and Nimba, West Africa. In: *Reaching into thought* (Ed. by Russon, A. E., Bard, K. A. & Parker, S. T.), pp. 211-232. Cambridge: Cambridge University Press.
- McGrew, W. C. 1992. *Chimpanzee material culture: implications for human evolution*. Cambridge, UK: Cambridge University Press.
- McGrew, W. C. 1998. Culture in nonhuman primates? *Annual Review of Anthropology*, **27**, 301-328.
- McGrew, W. C. 2004. *The cultured chimpanzee: reflections on cultural primatology*. Cambridge: Cambridge University Press.
- McGrew, W. C. & Tutin, C. E. G. 1978. Evidence for a Social Custom in Wild Chimpanzees. *Man*, **13**, 234-251.
-

-
- Menzel, E. W. 1968. Responsiveness to objects in free-ranging Japanese monkeys. *Behaviour*, **26**, 130-150.
- Mithen, S. 1999. Imitation and cultural change: a view from the Stone Age, with specific reference to the manufacture of handaxes. In: *Mammalian social learning: comparative and ecological perspectives* (Ed. by Box, H. O. & Gibson, K. R.), pp. 389-399. Cambridge: Cambridge University Press.
- Morand-Ferron, J., Lefebvre, L., Reader, S. M., Sol, D. & Elvin, S. 2004. Dunking behaviour in Carib grackles. *Animal Behaviour*, **68**, 1267-1274.
- Morrison, J. A. & Menzel, E. W. 1972. Adaptation of a free-ranging rhesus-monkey group to division and transplantation. *Wildlife Monographs*, **31**, 6-78.
- Nishida, T., Matsusaka, T. & McGrew, W. C. 2009. Emergence, propagation or disappearance of novel behavioral patterns in the habituated chimpanzees of Mahale: a review. *Primates*, **50**, 23-36.
- Oswalt, W. H. 1976. *An anthropological analysis of food-getting technology*. New York: John Wiley.
- Page, E. B. 1963. Ordered hypotheses for multiple treatments - a significance test for linear ranks. *Journal of the American Statistical Association*, **58**, 216-230.
- Perry, S., Baker, M., Fedigan, L., Gros-Louis, J., Jack, K., MacKinnon, K. C., Manson, J. H., Panger, M., Pyle, K. & Rose, L. 2003. Social conventions in wild white-faced capuchin monkeys - Evidence for traditions in a neotropical primate. *Current Anthropology*, **44**, 241-268.
- Piersma, T. & Drent, J. 2003. Phenotypic flexibility and the evolution of organismal design. *Trends in Ecology & Evolution*, **18**, 228-233.
- Ramsey, G., Bastian, M. L. & Van Schaik, C. 2007. Animal innovation defined and operationalized. *Behavioral and Brain Sciences*, **30**, 393-437.
- Reader, S. M. & Laland, K. N. 2002. Social intelligence, innovation, and enhanced brain size in primates. *Proceedings of the National Academy of Sciences of the United States of America*, **99**, 4436-4441.
- Reader, S. M. & Laland, K. N. 2003. *Animal innovation*. Oxford: Oxford University Press.
- Reader, S. M. & Macdonald, K. 2003. Environmental variability and primate behavioural flexibility. In: *Animal Innovation* (Ed. by Reader, S. M. & Laland, K. N.), pp. 83-116. Oxford: Oxford University Press.
- Rendell, L. & Whitehead, H. 2001. Culture in whales and dolphins. *Behavioral and Brain Sciences*, **24**, 309-382.
- Rijksen, H. D. 1978. *A Field Study on Sumatran Orangutans (Pongo pygmaeus abelii Lesson 1872). Ecology, behaviour and conservation*. Wageningen: H. Veenman & Zonen BV.
- Rumbaugh, D. M. 1977. *Language learning by a chimpanzee: The LANA project*. New York: Academic Press.
- Russon, A. E., Kuncoro, P., Ferisa, A. & Handayani, D. P. 2010. How Orangutans (*Pongo pygmaeus*) Innovate for Water. *Journal of Comparative Psychology*, **124**, 14-28.
- Russon, A. E., van Schaik, C. P., Kuncoro, P., Ferisa, A., Handayani, D. P. & Van Noordwijk, M. A. 2009. Innovations and intelligence in orangutans. In: *Orangutans: Geographic variation in behavioral ecology and conservation* (Ed. by Wich, S. A., Utami Atmoko, S. S., Mitra Setia, T. & van Schaik, C. P.), pp. 279-298: Oxford University Press.
- Sachs, L. 1999. In: *Angewandte Statistik: Anwendung statistischer Methoden.*, pp. 397; 664-668. Berlin: Springer Verlag.
- Sanz, C. M. & Morgan, D. B. 2009. Flexible and Persistent Tool-using Strategies in Honey-gathering by Wild Chimpanzees. *International Journal of Primatology*, **30**, 411-427.
- Savage-Rumbaugh, E. S. 1986. *Ape language: From conditioned response to symbol*. New York: Columbia University Press.
-

- Schoning, C., Humle, T., Mobius, Y. & McGrew, W. C. 2008. The nature of culture: Technological variation in chimpanzee predation on army ants revisited. *Journal of Human Evolution*, **55**, 48-59.
- Sol, D. 2003. Behavioural innovation: a neglected issue in the ecological and evolutionary literature? In: *Animal Innovation* (Ed. by Reader, S. M. & Laland, K. N.), pp. 63-82. Oxford: Oxford University Press.
- Sol, D. & Lefebvre, L. 2000. Behavioural flexibility predicts invasion success in birds introduced to New Zealand. *Oikos*, **90**, 599-605.
- Sol, D., Lefebvre, L. & Rodriguez-Teijeiro, J. D. 2005. Brain size, innovative propensity and migratory behaviour in temperate Palaearctic birds. *Proceedings of the Royal Society B-Biological Sciences*, **272**, 1433-1441.
- Stoinski, T. S. & Whiten, A. 2003. Social learning by orangutans (*Pongo abelii* and *Pongo pygmaeus*) in a simulated food-processing task. *Journal of Comparative Psychology*, **117**, 272-282.
- Sugiyama, Y. 1997. Social tradition and the use of tool-composites by wild chimpanzees. *Evolutionary Anthropology*, **6**, 23-27.
- Tennie, C., Call, J. & Tomasello, M. 2009. Ratcheting up the ratchet: on the evolution of cumulative culture. *Philosophical Transactions of the Royal Society B-Biological Sciences*, **364**, 2405-2415.
- Tomasello, M. 1996. Do apes ape? In: *Social learning in animals: the roots of culture* (Ed. by Heyes, C. M. & Galef, B. G.), pp. 319-346. London, UK: Academic Press.
- Tomasello, M. 1998. Emulation learning and cultural learning. *Behavioral and Brain Sciences*, **21**, 703-704.
- Tomasello, M. 1999a. *The cultural origins of human cognition*. Cambridge, MA: Harvard University Press.
- Tomasello, M. 1999b. The human adaptation for culture. *Annual Review of Anthropology*, **28**, 509-529.
- Tomasello, M. 2001. Cultural transmission - A view from chimpanzees and human infants. *Journal of Cross-Cultural Psychology*, **32**, 135-146.
- Tomasello, M. & Call, J. 2004. The role of humans in the cognitive development of apes revisited. *Animal Cognition*, **7**, 213-215.
- Tomasello, M., Kruger, A. C. & Ratner, H. H. 1993a. Cultural Learning. *Behavioral and Brain Sciences*, **16**, 495-511.
- Tomasello, M., Savage-Rumbaugh, S. & Kruger, A. C. 1993b. Imitative learning of actions on objects by children, chimpanzees, and enculturated chimpanzees. *Child Development*, **64**, 1688-1705.
- Tomasello, M. & Stahl, D. 2004. Sampling children's spontaneous speech: how much is enough? *Journal of Child Language*, **31**, 101-121.
- van Noordwijk, M. A., Sauren, S. E. B., Nuzuar Abhulani, A., Morrogh-Bernard, H., Utami Atmoko, S. S. & van Schaik, C. P. 2009. Development of independence: Sumatran and Bornean orangutans compared. In: *Orangutans: geographic variation in behavioral ecology* (Ed. by Wich, S. A., Utami Atmoko, S. S., Mitrasetia, T. & van Schaik, C. P.), pp. 189-203. Oxford: Oxford University Press.
- van Noordwijk, M. A. & van Schaik, C. P. 2005. Development of ecological competence in Sumatran orangutans. *American Journal of Physical Anthropology*, **127**, 79-94.
- van Schaik, C. 2009. Geographic variation in the behavior of wild Great Apes: Is it really cultural? In: *The question of animal culture* (Ed. by Laland, K. N. & Galef, B. G.), pp. 70-98. Cambridge, Massachusetts; London, England: Harvard University Press.
- van Schaik, C. P. 2006. Why are some animals so smart? *Scientific American*, **294**, 64-71.

-
- van Schaik, C. P., Ancrenaz, M., Borgen, G., Galdikas, B., Knott, C. D., Singleton, I., Suzuki, A., Utami, S. S. & Merrill, M. 2003. Orangutan cultures and the evolution of material culture. *Science*, **299**, 102-105.
- van Schaik, C. P., Deaner, R. O. & Merrill, M. Y. 1999. The conditions for tool use in primates: implications for the evolution of material culture. *Journal of Human Evolution*, **36**, 719-741.
- van Schaik, C. P. & Knott, C. D. 2001. Geographic variation in tool use on Neesia fruits in orangutans. *American Journal of Physical Anthropology*, **114**, 331-342.
- van Schaik, C. P., van Noordwijk, M. A. & Wich, S. A. 2006. Innovation in wild Bornean orangutans (*Pongo pygmaeus wurmbii*). *Behaviour*, **143**, 839-876.
- Whiten, A. 1989. Parental encouragement in *Gorilla* in comparative perspective: implications for social cognition. In: *The mentality of gorillas and orangutans* (Ed. by Parker, S. T., Miles, H. L. & Mitchell, R. W.), pp. 342-366. Cambridge: Cambridge University Press.
- Whiten, A. 1998. Imitation of the sequential structure of actions by chimpanzees (*Pan troglodytes*). *Journal of Comparative Psychology*, **112**, 270-281.
- Whiten, A. 2005. The second inheritance system of chimpanzees and humans. *Nature*, **437**, 52-55.
- Whiten, A., Goodall, J., McGrew, W. C., Nishida, T., Reynolds, V., Sugiyama, Y., Tutin, C. E. G., Wrangham, R. W. & Boesch, C. 1999. Cultures in chimpanzees. *Nature*, **399**, 682-685.
- Whiten, A., Goodall, J., McGrew, W. C., Nishida, T., Reynolds, V., Sugiyama, Y., Tutin, C. E. G., Wrangham, R. W. & Boesch, C. 2001. Charting cultural variation in chimpanzees. *Behaviour*, **138**, 1481-1516.
- Whiten, A., Horner, I., Litchfield, C. A. & Marshall-Pescini, S. 2004. How do apes ape? *Learning & Behavior*, **32**, 36-52.
- Whiten, A., Horner, V. & de Waal, F. B. M. 2005. Conformity to cultural norms of tool use in chimpanzees. *Nature*, **437**, 737-740.
- Whiten, A., Horner, V. & Marshall-Pescini, S. 2003. Cultural panthropology. *Evolutionary Anthropology*, **12**, 92-105.
- Whiten, A., McGuigan, N., Marshall-Pescini, S. & Hopper, L. M. 2009a. Emulation, imitation, over-imitation and the scope of culture for child and chimpanzee. *Philosophical Transactions of the Royal Society B-Biological Sciences*, **364**, 2417-2428.
- Whiten, A. & Milner, P. 1984. The educational experiences of Nigerian infants. In: *Nigerian children: developmental perspectives* (Ed. by Curran, H. V.), pp. 34-73. London: Routledge and Kegan Paul.
- Whiten, A., Schick, K. & Toth, N. 2009b. The evolution and cultural transmission of percussive technology: integrating evidence from palaeoanthropology and primatology. *Journal of Human Evolution*, **57**, 420-435.
- Whiten, A., Spiteri, A., Horner, V., Bonnie, K. E., Lambeth, S. P., Schapiro, S. J. & de Waal, F. B. M. 2007. Transmission of multiple traditions within and between chimpanzee groups. *Current Biology*, **17**, 1038-1043.
- Whiten, A. & van Schaik, C. P. 2007. The evolution of animal 'cultures' and social intelligence. *Philosophical Transactions of the Royal Society B-Biological Sciences*, **362**, 603-620.
- Wich, S. A., Utami-Atmoko, S. S., Setia, T. M., Rijksen, H. D., Schurmann, C. & van Schaik, C. 2004. Life history of wild Sumatran orangutans (*Pongo abelii*). *Journal of Human Evolution*, **47**, 385-398.
-

- Wood, D. 1989. Social interaction as tutoring. In: *Interaction in human development* (Ed. by Bornstein, M. H. & Bruner, J. S.), pp. 59-80. Hillsdale, NJ: Lawrence Erlbaum Associates.
- Zweifel, N. 2008. Dietary differences between two orangutan populations in Central Kalimantan, Indonesia. Indications of individual and social learning. In: *Anthropology*. Zurich: University of Zurich.
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