On the individual learning of primate material culture

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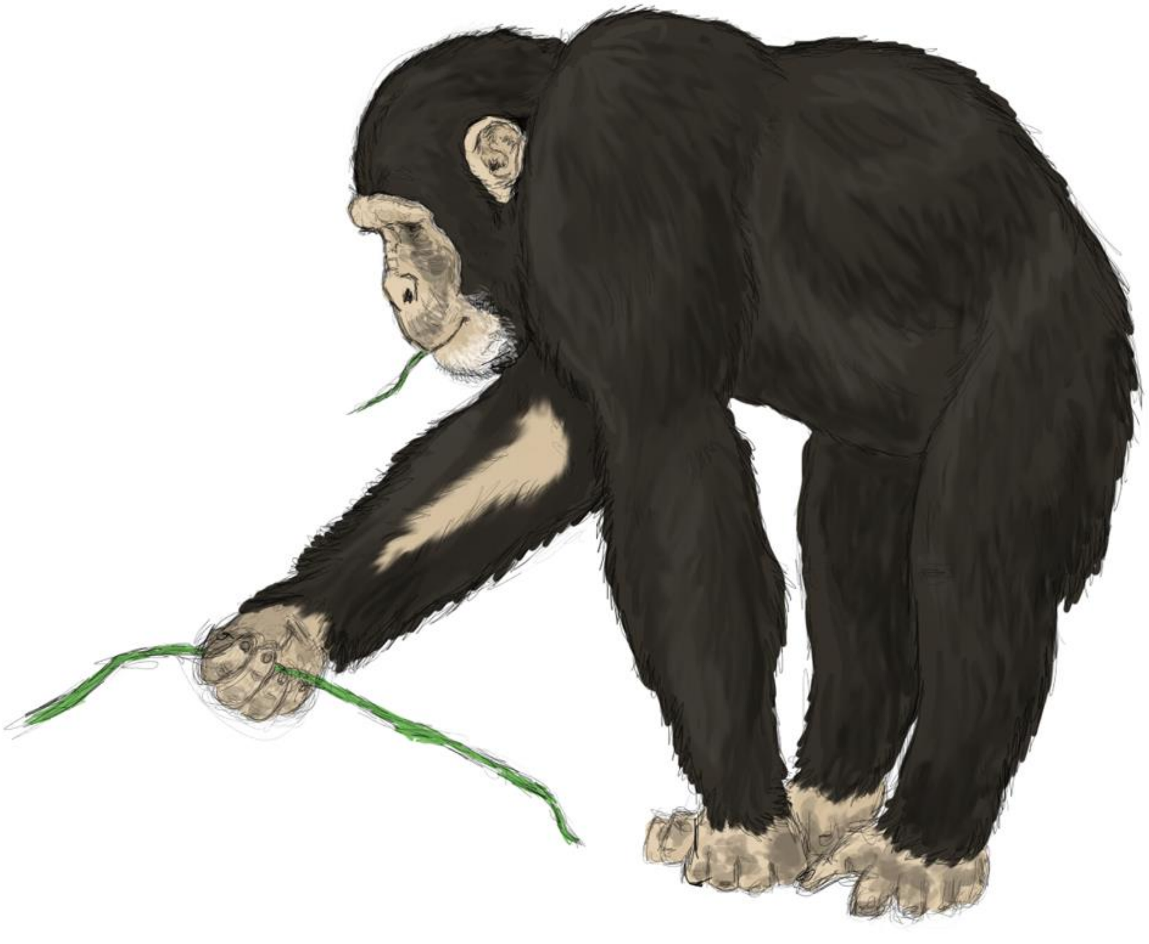
To my parents, and theirs.

"Anything which I have done which you may consider worthwhile, has been made possible by the genius of my mother and father"
-Howard Hughes



Chimpanzee algae scooping (drawing by William Daniel Snyder, 2018)

Acknowledgments

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Look at that, we did it!

Abstract

The cognition behind tool-use in primates is studied across a wide variety of fields, ranging from animal behaviour, biology, archaeology, anthropology, history, to psychology. This thesis encapsulates an interdisciplinary approach to studying and interpreting the phylogenetic origins of individual learning behind tool-use in non-human primates. The introduction chapter presents the background to this thesis, introducing concepts such as the Zone of Latent Solutions hypothesis (Tennie et al., 2009), Vygotsky's (1978) ZAD and ZPD theories, and the current state of animal tool-use research. Chapter II provides a literature review of individual learning of tool-use across animal species, presenting a novel picture of animal tool-use: one in which individual learning, rather than social learning, can drive and sustain animal material culture. Chapter III then discusses the positive results of four independent experimental studies on the individual learning abilities of naïve, captive chimpanzees (*Pan troglodytes*) across wildlife parks in Europe and a sanctuary in Africa. Chapter IV discusses the results of a study with naïve long-tailed macaques (*Macaca fascicularis fascicularis*) that failed to reinnovate the pound-hammering behaviour observed in a wild subspecies. Similarly, Chapter V presents the results of a study on the stone knapping abilities of naïve chimpanzees, in which the chimpanzees did not individually or socially learn how to make flakes, contrary to predictions. The last two chapters (IV and V) explore some possible explanations for the lack of reinnovation observed in these two populations. Finally, the discussion (in chapter VI) summarises the main findings and presents some limitations and objections to the studies, alongside recommendations for future work.

Abstrakt

Die dem Werkzeuggebrauch bei Primaten zugrundeliegenden kognitiven Prozesse werden von einer Reihe akademischer Disziplinen erforscht, etwa der Verhaltensbiologie, Archäologie, Biologie, Anthropologie, Geschichte und der Psychologie. Die vorliegende Arbeit stellt einen interdisziplinären Zugang zur Erforschung der evolutionären Ursprünge des dem Werkzeuggebrauch in nicht-menschlichen Primaten zugrundeliegenden individuellen Lernens dar. Die Einleitung erläutert den theoretischen und empirischen Hintergrund der Arbeit: sie führt Konzepte wie die Hypothese der „Zone der Latenten Lösungen“ (Tennie et al., 2009) sowie Vykotskys (1978) Theorien ein und beschreibt den aktuellen Forschungsstand zum Werkzeuggebrauch im Tierreich. Kapitel 2 präsentiert die Ergebnisse einer Literaturrecherche zum individuellen Lernen von Werkzeuggebrauch in nicht-menschlichen Tieren und zeichnet ein neues Bild vom Werkzeuggebrauch in Tieren: eines, in dem Tiere *individuell* statt sozial lernen, Werkzeuge zu gebrauchen. Kapitel 3 stellt die Ergebnisse vierer unabhängiger experimenteller Studien zu den individuellen Lernfähigkeiten von im Werkzeuggebrauch unerfahrenen Schimpansen (*Pan troglodytes*) aus verschiedenen Tierparks in Europa und einem Schutzgebiet in Afrika dar. Kapitel 4 präsentiert eine Studie zum individuellen Lernen von einer im Werkzeuggebrauch unerfahrenen Spezies von Makaken (*Macaca fascicularis fascicularis*), die zeigt, dass diese Affen die Verhaltensweise „poundhammering“, welche in einer anderen, wilden Subspezies (*Macaca fascicularis aurea*) beobachtet wurde, nicht spontan erfinden. In ähnlicher Weise zeigt Kapitel 5, dass im Anfertigen von Steinwerkzeugen unerfahrene Schimpansen weder individuell noch sozial lernen, Steinwerkzeuge herzustellen. Die empirischen Kapitel 3 bis 5 führen theoretische und methodische Neuerungen für das Studium des Werkzeuggebrauchs bei Primaten ein und führen einige Erklärungsmöglichkeiten für die negativen Ergebnisse in Kapitel 4 und 5 an. Das letzte Kapitel fasst die Hauptergebnisse zusammen, weist auf Einschränkungen der Arbeit hin und gibt Empfehlungen für künftige Studien.

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1.1 General Introduction

"It would seem that the traits identified as cultural are not difficult for chimpanzees to invent, and that invention has occurred independently in many sites"
-Byrne (2007, 579)

From New Caledonian crows making and using different tools across geographical regions to retrieve food (Hunt, 1996; Hunt & Grey, 2003), dolphins adopting marine sponges (most likely) as hunting tools (Krützen et al., 2005; Mann et al., 2008; 2012), octopods using coconut halves as defensive structures (Finn et al., 2009), orangutans presenting clear interpopulational differences in their tool complexes (Fox et al., 2004), to chimpanzees, who display, so far, one of the most extensive and sophisticated tool-use repertoires in non-human animals (Goodall, 1986; McGrew, 1992, 2004; Tomasello & Call, 1997, Wynn et al., 2011), tool-use in the animal kingdom is as varied as it is sophisticated. Once considered unique to humans, these observations have led many to suggest that non-human animals also have "culture". However, the learning mechanisms behind these tool-use behavioural repertoires, and consequently the type of culture observed in non-human animals, are still heavily debated topics. Examining the cognitive mechanisms behind non-human animal (henceforth: animal), and in particular primate, tool-use inherently generates insight that can be applied to these and various other research questions (Mesoudi, 2011).

Firstly, expanding our existing understanding of animal cognition and behaviour is a naturally interesting and valuable pursuit. Secondly, research on the behaviour and cognition of extant animals, and in particular non-human primates (henceforth: primates), can be used to draw insight on the potential behaviours and cognition of early hominins, and subsequently to shed light on the evolution of our own modern human cognition and material culture (Liebal & Haun, 2018). The advent of tools in the archaeological record has been heralded as one of the catalysts of a human culture, and indeed material culture (here defined as the tools, artefacts, technology, instrumental skills and knowledge that allow individuals to interact with and shape their environment; Boesch, 2003; Legare & Nielsen, 2015) has played a crucial role in human evolution (Stout et al., 2000; Coolidge & Wynn, 2005; Gergely & Csibra, 2006). The close phylogenetic ties between extant chimpanzees and humans have allowed researchers to draw insight from the material culture and behaviour of these great apes to that of the last common ancestor at circa 14mya (Tavaré et al 2002; Whiten et al., 2003), and perhaps even beyond (Reindl et al., 2016; Tennie et al, 2016; 2017).

Lastly, examining the behaviour and cognition of animals may aid in the conservation efforts of the species, many of which continue to have a critically endangered status in the wild (see the IUCN Red List of Threatened Species). Understanding the cognitive mechanisms behind the behaviours of these endangered species can, for example, help ensure that animals that are reintroduced into the wild from captivity are equipped with the basic skills required to thrive in their natural habitat (Sutherland, 1998). Finally, through outreach and the media, sharing animal behaviour research with the general public helps draw attention to conservation efforts and fundraising initiatives (Kuhar et al., 2010). In summary, the study of animal tool-use is not only of interest to ethologists, but insight from this line of research can provide invaluable data for those interested in the many aspects of cultural evolution.

The theoretical and empirical work presented in this thesis focuses primarily on examining the acquisition of tool-use behavioural forms in primates. The aim of this research was to expand current understanding of the learning mechanisms behind material culture in extant primates and to contribute novel comparative data to the study of material culture and cognition in early hominins. By empirically testing the emergence of behaviours in naïve primates, the role of various learning mechanisms in catalysing the emergence of these behaviours can be isolated. This allows for hypothesises to be made on how wild primates create and sustain their tool-use cultures, and how early hominins may have done the same. The theoretical contributions of the work included in this thesis spanned from introducing new methodological advances to identify the cognitive mechanisms behind tool-use behaviours, to discussing novel, alternative, interpretations for the data retrieved from these, and related, studies. The experimental contributions of this thesis provide some of the first investigations into primate material culture using a new targeted testing methodology to isolate the roles of individual and social learning in the acquisition of behavioural forms. The general introduction presents an overview of the current state of the field of animal (focusing particularly on primate) tool-use alongside describing the theoretical background and framework for the empirical work and discussions in the following chapters (see also Appendix III for definitions of some of the terms used throughout the thesis).

1.2 Theoretical and empirical background

1.2.1 Culture

One of the most controversial and heavily debated concepts across various fields is that of "culture", which has been defined in a variety of ways across the fields and timeframes. Kroeber & Kluckhohn (1952) listed 168 definitions of "culture" present in the literature available at the time, and it is likely that even more have been introduced since then. Culture has been defined both in a strict sense, limiting it largely only to humans (e.g., "*culture is a mental construct consisting of ideas";* Taylor 1948, 101; see also Holloway, 1969) and in a very broad way, expanding the potential of possessing culture to almost all social animals (e.g., "*Those group-typical behaviour patterns shared by members of a community that rely on socially learned and transmitted information",* Laland & Hoppitt, 2003, 151). What most definitions of culture seem to have in common however is a strong emphasis on the role of social learning, defined as *"The learning about other agents, or the inanimate world, that is influenced by the observation of, or interaction with, another individual and its products"* (Heyes, 2012, 2185), in creating and sustaining cultural behaviours. Social learning has been described as the "*necessary ingredient"* of culture (Whiten et al., 2011,941). Yet, several forms of social learning exist (see Whiten et al., 2004 and Appendix III for definitions of some of these forms). Traditionally, a distinction has been made between high-fidelity and low-fidelity social learning in the literature. *High-fidelity* social learning mechanisms are those that transmit the information of a behaviour (the goals, actions and results; Tomasello et al., 1993) to a faithful enough degree to allow for the actual form of the behaviour (i.e., the main action-components of the behaviour[1]) to be replicated. On the other hand, *low-fidelity* social learning mechanisms are those that only transmit general information unrelated to the form of

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[1] Behavioural forms may consist of one or more action forms in a linear or hierarchical relationship.

the behaviour, (i.e., they do not allow for the copying of the behavioural form itself; Tennie et al., submitted). Thus, low-fidelity social learning mechanisms merely encourage or increase the likelihood that an individual will reproduce the behavioural form independently by, for example, focusing its attention on a certain location or stimulus for a target behaviour to emerge (e.g., through local or stimulus enhancement; Thorpe, 1963). Tennie et al., (submitted) suggest that high-fidelity and low-fidelity social learning should be renamed “copying social learning” and “non-copying social learning” respectively to better reflect the differences between the types of information these two categories of social learning provide. In principle the new terms suggested by Tennie et al., (submitted) do help clarify the different down-the-line effects of high and low-fidelity social learning mechanisms. Indeed, the use of “copying” and “non-copying” emphasises the pivotal fact that “copying social learning” mechanisms can transmit the form of the behaviour, and therefore can also sustain human forms of culture, such as cumulative culture and culture-dependent traits.

Cumulative culture is the gradual accumulation of knowledge, modifications and improvements of traits over time (Boyd & Richerson, 1985; Tomasello et al., 1994; Dean et al., 2012). This extensive accumulation of knowledge and skills over time creates culture-dependent traits (CDTs): traits that are too complex to be reinnovated by a single individual in her lifetime (Reindl et al., 2017). Culture-dependent traits require social learning (most often high-fidelity forms of social learning) to be acquired by an individual (Reindl et al., 2017). Cumulative culture (and so also culture-dependent traits) has been argued to be unique to human forms of culture (see following section for more discussion).

On the other hand, “non-copying” social learning mechanisms can only increase the *frequency* of the behaviour within populations, but cannot transmit the form itself. These forms of low-fidelity social learning can only encourage the acquisition of behaviours that are already within the individual learning abilities of animals. Behaviours that do not require high-fidelity social learning to be acquired (i.e., not culture-dependent traits) are said to be “reinnovated” when they are individually acquired by naïve animals (individuals who have never seen the behaviour beforehand; Bandini & Tennie 2017). The new terms proposed by Tennie et al., (submitted) encapsulate the crucial differences between these forms of social learning. However, as this thesis contains two published studies that refer to low and high-fidelity social learning (these papers were published before the new terms were coined by Tennie and colleagues), these original terms will be used throughout the thesis.

Once a distinction has been made about the social learning mechanisms involved in the behaviours under examination, the type of culture can be identified. For human cumulative culture, it is likely that high-fidelity social learning is required (Tomasello et al., 1993; Tennie et al., 2009; Dean et al., 2012). However, for other forms of culture, it may be that social learning is not required for the behaviours to be reinnovated, but low-fidelity social learning is involved in increasing the frequency of these behaviours (as discussed above). This second form of culture can be considered a "soft" culture (Neadle et al., 2017), which is most likely the type observed in most animal species, and constitutes the definition of culture adopted in this thesis. The next section will discuss in more detail the differences between human and animal culture.

1.2.2 Human culture

The vast success of our species and our colonization of almost every ecological niche on the planet is often attributed to our ability to sustain, transmit, and accumulate cultural knowledge (Boyd et al., 2011; Dean et al., 2012; Henrich, 2015). This ability to acquire and transmit cultural information has been referred to as a "second-inheritance" system, due to the hypothesised similarities between the transmission methods of cultural traits and genes[2]. In the current literature, the environment, an inherited trait that plays an important role in behaviours, has also been included in this process; in which genetic, cultural and environmental inheritance systems all play a complex role in human evolutionary processes (the "triple-inheritance" system; Richerson & Boyd, 1989; Kendal et al., 2010).

In terms of the cultural aspect of the triple inheritance system, as mentioned above,

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[2] Cultural traits have, in the past, also been referred to as "memes", a term originally presented in Dawkins, (1976). This term is now generally no longer used in the cultural evolution literature (Reader & Laland, 1999; although see also Dennett, 1998).

high-fidelity social learning mechanisms, such as imitation and some forms of teaching (alongside innovative processes) have been suggested to be the driving mechanisms behind the cumulative nature of human culture (e.g., see Tomasello, 1999, 39: "*cultural evolution depends on two processes, innovation and imitation, that must take place in a dialectical process over time such that one step in the process enables the next*" and see also Enquist et al., 2010; Lewis & Laland, 2012). These mechanisms allow humans to learn and subsequently transmit the actual form of cultural traits to a faithful enough degree to allow for innovations and modifications on existing traits to be made. The improved traits are then passed on, and new modifications can be made on top of these. The classical example of a product of cumulative culture is the computer, which is the result of a long series of inventions, starting from the abacus and culminating in the compact, lightweight laptop that many of us use daily. No single individual could independently reinnovate a computer in his or her lifetime, making this object a clear example of a culture-dependent trait. Most of the traits in modern human culture are the product of this accumulation of knowledge and skills over space and time (Lehman, 1847; Dean et al., 2012; although see also Vaesen et al., 2018 for an alternative view on the increase in complexity of human culture).

Although many agree that high-fidelity social learning is required for the sustenance of our modern culture, proponents of the Cultural Attractor Theory (CAT; Sperber 2012; Morin, 2012, 2015; Scott-Phillips, 2017) contend that social learning only plays a minor role in human culture, and that the transmission and stability of cultural traits can be attributed to the "attractive" nature of these traits. CAT argues that it is the intrinsic "attractive" nature of certain traits that makes them more salient to humans, therefore increasing the likelihood of humans converging on the same behavioural forms (Morin, 2012). Whilst CAT may provide some new perspectives on why certain traits seem to be persistently transmitted across generations, it does not explain why humans developed such seemingly unique high levels of attention towards social information across contexts (see for example, the "over-imitation" phenomenon observed in young children across cultures; Lyons et al., 2007; Nielsen & Tomasello, 2010). Furthermore, the countless examples of humans' reliance on social information for survival (e.g., the many cases of explorers stranded in harsh environments who only survived due to local communities that had accumulated, across generations, the knowledge to survive in these environments; Henrich, 2015; Muthukrishna & Henrich, 2016) all suggest that social learning must play an important role in our modern culture. Thus, whilst CAT can provide an additional (and compatible) explanation of why certain cultural traits are transmitted, it cannot be used as a viable full alternative explanation for the triple-inheritance theory (Richerson & Boyd, 1989). In summary, it seems likely that humans' remarkable (and potentially unique; Dean et al., 2012) ability to faithfully acquire and transmit cultural traits may be the distinguishing feature of our culture compared to that of other animals (Laland & O'Brien, 2011; Henrich, 2015).

1.2.3 Non-human animal culture

Many researchers have claimed that non-human animals also possess culture (following the definition of culture that emphasises a dependence on social learning; Goodall, 1986; Whiten et al., 1999, 2000, 2001; de Waal, 2001; van Schaik, 2003; West et al., 2003; Krützen et al., 2005; de Waal & Ferrari, 2011; Rendell & Whitehead, 2011; Aplin et al., 2015; Robbins et al., 2016). Others have further argued that some animals demonstrate human-forms of cultural behaviours, which (must) rest on high-fidelity social learning (e.g., Whiten et al., 1999; 2001, Marshall-Pescini & Whiten, 2008; de Waal & Ferrari, 2011; Yamamoto et al., 2013; Gruber et al., 2015; Davis et al., 2016; Sasaki & Biro, 2017). Of the tool-using animal species, chimpanzees (*Pan troglodytes*) are often used as a case species for animal "culture", due to their extensive tool-use repertoires, population-wide patterns of behaviours and their close phylogenetic ties to humans (Goodall, 1986; Mcgrew, 1992, 2004; Tomasello & Call, 1997, Whiten et al., 1999; 2001; de Waal & Ferrari, 2011; Wynn et al., 2011; Gruber et al., 2015). For example, de Waal & Ferrari, (2011, 203) confidently state: "*Exposed to models of their own species, chimpanzees reliably and faithfully imitate tool-use, foraging techniques and arbitrary action sequences*". However, despite the significant body of work investigating the learning mechanisms behind chimpanzee tool-use repertoires, there is still much debate around whether these repertoires are sustained via low-fidelity social learning (e.g., Luncz et al., 2012; Gruber et al., 2012; 2015), a mix of low and high-fidelity social learning (such as in human culture e.g., Whiten et al., 1999; 2001; de Waal & Ferrari, 2011), or a mix of (primarily) individual learning with low-fidelity social learning facilitating the acquisition (e.g., Tennie et al., 2009; Bandini & Tennie, 2017). To address this question, the first step is to understand whether chimpanzees are *able* to acquire behavioural forms via any type of social learning. The following step is then to explore whether the emergence of the tool-use repertoires of wild chimpanzees and other primates necessarily rest on these social learning mechanisms. A brief history of the studies addressing these questions is provided in the following section.

1.2.4 History of studies on chimpanzee culture

Two pioneers of the study of chimpanzee tool-use were McGrew (1979) and Goodall (e.g., 1970; 1985), whose seminal reports on wild chimpanzees provided some of the first systematic reviews of chimpanzee behaviour. Although these reports were of an observational nature, Goodall (1970; 1985), in particular, made strong claims on the learning mechanisms behind the behavioural repertoires she was observing, arguing that similarly to human culture, high-fidelity social learning also underlies chimpanzee culture: "*in a species which is so well known for its imitative abilities, it seems sensible to suppose that most, if not all, of the behaviours outlined above [. . .] are passed down from one generation to the next through observational learning*[3] *in a social context*" (Goodall, 1970,161). Despite the lack of experimental evidence for this view at the time, the assumption that chimpanzees depend on social learning, and that they do not possess any individual learning abilities (e.g., see Kummer & Goodall; 1985, 203: "*primates are remarkably ill-equipped with innate technologies*") remained uncontested and pervasive in the literature for many years. The discovery of variations in behavioural repertoires between wild chimpanzee populations further consolidated the view that these differences were the product of high-fidelity social learning (e.g., Whiten et al., 1999; 2001). Following up on these early reports, and to examine the breadth of the differences between population behavioural repertoires, Whiten and colleagues (1999; 2001) carried out an extension of the original survey of chimpanzee behaviours across African field sites by McGrew (1979).

1.2.5 The method of exclusion

Whiten et al (1999; 2001) mapped the chimpanzee behaviours observed at the time across six long-term field sites in Africa. Based on these records, behaviours in each

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[3] By observational learning, Goodall was most likely implying high-fidelity forms of social learning. such as imitation.

population were then categorised as "*customary*", "*habitual*", "*present*", "*absent*", or "*ecological explanation*" (the latter defined as: *"absence is explicable because of a local ecological feature";* Whiten et al., 1999, 6). Behaviours that were found to be either *customary* or *habitual* in one site, but *absent* and not due to ecological explanations at another were considered "*putative cultural traits*" (Whiten et al., 1999, 6). A total of 39 cultural traits were identified following this method. It was then argued that the presence of one or more of these 39 behaviours in a chimpanzee community could be confidently attributed to social learning, as other potential external factors, such as genetics and environmental influences, had been ruled out (an impossibility, in reality). This method was thus named the "method of exclusion" (henceforth: MOE. This method is also known in the literature as: "method of elimination", van Schaik, 2003; "geographical method", van Schaik et al., 2003; van Schaik, 2009; "ethnographic method", Laland & Janik, 2006 or the "group comparison method", Fragazy & Perry 2003).

Whiten et al., (1999, 4) suggest that, at least for some of the putative cultural behaviours, high-fidelity social learning must be assumed: "*it is difficult to see how such behaviour patterns could be perpetuated by social learning processes simpler than imitation*". This new method (MOE) of identifying differences in the behavioural repertoires of wild animals sparked a flurry of research into the behaviours of several other species, and similar reports were published soon after for orangutans (*P. pygmaeus*; van Schaik et al., 2003), gorillas (*G. gorilla*; Robbins et al., 2016), capuchins (*C.apella*; Perry, 2011), spider monkeys (*A. geoffroyi*; Santorelli et al., 2011) and dolphins (*Tursiops sp*; Krützen et al., 2015).

Although the method of exclusion has some commendable points, not the least that it encourages systematic reviews into wild animal behaviours and collaboration between researchers across different field sites, some have argued that this method tends to create false positives in favour of the cultural hypothesis (Galef, 1992; Laland & Hoppitt, 2003; Laland & Janik, 2006). One of the strongest criticisms of the method of exclusion is that it does not (and cannot) fully exclude the potential impact of environmental and genetic factors on the emergence of behaviours. For example, an in-depth study on one of the 39 behaviours, "ant dipping" in chimpanzees (which was categorised as a cultural behaviour in Whiten et al.s' (1999) original report, based on the fact that differences in the length of tools used by the chimpanzees were found across sites) revealed that the variation in stick length could be attributed to the differences in levels of aggression of the ants between sites, rather than any cultural learning (Humle & Matsuzawa, 2002; see also Humle et al., 2009).

The second external factor that the method of exclusion claims to control for is the influence of genes. Yet only one behaviour in the original (Whiten et al., 1999) review was excluded due to a potential influence of genetics, raising doubts on how rigorously this factor was controlled for (Laland & Janik, 2006). Indeed, the role of genetics in wild chimpanzee behaviours remains a contentious issue. Two independent studies (Lycett et al., 2007; Langergraber et al., 2010) carried out phylogenetic analyses of the behavioural differences observed in wild chimpanzee populations, generating inconsistent results. Whilst Lycett et al., (2007; 2010) found no correlation between genes and chimpanzee behavioural repertoires, Langergraber et al., (2010) found that some behaviours could be explained by genetic differences between populations. Thus, the role of genetics in chimpanzee behavioural repertoires remains inconclusive (see also Hopkins et al., 2014). It is unlikely, however, that ant-dipping is the only behaviour for which factors other than cultural learning play a bigger role than previously hypothesised (Galef & Griffin, 1995; Laland & Janik, 2006). With more research into the specific behaviours, it is possible, indeed probable, that other factors (such as the environment or genes) will be identified in the emergence of some of the other behaviours classified as cultural by Whiten et al., (1999; 2001).

Furthermore, the method of exclusion poses several theoretical problems inconsistent with its core aim of identifying cultural behaviours. Firstly, it is logically impossible to demonstrate the absence of an influence (as McGrew, 1977, 368, states: "*absence of evidence does not provide evidence of absence*"). Secondly, it is highly unlikely that any behaviour is influenced by only one single factor. Thus, rather than assuming that behaviours can *either* be driven by environmental factors, genetics, individual learning or social leaning exclusively, it is much more likely and more parsimonious to assume instead that *each* of these factors influence the emergence and form of a behaviour (similarly to the logic behind the "triple-inheritance theory"; see also Barrett, 2018). Thus, although the contributions of each factor towards the shaping of the form of behaviours may vary, trying to place behaviours into mutually exclusive categories is most likely an impossible and unproductive task (much like the old nature-nurture debate; Laland & Janik, 2006; Barrett, 2018). Despite the clear shortcomings of the MOE, findings from these studies are still used by some as evidence to demonstrate the existence of cultural behaviours across species (and even for claims of the mechanisms behind these behaviours), and experimental studies on the cognition behind animal, and in particular chimpanzee, tool-use reflect this view (e.g., Byrne et al., 2003; Gruber et al., 2015; Davis et al., 2016).

1.2.6 Experimental tests for social learning in animals

"Primates can [...] solve only those problems that are of the same degree of difficulty as those they can solve alone"
-Vygotsky (1978, 88)

Whilst acting director of the chimpanzee research station of the Prussian Academy of Sciences on the Island of Tenerife, Wolfgang Köhler (1887-1967) carried out some of the earliest experimental tests on the tool-use abilities of captive chimpanzees. In retrospect, it could be said that Köhler was most interested in what chimpanzees were able to achieve independently of social information. Through a series of experiments that most often involved placing food out of immediate bodily reach, Köhler was able to observe the spontaneous problem solving and tool-use capabilities of the chimpanzees. Contrary to the widespread belief that chimpanzees were not able to use tools or solve problems without some form of social input, Köhler discovered that his subjects were able to solve almost all the tasks independently through what he called "*insight learning"* (Köhler 1925, 190; by "insight learning" Köhler was referring to an individual learning-focused mechanism). Thus Köhler became one of the first to suggest that chimpanzees do not strictly require social information to innovate and reinnovate some aspects of their tool-use repertoires.

Despite Köhler's findings, moving forward, the field continued to focus primarily on identifying the social learning abilities of chimpanzees. To test the view that chimpanzees depend on high-fidelity social learning for their tool-use repertoires (as suggested by Kummer & Goodall, 1985; Whiten et al., 1999; 2001), methodologies from early ethology studies were adapted to test primates. For example, one early study on social learning was carried out with captive budgerigars (*Melopsittacus undulates*). Dawson & Foss (1965) provided two groups of budgerigars with a baited container that could be opened either using the beak or a foot. One individual from each group was trained (out of view of the rest of the group) in one of the two methods. Once the demonstrators reliably only used the method they were trained in, they were placed back into their respective groups. The authors then observed whether the rest of the group was more likely to adopt the demonstrated (or “seeded”) technique or if they chose at random (Dawson & Foss, 1965). The budgerigars were found to use the demonstrated technique more often than the alternative method to open the bottle, and Dawson & Foss (1965) argued that the subjects were imitating the actions of their demonstrator. However, firstly, these results were not replicated in a follow-up study and the authors of the replication study reported a number of ambiguities with the original study (Galef et al., 1988). Secondly, in the light of new understanding on the different forms of social learning, it seems more likely that the budgerigars were simply learning about the affordances of the lid, as the two methods produced different environmental results: when the demonstrator used its beak to open the bottle, the lid twisted off, whilst when the foot was used, the lid came off without the twisting action (Zentall & Akins, 2001). These two effects are simple enough that they are most likely within the individual learning abilities of the birds. Therefore, a more parsimonious interpretation of this study is that the budgerigars were replicating the effects of the behaviour, rather than the actions. These findings demonstrate that social learning influenced the birds to a certain degree, but the social learning mechanisms at work were most likely of a low-fidelity type (therefore unable to sustain imitation as Dawson & Foss (1965) originally hypothesised).

Dawson & Foss’s (1965) method of training demonstrators in two alternative methods and seeding the methods in naïve groups was then adopted by Whiten et al., (1996), who initiated a long tradition of testing chimpanzees following this “two-target” method. Many studies across a wide number of species have now been carried out using this methodology (e.g., Whiten et al., 1996; Whiten, 1998; Whiten et al., 2005; 2008, Custance et al., 2001; Stoinski et al., 2001; Atkins et al., 2002; Miller et al., 2009; Kis et al., 2015; Whiten et al., 2015). Results from these tests consistently demonstrate that many animal species are capable of socially learning simple techniques to retrieve food rewards, and that naïve subjects are more likely to adopt the technique that was demonstrated rather than the alternative method (see references above). Data from these studies have been used as evidence not only for the existence of social learning in different animal species (which is irrefutable), but some have further argued that the social learning mechanisms being adopted are similar to those in human culture (i.e., they are of a high-fidelity type, Whiten et al., 1996; 1998). Yet, although two-target tests provide a simple way of identifying whether animals can socially learn the solutions to casually-clear problems (these tests usually involve sliding a door to the left or the right, or opening a puzzle box by "poking" or "lifting" a lever; Whiten et al., 2015), they cannot identify whether the social learning mechanisms at play are of a high or low-fidelity type due to the inherent confounds of the testing method (see above). Thus, two-target tests can provide information on which species are able and motivated to attend to social demonstrations, but they cannot identify whether these animals have high-fidelity social learning skills and, crucially, they cannot identify whether they can acquire culture-dependent traits (as the solution of these tasks most likely lie within their individual abilities; Bandini & Tennie, 2017). Indeed, in almost all two-target tests carried out with chimpanzees so far, at least one individual has spontaneously reinnovated the alternative non-seeded technique (see Tennie et al., submitted, Bandini & Harrison, in prep, and individual learning database described chapter II). If these tests generated solutions that could only be acquired through powerful high-fidelity social learning mechanisms, then no individual should reinnovate the non-seeded technique (as it should be outside their individual learning capabilities). The fact that at least one subject has (almost) always reinnovated the alternative solution to the seeded one suggests that both solutions are relatively easy and do not, in any case, necessitate social learning to emerge. Therefore, whilst these tests can identify general copying abilities across the animal kingdom, they do not identify any "special" or "human-like" copying abilities (Bandini & Tennie, 2017).

Based also on the results of these two-target tests, and despite the large bias in the literature in favour of primates, chimpanzees, and indeed all primates, continue to be conspicuously absent from the list of candidate species possessing *cumulative* culture (so far, only some species of birds and whales are on the list, due, primarily, to their seemingly complex vocal learning abilities; Laland & Hoppitt, 2003). What is clear from past studies is that whilst chimpanzees and other primates are motivated to attend to social information, currently, two-target studies do not identify behaviours that require social learning to emerge or behaviours that are beyond chimpanzees' own individual learning abilities.

However, a study on action copying in chimpanzees by Tennie and colleagues (2012) identified a novel behaviour that was beyond the individual and social learning abilities of chimpanzees. The authors trained a chimpanzee (Mawa: male, 22 years old) at Ngamba Island Chimpanzee Sanctuary, Uganda, to show a novel "praying" action (i.e., Mawa would *"squat and raise both arms [...] his hands placed one over the other with both palms facing his head"* Tennie et al., 2012, 12). This behaviour had never been seen as part of the chimpanzees' natural behavioural repertoire at Ngamba Island and therefore was considered to be a "*novel target action"* (Tennie et al., 2012, 4). Once Mawa was trained to reliably show the new behaviour in exchange of a food reward, he was placed back into his group to act as a demonstrator. No other chimpanzee in the group acquired the target behaviour (Tennie et al., 2012). Thus, the chimpanzees were seemingly unable or unmotivated to copy the actions of a novel behaviour that was outside of their individual learning abilities (Tennie et al., 2012).

Recent research from neuroscience supports this conclusion. Hecht et al., (2012), examined the brain images of chimpanzees, macaques and humans using brain stimulations, and found evidence for differences across the species in the response of their mirror systems to the observational learning process. Whilst humans mirror systems responded to watching the actions and the results of a behaviour, chimpanzees', and to an even greater degree, macaques' mirror systems only responded to viewing the end product of a behaviour, and did not demonstrate any response towards viewing the actions being performed (Hecht et al., 2012). Similarly, an eye-tracking study on humans, bonobos, chimpanzees, orangutans and rhesus macaques demonstrated that humans viewed the target actions in the presented movies for a much longer time than the other primates (Kano et al., 2018). Although the chimpanzees and orangutans watched the target actions for a longer period than the bonobos and macaques, their attention was considerably shorter and less focused compared to that of the human participants (Kano et al., 2018; although note that eye-gaze towards the video does not necessarily translate into automatic retention of the content. Thus, even if chimpanzees and orangutans did pay more attention to the actions than the other primates, this does not necessarily enhance their ability to reproduce these actions). Cumulatively, these studies provide mounting evidence for the view that non-human great apes only have a limited (if any) ability to retain social information on actions (and therefore have limited action copying abilities, compared to humans).

1.2.7 Data from enculturated great apes

Although it seems that unenculturated primates (including *"enriched captive apes"*: apes living in conspecific groups in captivity, not under deprived conditions, and without extensive human contact and/or training; Henrich & Tennie, 2017) are unable to socially learn behaviours that they cannot also individually learn, evidence from *enculturated* apes (captive individuals who have received extensive human contact and training; Henrich & Tennie, 2017) suggests that these subjects may be able to "learn how to learn" (Heyes, 2015; 2016). One famous example of this phenomenon is Kanzi, a male bonobo raised primarily by Dr. Savage-Rumbaugh in a hybrid panhuman family at a primate research facility in Iowa, USA. Kanzi was exposed from a young age to human language training through his mother, who was undergoing extensive training with a lexigram. Gradually Kanzi also starting using the lexigram, alongside showing (after training) many other typically "human" behaviours (although the evidence is highly anecdotal; Savage-Rumbaugh et al., 1993).

In a more systematic study, Toth et al., (1993; 1999) and Schick et al., (2009) investigated the cognition behind the manufacture and use of early hominin stone tools by providing Kanzi, and later his sister, Panbanisha, with the materials needed to make Oldowan flakes (hammerstones, cores and a baited puzzle box that could only be opened by cutting it open with a flake) and demonstrations on how to make and use a flake to open a baited puzzle box. After the demonstrations, Kanzi was able to make and use flakes without help from his human trainers. Kanzi's flakes displayed similar properties to those found in the archaeological record for early hominins (Toth et al., 1993; Harmand et al., 2015). As currently there is no evidence for wild bonobos spontaneously making or using stone flakes in the wild (although there are reports of chimpanzees in Côte d'Ivoire, and capuchins in Brazil unintentionally making these tools; Mercander et al., 2002; 2007; Proffitt et al., 2016. See also chapter V), it seems that Kanzi, after extensive training in this, and other “unnatural” tasks, was able to express a behaviour outside of wild bonobos’ normal tool-use repertoires. However, a baseline condition, in which Kanzi was provided with the materials to make flakes, but no training in the behaviour, is missing. Thus, it is possible that Kanzi could have made flakes even without demonstrations. Indeed, captive capuchins were able to make and use flakes without social information in a similar setup (Westergaard & Suomi, 1994). As naïve, captive capuchins were able to make flakes without requiring demonstrations; it is also possible that Kanzi, if he had been allowed to independently explore the materials, would have spontaneously reinnovated the knapping process. This subject is further explored in chapter V.

Studies with enculturated apes, such as Kanzi, or Viki, the chimpanzee who was trained in human language (Hayes & Hayes; 1952), suggest that highly enculturated animals that have been exposed to humans and extensive training regimens in species-atypical conditions may be able to express behaviours that are outside of their normal behavioural repertoires. The extensive human contact and training regimes that these animals are exposed to may have long lasting effects on their cognition, perhaps even providing them with the abilities required to copy behaviours. Damerius et al., (2015) found that semi-wild orangutans that had been exposed to humans for a long time and demonstrated a confident and trusting relationship with their carers (measured via the HOI; Human Orientation Index; Damerius et al., 2015), performed better in a cognitive test battery. This preliminary evidence suggests that prolonged exposure and interaction with humans may have an effect on the cognition of primates, leading to higher performance on (human-created) cognitive tasks (Shaw & Shmeltz, 2017). In Kano et al.s’ (2018) eye-tracking study, the authors found that chimpanzees who had previously participated in cognitive experiments and who were familiar with watching movies viewed target actions longer than chimpanzees who did not have any experience with these types of tests. Furthermore, a recent study on the fronto-parieto-temporal regions of primate brains demonstrated that chimpanzees who had been trained extensively in the traditional “do-as-I-do” paradigm (i.e., they were trained to repeat demonstrated actions) showed noticeable changes in their brain’s white matter integrity, suggesting that learning how to copy actions increases the ability to do so and has a lasting effect on neural systems (Pope et al., 2018). These findings suggest that modern humans' seemingly exceptional ability to attend to and copy actions may be both a product and a driver of our cultural evolution (see also Heyes, 2018). It is particularly interesting therefore that non-human primates who (most likely) do not spontaneously copy actions, are seemingly capable of learning this ability after extensive human training (e.g., Kanzi and Viki, see above; Heyes, 2015). This suggests that our motivation and/or need to copy actions may have emerged after the split with our last common ancestor, but the potential cognitive requirements to do so were already present before the split.

However, for the current purposes, although Kanzi and other enculturated apes can provide interesting data on what non-human primates are capable of learning and reinnovating after extensive human exposure and training, they do not provide any information on the social learning or cognitive abilities of extant wild unenculturated primates (as enculturated individuals such as Kanzi are reared in species-atypical conditions and therefore are not representative of the natural conditions and cognition of wild primates; Bjorklund, 2018). Taking into account the potential effect that human rearing and training has on non-human animals, and the neurocognitive evidence supporting the view that non-human primates do not attend to actions (Hecht et al., 2012; Pope et al., 2018), it is more likely that individuals such as Kanzi (currently at least) developed their copying abilities during their extensive enculturation process rather than demonstrating any widespread copying abilities present in wild non-human great apes.

1.3 The Zone of Latent Solutions hypothesis

The question of how naïve, unenculturated, wild animals acquire and express their behavioural repertoires therefore remains debated. The current null culture hypothesis: i.e., that that these behavioural forms are dependent on high-fidelity social learning (Whiten et al., 1999; 2001) lacks supporting evidence (and is unsubstantiated by neurocognitive studies; see above). Thus, alternative approaches, such as environmental or genetic explanations, should be sought. Although an environmental or genetic approach may seem more likely than the culture hypothesis (as this view is unsupported by the data), the most parsimonious explanation is an equifinal one, in which more than one factor contributes to the acquisition and sustenance of animal behavioural forms.

To this end, in 2009, Tennie and colleagues proposed the “zone of latent solutions” (ZLS) hypothesis. The ZLS provides an alternative explanation for animal behaviour by suggesting that the acquisition of behavioural forms rests primarily on individual learning mechanisms. Tennie et al., (2009) argue that, in contrast to the culture hypothesis, animals do not depend on social learning to acquire their behavioural forms. Instead, these forms are “latent solutions” that each individual of a species (if in the appropriate situation and motivational state, amongst other factors, see Bandini & Tennie, 2018 and chapter IV) can independently reinnovate through individual learning. Behaviours within the ZLS of a species range on a continuum: they can emerge almost automatically (for example, yawning, which is unconsciously released) or they can emerge more indirectly via individual learning (Reindl et al., in press). The crux of this approach is that latent solutions do not *require* any form of social learning to emerge. However, low-fidelity social learning does play a role in animal behaviour. These types of social learning greatly increase the likelihood that individuals will express the behavioural form by encouraging their attention towards the materials of the behaviour, or by placing them in a favourable situation (e.g., mechanisms such as local enhancement may encourage interest towards the areas in which the required materials of a behaviour can be found; Thorpe, 1963; Whiten et al., 2004). Thus, social learning opportunities harmonise the frequency of the behaviours within and across populations. Once a behaviour has been reinnovated, social learning biases, such as when to acquire social information and from whom to acquire it (Hoppitt & Laland, 2013) then influence which individuals in the group will express similar behaviours. These social learning biases promote general trends in behaviours within populations: if most individuals in a group are more likely to attend to social information provided by innovator A due to certain characteristics (perhaps the hierarchy of the individual in the group, or their age and/or sex; Hoppitt & Laland, 2013), rather than innovator B, then the majority of the group will reinnovate the behavioural form expressed by individual A. However, in another population, innovator B might be favoured, creating slight variations in the behavioural repertoires of the two populations. These low-fidelity social learning strategies then lead to the population-wide differences in behavioural repertoires observed in some wild animals (e.g., chimpanzees; Whiten et al., 1999; 2001; orangutans; van Schaik et al., 2003; New Caledonian crows; Kenward et al., 2005). Although it might then seem, on first observation, that population differences are only the product of social learning, only the frequency of the behaviour is socially influenced. The acquisition of the behavioural form is nevertheless individually learnt. Thus, the population differences in animal behavioural repertoires can be considered “socially mediated serial reinnovations” (SMSR; Bandini & Tennie, 2017).

Although the ZLS approach may seem iconoclastic in that it reverses the currently accepted culture hypothesis (Kummer & Goodall, 1985; Whiten et al., 1999; 2001; Gruber et al., 2015; Davis et al., 2016), by suggesting that social learning plays a supporting rather than major role in animal behaviour, this approach was founded on the work of several influential psychology and primatology researchers (see section below) and on the growing body of evidence supporting a dual role of individual and low-fidelity social learning in animal material culture (Tennie et al., 2008; Hoppitt et al., 2012; Allritz et al., 2013; Menzel et al., 2013; Reindl et al., 2016; Bandini & Tennie, 2017; Neadle et al., 2017; Barrett et al., 2018 and see also chapter II).

1.3.1 Historical background to the ZLS hypothesis

The ZLS hypothesis contributes to the early work of one of the classics of psychology, Lev Vygotsky (1896-1934). Vygotsky formulated some of the most influential theories on learning in (human) children. Vygotsky argued that children require social learning to acquire all but their most basic tool-use abilities, and introduced the *zone of actual development* (*ZAD*) and the *zone of proximal development (ZPD)* concepts to explain children’s’ learning in society (Vygotsky, 1978). The ZAD encompasses all behaviours that an individual is capable of achieving independently at a given ontological point (Vygotsky, 1978). The behaviours within each individual’s ZAD are not fixed, and can vary between individuals. On the other hand, the ZPD consists of behaviours and skills that first require some form of social learning to emerge at the appropriate developmental stage (Vygotsky most often cites active teaching as the form of social learning at work). Once the behaviours that were in the ZPD are acquired (through social learning), they are then integrated into the ZAD of the individual – they become part of the ZAD. Similarly to the ZAD, and because the ZAD grows, the ZPD is continuously growing (the ZPD concept can be seen as a precursor to the “ontogenetic cultural intelligence hypothesis”; Herrmann et al., 2007; Tennie & Over, 2012). There are always behaviours that are even outside the reach of the ZPD, as some behaviours, no matter the amount of teaching or social learning available, will not be accessible until the individual reaches the appropriate developmental age (or until the appropriate precursor skills are acquired and placed within the ZAD of the individual; see Reindl et al., in press).

The aim of ZAD and ZPD concepts was to explain how (human) individuals acquire novel behaviours and integrate them into their behavioural repertoires, therefore also in part explaining the cultural component of human development (Vygotsky, 1978). The ZAD and ZPD concepts inspired Tennie and colleagues (2009) to envision a *zone of latent solutions (ZLS)*, which describes the learning mechanisms in species that do not rely so heavily on social learning mechanisms, therefore also providing the missing phylogenetic baseline of the ZAD. Whilst Vygotsky examined learning processes on an (exclusively human) individual level, the ZLS approach instead provides information on a species level, and examines both human and non-human learning abilities. Thus, the ZLS can be seen as an extension of Vygotsky's (1978) original theories, filling in some of the theoretical gaps left by the ZAD/ZPD concepts. Vygotsky assumed that children have barely any spontaneous tool-use abilities (children's spontaneous abilities are "*practically zero"*, Luria & Vygotsky 1978, 114), yet considering the adaptive value of tool-use for humans (Laland et al., 2000) and that for the cumulative cultural process to start, individuals must first innovate some behaviours spontaneously, it seems unlikely that humans have no individual learning abilities. Thus, the ZLS also provides a behavioural baseline for humans (i.e., behaviours that individuals can reinnovate without social information) and evidence for this ZLS in humans was provided by Reindl et al., (2016), who demonstrated that naïve children (between the ages of 2-3.5 years) were able to solve a variety of novel tool-use problems based on those practiced by wild great apes, without any social information.

Therefore, whilst Vygotsky (1978) emphasized the importance of social learning for human children to acquire their behavioural repertoires, the ZLS instead works on the assumption that there are some behaviours that even humans can acquire purely through individual learning – unaided by high-fidelity social learning mechanisms. The behaviours that are independently acquired (i.e., the behaviours within humans'

ZLS; Reindl et al., 2016) can be viewed as a baseline for Vygotsky's (1978) ZAD. Tennie et al., (2016) describe a hypothetical thought experiment: the "island test" to envision which behaviours are within the ZLS of humans and other species. The island test involves imagining a scenario in which a naïve child is placed on a deserted island with all the materials of the target behavioural form being examined. Once the child reaches the appropriate developmental stage, would she be able to reinnovate the same behavioural form, in the absence of any cultural models? If the behavioural form can be reinnovated in these conditions, then it would fail the island test for cumulative culture, and would instead be considered a latent solution. If the behaviour does not appear in these conditions, then it is most likely a culture-dependent trait, which requires some form of social learning to be acquired (Tennie et al., 2016; Reindl et al., 2017). These behaviours would lie in Vygotsky's (1978) ZPD. The ZLS approach does not make any modifications to the ZPD, but instead argues that this zone is most likely *unique* to humans (one possible exception to this might be whale and bird song, but further research into acquisition methods is still required; Garland et al., 2011). Thus, whilst humans can learn new behaviours beyond their ZLS (to go into their ZPD), other animals are restricted to reinnovating behaviours within their ZLS (as they seemingly cannot copy or reinnovate behaviours outside of their ZLS; Köhler, 1925; Tennie et al., 2009; Bandini & Tennie, 2017). Reindl et al., (in press) name this phenomenon the "ZLS-only" account, whilst humans, who can go beyond their ZLS (through copying forms of social learning such as imitation and active teaching, but also potentially due to our ability for language, theory of mind and enhanced shared intentionality and cooperative actions; Tomasello 1999; Tennie et al 2009; Boyd et al 2011; Csibra and Gergely 2011; Kline 2015), are placed in the "ZLS-plus" category, in which the ZLS can only explain the baseline of our culture (Reindl et al., in press).

In his early work, Köhler (1925) also came close to suggesting a version of the ZLS for chimpanzees when he argued that his subjects had individually reinnovated their tool-use behaviours without social learning. Köhler also briefly suggested that chimpanzees might not be able to learn behaviours outside of their own individual learning repertoire: "*It is most difficult for chimpanzees to imitate anything, unless they themselves understand it"* (Köhler, 1925, 157). The ZLS approach therefore combines Vygotsky's (1978) early theoretical work with Köhler's (1925) experimental work and contributes a crucial behavioural baseline to provide an alternative approach to explain the unique nature of human culture in the animal kingdom.

1.3.2 The Latent Solutions Testing methodology

To test its theoretical predictions, the ZLS hypothesis can be experimentally investigated following the latent solutions (LS) testing methodology (Tennie & Hedwig, 2009). LS tests provide a relatively simple way for researchers to isolate and identify the necessity of individual and social learning in the emergence of behaviours. Naïve subjects (who have never seen or been in trained in the target behaviour before) are provided with all the materials of the behaviour. No demonstrations or social information on the main components (i.e., actions or results) of the behaviour are provided before testing, to ensure that social learning does not and cannot influence the acquisition of the behaviour. If the target behaviour emerges under these conditions (i.e., without social learning), then logically it can be concluded that the behaviour was, and can be, reinnovated through individual learning, and that social learning is not required for it (Tennie & Hedwig, 2009; Bandini & Tennie, 2017). Thus, latent solution tests are tests for cultural dependency. Behaviours that emerge under these conditions are latent solutions within the species ZLS. LS type tests are most often (and most easily) carried-out with captive individuals, as the previous knowledge and rearing histories of captive individuals are recorded (as it is essential for these tests that the subjects are naïve to the behaviour before testing). Whilst the original testing methodology (Tennie & Hedwig, 2009) and previous LS tests only involved this asocial baseline condition (Tennie et al., 2008; Allritz et al., 2013; Menzel et al., 2013; Reindl et al., 2016; Bandini & Tennie, 2017; Neadle et al., 2017), chapter IV presents a new extended LS testing methodology that includes social learning conditions for when the target behaviour does not emerge in the baseline condition (Bandini & Tennie, 2018). The extended LS testing methodology offers social information on the target behaviour in a step-wise manner, allowing for the level and amount of social learning required for the behaviour to emerge to be identified (Bandini & Tennie, 2018; and see chapter IV for a more detailed explanation).

Data collected from LS studies with captive subjects can then be generalised to make species-wide claims. This approach has led some to argue that latent solutions must therefore by fully genetically encoded for (e.g., Moore, 2013). However, whilst predictions on the individual learning capabilities of wild animals can be made based on data from captive individuals due to their genetic relationship, LS are not only adaptations and exaptations (i.e., traits that adapted for uses other than those they first evolved for; Gould & Lewontin 1979), they are also behaviours that are individually learnt and emerge via a mix of ontogenetic, genetic and environmental factors (Tennie et al., 2009; Bandini & Tennie, 2017; Reindl et al., in press). LS tests address both these factors. On a genetic level, it is assumed that all (normally developing) members of the species should possess the relevant genetic information to show behaviours within their ZLS. On an environmental level, the LS testing conditions (in which all the materials of the behaviour are provided), manipulate the environment of the test subjects in such a way as to replicate the conditions encountered by wild individuals, and allow for the learning of the affordances of the new environment (Gibson, 1979). Thus, insight from (enriched; Henrich & Tennie, 2017) captive individuals can be generalised to their wild counterparts, similarly to the approach taken in previous studies on animal cognition (e.g., Köhler, 1925).

1.3.3 ZLS standards

To strengthen the reliability of these species-wide claims, Bandini & Tennie (2017) introduced two standards that address the differences in relative complexity of animal behavioural forms: the single and the double-case ZLS standards. Behaviours that are perceived to be more complex (such as chimpanzee nut-cracking, Boesch et al., 1994) are very unlikely to emerge by chance (for example during display or play sessions). Therefore, the observation of one individual spontaneously showing the behaviour is sufficient to conclude that all individuals of the species are theoretically capable of reinnovating the behaviour without social learning. Thus, for more relatively complex behaviours, the single-case ZLS standard is applied, and the observation of one reinnovation of the behaviour is sufficient to make claims on the species-wide ZLS. On the other hand, for more relatively simple behaviours (such as chimpanzee stick tool-use behaviours, which generally only involve one tool and one step to solve the problem) it is possible (albeit still unlikely) that the behaviour could appear by chance in a different context. For these behaviours, the double-case ZLS standard is applied, and at least two, independent, reinnovations of the behaviour are required before it can be argued to be within the species' ZLS (Bandini & Tennie, 2017). Bandini & Tennie (2018) also provide a method to determine with confidence that a behaviour is outside of the species' ZLS when the target behaviour does not appear in any of the individual or social learning conditions in the extended LS testing methodology (Bandini & Tennie, 2018). Using a cumulative binomial distribution formula, the minimum sample sizes (based on the two ZLS standards described above) required to generalise negative findings to the species are provided (see Bandini & Tennie, 2018 and further discussion in chapter IV).

1.3.4 Previous LS studies

One of the first LS studies in great apes was carried out by Tennie et al., (2008), who tested the learning mechanisms behind gorilla nettle processing (*Gorilla berengei*; Byrne & Byrne, 1991). Wild mountain gorillas in Rwanda, Africa, have converged on the same method to process nettles, and the apparent complexity of this processing technique has led some to argue that the form of this behaviour must rely on imitation ("*These patterns of variation suggest that […] logical organisation is copied by program-level imitation"* Byrne & Byrne, 1993, 243). However, when Tennie et al., (2008) provided naïve, captive gorillas with similar nettles as those consumed in the wild and no social information on the technique (in an LS test), these naïve gorillas spontaneously reinnovated the same step-wise approach as their wild counterparts. Thus, it is likely that rather than relying on social learning, this behaviour is a latent solution that all individuals (even of different subspecies) can reinnovate under the right circumstances. Similar findings have been reported for leaf-swallowing in chimpanzees (Allritz et al., 2013), food washing and placer mining across all species of great apes (Menzel et al., 2013), 11 tool-use behaviours in human children (Reindl et al., 2017) and food cleaning in gorillas (Neadle et al., 2017), alongside the studies presented in chapter III.

1.4 Summary and aims of the thesis

The main aim of this thesis was to explore primates' individual learning abilities and identify tool-use behaviours within their ZLS. The ZLS hypothesis is still relatively new in the literature, and more experimental evidence is required to test the predictions it makes in relation to human and non-human primate cultural behaviours. Although the focus of the field has remained for many years on social learning, some work on the individual learning abilities of non-human animals has already been carried out (before the ZLS approach was introduced). Chapter II consists of a systematic review of previous studies in which the spontaneously acquisition of tool-use behaviours was found across species. Chapter II provides, for the first time, a comprehensive review of the experimental evidence on the individual learning of animal tool-use.

Chapters III-V discuss the results of six experimental tests on the individual learning abilities of naïve chimpanzees (*Pan troglodytes*) and long-tailed macaques (*Macaca fascicularis*) across zoological institutions and sanctuaries in Europe and Africa. These studies applied both the original LS testing methodology (Tennie & Hedwig, 2009) and introduced and applied the extended LS testing methodology (Bandini & Tennie, 2018) to examine the ZLS of extant primates and to draw inferences on the evolution of our own material culture. The final chapter summarises the main findings of this thesis and discusses the theoretical implications for the study of primate material culture. Limitations of this work are highlighted and potential directions for future research are also provided in the discussion chapter.

Ethical approval for all studies presented in this thesis was granted by The University of Birmingham AWERB committee (reference UOB 31213) alongside the host zoos following SSSMZP, EAZA, BIAZA and WAZA protocols on animal research and welfare.

Chapter II: *A review of the role of individual learning in animal tool-use*

2.1 Introduction

"The natures of animals are untutored"

-Hippocrates (Epidemics vI, 32)

The notion that tool-use is unique to humans has now been conclusively disproved by the ever-growing number of observations of animals using tools across various contexts (e.g., Whiten et al., 1999; 2001; Ottoni & Mannu, 2001; Perry, 2001; Van Schaik et al., 2003; Krützen et al., 2005; Finn et al., 2009; Kenward, 2011; Robbins et al., 2016). Yet the mechanisms behind the emergence and sustenance of these tool-use repertoires are still heavily debated. The current null hypothesis is biased towards a social learning approach, in which animal tool-use repertoires are thought to depend on social learning mechanisms. The ZLS hypothesis (Tennie et al., 2009; see general introduction), on the other hand, proposes that most (if not all) non-human animal (henceforth: animal) tool-use behavioural forms are within the ZLS of the species, and can be acquired primarily via individual learning. Low-fidelity social learning then plays a role in catalysing and harmonising the frequency of the behaviours, creating the regional differences in repertoires observed in some animals (e.g., chimpanzees; Whiten et al., 1999; 2009; orangutans; van Schaik et al., 2003 and New Caledonian crows; Hunt & Grey, 2003). Although social learning is still favoured over individual learning as the driver of the behavioural forms of animal tool-use, several examples of spontaneous reinnovations without social learning by naïve animals are found in the literature. The aim of the review presented in this chapter was to create a database of these examples, collecting experimental and observational studies in which tool-use behaviours emerged spontaneously (i.e., they were reinnovated by naïve individuals who were not exposed beforehand to any social information on the behavioural form) in wild and captive animals. Most of the studies included in the database describe behaviours first observed in captive individuals (where the subject's previous knowledge and experience was known and controlled for). However, the database also includes observational accounts of the innovation (or reinnovation) of behaviours in the wild (where it was known that the innovator had not seen the behaviour beforehand). Due to the pervasive focus on social learning in the literature, accounts of the individual learning of tool-use behavioural forms by naïve animals have been largely overlooked, and their importance rarely examined. This chapter highlights the extent of individual learning in the tool-use repertoires of a wide range of species, suggesting that animal individual learning abilities may have been systematically underestimated (e.g., *"primates are remarkably ill-equipped with innate technologies*" Kummer & Goodall, 1985, 203).

2.2 Materials and Methods

A literature search was carried out using the terms: animal "*innovations*", "*inventions*", "*novel behaviour"*, "*spontaneous*", "*individual learning"*, "*problem-solving" "trial and error"* and "*tool-use"*, following the terms used in previous literature reviews on animal tool-use and innovation (e.g., Reader & Laland, 2001). Although some studies on individual learning were already known to the author before starting the review, these were only added into the individual learning database if they were found following the systematic approach described below. This procedure was carried-out to ensure that the process was as unbiased as possible. The online search engines *Google Scholar* and *Web of Science* were used to search for relevant literature across journals. Once the literature search using these terms was exhausted, references from within the already-accessed papers were examined to find ones that cited other relevant studies on the spontaneous expression of tool-use behavioural forms by naïve animals. Over 200 research papers were then thoroughly read to ascertain that they i) described the *spontaneous* (i.e., without social learning) emergence of a behavioural form and ii) that the individual who showed the behaviour was naïve to the target behaviour beforehand, and had not received any training or exposure to the behaviour before testing or before the first observation (as described by the authors of the study). Studies were excluded if it was clear that the subject had pre-existing knowledge of the behaviour that was later reinnovated, or if the subject was enculturated or deprived (see general introduction and Henrich & Tennie, 2017). The studies that were included in the final individual learning database consist of reports of the first time a tool-use behavioural form was observed in a population of wild animals, studies with captive subjects in which a new behaviour was actively encouraged by the experimenters, studies in which the main research aim was not to encourage individual learning, but reinnovations nonetheless occurred, and simple observational reports describing the emergence of behaviours in captive populations (see the “individual learning database” in the supplementary files in the provided CD).

The individual learning database is divided by species, and includes the name of the species (Column one), the title of the relevant paper (Column two), the authors (Column three), the testing methodology (or observational method) applied in the study (Column four), a brief summary of the main findings (Column five), which standard (i.e., the double or single ZLS-case) is applied, based on the assumed complexity of the behavioural form (Column six; see Bandini & Tennie, 2017 and general introduction), interpretation of the findings by the authors (Column seven; Quotes were taken directly from the papers to avoid any subjective interpretations by the author; compare to Reader & Laland, 2001). The last column includes EB’s personal interpretation of the findings of the study (Column eight) with regards to the ZLS hypothesis. The studies were either classified as *Potential ZLS or ZLS. Potential ZLS* studies were those that described behaviours that are *most likely* in the species’ ZLS, but cannot (yet) be confidently labelled latent solutions as they either did not meet the requirements of the single or double-case ZLS standards, or they were observations of behaviours in the wild, and therefore require further experimental testing (observations of behaviours in the wild require experimental testing as, although the authors suggest that the individuals were naïve to the behaviour before the first observation, this cannot be confidently confirmed for wild animals as researchers do not follow their subjects all day every day. Thus, to be confident in classifying a behaviour as a latent solution, captive subjects (whose rearing history and pre-existing knowledge on the target behavioural form can be controlled for) need to be tested before the behavioural form can be assumed to be within the species’ ZLS). *Potential ZLS* behaviours are still likely to be in the ZLS of the species, but require further examination following the standards described in the introduction chapter. On the other hand, *ZLS* behaviours are those that met the requirements of the single or double-case ZLS standards (respectively), and were observed in individuals who were clearly naïve to the behaviour beforehand. These behaviours can be confidently assumed to be in the ZLS of the species (see introduction).

2.3 Results

107 studies that fit the requirements described above were found by EB between 2016 and 2018. All the relevant studies are included in the individual learning database (see supplementary files in the provided CD). Of these studies, 75.8% were articles on primates (including, in alphabetical order: baboons (*Papio papio; cynocephalus anubis*); bonobos (*Pan paniscus*); capuchins (*Cebus paella; capucinus; nigritus; libidinosus*); chimpanzees (*Pan troglodytes*; *schweinfurthii*); orangutans (*Pongo pygmaeus abelii*); gibbons (*Hylobatidae*); golden lion tamarins (*Leontopithecus rosalia rosalia*); gorillas (*Gorilla beringei beringei*; *gorilla gorilla)* and macaques (*Macaca tonkeana; fascicularis fascicularis; nemestrina; silenus; mulatta; fuscata*). 15.4% were studies with birds (including: canaries (*Serinus canaria*); goffin cockatoos (*Tanimbar corella*); hawaiian crows (*Corvus hawaiiensis*); hyacinth macaws (*Anodorhynchus hyacinthinus*); kea parrots (*Nestor notabilis*); new caledonian crows (*Corvus moneduloides*); northern blue jays (*Cyanocitta cristata*); pigeons (*Columba livia domestica*); rooks (*Corvus frugilegus*) and woodpecker finches (*Cactospiza pallida*). 8.8% were other animals (including: Asian elephants (*Elephas maximus*); dingos (*Canis dingo*); octopods (*Amphioctopus marginatus*) and otters (*Enhydra lutris nereis*). No control for research effort or for the frequency of the species in the wild was carried out for this review; therefore it is likely that the larger number of spontaneous tool-use reports in primates and birds is partially a product of the research bias towards these species in the literature (Sayers & Lovejoy, 2008).

Of the reports included in the database, 76.6% described studies with captive subjects, and 23.4% were observations of behaviours in the wild. Fourteen different tool-types were found, 64.3% of which were man-made objects. Materials used as tools were primarily sticks and stones: 56.2% of the studies included in the database involved stick tools and 18.1% stone tools. However, other objects were used as tools as well: 0.9% involved newspaper, 2.9% boxes, 4.8% wires, 4.8% leaves, 2.9% cups and containers, 3.8% string and human hair, 1.9% the doors of their enclosures, 0.9% sponges, 0.9% coconuts and 1.9% used water as a tool. The studies were classified as demonstrating either a *potential ZLS* behaviour, or a *ZLS* behaviour. 64.2% of the studies were classified as *ZLS* behaviours and 35.8% were *potential ZLS* behaviours.

2.4 Discussion

Here the studies most relevant to the topic of this review will be discussed, i.e., those that demonstrate that animals across species can reinnovate behavioural forms within their tool-use repertoires. Specific accounts on the reinnovation of behavioural forms were chosen as case examples from species that have been suggested to depend on social learning to acquire their behaviours (e.g., chimpanzees; Whiten et al., 1999; 2001). Furthermore, reports of tool-use from species that do not regularly use tools in the wild (e.g., gorillas; Robbins et al., 2016) were included as they provide some of the most compelling cases for the view that animals can reinnovate behaviours within their ZLS. Lastly, clear examples of anthropocentric and social learning-biased interpretations of data are also discussed. In the last section, some of the potential factors that influence the acquisition of behaviours within the ZLS are presented.

2.4.1 Individual learning in Primates

2.4.1.1 Chimpanzees

Kummer & Goodall (1985, 208) describe one of the first instances of spontaneous tool-use in wild chimpanzees - in Gombe, Tanzania: "*One new behaviour that did spread through the community at Gombe was the use of sticks as levers to try to open banana boxes […] three adolescents began,* ***independently****, to use sticks to try to prize open the steel lids […] over the next year, the habit spread until almost all members of the community […] were seen using sticks in this way"* (emphasis placed by author). Although the previous tool-use knowledge of the Gombe chimpanzees is not reported, this observation was included here because the banana boxes were man-made objects introduced by the researchers, making it unlikely that the chimpanzees had already encountered this specific problem in the wild. Indeed, many of the first observations of tool-use in animals were the product of animals interacting with novel, man made or introduced materials and objects (e.g., Köhler, 1925; Lefebvre, 1995). Subsequently, many early researchers interpreted new observations of animal tool-use from an anthropocentric point of view. Indeed, despite writing that the chimpanzees showed the behaviour "independently" (i.e., without requiring social models; see quote above), Kummer & Goodall (1985, 213) also argue (without providing further evidence) that the chimpanzees were learning the behaviour from each other: “*That many individuals learnt as a result of watching their companions is suggested by the fact that one female was observed to behave thus on her very first visit to camp”.* The authors interpret this instantaneous reinnovation as evidence that the chimpanzee must have socially learnt the behaviour by watching others beforehand. Although it is possible that this particular chimpanzee had observed other individuals before approaching the banana box, a more parsimonious interpretation for the fact that three individuals (Kummer & Goodall, 1985) showed the same behaviour during their first interactions with the box is that each individual was able to reinnovate the behaviour independently. Although Kummer & Goodall (1985) present some of the first accounts of wild chimpanzee tool-use behaviours, this report provides an example of how social learning was often favoured in the literature, even when an individual learning explanation was more parsimonious, and better supported by the data. This phenomenon could be considered an “illusion” of cultural dependency.

Indeed, it is only with more controlled cases of innovations that learning mechanisms can be identified with confidence in wild populations. Hobaiter et al., (2014) report one of the rare occurrences in which the emergence of tool-use behaviours in wild chimpanzees was tracked as the frequencies increased within the community. The authors describe the emergence of two tool-use behaviours in the chimpanzees of Budongo Forest, Uganda: moss-sponging and leaf-sponge re-use. The tools were used to retrieve water from a waterhole that had recently been flooded (Hobaiter et al., 2014). The authors followed the increases in frequency of these two behaviours within the Sonso chimpanzee community. Using network-based diffusion analysis for the first behaviour, Hobaiter et al., (2014) attributed at least 85% of the newly observed events of moss-sponging to social learning, arguing that for each new observation, naïve chimpanzees enhanced their chances of developing moss-sponging by a factor of 15. Thus, (low-fidelity) social learning most likely played a role in increasing the frequency of this behaviour within the community. Yet, even though the frequency of the behaviour may have increased through low-fidelity social learning, this leaves open the question as to whether the form of the behaviour is *reliant* on social learning. Indeed, this study was included in the database because, after the original innovation of moss-sponging by the alpha male, the alpha female also reinnovated the behaviour independently before having observed the male moss-sponging (researchers were able to closely observe the chimpanzees during the study period, allowing for conclusions to be made on the background knowledge of each of the group members; Hobaiter et al., 2014). Therefore, it seems likely that although low-fidelity social learning facilitates the individual acquisition of the behavioural form by the rest of the group, moss-sponging is not a culture-dependent trait, as it was also reinnovated through individual learning by (at least) two separate individuals, in the absence of social learning (fulfilling both the single-case and the more conservative double-case ZLS standard). In a follow-up study on the spread of moss-sponging three years after its innovation, Lamon et al., (2017, 6) agree with the ZLS approach to explaining the increase in frequency of this behaviour: "*Of course, each moss-sponger has to individually learn the behaviour, but in all likelihood, this was facilitated by the social influence exerted by other group members that acted as models*".

On the other hand, for the second behaviour, leaf-sponge re-use, the social network analysis failed to show a role of social learning in the increase in frequency of the behaviour, as eight naïve chimpanzees independently reinnovated the same behavioural form (Hobaiter et al., 2014). Thus, this study suggests that both moss-sponging and leaf sponge-reuse seem to be within chimpanzees' individual learning abilities (i.e., their ZLS), and although the frequency of moss-sponging reinnovations may have been more heavily influenced by low-fidelity social learning than leaf-sponge re-use, it is not dependent on these forms of social learning to be acquired by chimpanzees (both of these behaviours were classified as *ZLS* behaviours in the individual learning database).

Several similar reports of reinnovations of stick and leaf tool-use behaviours by naïve individuals were also found in *captive* chimpanzees. As discussed in the introduction, Wolfgang Köhler (1914-1920) spent many years investigating the cognition behind captive (unenculturated) chimpanzee stick tool-use, and concluded that many of these behaviours, such as using a stick to retrieve out-of-reach foods, can emerge via "*insight learning"*[4]. Following Köhler's early work, Paquette (1992) installed an

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[4] We would now refer to "insight learning" as "individual learning", as "insight" implies a sole, or primary, role of genetics in the emergence of a behaviour. However, it is more parsimonious to assume that genetics play a role alongside other factors such as the environment and individual and social learning (see general introduction and Reindl et al., in press).

artificial termite mound in the enclosure of naïve, captive chimpanzees to examine the origins of the wild termite-fishing behaviour (in which chimpanzees use sticks to retrieve termites from deep inside their underground nests, e.g., see Whiten et al., 1999). Upon finding that the naïve chimpanzees spontaneously demonstrated the same termite-fishing behaviour as their wild counterparts, Paquette (1992, 17) concludes: *"the speed with which the group of experimentally naive chimpanzees discovered and learned tool-use suggests that wild chimpanzees of different populations independently discovered the fishing behaviour"*. Similarly, Kitahara-Frisch & Norikoshi (1982) examined the origins of sponge-making (a behaviour in which wild chimpanzees use leaves as sponges to absorb liquids such as water or honey; Frisch & Norikoshi, 1982, 42) and found that captive chimpanzees showed the same form of sponge-manufacture and use as their wild counterparts. The authors conclude that, contrary to previous claims, "*the example of the mother is by no means necessary for the habit to appear in young animals. This observation raises the question of whether the acquisition of so-called proto-cultural habits does not rely as much, at least, on independent reinvention as on transmission through imitation learning"*. The interpretation of the results of many of the studies included in the individual learning database often agree with those proposed by the ZLS approach[5] and provide mounting evidence for the view that simple stick tool-use may be within the ZLS of all chimpanzees.

Whilst several accounts of reinnovations of stick tool-use were found in the literature, reinnovations of stone-tool behaviours, such as nut-cracking, were rarer across both wild and captive chimpanzees. Nut-cracking is often considered to be one of the most complex behaviours within chimpanzees' repertoires as it involves the use of at least two objects (hammerstone and an anvil) and a set of steps that must be followed in the appropriate order to reach the end goal (complex behaviours have been loosely defined in the literature as those that involve multiple tools and/or multiple steps to

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[5] For example, see Kitahara- Frisch et al., (1982); Epstein et al., (1984); Anderson, (1985); Visalberghi & Trinca, (1989); Köhler, (1925); Birch, (1945); Tokida et al., (1994); Westergaard & Suomi, (1994); Fontaine et al., (1995); Paquette et al., (1995); Visalberghi et al., (1995); Beck, (1996); Weir et al., (2002); Morimura, (2003); Breuer et al., (2005); Pouydebat et al., (2005); Kenward et al., (2005); Morgan & Abawe, (2006); Mendes et al., (2007); Yamamoto et al., (2008); Ausperg et al., (2011); Foerder et al., (2011); Ausperg et al., (2012); Rutz et al., (2016); Bandini & Tennie, (2017); Laumer et al., (2017); Neadle et al., (2017); Bandini & Tennie, (in prep); Bandini et al., in (prep); Tennie et al., (in prep).

achieve the final goal; Maulman et al., 2012). The assumed complexity of nut-cracking (and the fact that it is a tool-use behaviour) has prompted researchers to assume that social learning must be required for the behaviour to be acquired (e.g., see Marshall-Pescini & Whiten 2008, 186: "*nut-cracking can be acquired in a matter of days by social learning"* and Inoue-Nakamura & Matsuzawa, 1997; Boesch & Boesch-Aschermann, 2000; Biro et al., 2003). Subsequently, the role of individual learning in nut-cracking has been under-examined. This neglect occurs despite the fact that some naïve chimpanzees in nut-cracking studies have been observed to reinnovate the behaviour without any social information. For example, in a study carried out by Marshall-Pescini & Whiten (2008) with semi-wild chimpanzees, a naïve subject was observed cracking nuts on a stationary anvil before the social demonstration conditions (Mawa, M, 22 years old). Mawa's reinnovation was, however, dismissed: *"given the speed and apparent purposefulness of his (Mawa's) actions during the first baseline trial [...] we infer that he was already familiar with this behaviour" (*Marshall-Pescini & Whiten, 2008, 190). Mawa was then used as a model for the rest of the group, and after nut-cracking was acquired by other chimpanzees, the authors propose that some form of imitation is at play: "*These results lend support to a view of imitation that is not limited to the reproduction of discrete actions but rather takes into account the copying of the sequential or hierarchical organization of a behaviour is at play"* (Marshall-Pescini & Whiten, 2008, 193). The authors also report that two other naïve chimpanzees in the group carried-out "*hitting motions"* on the ground, similar to those Mawa used, whilst watching Mawa crack open the nuts (Marshall-Pescini & Whiten, 2008, 192). These observations were used as further evidence for the view that the naïve chimpanzees were imitating Mawa. However, only one of the individuals (Baluku) showed this hitting motion in more than one demonstration session, and Baluku might be more enculturated than the other individuals (see Tennie et al., 2012). Additionally, this hitting action is not new to chimpanzees, and has been observed in other contexts as well (Marshall-Pescini & Whiten, 2008), therefore it is more likely that Baluku (alongside other chimpanzees) already possessed this behavioural form within his repertoire, and was only socially stimulated by Mawa to show it (through low-fidelity forms of social learning, such as stimulus enhancement; Thorpe, 1963). Thus, although Mawa's previous nut-cracking experience is unknown, the chance that he reinnovated the behaviour via individual learning remains a possibility (and indeed may be the most parsimonious interpretation of these findings), until it is proven otherwise (e.g., if it is found that Mawa could a) copy actions and b) clearly copied the behaviour from another chimpanzee or human. Personally, neither of these scenarios seem very likely, as non-human animals appear unable to copy actions (unless enculturated, see general introduction for further discussion of this and Tennie et al., 2009)). Thus, Mawa's spontaneous nut-cracking, and Bakulu's hitting action in response, support the view that this behavioural form can be reinnovated by naïve chimpanzees under the right circumstances.

In a similar study on the origins of nut-cracking (but with captive subjects), Hirata et al., (2009) report that their demonstrator reinnovated nut-cracking before training started on the behaviour (after the chimpanzee had been exposed to artificial shelled nuts, hammerstones and stationary anvils over 65 testing sessions and after a 1.5 year break from testing). Hirata et al., (2009) nevertheless conclude that nut-cracking requires social learning to emerge, whilst acknowledging, *"it is also true that they (the group) did not show evidence of immediate true imitation […] their behaviour did not clearly improve immediately after observing successful nut-cracking by a peer"* (Hirata et al., 2009, 21). Data from these studies negates the view that social learning is a necessary factor in the emergence of this behaviour, and indeed spontaneous nut-cracking has also been observed in naïve capuchins (see below) and in a captive orangutan (*C.Tennie, pers.comm).* Thus, similarly to stick tool-use behaviours, it is possible that nut-cracking may be in the ZLS of chimpanzees, and even in that of other primate species. However, it is important to note that although isolated examples of nut-cracking reinnovations have been reported, these accounts are much rarer than for other behaviours. Furthermore, in many previous studies of nut-cracking, not all the chimpanzees in the group started cracking nuts when the materials were provided, even after social demonstrations (e.g., Inoue-Nakamura & Matsuzawa, 1997; Boesch & Boesch-Aschermann, 2000; Biro et al., 2003; This is also true in the wild, where only some populations crack nuts, even if the same nuts are found elsewhere; McGrew et al., 1996; Morgan & Abawe, 2006). Furthermore, long-tailed macaques (*Macaca fascicularis fascicularis*) also failed to reinnovate nut-cracking in a LS test (Bandini & Tennie, 2018 and chapter IV). Thus, nut-cracking may be a behaviour that is at the limit of the individual learning abilities of primates, and therefore requires a much longer period of exposure to the materials (perhaps during a sensitive learning period; Inoue-Nakamura & Matsuzawa, 1997) and/or some forms of social facilitation before it is reinnovated. Similarly, nut-cracking was also the only behaviour out of the test battery carried out by Reindl et al., (2016) that naïve human children failed to reinnovate (however, this might have been due to the fact that children are often discouraged from breaking and destroying objects; Reindl et al., 2016). Future studies should test naïve subjects (especially chimpanzees, who show the highest potential for reinnovating nut-cracking, and indeed some chimpanzees have already shown this ability; see above. This research effort is currently being carried out by *D.Neadle*) with extended baseline conditions in which subjects can freely manipulate the materials of the behaviour, to explore the conditions required for this behaviour to emerge.

2.4.1.2.Gorillas

Although gorillas do not commonly use tools in the wild, sporadic cases of spontaneous tool-use by gorillas in the wild and in captivity have been reported. One such report comes from Kinani & Zimmerman (2015), who describe, for the first time, a female juvenile gorilla (*Gorilla beringei beringei*) using a stick to fish for ants in Volcanoes National Park, Rwanda. The authors describe the behaviour as being similar to chimpanzee ant-dipping (which was classified as a "*putative cultural trait";* Whiten et al., 1999*;* for chimpanzees before it was discovered that the environment played a major role in shaping the form of the behaviour; see general introduction). This is the first report of ant-dipping (and indeed, any stick tool-use) in wild gorillas, providing the first tentative evidence for the view that this tool-use behavioural form is not a culture-dependent trait for gorillas (and therefore is likely to be within the species' ZLS). Further evidence of gorillas' spontaneous tool-use is offered by Lonsdorf et al., (2008), who exposed captive gorillas to an artificial termite mound in their enclosure. The authors report that although not all the gorillas in the group used tools, the alpha male fished for the bait using a stick on the first day of the study, demonstrating the same behavioural form as wild chimpanzees, despite being naïve (Lonsdorf et al., 2008). Similarly, Nakamichi (1999) observed a western lowland gorilla (*Gorilla gorilla gorilla*) at the San Diego Wild Animal Park throw sticks into the foliage of trees to knock down leaves and seeds (which were later consumed), and Fontaine et al., (1995) describes how a group of gorillas in a zoo in Gabon spontaneously used sticks to reach objects outside of their enclosure and coconut fibres as sponges to absorb water, demonstrating similar behavioural forms as chimpanzees and other primates who regularly use tools (Fontaine et al., 1995). Although the behaviours described above are not particularly complex (following the current definition in the literature; e.g., Meulman et al., 2012), these reports demonstrate that gorillas are capable of (spontaneously) using tools when motivated. Thus, despite rarely showing tool-use behaviours in the wild, gorillas have demonstrated a surprisingly extensive ability to innovate and reinnovate various tool-use behaviours via individual learning (e.g., Wood, 1984; Natale, 1988; Fontaine et al., 1995; Boysen et al., 1999; Nakamichi, 1999; Pouydebat et al. 2005; Tennie et al., 2008; Lonsdorf et al., 2008; Manrique et al., 2013; Neadle et al., 2017).

2.4.1.3. Capuchins

Capuchins exhibit one of the most extensive natural tool-use repertoires in (non-human) primates (only second to chimpanzees), and a clear ability to individually learn these repertoires. One example of a stone-tool behaviour comes from wild bearded capuchins (*S.libidinosus*) in Serra da Capivara National Park in Brazil. These capuchins have been observed deliberately pounding standing stones with smaller hammerstones to break open fragments of the larger stones (Proffitt et al., 2016). This behaviour, named stone-on-stone (SoS) percussion, involves an individual selecting a smaller pounding stone and using it to strike the cobbles embedded in a conglomerate of standing stones using one or both hands (Proffitt et al., 2016). The purpose behind SoS percussion is still unclear, but it may be that the monkeys break stones open to ingest powdered lichens or quartz from inside (support for this possibility comes from a report of a captive capuchin (*Cebus nigritus*) that was also observed practicing SoS and then licking the lichens inside the stone; Bortolini et al., 2007). An interesting by-product of this behaviour is that by pounding the stones together, the capuchins produce conchoidal flakes indistinguishable from those made by early hominins (according to the authors; Proffitt et al., 2016). This is the first observation of SoS behaviour, and the production of flakes, in wild capuchins. Although the learning mechanisms behind the acquisition of this behaviour in the wild remain to be identified, an earlier experimental test with captive capuchins (*Cebus apella*) describes how a similar stone pounding behaviour, including the production (and use) of flakes, was reinnovated spontaneously by naïve capuchins (Westergaard & Suomi; 1994). The captive capuchins tested by Westergaard & Suomi (1994) were also able to use the flakes they made as tools, and used them to cut open the acetate top of a baited testing apparatus (similarly to the testing conditions the bonobo Kanzi faced; Toth et al., 1993; see also chapter V for further discussion of this study). This study is particularly interesting as it demonstrates that naïve capuchins are not only able to reinnovate a wild behaviour (SoS percussion), but they are also able to make and use flakes in a similar way as hypothesised for early hominins (Proffitt et al., 2016) –all without requiring social learning beforehand. This data from wild and captive capuchins holds important implications for early hominin flake knapping. Considering the relative ease of the reinnovation of the behavioural form by these monkeys, it may be that early hominins could also individually reinnovate stone knapping (Tennie et al., 2016; 2017), rather than having to rely on more complex social learning mechanisms (the currently preferred hypothesis for early hominins, see chapter V for a more in-depth discussion).

Ottoni & Mannu (2001) also describe a stone tool behaviour in wild capuchins. The wild bearded capuchins of the Ecological Park of the Tiete River (São Paulo, Brazil) are provisioned daily with fruit and protein, but spend the majority of the day foraging for naturally occurring food sources (Ottoni & Mannu, 2001). During one of these foraging sessions, the monkeys were observed cracking open mature *Syagrus* nuts using a hammerstone on an anvil, similarly to how wild chimpanzees crack nuts. The authors conclude that nut-cracking is driven by "*some kind of observational learning, albeit restricted to stimulus enhancement, as a starting point of a long process of individual improvement by trial-and-error*" (Ottoni & Mannu, 2001, 357). Similarly, in a study on nut-cracking in captive capuchins, Visalberghi (1987) provided naïve subjects with stones and encased almonds, but no social information on the behaviour. Over a period of ten trials, two males successfully used stone tools to crack open the almonds (Visalberghi, 1987). Although the rest of the group (40 individuals) had ample opportunities to observe the two males cracking nuts, no other individual from the group reinnovated nut-cracking (see below for further discussion). Nut-cracking has now also been observed in other species of capuchins, including wild *Cebus libidinosus* (Waga et al., 2006), *Sapajus apella* (Izawa & Mizuno, 1976), *Cebus apella* (Struhsaker and Leland, 1977) and in another captive population of *Cebus apella* in captivity (Antinucci & Visalberghi, 1986). These findings strongly support the view that nut-cracking may be in the ZLS of capuchins, as it can be reinnovated via individual learning. Various other spontaneous tool-use behaviours have been observed in capuchins (Westergaard & Fragaszy, 1987; Visalberghi & Trinca, 1989; Fernandez, 1991; Boinski, 1998; Bortolini et al., 2007), making capuchins a promising species for the study of individual learning in primate tool-use.

2.4.1.4 Macaques

Some populations of *Macaca fascicularis aurea* (*Mfa)*, a subspecies of long-tailed macaques, frequently use stone tools and two different methods (pound-hammering and axe-hammering) to pound open encased foods in Southeast Asia (Malaivijitnond et al., 2007). The closely related subspecies, *Macaca fascicularis fascicularis (Mff*), have, however, never been observed to use tools, despite sharing an environment and even interbreeding with *Mfa* (Gumert & Malavijitnond, 2012; Luncz et al., 2017 and see chapter IV). Despite having access to social information on tool-use (i.e., *Mfa* who could act as demonstrators of the tool-use behaviours), *Mff* continue not to use tools in the wild. However, Zuberbühler et al., (1996) observed a captive *Mff* spontaneously using a stick to retrieve apples that had fallen just out of reach outside the enclosure. The behaviour was then also observed in other members of the group. Stick manipulation was found to slightly increase when the original innovator was raking in apples. However, the small increase of manipulation of sticks (perhaps via social facilitation) did not always result in tool-use by the other members of the group. The authors therefore conclude: "*We cannot conclude from these data that stimulus enhancement is a necessary prerequisite to becoming a skilled animal, because MD, the inventor of the technique, most likely developed his skill by means of individual learning" (*Zuberbühler et al., 1996, 10). Naïve *Mff* have also been reported using human hair as dental floss (Wantabe et al., 2007), and Tonkean macaques (*Macaca tonkeana*) have been observed spontaneously using sticks to retrieve honey from an out-of-reach apparatus (Anderson, 1985), sticks to rake food into the enclosure (Ueno et al., 1998), and making climbing structures out of sticks and browse (Westergaard, 1987; Westergaard & Lindquist, 1987; Ducoing & Thierry; 2005). Japanese macaques (*Macaca fuscata*) also use human hair as dental floss (Leca et al., 2010) and use stones (and infants) to push fruit out of a tube (Tokida et al. 1994). Lion-tailed macaques (*Macaca silenus*) use probes to extract syrup from a baited apparatus (Westergaard, 1988) and Rhesus macaques use cup-like containers to transport water around their enclosures (Parks & Novak 1999). These reports demonstrate that, similarly to gorillas (who do not often practice tool-use in the wild), various species of macaques can reinnovate some tool-use behaviours when in the appropriate context.

2.4.2 Individual learning in birds

2.4.2.1. Crows

In comparison to primates, the case for individual learning in bird material culture seems to be less debated, perhaps due to the fact that birds are less likely to be anthropomorphised and therefore human-like cognition is not immediately assumed for these animals. Indeed, several accounts exist of naïve birds in the wild and in captivity innovating and reinnovating wild behaviours (e.g., Colias & Colias, 1964; Epstein et al. 1984; Jones & Kamil, 1973; Tebbich et al. 2001; 2007; Bird & Emery, 2009; Taylor et al., 2010; Overington et al. 2011; Auersperg et al. 2012). Some of the most impressive accounts of the individual learning of tool-use come from New Caledonian crows (*Corvus moneduloides),* who possess sophisticated stick tool-use repertoires, rivalling even those of non-human primates (Weir et al., 2002). Similarly to chimpanzees, some New Caledonian crow tool-use is subject to regional variation. In the chimpanzee case however, this variation has been used as evidence for the view that the behavioural forms are dependent on social learning (Whiten et al., 1999; 2001; Gruber et al., 2015). Yet this claim has not been made (so far) for wild New Caledonian crows (Hunt, 1996; although see also Logan et al., 2015 for an experimental test on the low-fidelity social learning abilities of New Caledonian crows). Furthermore, subsequent experimental studies with captive New Caledonian crows demonstrated that naïve crows can spontaneously make and use some of the same tools as their wild counterparts, without social learning. The authors state: "*In the light of our findings, it is possible that the high level of skill observed in wild adult crows is not socially acquired"* (Kenward et al., 2005, 121). Naïve New Caledonian crows are also capable of reinnovating tool bending (Weir & Kacelnik, 2006) and metatool-use (i.e., the ability to use one tool on another; Whiten & Byrne, 1997; Taylor et al., 2007). These findings led Kenward et al., (2005, 121) to conclude that: *"the ability of this species to manufacture and use tools is at least partly inherited and not dependent on social input".*

Another strong example of individual learning in birds comes from Hawaiian crows (Alalā; *C. hawaiiensis).* Hawaiian crows are extinct in the wild and currently only exist in captivity, but it is likely that in their past natural state these crows also used tools (similarly to New Caledonian crows; Rutz et al., 2016). In an experimental study with captive Hawaiian crows, 78% of the population spontaneously used tools to probe for out-of-reach food, without social demonstrations (Rutz et al., 2016). Similarly to Kenward et al.s' (2005) conclusion for New Caledonian crows, Rutz et al., (2016, 405) also suggest that the observed behavioural repertoire is therefore a product of individual learning: *"Alalā clearly possess a propensity to "discover" tool-assisted foraging solutions independently".*

2.4.2.2. Other birds

Similarly to primates, several species of birds that do not use tools in the wild spontaneously reinnovate tool-use when provided with the materials in captivity. One example of this phenomenon are captive born and raised blue jays (*Cyanocitta cristata*), who do not use tools in the wild, but were observed tearing up pieces of newspaper and using them to rake out-of-reach food pellets from outside their cage (Jones & Kamil, 1973). Although – similarly to the case for many primates – the authors interpreted this finding as the product of social learning ("*the fact that to date we have found six jays in our colony demonstrating tool-using behaviour is more likely the result of […] observational learning or imitation than the result of the independent acquisition of this behaviour by each of the six jays"*, Jones & Kamil, 1973, 1078), in the light of new understanding on the role of individual learning in animal tool-use, it seems more likely that blue jays can reinnovate this behavioural form without requiring social learning, but the increase in frequency of the behaviour observed in this captive group was facilitated by social learning of different types than the ones indicated by these authors, namely by low-fidelity social learning (that merely fosters the likelihood of individual reinnovation; Tennie et al., 2009).

Most other cases of spontaneous tool-use in birds have been cited as examples of individual learning, rather than of imitation and/or other forms of social learning. For example, when captive Goffins cockatoos were observed making and using stick tools to rake in food from outside the enclosure, the authors argue that their "*observations* *prove that innovative tool-related problem-solving is within this species' cognitive resources"* (Auersperg et al., 2012, 2). When captive Rooks (*Corvus frugilegus*) used stones to collapse a platform to retrieve a worm, the authors similarly concluded that the reinnovation was an individually learnt solution to a new problem (Bird & Emery, 2009). And when naïve pigeons solved a task inspired by Köhler's (1925) work with chimpanzees, in which the pigeons had to use boxes to reach a banana hanging outside their enclosure, the authors conclude that that they "*have on hand an instance of insightful problem solving"* (Epstein et al., 1984, 62). Indeed, albeit some minor exceptions, contrary to the primate case, the view that bird tool-use is the product of individual learning is pervasive throughout the literature (e.g., Tebbich et al., 2001; 2007; Tebbich & Bshary, 2004; Auersperg et al., 2001; 2016).

2.4.3 Individual learning in other animals

Although most reports of animal spontaneous tool-use come from primates and birds, other animal species have also demonstrated the ability to individually reinnovate tool-use behaviours. For example, a dingo (*Canis dingo*) was recorded moving objects around his enclosure, including a table, to climb on to reach food or to observe other animals outside his enclosure (Smith et al., 2011). The dingo's behaviour (using a table to access out-of-reach food) is reminiscent of Köhler's (1925) early studies in which chimpanzees used boxes to reach hanging bananas. Furthermore, Chevalierskolnikoff & Liska (1993) describe over 20 tool-use behaviours that were reinnovated, without social learning, by captive African and Asian elephants. Behaviours included: "*reach toward food with stick held in the trunk"; "Rub the body with a stick"; "probe musth gland with stick"* (Chevalierskolnikoff & Liska, 1993, 210). A recent observational report describes the use of two coconut halves as a protective shell by an octopus (*Amphioctopus marginatus;* Finn et al., 2009), and orphaned, captive juvenile sea otters (*Enhydra lutris nereis)* were found to reinnovate the same stone tool pounding behavioural forms as observed in wild adult otters (Nicholson et al., 2007). These studies demonstrate that tool-use is not restricted to primates and birds, but that many other animals possess the ability to use tools, and crucially, the ability to individually learn their behavioural forms.

2.5.Factors influencing the emergence of reinnovations

The individual learning database provides insight into the extent of individual learning of material culture in the animal kingdom. However, the studies included in the individual learning database also demonstrate that not all individuals, although capable of doing so, will reinnovate all the behaviours within their potential capabilities. Some of the factors that may influence the reinnovation of behaviours in the ZLS are discussed below.

2.5.1 Environment

The environment is one of the most important contributing factors to the reinnovation of behavioural forms. Species with the most extensive tool-use repertoires are often ones that have invaded new niches (Alcock, 1972). Colonising new areas requires the innovation of behaviours and foraging techniques, placing the species under new selective pressures (Miller, 1956). These acquired characteristics then can even shape the environment itself (e.g., “niche-construction” theory; Odling-Smee et al., 1996), resulting in the environment playing a role as both an explanation and explanandum for animal tool-use.

One concrete example of how the environment can influence the likelihood of tool-use emerging is encapsulated by the concept of the “captivity effect” (van Schaik et al., 1998). The captivity effect describes the observation that captive animals seem to outperform their wild counterparts in both the diversity and frequency of behaviours, such as tool-use (van Schaik et al., 1998). The safer and more predictable environment provided by captivity, regular provisioning, the lack of predators, and higher levels of free time and energy afforded by captive settings have all been cited as factors behind the increased levels of tool-use in captive animals (Haslam, 2013). Thus, among other factors, the increased opportunities to explore new behaviours afforded by captive environments most likely enhance the likelihood that animals will reinnovate behaviours within their repertoires (see general conclusion for further discussion of the captivity effect).

The environment in the wild may also influence the emergence of tool-use behavioural forms. To explain the advent of tool-use in wild species, some have argued that encounter rates with certain food types or resources greatly encourage the emergence of associated tool-use behaviours in wild animals (the *opportunity hypothesis*; Koops et al., 2013; 2014). Others have argued instead that tool-use emerges as a direct response to times of scarcity of preferred food sources (the *necessity hypothesis*; Fox et al., 1999; Fox et al., 2004; Koops et al., 2014). Koops et al. (2013; 2014) directly tested the two opposing hypotheses on wild primates (focusing especially on chimpanzees) and found that access to the appropriate resources and food sources (i.e., the opportunity hypothesis) was the most compelling explanation for the regional variation observed in chimpanzee tool-use behaviours. The opportunity hypothesis may therefore explain at least parts of both the regional variation in tool-use repertoires observed in some species of wild primates and also the increased levels of tool-use behaviours observed in captive animals. However, it is important to note that although captive environments may foster tool-use, this does not necessarily then imply that captive animals are capable of reinnovating behaviours that their wild counterparts cannot (i.e., of going beyond their ZLS, except in the case of enculturated apes, see general introduction), but rather that captivity merely increases the likelihood of reinnovating behaviours that are within the individual learning abilities of all members of the species (see chapter VI for further discussion of this issue).

2.5.2 Genetics

The role of genetics in animal tool-use is still poorly understood. As mentioned in the general introduction, Langergraber and colleagues (2010) directly examined the role of genetic influence on the 39 chimpanzee tool-use behaviours identified by Whiten et al., (1999; 2001) as “cultural” (i.e., relying on social learning, according to Whiten et al., 1999; 2001; see general introduction) and concluded that “*genetic differences cannot be excluded as playing a major role in structuring patterns of behavioural variation among chimpanzee groups”* (Langergraber et al., 2010, 409). However, using cladistics analysis on the same 39 chimpanzee behaviours, Lycett et al., (2007, 547) argue instead that their data *“support the suggestion that the behavioural patterns are the product of social learning and, therefore, can be considered cultural”*. These two contrasting studies demonstrate only that the role of genetics in animal tool-use is still unclear and heavily debated. Yet, it is likely that alongside the environment, genetics play an important role in the emergence of behaviours. This role is most clearly observed in studies in which very closely related subspecies were found to differ in their tool-use abilities (e.g., long-tailed macaques; Luncz et al., 2017; chapter IV and otters; Ladds et al., 2017), even when they share the same environment and/or are placed in the same testing conditions. Furthermore, measurements of intelligence (which may be correlated to the ability to use tools; Reader & Laland, 2001) have also been suggested to be heritable in chimpanzees (Hopkins et al., 2014), and, dolphin sponging behaviour (in which dolphins use sponges as foraging tools; Krützen et al., 2005), has been suggested to be predicted by genetic relatedness with other spongers in the community (Krützen et al., 2005; although see Sergeant et al., 2007 for a contrasting view). In summary, further research is still required into the role of genetic differences in the tool-use abilities of animals. In the meanwhile, this factor should be kept in mind as an influence on the reinnovations of behaviours in animals, even on a subspecies level.

2.5.3 Pre-existing techniques

An individual's background knowledge of the materials of the target behavioural form may also influence the reinnovation of the behavioural form in naïve animals. Gruber and colleagues' (2009; 2011) work with the Sonso and Kanywara chimpanzee communities in Uganda provides relevant data for discussions on the role of these factors in the acquisition of a novel behaviour. Despite neighbouring each other, the two communities adopt different methods to acquire honey from trees: Sonso chimpanzees most often use their hands or leaves to access the honey, whilst Kanywara chimpanzees generally use stick tools (Gruber et al., 2009). To examine the stability of these differences, Gruber et al., (2009; 2011) placed an artificial log with two honey-filled cavities in both groups, to encourage the Sonso chimpanzees to switch their method to the Kanywara stick-tool-use approach. However, contrary to expectations, the Sonso chimpanzees remained with their pre-existing technique of using leaves to scoop up the fluid, even from the narrower cavities of the artificial log, and the Kanywara chimpanzees continued to use sticks for the remainder of the experiment. The stability in methods remained even after the researchers placed sticks inside the holes in the Sonso chimpanzees' log (the chimpanzees simply removed the sticks and continued to use leaves to absorb the honey). Gruber et al., (2009, 1809) argue that the Sonso chimpanzees' reliance on community-specific techniques, rather than switching to stick tool-use *"supports a culturally based rather than an individual acquisition of the behaviour"*. The authors further argue that the Sonso chimpanzees are “*unable”* to use sticks because they have never observed another individual using a stick to retrieve honey. On the other hand, the Kanywara chimpanzees, who regularly use sticks, have ample opportunities for naïve individuals to socially learn stick tool-use for honey dipping (according to Gruber et al., 2009). However, a more parsimonious explanation for these findings is that, whilst low-fidelity social learning may have encouraged the chimpanzees to initially adopt either a leaf or stick based approach to this task (simple increases in exposure to either leaves or sticks around the problem-space most likely influences which method an individual chooses; e.g., “Founder effects”; Tennie et al., 2009; Tennie & Hopper, 2011), both behaviours are within the chimpanzees’ ZLS (and therefore all individuals, in both communities, are technically capable of reinnovating either technique). Thus, although capable of using sticks, the Sonso chimpanzees may have not switched to stick-use simply because they already had a pre-existing, efficient, technique to reach the same end goal (Tennie & Hopper, 2011). Indeed, chimpanzees seem hesitant to switch to a new technique if it is not significantly more efficient than their previous method (Hrubesch et al., 2009; Davis et al., 2016; Harrison & Whiten, 2018). Thus, the existence of an already efficient technique may hinder the exploration of new methods if the end result is the same, and the new method is not vastly more efficient (no data exists on differences in efficiency between the leaf and stick methods, but it is likely that if differences do exist, they are minimal and thus hard to observe for this behaviour; see Tennie & Hopper, 2011). Therefore, the chimpanzees’ relative inflexibility observed in Gruber et al.s’ work (2009; 2011) may not be a reflection of the Sonso chimpanzees’ dependence on social learning, but rather may reveal a form of “functional fixedness”, in which the subjects’ past experience with objects in different contexts hinder their ability to reinnovate alternative behavioural forms with these tools (functional fixedness via individual learning; Hanus et al., 2011). This phenomenon may, therefore, have obstructed the Sonso chimpanzees from switching to a new method with tools that they already used for other purposes (a similar case was found for the long-tailed macaques discussed in chapter IV). This inflexibility may constitute a limiting factor for non-human tool-use (Brosnan & Hopper, 2014).

Previous experience with the materials of a behaviour does not, however, always play a limiting role on the reinnovation of behaviours. Indeed, several studies have demonstrated that the opportunity to manipulate components of a behaviour for an extended period (or during an ontogenetic sensitive learning period) is beneficial for subsequent reinnovations of the behavioural from (e.g., Tebbich et al., 2001; Biro et al., 2003; Tan et al., 2017; and see chapter VI for further discussion).

2.5.4 Social learning

Although the studies described in this review highlight the importance of individual learning in the acquisition of tool-use behavioural forms, low-fidelity forms of social learning also play a significant role in the increases in frequencies and in the later sustenance of animal tool-use behavioural forms. Over 20 different animal species have been found to attend to social information through various low-fidelity social learning mechanisms (e.g., Custance et al., 2001; Stoinski et al., 2001; Atkins et al., 2002; Miller et al., 2009; Reader & Biro, 2010; Kis et al., 2015; Whiten et al., 2015), and it is undoubtable that these forms of low-fidelity social learning greatly facilitate the frequency of reinnovation of behaviours, making it more likely that the rest of the group will acquire the behaviour once it has been reinnovated (through simple low-fidelity social learning mechanisms such as local and/or stimulus enhancement; Thorpe, 1963). However, this process is not infallible, and despite opportunities for individual and social learning, some individuals in a group may never express the target behaviour. In fact, many of the studies in the individual learning database describe reinnovations in only some subjects within their samples, whilst other members of the group never express the behaviour despite ample exposure to the reinnovators. Evidence from wild chimpanzees also suggests that very few innovations "catch-on", despite opportunities for social learning (Nishida et al., 2009). Tebbich et al., (2001) directly examined this phenomenon by measuring the rates of acquisition of a novel tool-use behaviour in naïve finches when exposed to a model and in a control group. The authors conclude: "*the presence of a model does not influence the ontogeny of tool-use: this behaviour was expressed in the absence of a model and the development was not slower without than with a model*" (Tebbich et al., 2001, 2192). Several other studies report similar results across various species[6].

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[6] For example: Menzel, (1970); Beck, (1978); Anderson, (1985); Sumita et al., (1985); Antinucci & Visalberghi, (1986); Visalberghi, (1987); Visalberghi & Trinca, (1989); Tokida et al., (1994); Zuberbühler et al., (1996); Nakamichi, (1999); Tebbich et al., (2001); Hayashi et al., (2005); Taylor et al., (2007); Bartolini et al., (2007); Yamamoto et al., (2008); Marshall-Pescini & Whiten, (2008); Geissmann, (2009); Hirata et al., (2009); Smith et al., (2011); Overington et al., (2011); Biro et al., (2013); Bandini & Tennie, (2018).

Collectively, these studies demonstrate that although low-fidelity social learning plays a role in increasing the frequency of reinnovations, it is not always the decisive predictor for the reinnovation of a novel tool-use behaviour (as other factors, such as sensitive learning periods, levels of motivation, development stages, etc. may hinder the reinnovation of specific behavioural forms).

2.6 Conclusion

This review has provided evidence from both wild and captive animals to support the view that some animal tool-use behaviours (if not all; see implications made by Tennie et al., 2009) are driven by individual learning, and that low-fidelity social learning, whilst facilitating the frequency and stability of these behaviours within populations, is not indispensable for these tool-use forms – as is demonstrated by their emergence across naïve individuals. Although the ZLS hypothesis is the first to explicitly describe this approach for animal tool-use, several studies (as discussed above and in the individual learning database) have already offered data consistent with this view. Indeed, despite never becoming a widespread approach, several early researchers concluded from their own work that individual learning plays a pivotal role in animal tool-use: "*Even the highest vertebrates, primates, have certain [...] forms of activity available, without specific training to develop them. They are present uniformly in all individuals of the same age group, and are invariably displayed if the general condition of the animals favours them"* (Menzel, 1970, 281).

Although individual learning may have a prominent role in encouraging the emergence of novel behaviours, it is the combination of individual learning and the various forms of low-fidelity social learning that allow for the successful sustenance of the rich animal tool-use behavioural repertoires (Reader & Laland, 2001; Heyes, 2011; Barrett, 2018). Furthermore, many external factors contribute to the likelihood of a behaviour being reinnovated. The importance of these factors (such as environmental and genetic influences) alongside recognising the equifinality (i.e., multifaceted nature) of novel behaviours (Barrett, 2018) should not be neglected. Currently, high-fidelity social learning is still the null hypothesis for most animal tool-use behaviours, and in particular for our closest living relatives, chimpanzees (Whiten et al., 1999; 2001; Gruber et al., 2015). Evidence from this review demonstrates instead that perhaps it is time to include individual learning as a serious alternative to the development of animal tool-use behaviours. As Byrne (2007, 285) elegantly asks: "*If a habit can be invented multiple times, perhaps it can be invented by every individual that has a real need of it?*"

2.6.1 Link to chapter III

This chapter provided a comprehensive overview of animal tool-use reinnovations. However, few of the studies included in the review specifically tested the individual learning abilities of our closest living relatives: chimpanzees, and none applied the LS testing methodology to a tool-use behaviour in chimpanzees (see general introduction). The following chapter fills this gap in the literature by presenting the results of four independent experimental studies on the learning mechanisms behind the acquisition of novel tool-use behaviours in naïve, captive chimpanzees. These studies constitute the first ZLS tests on tool-use behaviours in non-human primates.

Chapter III: Testing the Zone of Latent Solutions with chimpanzees

This chapter includes a slightly modified version of the (published) paper:

Bandini, E & Tennie, C. (2017). Spontaneous reoccurrence of “scooping”, a wild tool-use behaviour, in naïve chimpanzees. *PeerJ, 5*, e3814.

Alongside slightly modified versions of the following two papers in preparation:

Bandini, E & Tennie, C. Full acquisition of “stick pounding behaviour” by naïve chimpanzees in the absence of observation opportunities. In prep.

Bandini, E, Neadle, D & Tennie, C. A tool-use behaviour, picking, is reinnovated by great apes. In prep.

For this chapter, the main texts of these papers were rearranged and combined to allow for better readability. Minor modifications have been made throughout the text to the Bandini & Tennie (2017) section, but otherwise the text is as published.

I am the primary author of the Bandini & Tennie (2017) publication. The original idea for this study was developed in collaboration with Claudio Tennie. I was primarily responsible for the design of the studies and I carried out all data collection and analysis. Claudio Tennie contributed to authorship by providing feedback and editing versions of this paper leading to its publication.

Link to open access article: https://peerj.com/articles/3814/

Chapter III: Testing the Zone of Latent Solutions with chimpanzees

3.1 *Introduction*

The studies presented in this chapter describe the results of four latent solutions tests on the acquisition of tool-use behavioural forms in naïve chimpanzees. This empirical work directly tests the two opposing hypotheses: the social learning and the ZLS approaches, on the emergence of four wild chimpanzee tool-use behaviours. As described in the general introduction, the only way to ascertain whether chimpanzee tool-use is best accounted for by a latent solutions approach, or whether social learning is required (as argued by Whiten et al., 1999; 2001), is to directly test whether these behaviours can be reinnovated by naïve individuals. The alternative approach, where high-fidelity social learning transmits the behavioural form, would instead predict that these forms cannot be spontaneously shown by individuals that are unconnected to the culture that keeps them in place. In such tests, subjects are considered naïve if they are in this sense unconnected, i.e., they have never been trained in and/or have never seen the behaviour before. To ensure ecological validity, subjects should be enriched captive apes (Henrich & Tennie, 2017). Subjects are provided with the necessary raw material and motivation (e.g., food baits) to develop the target behavioural form (LS test; see general introduction). If the naïve subjects develop the target form, this demonstrates that social learning (of either low-fidelity or high-fidelity type) is not necessary for explaining the acquisition of the tested behavioural form (and it becomes unparsimonious to assume that social learning is responsible for the form in the wild).

In this chapter, four wild chimpanzee tool-use behavioural forms (referred to by their target actions: scooping, picking and pounding) were experimentally tested following the LS methodology to assess whether these behaviours are latent solutions (and therefore will emerge without social information), or whether they require social learning to be acquired (and therefore should not emerge in the LS testing conditions; providing evidence for the social learning hypothesis).

3.2 Behaviour Descriptions

3.2.1 Scooping

Algae scooping (not to be confused with *algae fishing*; Boesch et al., 2016), is a behaviour observed in wild chimpanzees in Bossou, Guinea. The behaviour involves feeding on aquatic algae using herbaceous tools (Humle et al., 2011). Chimpanzees in the wild use tools to feed on *Spirogyra sp.,* a common form of algae in Bossou that often covers the surface of ponds, streams and lakes (Humle et al., 2011). Although algae scooping has also been described elsewhere (Sakamaki, 1998; Devos et al., 2002), Humle and colleagues (2011) provide the only description of the actual form of the behaviour. The authors (Humle et al., 2011) divided algae scooping in wild chimpanzees into six steps: (1) select a stalk or stick, (2) detach it from the branch or bush, (3) modify its length, (4) remove the leaves, (5) insert it into the water and (6) *scoop the algae*, using a "*gentle swivelling action of the wrist"* (Humle et al., 2011, 199). This study focused on the behavioural form of *scooping* and the accompanying actions (steps 1, 5 and especially 6) because the selection, procurement and modification of sticks (steps 1-3) are already known to be widespread behaviours in chimpanzees, strongly suggesting that they can be individually innovated (see Whiten et al., 1999; Gruber et al., 2010 for reviews of tool-use in wild and captive apes). Likewise, the focus of this study was not on how chimpanzees might learn that algae are edible or where they can be found. While such learning can also be, and presumably often is, socially mediated in chimpanzees (e.g., via local and/or stimulus enhancement; see description of social learning terms in Appendix III and in Whiten et al., 2004), this kind of information (what and where) does not require the copying of behavioural forms from other individuals. Thus, the question of how individuals learn what exactly to do at the location or with the new type of food would remain unanswered. Consequently, when examining whether high or low-fidelity social learning mechanisms are required for animal tool-use behaviour to emerge, logically, the experimental focus must be on the *behaviour* (the actions) itself. Here the focus was on examining the necessary learning mechanisms behind the scooping tool-use actions (identifying the need for a stick, inserting the stick and using it to scoop by applying a "*swivelling action of the wrist"*; Humle et al., 2011, 119) by testing whether they would reappear spontaneously in naïve chimpanzees without the aid of social learning.

At the time of Whiten et al.s' (1991; 2001) reports on cultural behaviours across chimpanzee populations, algae scooping failed to meet the requirements for "*putative cultural variants"* as the absence of the behaviour in other communities was explained by a lack of suitable algae (Whiten et al., 1999; 2001). However, since the two reports, feeding on algae has been observed in two other chimpanzee communities: in Odzala National Park, Republic of Congo (Devos et al., 2002) and in Mahale National Park, Tanzania (Sakamaki, 1998). In Odzala National Park, three chimpanzees were observed feeding on aquatic algae. Two chimpanzees used their fingers, whilst one (male, unknown age) used the stem of a sedge to scoop the algae (Devos et al., 2002). In Mahale, Tanzania, a female chimpanzee (Sally, unknown age), fed on aquatic algae without using a tool (Sakamaki, 1998). Following the requirements outlined in Whiten et al., (1999; 2001), algae scooping would now be classified as a *"putative cultural variant"* as it is habitual in one community (Bossou, Guinea), but absent without environmental explanations in Mahale, Tanzania (as edible algae exist in this community as well). Thus, algae scooping would now be categorised as a cultural behaviour, the emergence of which, as discussed above, would be considered to depend on social learning (Whiten et al., 1999; 2001).

3.2.2. Picking

The second experiment tested the acquisition of another wild chimpanzee behaviour: *marrow picking* (Boesch & Boesch, 1989; Boesch & Boesch, 1990). Wild chimpanzees in Taï National Park, Ivory Coast, have been observed to hunt and then consume the bone marrow of colobus monkeys (*Colobus badius*; Boesch & Boesch, 1989; Boesch & Boesch, 1990). To access the bone marrow, chimpanzees first open the ends of long bones with their teeth and then use small sticks to retrieve the marrow from inside the bone shaft (Boesch & Boesch, 1990). This tool-use behaviour is known as *marrow picking* (Boesch & Boesch, 1990) and has been observed regularly in Taï chimpanzees at the end of meat-eating bouts. Other than in Taï National Park, marrow picking has only been observed on one occasion in Goualougo Triangle, Republic of Congo (≈2600km from Taï), where Sanz and Morgan (2007) reported one individual using a twig segment to extract marrow from the bones of a duiker. The behaviour and the tools used in Goualougo Triangle are similar to the ones reported by Boesch & Boesch (1990) for Taï chimpanzees. Marrow picking was categorised as one of the 39 cultural behaviours by Whiten et al., (1999) as it was customary in Taï National Park and absent at all other sites (but not due to environmental explanations) at the time of the study (and it is only considered a rarity in Goualougo Triangle, which does not have an effect on the original classification of marrow picking as a cultural trait as chimpanzees hunt colobus monkeys at other sites across Africa (e.g., in Gombe National Park, Tanzania; Stanford et al., 1994), but have only been observed to use tools to eat the bone marrow in Taï National Park and Goualougo Triangle).

3.2.3 Pounding

Two pounding experiments were carried out to test two of the pounding behaviours observed in wild chimpanzees: *pestle pounding* and *insect pounding*. These two behaviours share the same required action (pounding) to retrieve different food sources (i.e., palm hearts in pestle pounding; Yamakoshi & Sugiyama, 1995 and ants and other insects in insect pounding; Sugiyama & Koman, 1979). Despite the similarities between these two behaviours, they are classified separately in the wild. Acknowledging this issue (which is observed even more prominently in the classification of some other behaviours, such as wild chimpanzee *ant dipping* and *termite dipping.* These two types of dipping are classified as separate behaviours, solely on the basis of the different food sources being retrieved (ants vs. termites), rather than being including under a larger "insect dipping" umbrella, for example. Further discussion of this issue can be found in the general discussion chapter), Whiten et al., (2001) explain that a certain level of subjective decision-making was employed in the lumping and splitting of behaviours in the original report: "*although it is important to acknowledge that it is difficult to establish objective rules for deciding such matters […] one can always split a category into the different ways of doing it, or alternatively, lump categories together that share a common feature*" (Whiten et al., 2001, 1488). Whiten et al., (1999; 2001) and subsequent reports following the method of exclusion (e.g., Perry, 2001; van Schaik et al., 2003; Santorelli et al., 2011; Robbins et al., 2016) all favoured a "splitting" approach, in which behaviours were classified separately, regardless of whether they shared common features such as the underlying actions. Following the established splitting method, two, separate, experiments were designed to test the acquisition of the pounding action in naïve chimpanzees. These two studies are described below.

3.2.3.1. Pounding Experiment I

The first pounding experiment tested the wild chimpanzee behaviour *pestle pounding*. Pestle pounding has been observed in chimpanzees in Bossou, Guinea (Yamakoshi & Sugiyama, 1995). Chimpanzees in this community use the leaf-petioles of oil-palm trees (*Elaeis guineensis*) as pounding tools to deepen the holes they make in oil-palm trees by pulling out the central shoots in the oil-palm crown. The chimpanzees then extract and eat the apical bud or meristem of the oil-palm tree (both of which are inaccessible without tools). Pestle pounding was first observed in Bossou in 1990, and by the time the first report was published in 1995, almost half of the group was observed practicing it (Yamakshi & Sugiyama, 1995). As pestle pounding is an easily identified behaviour in which the chimpanzees make a loud, recognizable pounding noise, the authors conclude *"this tool-using behaviour was invented recently and has since spread widely throughout the group"* (Yamakshi & Sugiyama, 1995, 489). Although the same species of tree (*Elaeis guineensis*) exists across most other chimpanzee sites, pestle pounding has, so far, only been observed in Bossou (Whiten et al., 2001). Following Whiten et al.s' (1999; 2001) requirements for a behaviour to be recorded as either *habitual* or *customary* at least one site, and absent at but not due to ecological reasons in at least one other site, pestle pounding was categorised as a *putative cultural behaviour* (Whiten et al., 1999; 2001).

The pounding action practiced by the chimpanzees whilst pestle pounding is described as: "*Picking up a removed leaf, the chimpanzees used its petiole as a pestle to repeatedly pound and deepen the hole, hands were used for pounding except for a few one-handed cases. They continually pounded an average of 10.0 times (n=38, S.D.=5.31) per PO component"* (Yamakoshi & Sugiyama, 1995, 493). Before pounding, the chimpanzees climb the palm trees and pull out the palm petioles, which they then use to pound the palm hearts. However, in the current study, only the crux of the behaviour was examined: i.e., the use of a tool and a pounding action to retrieve a desirable food (see above in the scooping section for a more detailed explanation behind this approach).

3.2.3.2. Pounding Experiment II

The second pounding experiment focused on testing *insect pounding*. This behaviour has been recorded under different names across various reports. Here Sugiyama & Koman’s (1979) definition as reported in Whiten et al., (2001, 1489) is followed: “*Probe used to retrieve insect by prodding it: take a small twig, remove the side branches and leaves, and so make a small stick. Next, they would beat and pound the bottom of the hole several times. On pulling the stick out a few termites would be attached to it, mostly broken and adherent. The chimpanzee would lick them off and again try to pound the bottom of the hollow”*. Insect pounding was categorised as a *rarity* in Whiten et al.s’ (2001) report on chimpanzee behaviours, as it did not reach habitual or customary status at any field site. Therefore, conversely to the other studies presented in this chapter, insect pounding did not reach the requirements to be classified as cultural trait (Whiten et al., 2001).

Although pestle and insect pounding share the same action (pounding) to reach the final goal (the food source), there are some small differences between these two behavioural forms. Firstly, a different food resource is being exploited (palm hearts vs. insects) and secondly, whilst the target action is identical between the two behaviours (indeed, in the first report of pestle pounding, the behaviour is described as being similar to other digging and pounding behaviours: “*the motor pattern which the chimpanzees employed is similar to that used for termite-nest digging but it is more exaggerated”,* Yamakoshi & Sugiyama, 1995, 489), pestle pounding requires a more forceful and aggressive form of pounding compared to insect pounding. The apparatuses and food rewards used as bait in experiments I and II address these small differences (see below).

3.3 General Methods

This section provides a description of the methods that were applied across the four studies presented in this chapter. The methods specific to the studies are described in more detail in the individual sections below.

3.3.1 Questionnaires

As emphasised in the general introduction chapter of this thesis, it is essential for LS studies that all the subjects are naïve to the target behaviour and the underlying actions before testing. Subjects must be naïve to ensure that any eventual reinnovations of the target behavioural form observed in the study are the product of individual learning rather than of social learning and/or previous experiences of the target actions or tools. Thus, to ensure that the subjects were completely naïve to the task and the target actions involved, a questionnaire was created on the past experiences of all the test subjects (see Appendix V for an example of the questionnaire, made in collaboration with *D. Neadle*). All the keepers of the animals involved in testing were asked to fill out the questionnaire. Once the questionnaires were completed and returned, individual interviews were carried out with each of the keepers to ensure that all the relevant information on the subjects' previous experiences (e.g., past research experiments carried out with the subjects, enrichment devices or tasks that had been provided and/or general behavioural observations) were controlled for. This process proved to be a (mostly) reliable method to control for the background knowledge of the chimpanzees (for example, Chester Zoo, UK, was first included as a possible testing facility for scooping, but was then later excluded after the questionnaires revealed that one of the chimpanzees in the group had been observed inserting a stick into a water bowl left outside of the enclosure). However, there was one case in which the questionnaire and the interviews were not successful in revealing all the relevant information on the chimpanzees' background, leading to some data potentially being excluded later in the analysis (see results and discussion section of the picking study below).

3.3.2 ZLS standards

As discussed in the introduction of this thesis, two ZLS standards (the single-case ZLS standard and the double-case ZLS standard; Bandini & Tennie, 2017) were created to ensure that data collected from captive subjects could be generalised to a species-wide level. As all the behaviours described in this chapter can be considered relatively "simple" behaviours, in that they only required the use of one tool (a stick tool) and one underlying target action, the studies here applied the double-case ZLS standard. Therefore, at least two, independent, reinnovations of each behaviour were required before the target behaviour could be confidently assumed to be within the ZLS of the species.

3.3.3 Filming

All experimental sessions were filmed by the researcher (EB) using a Sony HDR-CX330E handycam video recorder. For the scooping and picking studies, in most testing sessions at least one other person (a research assistant or collaborator) also filmed the testing conditions, to ensure that all behaviours that emerged during testing were recorded. Behaviour coding was then carried out from the video after testing (except for the first scooping experiment, in which EB also live coded), and reliability coding was carried out from video (either all the videos were coded, or a percentage of videos were coded; see individual methods section below). All analysis was run in R version 3.4.1 (2017-06-30).

3.3.4 Ethical Statement

All of the studies presented in this chapter were reviewed and approved by the University of Birmingham AWERB committee (reference UOB 31213) and by the host zoos following guidelines provided by the SSSMZP, EAZA, BIAZA and WAZA on animal welfare and research in zoological institutions. These studies adhered to legal requirements of the UK, Italy and Zambia, where the research was carried out, and adhered to the ASP principles for the Ethical Treatment of Primates. All the subjects in these studies voluntarily participated in the experiments, and were free to stop participating at any time (as the testing apparatuses were simply placed within, or just outside, of the enclosure, individuals could choose when/if to interact with the apparatus). Subjects kept their regular cleaning and feeding schedules during testing and had access to water *ad libitum*. Subjects live in natural-type social groups and were fed a daily appropriate and varied diet. Furthermore, the animals included in these studies regularly participate in research activities (such as the ones presented in this chapter) and have access to enrichment devices (none of which involved the target actions being tested in these studies, however).

3.3.5 Scooping Methods

3.3.5.1 Subjects

Twenty-one captive chimpanzees, ranging from 7 to 49 years of age (M_{age}=31.33, SD=10.09), based in Twycross Zoo in the United Kingdom took part in this study (see Appendix II for demographic information on the subjects). All the chimpanzees were housed in social groups and had access to two indoor enclosures, two outdoor enclosures (with observational windows for visitors) and two indoor management areas, which were out of view of visitors. Throughout the enclosure the subjects had access to enrichment apparatuses such as climbing ropes, hanging feeders and were regularly provided with other enrichment devices.

The chimpanzees were housed in two groups. Group 1 (n=6; M_{age}=28.60, SD=8.36) and Group 2 (n=15; M_{age}=31.33, SD=10.90). Wild born individuals were originally from the Democratic Republic of Congo or of unknown origins, whilst the majority of the captive born individuals were born at the testing institution. Owing to zoo management requirements, it was not possible to test each individual separately; so subjects were tested in their normal group settings. The groups were kept separately, and no observation between the two groups was possible during testing. The testing was carried out in the subjects' respective communal management areas.

As mentioned previously (see *Questionnaire* section above), to ensure the naivety of the subjects, the chimpanzees' keepers were asked for a detailed description of any tool-use they may have seen and all past research and enrichment exercises the subjects had participated in that might have been similar to the one presented here. The keepers independently confirmed that none of the chimpanzees at their institution had previously been exposed to any tasks, behaviours or materials similar to the ones provided in the current study. The keepers reported that the chimpanzees did have access to sticks before this study, but as the focus was not on general stick use (which is already known to be widespread in great apes, suggesting that it has already been reinnovated multiple times) previous contact with sticks did not present a problem for the aims of the study. Crucially, the keepers confirmed that the tested subjects were naïve to the problem of having to retrieve out of reach food and to the scooping action. Thus, it is highly unlikely that the subjects in this study, despite having had access to sticks, had previous experience with the problem of retrieving food from a body of water using sticks (there were no water surfaces in the enclosure). Furthermore, the keepers also confirmed, through the questionnaire and in person, that the chimpanzees did not have any experience with the *swivelling* action required for the scooping behaviour seen in the wild (Humle et al., 2011). Although the ideal conditions would involve testing a group of chimpanzees raised in a fully controlled environment, these conditions do not exist (and would, in any case, lead to ethical problems). Therefore, the best available option involves testing captive chimpanzees whose previous experiences can be confidently accounted for (as was done in these studies).

3.3.5.2 Procedure

A square plastic container (16cm x 66cm x 20cm) was placed outside the enclosure mesh and filled with room-temperature water (Fig. 1). Three bamboo sticks, modelled on the sticks collected in the field (Humle et al., 2011) in Bossou (min. 35cm and max. 98cm long, mean: 66.5cm- diameter min. 5mm, max 30mm, mean: 17.5mm), were placed around the enclosure prior to the chimpanzees entering the management area (again, given the focus on scooping actions, the provision of detached sticks did not present a problem for the study design). Prior to testing, food (bread) was left to harden for a week so that it would float on the top of the water. The bread was cut into “half-moon” shapes, to allow for it to be retrieved using a scooping action, similarly to algae in the wild. Three pieces of prepared bread pieces (half-moons) per testing session were placed simultaneously in the water container right before testing began. See Fig. 1 below for the experimental set up.

Fig. 1: Scooping experimental set-up. Container with bread crusts in the foreground and one of the sticks inside the enclosure (photograph by EB).

Testing began at around 12.30pm each day. Once the chimpanzees were allowed into the management area, a 30-minute testing period commenced. The test was live coded by E1 (EB) and filmed by E2 (research assistant, *F.Rocoque*). All chimpanzees then had potential access to the apparatus. Each group was tested three times: twice on consecutive days, and then a third time after 28 days. The testing session started when the chimpanzees were allowed into the management areas and ended after a total of 30 minutes.

3.3.5.3 Coding

It was live coded whether the subjects used a tool to retrieve the food; if they used a scooping technique (following the description by the Humle et al., 2011) or a different technique; whether there were any instances of stick modification; and whether the attempt was successful or not (see table one below for a description of the behaviours coded). A naïve coder, who was not familiar with the hypothesis or aims of the study second coded all of the videos to test for interrater reliability.

Table 1: Behaviours coded in the scooping study and their descriptions

Method	Description
Scooping	Individual holds a stick in the hand(s) and inserts it into the bucket of water. The individual then uses the stick and *a gentle swivelling action of the wrist* (Humle et al., 2011) to retrieve a piece of the floating bread. This is analogous to descriptions of the wild scooping behaviour.
Side Technique	Individual holds a stick in the hand(s) and places it on the upper part of the floating bread crust. The individual then uses the stick to push the piece of bread towards one of the sides of the bucket. Then, pressure is placed on the crust to slide it up the edge of the container and onto the rim. Once the bread is on the rim, it is pulled towards the mesh and retrieved with a finger(s).
Stick Modification	Individual modifies the provided stick in any way to make it more or less adapted to the task.
Successful Attempt	Individual is successful in retrieving the bread using the chosen technique. A successful attempt was recorded if the individual managed to retrieve a piece of bread, including the smaller pieces that formed when the crusts started to disintegrate, and transport it to the mesh
Unsuccessful Attempt	Individual was not successful in retrieving the bread using the chosen technique.

3.3.6 Picking Methods

3.3.6.1 Subjects

The subjects in this study were 25 captive chimpanzees (M_{age}=32.35; SD=10.79), 21 based in Twycross Zoo and four housed in the Bioparco di Roma, Italy (henceforth: BP). The first test was carried out at Twycross Zoo (see section above: the subjects were divided into two social groups: Group 1 (*n*=6; M_{age}=28.60, SD=8.36) and Group 2 (*n*=15; M_{age}=31.33, SD=10.90)). The four individuals (*n*=4; 3 females, M_{age}=31.25, SD=9.17) at BP are kept in one social group (see Appendix II for demographic information on the subjects). The BP chimpanzees were captive-born and reared in captivity (although no records exist on whether they were hand or parent reared).

All great ape keepers across both facilities were provided with the questionnaire on the subjects' previous experiences, to assess whether the chimpanzees had participated in any similar tasks as the one presented by the picking study. All the keepers independently confirmed via the questionnaires and in person that the chimpanzees at both Twycross zoo and BP were naïve to this task, and did not have any previous experience of retrieving food from inside tubes using a tool (but see section below on limitations of this study in which a potential inaccuracy during the questionnaire process of this study is discussed).

3.3.6.2 Procedure

As with the previous studies, the chimpanzees were tested in their social groups. No contact between the groups at Twycross Zoo occurred before or during this experiment. The materials were placed in the enclosure before the subjects could enter the testing area. Due to local constraints, it was not possible to use monkey bones and/or bone marrow for the purposes of this study. Therefore, to replicate the long bones of mammals prototypical to marrow picking in wild chimpanzees (Boesch & Boesch, 1990; Whiten et al., 2001; Sanz & Morgan, 2007) white non-toxic PEX barrier pipe was used and cut to a standardised length (diameter=15mm, length=15cm). The resulting tube was sealed at one end using a white non-toxic push fit stop-end (diameter= 30mm, length=32mm) fitted 27mm over the end of the tube and secured with an e-poxy adhesive (see Fig. 2; adhesive became non-toxic when cured for 24hrs). The tube was then filled with 10g of smooth peanut butter (warmed for 60 seconds in a microwave), using a long syringe. This ensured that the peanut butter remained at the bottom of the tube, avoiding the sides, preventing the subjects from licking or picking the butter out with fingers. The tube's diameter was sufficiently narrow that none of the subjects could fit their fingers inside. As with bones in the wild marrow picking behaviour, it is possible that the apes damage the tubes with their teeth to avoid having to use a tool, however due to the sturdy construction of the tubes, this would take considerable time (and in any case, more time than using a tool to retrieve the peanut butter). Thus, a tool was required to complete the task most efficiently; and sticks were provided. Sticks were taken from a garden willow trellis and cut to 20cm in length, diameter was ~5mm, with a maximum of 7.5mm (see Fig. 2), sizes were taken from reports of wild chimpanzee marrow picking tools (Boesch & Boesch, 1990). Filled tubes were refrigerated for at least 24 hours prior to testing to set the peanut butter at the base of the tube.

Fig. 2: Filled picking tubes (left) and sticks (right) placed in the subjects' enclosure (photograph courtesy of D.Neadle).

The first test was carried out with chimpanzees at Twycross Zoo. As this was a novel task, and the subjects were unfamiliar with the materials, the keepers requested that only one tube and three sticks be placed into Group 1 on the first day of testing. Thus, Group 1 on day one only received one tube and three sticks. After the first testing session, it was established that the materials were appropriate for the chimpanzees, and following sessions all included providing the three tubes and three sticks inside the enclosures. In accordance with previous LS tests (see above), prior to the subjects entering their usual day areas, the tubes and the sticks were spread into the enclosure (outside of 1m radius of tubes). Three tubes and three sticks were provided before each trial and placed throughout the day enclosures (open to the public and viewable through glass partitions). The tubes and sticks were placed in the enclosure during the usual morning scatter feed between 8 and 10 am. Each group was tested twice over a period of four weeks.

As chimpanzees at Twycross Zoo had access to four different enclosures (two indoor and two outdoor) during testing, five different researchers (EB, *D.Neadle, C.Williams, P.Cowdell*, and *R.Tinsley*) were posted in each enclosure with a camera to ensure that all interaction with the testing apparatus was coded and filmed. The exact same procedure was repeated at BP, except that only EB was present as the chimpanzees were easily visible in both the indoor and outdoor enclosures. Three tubes and three sticks were placed in the outdoor enclosure whilst the subjects were in their management area. Once the individuals entered the enclosure, a maximum 30 minute-testing period began. The chimpanzees had access to their outdoor and indoor enclosures throughout the whole testing sessions. When in the indoor enclosure, individuals could not observe the outdoor area, and vice versa. Subjects at the BP were tested twice following protocol from Twycross Zoo.

3.3.6.3 Coding

Behaviours were coded from video. See table 2 for behaviour descriptions. 25% of the videos were second-coded by a naïve coder (*A.Cope*) to assess the interrater reliability. Videos for second coding were selected following the protocol outlined by *D.Neadle*: during the first round of coding by EB, all the videos were assigned a sequential number (e.g., 1-*n*). After coding, the numbers were placed into a random number generator in Excel until 25% of the videos were selected for interrater reliability testing (see also Neadle et al., in prep). The second coders observations were then compared to EB’s using a Cohen’s Kappa calculation.

Table 2: Behaviours coded in the picking study and their descriptions

Method	Description
Picking	Individual holds a stick held in the hand(s) and inserts it into one end of the tube. Once the stick comes in contact with the peanut butter, the subject then removes the now peanut butter coated stick (or similar) and consumes the peanut butter using his/her mouth. This is analogous to marrow picking.
Picking (other)	The subject uses an object, other than the sticks provided, to dip into the tube and retrieve the peanut butter.
Hand	The subject used their fingers to try to access the peanut butter from inside the tube (without having destroyed it first), by inserting the tip of a finger into the tube and licking any residue of peanut butter from the finger.
Mouth	The subject puts the tube directly in the mouth and tries to extract the peanut butter by either sucking the tube, chewing the end or using the tongue to extract any residue of peanut butter near the tip of the tube.
Hand/Mouth	The subject uses first their finger and then their mouth to suck and extract the peanut butter from the top of the tube.
Mouth/Hand	The subject first attempts to use their mouth or tongue to extract the peanut butter, and then their finger(s).

3.3.7 Pounding experiment I methods

3.3.7.1 Subjects

The subject sample for the first pounding study consisted of (n=93; M_{age}=18.1, SD=10.2), four groups of chimpanzees housed at Chimfunshi Wildlife Orphanage (henceforth: Chimfunshi) in Zambia, Africa (See table in Appendix I for demographic information on the subjects). Apart from Groups 3 and 4, who can occasionally see each other through a small gap in the mesh of the two adjoining enclosures, none of the other groups of chimpanzees at Chimfunshi are in view of each other (see Appendix I for an aerial view of the enclosures at Chimfunshi). The apparatus was placed in an area of the enclosures of Groups 3 and 4 in which it was impossible for the other group to see the apparatus or any of the subjects interacting with it.

3.3.7.2 Study Site

Chimfunshi is located in the Copperbelt region of Northern Zambia, Africa (S12 deg 21.924 E027 deg 28.912; see Appendix I). The chimpanzees live under semi-wild conditions in fenced enclosures ranging between 20 and 80 hectares. Individuals spend most of the day and all night outdoors, and only come indoors for their daily feeds (11.30-13.00 and 14.30-16.00). Subjects have access to water *ad libitum* and are fed a daily rich and varied diet, alongside having access to fruiting tress inside their enclosures. As interaction between keepers and visitors and the chimpanzees is kept at a minimum (to preserve the natural state of the animals), no enrichment devices, toys or tasks are provided to the chimpanzees. However, the chimpanzees do occasionally participate in research studies such as the one presented here.

Following the protocol to ensure the nativity of the subjects, prior to testing, the keepers at Chimfunshi and the Chimfunshi Research Advisory Board (CRAB) were provided with the questionnaire, and all confirmed that the chimpanzees did not have any previous experience with similar tasks during past experiments or enrichment exercises.

3.3.7.3 Procedure

Due to management restrictions at Chimfunshi and so as not to interfere with the chimpanzees’ daily diet, the originally described food rewards (palm hearts) could not be used to bait the apparatus. However, similarly to the previous two studies, the focus of this study was not to identify the cognitive mechanisms behind learning which foods are edible (which may indeed be socially mediated; see also general discussion chapter). Rather, the aim of the study was to examine the crux of the behaviour: the use of sticks to pound food. Thus, the pounding apparatus was baited with boiled potatoes, in order to replicate as closely as possible (without using palm hearts) the hardness and consistency of palm hearts.

The testing apparatus (Fig. 3) was set-up near the indoor management area when the chimpanzees were not present. The testing apparatus measured 21cm x 21cm x 16cm, with the diameter of the top of the apparatus measuring approx. 1.6cm. A hard-boiled potato (boiled for approx. three minutes, weighing between 145g to 190g) was inserted into the testing apparatus before attaching it to the mesh. The potato was boiled so as to make it palatable, but was left hard enough so that it required forceful pounding with a stick to break it into smaller pieces, to recreate as closely as possible the conditions encountered by wild chimpanzees during pestle pounding bouts. The lid of the testing apparatus was sealed, apart from one small hole on the top, which was large enough to allow a stick to go through, but too small for more than one finger to be inserted into the apparatus (only the tip of the finger- to approx. under the finger nail-could be inserted into the apparatus). The testing apparatus was then attached to the mesh via a backing panel and metal wires at a rough height of one meter, in an area that was accessible to all the chimpanzees when they arrived for their daily feed. The apparatus was attached to a section of the mesh in the enclosures of Groups 3 and 4 where it was impossible for the other group to see the apparatus or interactions with it.

Fig. 3: Experimental set-up in the first pounding experiment (camera still by EB).

Testing was carried out over six weeks by EB. Each group was tested twice over the six weeks. Tests were carried out after the daily feeds (between 11.30-13.30) as the chimpanzees were most often near the indoor areas right after feeding. Tests started when an individual started manipulating the apparatus and ended after a maximum of 30 minutes.

3.3.7.4 Coding

The videos were coded for all events of interaction with the testing apparatus (see table 3 below). For all tool-use bouts, the time of start of manipulation and end were recorded, alongside what tool was used (small or large), whether the tool was shared or taken by another individual, whether the attempt was successful in retrieving the baited food or not, and if the stick tool was modified in any way before or during a manipulation bout. Tool sharing was coded when an individual allowed another one to take the stick from their hand or mouth. Furthermore, the grip of the stick (i.e., how the stick was held in the hand) was recorded (when it was clear enough from the video) and how many times the stick was pounded (an instance of pounding started as the stick entered the apparatus and ended when it was pulled out) before food was retrieved from the end was also counted. Coding was carried out after testing from video. All videos were first coded by EB and then 25% of the videos were second-coded by a naïve coder to assess interrater reliability (following the procedure described above and in Neadle et al., in prep).

Table 3: Behaviours coded in the pounding studies and their descriptions

Method	Description
Interaction	Individual approaches the testing apparatus and begins manipulating it, without a tool. This type of manipulation most often involves an individual inserting their finger into the top of the apparatus, attempting to probe inside the apparatus, or using their whole body to attempt to break or remove the apparatus from the mesh.
Stick insertion	Individual holds a stick tool in hand(s), and inserts it into the apparatus. Crucially, these events are not coded as pounding, as they do not involve the forceful pounding action observed in the wild behaviours.
Pounding	Individual inserts a stick into the apparatus and performs the forceful action of hitting it to the bottom of the apparatus, once or several times to attempt to break the food source inside the apparatus (as described by Sugiyama & Koman, 1979; Yamakoshi & Sugiyama, 1995).
Successful Attempt	Individual is successful in retrieving some of the baited food using the chosen technique.
Unsuccessful Attempt	Individual was not successful in retrieving any of the baited food using the chosen technique.
Other Apparatus Manipulation	Individual manipulates the apparatus in a way not described by any of the categories above (this manipulation does not result in any food retrieval).

3.3.8 Pounding experiment II methods

3.3.8.1 Subjects

The second pounding experiment was tested opportunistically at Chimfunshi. The sample for this study (*n*=17; $\mathrm{M}_{\mathrm{age}}$=19.7, SD=5.6) consisted of individuals in the “orphanage group” (thus called as these chimpanzees are kept in an enclosure near to the owner’s living quarters, which originally housed the first chimpanzee adopted at Chimfunshi). The individuals in the orphanage group were not included in pounding experiment I. The chimpanzees in the orphanage group (*n*=14; M_{age}=18.6, SD=4.1) were tested in their normal social group setting (more on this below). Additionally, chimpanzees that were, at the time, being kept separately from the rest of their group due to health or introduction reasons were also included in the sample. These subjects consisted of: LJ (Female, age 31; see table 1) who was being introduced into Group 4 (previously LJ was in Group 2) at the time of testing and so was temporarily housed alone in the indoor management areas of Group 4, and DN and DB (mother: DN and child: DB pair, see table 4 below; individuals in ***bold and italics*** were tested separately). DN and DB were being kept in the indoor management areas of Group 1 as DN was receiving medical treatment at the time of testing.

Table 4: Demographic information on the subjects in the second pounding study

Name	Sex	Approx.DoB	Origin	Rearing
Alice	Fem	12/31/1994	Wild	Hand-raised
Bili	Male	12/31/1995	Wild	Hand-raised
Careen	Fem	01/04/1999	Unknown	Unknown
Carle	Male	03/25/2008	Captive	Mother-Group
Cindy	Fem	12/31/1995	Wild	Hand-raised
DeeDee	Fem	06/14/2001	Captive	Hand-raised
Dominique	Male	09/17/2002	Captive	Hand-raised
Gus	Male	12/31/1997	Unknown	Unknown
Hans	Male	12/31/1996	Unknown	Unknown
Karla	Fem	12/31/1998	Captive	Unknown
Kitty	Male	11/14/2006	Captive	Mother-Group

Madona	Fem	12/31/1994	Wild	Hand-raised
Mads	Fem	04/04/1998	Captive	Unknown
Sims	Male	12/31/1997	Wild	Hand-raised
Little Judy	Fem	05/15/1991	Captive	Mother-Group
Donna	Fem	12/31/1979	Wild	Hand-raised
Debbie	Fem	11/12/2015	Captive	Mother-Group

Although CRAB and the keepers confirmed that none of the subjects at Chimfunshi had any previous experience of the target pounding action, it is important to note that the individuals in the orphanage group were in contact with humans on a daily basis during testing. These chimpanzees are highly habituated to humans, and regularly go on “bush walks” with tourists, which involve a group of three to five tourists walking with the chimpanzees around their enclosure for around an hour, each day. The chimpanzees voluntarily interact with the humans, encouraged by treats such as dog biscuits and grapes throughout the walk. Thus, although the chimpanzees in the orphanage group did not have had direct experience of the task and the target action under investigation, they did have extensive and daily experience interacting with humans. This exposure to humans may have affected their performance in the task (e.g., see Forss et al., 2016 and discussion section below). However, the chimpanzees in the orphanage group were never trained in tool-use behaviours (of the type presented here, or any other) and had never been shown how to use any kinds of tools. Thus, these chimpanzees were still considered to be naïve to the pounding target action, but their background of human exposure was kept in consideration when analysing the data (see discussion section).

3.3.8.2 Procedure

The testing apparatus (Fig. 4) consisted of a long tube, baited at the bottom with a small, soft, pear (weighing between 120g-150g). The apparatus measured 35cm x 20cm x 24cm and was attached to the mesh via the same backing and wires as the pounding apparatus in the first experiment, at roughly one meter from the ground, and could be baited by the experimenter from the outside. The entrance to the tube was slightly bigger than the apparatus used in the first pounding experiment (diameter 6cm) but still did not allow the chimpanzees to reach their whole hands or single fingers to the bottom of the tube. As the subjects who were tested independently from the rest of their groups (LJ; DN & DB) were kept inside in their indoor management areas during testing, three sticks (measuring 20cm in length, diameter: ~5mm, max. 7.5mm) were inserted into the testing rooms before the subjects were allowed in. The three sticks were spread around the enclosure by the keepers, and were placed at least one meter out of radius of the apparatus. For the orphanage group, the apparatus was attached to the mesh of the enclosure at a height of one meter from the ground so that it faced into the outside area of their enclosure (as this is the area in which the chimpanzees spent the majority of their day). To ensure that this test remained comparable to the one carried out with LJ and DN & DB, three sticks with the same measurements (20cm in length, diameter: ~5mm, max. 7.5mm) were placed throughout the outside enclosure, however the chimpanzees in the orphanage group also had access to naturally occurring sticks.

Fig. 4: Experimental set-up for the second pounding study (photograph by EB).

As in the previous experiment (pounding experiment I), testing on the second pounding experiment was carried out over six weeks by EB. Each group and individual was tested twice over the six weeks. Tests were carried out after the daily feeds (between 11.30-13.30). The testing session started when an individual began manipulating or inspecting the testing apparatus and ended after a maximum of 30 minutes.

3.3.8.3 Coding

Coding followed the same procedure as in the previous experiment, and the same behavioural categories were coded from video (see table 3 above). All videos were first coded by EB. 25% of the videos were then second-coded by a naïve coder (*P.Cowdell*), who was not familiar with the aims and hypothesis of this study, or of the previous study, to assess interrater reliability.

3.4 Results

3.4.1 Scooping results

3.4.1.2 Reliability Coding

The naïve coder coded from video all the same categories that had been lived coded. The overall Cohen's Kappa was calculated (for a total of 164 instances): there was very good agreement (Cohen, 1968) between the two coders, *k* = .870.

3.4.1.3 Experimental results

Within the first ten minutes of testing (HO: 6 minutes 23 seconds and LO: 7 minutes 9 seconds), two females, HO (female, 33 years, see table 5) in Group 1 and LO (female, 37 years) in Group 2, independently retrieved the floating food using stick tools and a scooping action (See CD with supplementary files for a video clip of individual HO scooping the bread).

Table 5: Demographic information on the reinnovators of the scooping task

ID	Sex	Age	Origin	Rearing
HO	Female	36y	Twycross Zoo	Parent
LO	Female	40y	Twycross Zoo	Hand

No other subject showed these behaviours, but note that, a) throughout the experiment, attempts to use the tools by other members of the group were actively discouraged by HO and LO, who dominated the testing apparatus. Thus, it is possible that other individuals might have used the scooping technique if they had been granted access to the apparatus. And b) because the chimpanzees could not be tested independently, data from individuals other than the first are generally un-interpretable with regard to the research question, as once one subject expresses the behaviour, other individuals can no longer be considered target-naïve. Thus, in a group setting, only the first occurrence per group counts in a LS test, as social learning can no longer be logically excluded afterwards. Given the absence of scooping demonstrations for HO and LO, as well as their established scooping-naivety at test (see above), these two individuals could not have socially learnt the behaviour, suggesting that both independently reinnovated it.

When scooping, HO and LO would insert the tool into the water, above or close to the crusts, and then gently rotate the wrist until the bread crust was wrapped around the stick. Once the bread crust was balanced on the tool, it was retracted towards the mesh. See Fig. 5 for an example of the scooping technique shown by HO. Thus, the reinnovated scooping actions in this study were very similar to the wild scooping behaviour: the wild chimpanzees, as well as the two captive chimpanzees in the current study, scooped using *a gentle swivelling action of the wrist* (as described by Humle et al., 2011, 119, for wild chimpanzees). Scooping was retested after a break of four weeks. In the second test, both HO and LO again monopolised the testing apparatus and proceeded to primarily use the scooping method (70% of cases) to retrieve the floating bread.

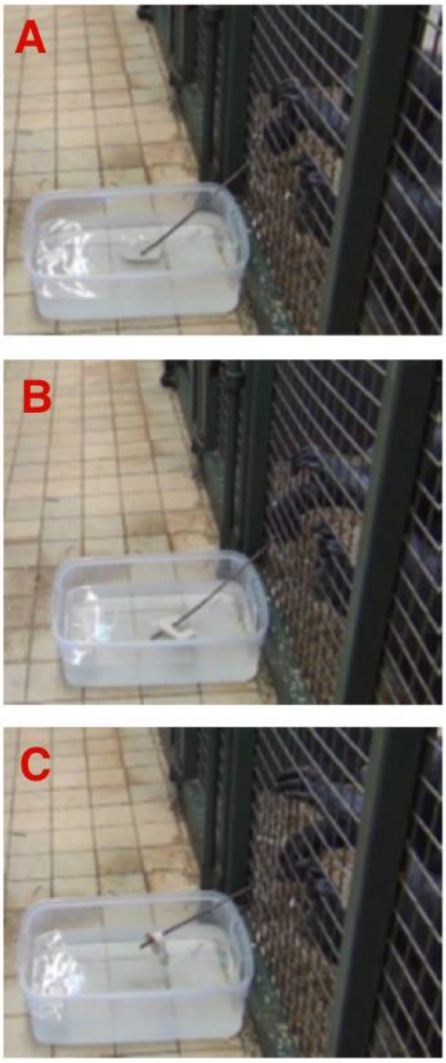

Fig.5: Scooping sequence. HO carrying out the scooping sequence. (A) HO inserts the stick under the bread, (B) using a "swivelling" motion of the wrist, HO scoops up the bread (Humle et al., 2011) and (C) HO retrieves the bread (camera stills by EB).

It may still be of some interest that, despite the focus of the study having been the scooping action, other steps of the wild algae scooping sequence were also recorded. The basic sequences of the wild and captive chimpanzees are very similar, although divergence exists between the order of some steps, with Bossou chimpanzees first modifying their sticks before inserting them into the water (most likely because they were detached directly from the tree or bush). Whilst the chimpanzees in this study were also observed to modify their sticks, they did so less frequently than their wild counterparts. Since the subjects in this study were provided with already detached sticks, they did not need to modify the length of the sticks as often as wild chimpanzees (and, as the sticks provided were already around the same length as that recorded in Bossou (Humle et al., 2011), further modification was not often necessary).

3.4.1.4 Tool Modification

However, some instances of tool modification were observed. A total of four instances of stick modification were recorded throughout the testing sessions – that is, stick modification happened in 30% of all retrieval attempts (including unsuccessful ones). All modifications occurred after the sticks were first inserted into the water. In all these instances HO and LO used their fingers or teeth to break off a small piece of the stick, perhaps to make it into a more manageable length to retrieve the bread crusts that had floated too close to the mesh (all instances of stick modification occurred when the crusts were closest to the mesh, see Fig. 6 for stills on the stick modification method).

Fig. 6: Stick modification sequence. HO modifying one of the provided sticks: (A) HO retrieves the longer stick from the apparatus, (B) HO uses her mouth to shorten the stick and (C) HO re-inserts the shortened stick into the water (camera stills by EB).

3.4.1.5 Latencies

In all three trials, both HO and LO retrieved all three pieces of bread crust (including small pieces which resulted from some disintegration of the bread crusts) within a maximum of six minutes. Mean retrieval time for each bread piece using the scooping technique in Group 1 (HO) was 4sec (SD=1sec); in Group 2 (LO): 8sec (SD=3sec; recorded from when the tool came in contact with the piece to when the individual started to feed). Mean retrieval time using the side technique in Group 1 (HO) was 20sec (SD=12sec); in Group 2 (LO): 7sec (SD=2sec).

3.4.1.6 Additional techniques

Due to slight differences in the overall physical setup between this experiment and the wild, it was expected that the captive chimpanzees would show additional new behaviours. This was indeed the case, and both HO and LO were observed to occasionally make use of the sides of the water container to retrieve the bread crusts. The basic sequence of this “side technique” was as follows: first, the stick was placed on the upper part of the bread crust, which was then pushed towards one of the sides of the bucket. Then, pressure was placed on the crust to slide it up the edge of the container and onto the rim. Once the bread was on the rim, it was pulled towards the mesh and retrieved with the fingers (see Fig. 7 for camera still of this method). All side technique attempts to retrieve the bread pieces were also coded. In both subjects, the scooping technique was more commonly used than the side technique: in HO 68.9% (20/29) of attempts were with the scooping technique and 31.1% (9/29) of the attempts were with the side technique. In LO 61.8% (55/89) of the attempts to retrieve the bread crust were carried out using the scooping technique and 38.2% (34/89) were using the side technique.

Fig. 7: LO demonstrating the side technique (camera still by EB).

3.4.1.7 Tool grip type

Individual variations in scooping technique were observed in the wild (Humle et al., 2011). Most frequently, Bossou individuals held the tool between the thumb and the index finger when scooping, but occasionally some gripped the tool between their middle and index fingers - although the exact number of times each variant occurred was not reported (Humle et al., 2011). Additionally, after scooping, some chimpanzees fed on the algae directly from the stick, whilst others, more rarely, gathered the algae off the stick with their fingers and then licked it off their hands. As in the wild, there were also individual differences between grips and feeding methods in the test subjects. To identify potential individual differences, all clear cases of finger positioning and feeding methodologies for HO and LO were coded (instances were not coded if the video was not clear enough to identify grip or feeding method). Table 6 below shows the frequencies of these variants between HO and LO.

Table 6. Number of times each action variant seen in the wild was performed by captive chimpanzees (only clearly visible instances were coded, including instances in which the stick was manipulated and no attempt was made).

Wild Behaviour (Humle et al., 2011)	HO/total	LO/total
Stick held between thumb and index finger	22/45	31/44
Stick held between middle and index finger	23/45	13/44
Direct mouth feeding	8/21	0/12
Use of fingers to feed	13/21	12/12

As can be seen in table 6, HO varied continuously between grips, and showed no preference for the middle and index grip whilst LO showed some preference for holding the stick between the thumb and index finger, similarly to Bossou chimpanzees. Furthermore, HO occasionally used the stick directly to feed, but preferred to use her fingers. LO only used her fingers to feed. Thus, overall, a comparable range of individual differences to wild chimpanzees were observed in this study.

3.4.2 Picking Results

3.4.2.1 Reliability coding

The naïve coder watched the videos and coded following the behaviour descriptions in table 2 above. A high level of agreement (Cohen, 1968) between coders, *k*=.086 was found.

3.4.2.2 Experimental results

In the first testing session at Twycross Zoo, three individuals across the two groups successfully retrieved the peanut butter from inside the tubes using the sticks provided. In Group 1, only one tube was placed inside the enclosure (under advisement from the testing institution, see methods section), only allowing one individual to participate in the test at a time. In this group, PT (male, 23 years old; see table 7) successfully retrieved the peanut butter from the tube using one of the sticks provided, thus showing the equivalent behaviour of wild marrow picking. PT was born and parent-reared in captivity at the testing institution. In Group 2, two individuals, KB (male, 13 years old) and VC (female, 26 years old) independently retrieved the peanut butter using the sticks provided. However, as it was not possible to control for the movements of all the individuals in the group, it cannot be discounted that the second individual, VC, solved the task after seeing the first one, KB, use the stick. Therefore, social learning cannot be ruled out from playing a role in the emergence of the behaviour in VC, and thus data from this individual is discounted. The first individual (KB) in Group 2 to spontaneously solve the task was also parent-reared in captivity. Both PT and KB independently used the same technique as their wild counterparts to retrieve peanut butter from inside the plastic tube, replicating the same behaviour as picking in the wild (see Fig. 8 for camera still of PT picking). The subjects were re-tested after a break of four weeks. The exact same procedure as the initial test was followed. In Group 1, the same individual (PT) successfully used the sticks provided to retrieve the peanut butter within the initial 10 minute testing period. PT was also recorded using other objects as tools, such as the stem of a spring onion to fish out the peanut butter. In Group 2, three individuals successfully used the sticks, including the original inventor, KB. The other two subjects, LO (female, 38 years old) and TL (female, 9 years old) had not interacted with the task in the first testing session. Again, it is impossible to rule out that these individuals observed KB use the sticks in the previous testing session, so it cannot be confidently stated that they were completely naïve to the task before expressing it. However, the second testing session found four individuals successfully manifesting the target picking action using the same technique as their wild counterparts.

Fig. 8: PT showing the picking technique (camera still by EB).

3.4.2.3 Bioparco di Roma Results

Two individuals (BG; male, 21 years old & SY; female, 21 years old; see Appendix II) spontaneously reinnovated the target picking behaviour at il Bioparco di Roma. Neither BG nor SY retrieved the sticks placed in the enclosure. However, as these individuals were tested in their outdoor enclosure (conversely to the Twycross Zoo subjects who were tested in their indoor enclosures), subjects at BP had access to naturally occurring sticks. Once the chimpanzees were allowed into their enclosure, BG and SY both took the tubes. BG took two of the tubes, and SY took the remaining one. BG initially attempted to break the tubes, but after 12 minutes of attempting to access the peanut butter without success, BG broke a twig of a nearby tree and used it to retrieve the peanut butter using the target picking method. The stick was then discarded and another one taken from the tree. BG repeated this action until the peanut butter in both tubes was finished.

After retrieving the tube, SY returned into the indoor enclosure. SY did not take any of the sticks with her into the management area, and as there were no sticks inside, she used a piece of bedding to retrieve the peanut butter from inside the tube, and continued to use the bedding for the whole 30 minute testing period. Neither BG nor

SY could see each other during testing, thus both naïve chimpanzees individually reinnovated the same picking behaviour. The experiment was re-tested following the same procedure after a period of a week. Again, BG and SY retrieved the tubes first, with BG taking two again and SY the remaining one (see video clip in supplementary CD of SY picking). Once again, neither individual took the sticks provided. Both individuals remained in the outside enclosure, but on separate platforms in the trees. BG used the twigs that he detached directly from the tree, whilst SY used a stick she found on the platform. Both individuals started using tools within 12 minutes of testing.

Thus, at least four naïve chimpanzees spontaneously reinnovated the target picking behaviour across two testing institutions, showing a comparable behaviour to the one observed in wild chimpanzees. The most prevalent method of accessing the peanut butter from the tube for all individuals was picking, however other methods were also attempted. The picking behaviour occurred in 76% (10/13) of attempts (see table 8).

Table 7: Demographic information on the picking reinnovators

ID	Sex	Age	Origin	Rearing
PT	Male	25	Twycross Zoo, UK	Parent
KB	Male	14	Bremerhaven Zoo, Germany	Parent
BG	Male	21	Bioparco di Roma, Italy	Unknown
SY	Female	21	Bioparco di Roma, Italy	Unknown

3.4.2.4 Latencies

As can be seen from table 8, chimpanzees from the UK and Italian zoos combined spent 46% of total testing time picking. In the Twycross Zoo sample, individuals PT and KB both expressed picking within three minutes, during the first trial, and in the Bioparco group, BG expressed picking within 12 minutes and 8 seconds during the first trial and SY reinnovated picking with 13 minutes and 4 seconds in the first trial.

Table 8. Mean time spent by subjects practicing each method of accessing peanut butter (SD in parenthesis)

Method	Time spent
Picking	01:42 (01:31)
Picking (other)	00:41
Hand	04:00
Mouth	00:52 (00:33)
Hand/Mouth	01:18 (00:45)
Mouth/Hand	02:25

3.4.2.5 Additional techniques

Picking with a tool occurred *after* attempting other methods first, these included: biting the tube and sucking the end of the tube and using fingers to attempt to access the peanut butter. These methods continued to occur even after picking with a tool was reinnovated. Indeed, after the first time picking was observed, subjects would often bite open the tubes with their teeth (perhaps to shorten them) and then continue to use sticks to retrieve the peanut butter from the (now) two pieces of tube. This behaviour could be considered analogous to another stage in the marrow picking process (Boesch & Boesch, 1989); in which wild chimpanzees were reported to crack open long bones with their teeth in order to use a stick to access marrow. Furthermore, one individual (PT) was observed using the stem of a spring onion for a previous scatter feed as a picking tool to retrieve the peanut butter (this was coded as picking: other; see table 2).

3.4.2.6 Tool grip type

When picking with a tool, the preferred finger grip of the stick was coded. Four main grips were observed. The stick was either held between the *middle and index fingers*, *the thumb and index*, with the *palm* or between *the thumb, middle, and index finger*. The most commonly observed grip type in chimpanzees was between the *middle and index finger*: observed in 47% (6/13) of cases. Unfortunately no data exists on the grip-types of wild chimpanzees when marrow picking, so the data collected in this study cannot be compared to wild chimpanzees.

3.4.3 Pounding Experiment I Results

3.4.3.1 Reliability Coding

The naïve coder watched 20% of the videos and coded all the same behaviours described in table 2 above. The reliability coder also coded whether a stick (as seen from the video) could be considered "large" or "small" (see below). Cohen's kappa was calculated, and there was substantial (Cohen, 1968) agreement between coders; k=0.78.

3.4.3.2 Experimental Results

One individual per group in three out of four of the groups (one individual in Groups 1, 2 and 4) tested with the pestle pounding apparatus used sticks and the target pounding action spontaneously. The only group that did not reinnovate pestle pounding was Group 3. As the groups included in this study are very large, only the first reinnovator in Group 4 (which is smaller than the other groups) could be confidently recognised (JK, male, 10 years old. See Fig. 9 and provided CD for a video clip of JK pounding), thus only the demographic for this individual is included in the table below. The observed pounding behaviour in the three groups consisted of individuals first retrieving a stick from their surroundings and carrying it over to the apparatus. The stick was then modified (if necessary) and inserted into the apparatus. The tool was then forcefully pounded into the apparatus one or more times, closely following the pounding behaviour observed in wild chimpanzees. The stick was then pulled out of the apparatus and the distal end of the stick sniffed and/or inserted directly into the mouth. This process was repeated several times. The pounding action observed in this study is similar to the one practiced by wild chimpanzees (see above; Sugiyama & Koman, 1979; Yamakoshi & Sugiyama, 1995).

Table 9: Demographic information of the pounding (exp. I) reinnovator (only one individual could be identified with confidence)

ID	Sex	Age	Origin	Rearing
JK	Male	10	Captive born	Parent

Fig. 9: JK showing the target pounding behaviour in the first pounding experiment (camera still by EB).

3.4.3.3 Pounding tools

The original sticks that were used as pounding tools by the chimpanzees in this study could not always be retrieved as the chimpanzees often carried the tools away with them into the forested area of their enclosures (which cannot be accessed due to health and safety regulations). However, a small sample of sticks was retrieved from group four. These sticks measured between 60-90cm long (M=76.9; SD=9.37) and .5-1.5cm wide (M=1.02; SD=0.499). The width of the sticks varied considerably between individuals. Although it was not possible to record the exact dimensions of the sticks, whilst coding from video, sticks could be classified as either “small” or “large” (see supplementary CD for a video clip showing the large and small sticks: large stick being used to pound into the apparatus by SK; small stick being held by JK near SK and the apparatus). 55% (11/21) of pounding events were carried out with a “large” stick, which may have made the forceful action more efficient, due to the larger diameter of the stick tools. Although potential differences in efficiency between the two types of sticks were not controlled for (as often an individual would start with a small stick, and then switch to a larger one, making it impossible to examine any differences in the amount of bait retrieved using different types of stick), in total, individuals spent (numerically) more time pounding with large sticks than small sticks (individuals spent on average 3:33 minutes (SD=1.23) more using a large stick than a small stick). However, the difference between time spent pounding with a large and a small stick was not statistically significant (Wilcoxon signed rank test; Z= -1.362, p=0.173). Mean number of times the stick was pounded was recorded for each pounding bout. Across all groups, individuals pounded on average 4.0 times (SD=1.3) per tool-use bout (Yamakoshi & Sugiyama, 1995, report an average of 10 pounding times per bout in the wild chimpanzees).

3.4.3.4 Interaction with the testing apparatus

Total interaction time with the apparatus (including both manipulation with and without tools) was measured per each group. Subjects in Group 1 spent 14:19minutes interacting with the testing apparatus; Group 2: 17:13minutes; Group 3: 18:03minutes; Group 4: 27:34minutes. In total, all four groups spent 1:17:27 manipulating the testing apparatus. A Kruskal-Wallis H test demonstrated no significant difference between the total interaction time of each group, $\chi^2(2)=2.424$, p=0.524, with a mean rank score of 37.21 for Group 1, 33.75 for Group 2, 29.44 for Group 3 and 40.32 for Group four.

Out of all interactions with the testing apparatus, 26% (19/74) of manipulations were pounding bouts. Individually, pounding made up 33% (5/15) of Group one’s interactions, 27% (6/22) of Group two’s and 28% (8/28) of Group four’s interactions (no pounding behaviour was recorded for Group 3). No observations of stick insertion were recorded in these groups. Out of the total testing sessions, time spent pounding was 4:06minutes for Group 1, 4:12minutes for Group 2 and 8:41minutes for Group 4 (totalling 16.59minutes for all three groups). Average time spent pounding was 1:05minutes (SD= 0.34).

3.4.3.5 Latencies

The latency in each of the groups was recorded: Group 1: 6:17min; Group 2: 4:42minutes; Group 4: 6:05minutes. The total mean time until tool-use was 5:54minutes (SD=0.97) across all three groups.

3.4.3.6 Tool grip type

Grip type was recorded every time an individual used a tool. However, not all videos allowed for a clear enough view to determine the grip-type of each individual, thus, only clear videos were coded (14% (3/21) of cases were excluded due to the view of the grip being blocked). Across all groups, two different grips were recorded: *holding the stick between the thumb and index* and *holding the stick in the palm, with all five fingers wrapped around the stick*. Of these two grip-types, palm grip was recorded in 67% (14/21) of cases, whilst holding the stick between the index and thumb was recorded in 19% (3/21) of cases. Subjects always held the stick in one hand (contrary to the wild, where chimpanzees have occasionally been observed holding the sticks with two hands; Yamakoshi & Sugiyama, 1995).

3.4.3.7 Tool sharing

Bouts of tool sharing were also recorded across all four groups. Tool sharing was observed relatively rarely, and only in Groups 1 and 4. In Group 1, tool-sharing events occurred in 41% (8/19) of pounding bouts, and in Group 4, tool-sharing occurred in 36% (7/19) of bouts. Tool sharing was never recorded in Group 2.

3.4.3.8 Tool modification

Modifications of the tools were rare, and only observed in Group 4. In only 15.8% (3/19) of pounding bouts was a modification of the tool recorded. Modification occurred, for example, when a chimpanzee (JK) brought the first tool to the apparatus, which was a frond made op of several smaller sticks (see also large/small stick clip in supplementary CD). JK then proceeded to remove the other fronds with his teeth, and used the middle (and largest) one to insert into the apparatus.

3.4.3.9 Food retrieval

The weight of the baited potato before and after testing was recorded, to examine how much was retrieved during pounding events. The potatoes weighed between, on average, 171g (SD= 17.26) prior to testing, and 144g (SD=9.45) after testing. On average 83% of the baited potato was retrieved during testing sessions.

3.4.4 Pounding Experiment II Results

3.4.4.1 Reliability coding

The naïve coder watched 25% of videos from the second pounding experiment and coded the same behavioural categories as in table 3. Again, there was a significant (Cohen, 1968) agreement between coders; k=0.74.

3.4.4.2 Experimental results

Data collected in the second pounding experiment were less clear than in the first experiment. Only one individual (LJ; female, 31 years, see the provided CD for a video clip of LJ pounding, and Fig. 10 below) out of the three tested groups reinnovated the second target pounding behaviour. One other individual (in the orphanage group) inserted a stick into the testing apparatus, but did not use the pounding action required to break and retrieve the pear. Therefore, this event was coded as "stick insertion" rather than "pounding" (see table 3 above). The individuals in the third group (DN & DB) did not interact with the apparatus in any of the testing sessions, potentially due to the fact that DN was receiving treatment for an illness at the time of testing, and might not have been motivated to interact with the apparatus (see more in discussion).

Table 10: Demographic information on the pounding (exp.II) reinnovator

ID	Sex	Age	Location of birth	Rearing
LJ	Female	23	Captive born-unknown	Parent

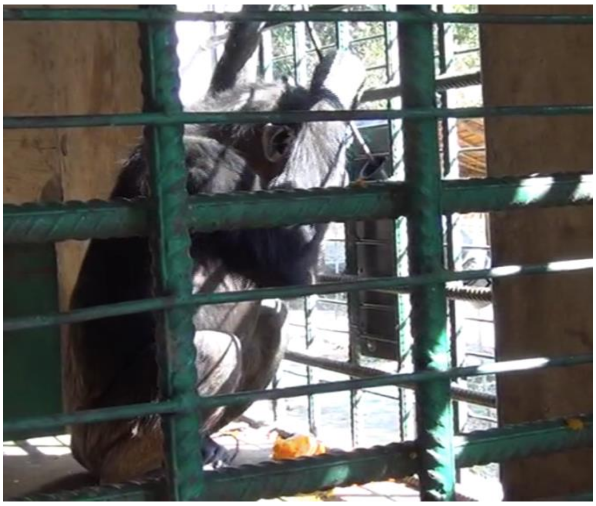

Fig. 10: LJ practicing the target pounding behaviour in the second pounding experiment (photograph by EB).

3.4.4.3 Pounding tool

The stick used by LJ to retrieve the pear measured 30cm x 4cm. Only one stick was used for both bouts of pounding. LJ’s total interaction time with the testing apparatus was 1:81min, and the latency until the first bout of pounding was recorded 46 seconds after testing started (the fastest reinnovation of the pounding behaviour recorded across both studies). Time spent pounding was 1:09min and 12% (2/17) of interaction bouts involved the target pounding action. LJ pounded on average 6 times (SD=1.2).

3.4.4.4 Interaction with the testing apparatus

Total interaction time for the orphanage group was 7:24minutes (no interaction was recorded for DW & DB). Total interaction time for all three groups was 9:05minutes.

3.4.4.5 Tool grip type

LJ held always held the stick in her palm (with all her fingers wrapped around it), before retrieving the stick and eating the pieces of pear attached to the distal end (no information exists on the grip-types used by wild chimpanzees).

3.4.4.6 Food retrieval

The pear was weighed before and after testing. Prior to testing, the pear weighed on average 126g (SD=7.07) and weighed 118g (SD=11.31) after testing, so 93% of the pear was retrieved during LJ’s pounding bouts.

3.4.4.7 Additional behaviours

In comparison to the first pounding test, relatively low levels of interaction with the testing apparatus were recorded throughout all three groups in this study. Across all three groups, total interaction with the testing apparatus was 15:05minutes, and DN & DB only sniffed the apparatus at the start of testing, and then retreated to the other side of the enclosure and did not interact with the apparatus during any subsequent tests. However, other behaviours directed to the testing apparatus were observed by the individuals from the orphanage group: For example, an instance of stick insertion was observed in this group, in which one individual (CD; female, 22 years old) inserted a small stick into the apparatus, but did not pound the bottom or to retrieve the food. This stick insertion bout lasted 28 seconds, and was only observed by CD (in 1/11 interactions).

Other manipulations of the apparatus consisted of individuals in the orphanage group inserting their fingers into the apparatus and pulling on the lip (which occurred in 45% (5/11) of interactions with the apparatus) and of the subjects attempting to go around the mesh to pull on the apparatus from the other side (in 36% (4/11) of interactions). Neither manipulation was successful for retrieving the food.

3.5 Discussion

3.5.1 General Discussion

The studies presented in this chapter provide empirical evidence for the view that some tool-use behavioural forms are within chimpanzees' ZLS (Tennie et al., 2009). The ZLS approach has, so far, been described primarily in a theoretical perspective for chimpanzee tool-use behaviours (previous explicit LS type studies with animals focused on non-tool-use behaviours; Tennie et al., 2008; Allritz et al., 2013; Menzel et al., 2013; Neadle et al., 2017; although see Reindl et al., 2016 for a LS study on tool-use in humans and see also individual learning table in chapter II). The four studies discussed in this chapter are the first ones to explicitly test which aspects of their material culture chimpanzees are capable of individually learning in the absence of social information. At least three behavioural forms were found to be within chimpanzees' ZLS. Although these studies focused on a small number of chimpanzee tool-use behaviours, the data presented here suggests that similar (e.g., stick) tool-use behaviours observed in wild chimpanzees may also be within the species' ZLS (although this remains to be tested).

The studies presented in this chapter do not, however, provide support for the alternative social learning hypothesis. As the target behavioural forms tested here reappeared in the absence of social information, at least for three of these behaviours, it can be logically concluded that social learning is not absolutely necessary for the behavioural form to be reinnovated (except for the second pounding experiment, for which at least one more reinnovation is required to meet the double-case ZLS standard and therefore confidently be included in the ZLS of chimpanzees). Given the findings presented in this chapter, a latent solution account is not only probable for the captive chimpanzee(s) in these studies who reinnovated the target behavioural forms in their particular groups, but also for the chimpanzees in the wild who "join in" on behaviours after they have been innovated via low-fidelity social learning mechanisms. The type of social learning used is most likely one that utilises each chimpanzee's ability to reinnovate the behaviour – but does not transmit the behavioural form itself (i.e., the social learning is not of a high-fidelity type). Thus, the results presented in this chapter strongly suggest that each individual chimpanzee is capable of reinnovating the behaviour independently, and that for those surrounded by others who have already expressed the behaviour, low-fidelity social learning mechanisms facilitate their own acquisition of the behaviour - increasing (and harmonising) the frequency of individuals reinnovating the behaviour in the wild population (via Socially Mediated Serial Reinnovations or SMSR; Bandini & Tennie, 2017 and see also general introduction). As each study generated slightly different discussion points, the following sections will discuss each study in more detail, before a general conclusion.

3.5.1.2 Scooping discussion

The same scooping behavioural form as observed in wild chimpanzees (Humle et al., 2011) re-appeared independently in two naïve chimpanzees. Thus, unlike human cumulative cultural behaviour, the observed patterns of scooping behaviour in the wild can be explained via SMSR, rather than requiring high-fidelity social learning mechanisms. As the scooping behaviour was independently reinnovated by two naïve chimpanzees, this fulfils the most conservative requirement for a latent solution (the double-case ZLS standard), and strongly suggests that chimpanzees elsewhere also have the potential to produce this behaviour individually (though they may of course still be socially influenced in, for example, where to feed and what to feed on when using this technique). Indeed, scooping in the wild has also been reported outside the potential "cultural reach" of Bossou (Humle et al., 2011), namely in Odzala National Park, Congo (around 3,000km apart; Devos et al., 2001). Why then, do we not see more populations engaged in algae (or other food) scooping? Perhaps this is due to local trade-offs between the necessity and the opportunity hypothesises (e.g., Fox et al., 1999; and see chapter II), a possible explanation for the fact that most wild innovations never "*catch on*" (Nishida et al., 2009) i.e., never lead to SMSRs.

3.5.1.2.1 Target scooping action

This study focused on the scooping action, the target behavioural form for which the role of social versus individual learning in its emergence was examined. Both wild (Humle et al., 2011) and naïve chimpanzees (in this study) show this behavioural form (in particular, they rotate their wrist to wrap the food around the tool, before retracting it towards them). This study suggests that this technique is rather easily reinnovated by individual chimpanzees, given a) the speed with which they expressed the technique, b) that two subjects did so and c) that none of the successful test subjects had an opportunity to observe this behaviour previously or during testing. Thus, this data renders it parsimonious to assume that the scooping technique in the wild also arises on an individual level – as a latent solution.

3.5.1.2.2 Individual differences

Individual differences in single actions during scooping behaviour observed in Bossou chimpanzees have been suggested as evidence for social learning: "*Individual variations in the different algae-feeding techniques described here also should be further explored. The patterns of intracommunity patterns of algae-feeding techniques may correlate with observational learning [...] and thus purport a social learning mechanism in their transmission*" (Humle et al., 2011, 120). However, comparable differences in action-level techniques were also found between the captive subjects in this study – despite the fact that these subjects could not have observed the Bossou chimpanzees. The existence of the small individual differences shown by naïve chimpanzees in this study suggests that these differences are also a product of individual, rather than social, learning. In general, a more convincing argument for social learning in the wild would have been similarity of details of tool behaviour within a community but systematic differences between groups (including this study), unrelated to ecological and/or genetic differences. Currently the evidence for such variations in wild chimpanzees is limited (Langergraber et al., 2010), and even when such differences are observed (Luncz & Boesch, 2014), they do not reflect differences on the level of behavioural form. The observed differences can instead be explained through low-fidelity social learning mechanisms such as stimulus enhancement (for example in explaining the use of wood hammers versus stone hammers when nut-cracking, as in Luncz & Boesch, 2014).

In conclusion, this study provided evidence that chimpanzee scooping, a tool-use behaviour, is a latent solution (just like other (non-tool-use) great ape behaviours that have been tested following the LS methodology (Tennie et al., 2008; Allritz et al., 2013; Menzel et al., 2013; Reindl et al., 2016; Neadle et al., 2017 and the studies presented in this chapter).

3.5.1.3 Picking Discussion

Similarly to the results of the previous study, the behavioural form of picking was observed in naïve, captive chimpanzees, without requiring social learning. Four individuals across two different testing institutions developed the same picking technique to retrieve peanut butter from plastic tubes, strongly suggesting that picking is a behaviour within the species' ZLS. Picking is rare in the wild, and the behaviour has not been described in detail yet, making comparisons between the steps seen in this study and the wild harder. However, the naïve chimpanzees in this study showed a comparable behaviour to their wild counterparts first by identifying the need for a tool (after failed initial attempts at sucking the food out of the tube) and then by using a stick tool to pick the food out of the tubes. These actions represent the crux of the wild picking behaviour (Boesch & Boesch, 1990).

3.5.1.3.1 Additional techniques

The subjects in this study also attempted to use other methods to access the peanut butter, such as tipping the tube into the mouth and using the tongue to retrieve the peanut butter, or using the tip of the finger to access any peanut butter left at the top of the tube. However, in the majority (76% or 10/13) of cases, the picking technique was used, suggesting that this was the most salient and efficient technique to retrieve the peanut butter. Interestingly, not all cases of picking were carried out with the sticks provided. In one case at Twycross zoo, PT used the stem of a spring onion to pick out the peanut butter, and at BP, none of the subjects used the tools that were provided, instead preferring to source their own tools, either using a twig picked from a tree, or using the (less efficient) bedding from the indoor enclosure. Furthermore, subjects varied in their grip of the tool, with most individuals holding the stick in their middle and index fingers, palm, followed by holding the stick in the palm (see results section above). The small differences in selection of tool and tool grip support the view that this behaviour is driven mainly via individual learning, as individual preferences would not be reinforced if the behaviour was being socially-copied (as discussed above).

3.5.1.3.2 Limitations of the study

Following the standard protocol (see methods section), questionnaires and independent interviews were carried out with the ape keepers before testing at both Twycross Zoo and BP. All the keepers confirmed that the chimpanzees in their care had never been exposed or participated in tasks similar to the picking test in this study, thus making them naïve to the target picking behavioural form. However, after the data was collected at Twycross Zoo, another researcher (*D. Neadle*, who was carrying out further testing on picking in the other great ape species; Bandini et al., in prep) was informed by one of the keepers that all the great apes at Twycross Zoo had been given tubes with food inside as a form of enrichment in the past (the keeper could not remember exactly when). The tubes were larger than the ones used for the picking experiment, however some of the great apes (the keeper could not recall exactly which species) used sticks to extract the food from inside. This report was not provided by any of the keepers (including the one who then remembered this incident and reported it to *D. Neadle*) during the initial questionnaire and interview stage, and none of the other keepers at Twycross Zoo remember giving the great apes these tubes. As this enrichment device is highly relevant for our study, yet none of the other keepers remembered giving it to the chimpanzees and it was not included in any of the questionnaire responses or the interviews, it is possible that the keeper who reported this to *D.Neadle* may have been mistaken, or may have been remembering enrichment provided to great apes at another zoo. However, even after investigation, we could not confidently assess whether the tubes had or had not been given to the chimpanzees in the past. Furthermore, similar tubes are often provided to captive great apes both as enrichment devices and as testing apparatuses for handedness studies, so it is not unquestionable that the chimpanzees at Twycross Zoo were given similar tubes filled with food beforehand. As it is essential for LS tests that subjects are completely naïve to the target action and the tasks, and currently it is impossible to confirm or dismiss the keeper's report, it must be acknowledged that there is a possibility that the first two chimpanzees who reinnovated the picking behaviour at Twycross Zoo (PT & KB) were not naïve to the task beforehand. If this was the case, and these chimpanzees had experience with tubes beforehand, then the data from Twycross Zoo would be uninterpretable for the purposes of this study. Therefore, PT and KB would have to be excluded from the dataset. Fortunately however, even after excluding PT and KB from the dataset, the data collected from BP is sufficient to draw conclusions on a species-wide level, as two chimpanzees (SY and BG) at BP individually reinnovated picking, still fulfilling the double-case ZLS standard. Thus, the conclusions drawn from this study can still be considered valid, even if the chimpanzees from Twycross Zoo must be excluded at a later date.

This experience highlights the importance of providing both questionnaires to the keepers and following up with individual interviews in order to establish the subjects' background before starting testing. However, it also demonstrates that even when following an established protocol, human error (i.e., the other keepers potentially forgetting about giving great apes the tubes as enrichment) can always occur. Although a frustrating experience, this was an opportunity to learn to be even more cautious when depending on important information from third parties (although asking keepers seems to be the only method currently feasible to assess the past experiences of subjects, perhaps more reliable methods will be developed in the future).

Thus, at least two (if not four) naïve chimpanzees reinnovated the same behavioural form of picking that is observed in wild chimpanzees, demonstrating that social learning is not *required* for the emergence of this behaviour in wild chimpanzees either, and adding another behaviour to chimpanzees' ZLS.

3.5.1.4 Pounding experiments I &II discussion

Similarly to the results of the previous two studies, naïve chimpanzees reinnovated the target pounding action in these two experiments without requiring social learning. Four individuals spontaneously reinnovated the pounding behaviour (one individual in group 1, 2 and 4 in the first experiment and LJ in the second experiment). In all groups that showed the behaviour, the naïve chimpanzees used sticks and a pounding action to retrieve the bait in the testing apparatus. These findings surpass the double-case ZLS standard and therefore suggest that stick pounding is a behaviour that can reinnovated via individual learning. This study adds to the growing body of evidence of the extensive individual learning abilities of chimpanzees. However, although four individuals reinnovated the pounding action (and indeed more subjects were observed expressing stick pounding, but only the first reinnovations were recorded in this study as the subjects were tested in their groups), and despite no significant difference in interaction time with the apparatus, no individuals in Group 3 in the first experiment, or in the orphanage group and DB & DN in the second experiment, reinnovated the target stick pounding behaviour. Some possible explanations for the lack of reinnovations observed in these groups and individuals are explored below.

3.5.1.4.1 Social tolerance

One possible explanation for the lack of reinnovation by individuals in Group 3 in the first pounding experiment is that this group has been found to be less socially tolerant than the other three groups at Chimfunshi. Social tolerance has been suggested to foster tool-use behaviours in both human and non-human animals (Cultural Intelligence hypothesis; Whiten & van Schaik, 2007; Hermann et al., 2007; van Schaik & Burkart, 2011; Forss et al., 2016; Ashton et al., 2018). Models have demonstrated that “high intelligence” (often equated with innovation) may be linked to social tolerance, with the most innovative groups also having the highest levels of social tolerance (van Schaik & Pradhan, 2003). This may also be due to the fact that more highly tolerant groups allow for more individual exploration without interruptions, in turn fostering innovations and reinnovations (van Schaik & Pradhan, 2003). Cronin et al., (2014) measured the levels of social tolerance in Groups 1-4 at Chimfunshi by examining both the naturally occurring social dynamics and experimentally testing their resource-sharing strategies. Whilst Groups 1, 2 and 4 had similar levels of social tolerance, Group 3 demonstrated the least socially cohesive structure and a general tendency to be less tolerant and more avoidant of the other group members (Cronin et al., 2014). Observational data collected (by EB) whilst testing Group 3 is consistent with Cronin et al.s' (2014) experimental findings. Furthermore, in a study on functional flexibility with Groups 3 and 4 at Chimfunshi, Harrison & Whiten (in prep) found distinct differences between the two groups, with Group 4 performing significantly better than Group 3 at a novel dipping task (*R.Harrison, pers.comm*). The authors suggest that the relatively poor performance of Group 3 in the dipping task, and their inflexibility when switching to more efficient techniques may be linked to their low levels of social tolerance. Similarly to Harrison & Whiten's (in prep) findings, it is possible that the individuals in Group 3 did not reinnovate the pounding behaviour examined in this study due to their relatively low levels of social tolerance. This interpretation is consistent with previous studies on the role of social tolerance in performance in novel behaviour acquisition tasks (van Schaik et al., 1999; Lonsdorf et al., 2008; Damerius et al., 2015; Forss et al., 2016; Harrison & Whiten, in prep).

Unfortunately, however, no data exists on the levels of social tolerance of the orphanage group. Yet, if it were found that this group also had low levels of social tolerance, this would lend further support to the cultural intelligence hypothesis (Whiten & van Schaik, 2007; Hermann et al., 2007; van Schaik & Burkart, 2011; Forss et al., 2016; Ashton et al., 2018). Whilst the different levels of social tolerance provide a potential explanation for the lack of reinnovation observed in Group 3, experimental applications of the cultural intelligence hypothesis are still relatively rare and controversial. Furthermore, currently, low levels of social tolerance cannot explain the lack of reinnovation by DB & DB and the orphanage group. Thus, other interpretations for the lack of reinnovations in studies I and II are explored below.

3.5.1.4.2 Motivation levels

Whilst the ZLS approach predicts that all individuals are technically *capable* of reinnovating the behaviours within their ZLS, this does not suggest that all individuals must always reinnovate the behaviour, even when they are in the appropriate ecological circumstances (Tennie et al., 2009; Bandini & Tennie, 2018). Other factors, such as genetics, developmental stage, levels of motivation, pre-existing techniques and even personality may play a role in whether some behaviours are reinnovated or not (see also Bandini & Tennie, 2018 and the following chapter). Indeed, these external factors may hinder the emergence of behaviours even when opportunities for social learning are provided. For example, several studies on the reinnovation of behaviours in both captive and wild populations across species reported that even after extensive exposure to knowledgeable demonstrators, the rest of the group does not always reliably acquire the target behaviour[7]. Thus, the lack of reinnovation of stick pounding observed in some of the subjects in the current study does not necessarily mean that these individuals are incapable of expressing the behaviour, but rather that they may have simply been limited by some of the external factors mentioned above. For example, it is possible that DN & DB’s and the orphanage groups’ lack of reinnovation may have been due to low levels of motivation to manipulate and explore the apparatus. This possibility is most notable for DN & DB, who did not interact with the testing apparatus at all during testing (see results). At the time of testing, DN & DB were being kept separately from the rest of their social group due to DN’s illness, and DN was still in recovery. Therefore, it is possible that DN was simply not interested in the test or the apparatus due to her poor health (and consequently, as DB is still a juvenile, her mother’s behaviour may have discouraged her from manipulating the apparatus as well). Furthermore, the stress of being kept separately from their social group (which is an uncommon occurrence at Chimfunshi; *T.Calvi*, *pers.comm*) may have also contributed to their perceived lack of interest in the apparatus.

The lack of reinnovation by the orphanage chimpanzees is, however, particularly surprising, given the extensive experience and interaction with humans that this group has on a daily basis. As described above, the chimpanzees in the orphanage group often participate in “bush walks” with both their (human) keepers and tourists. Therefore, these chimpanzees could be considered to possess a higher level of enculturation compared to all the other groups at Chimfunshi (enculturation has been suggested to improve the performance of apes on cognitive tasks; see general

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[7] For example, Menzel et al., (1970); Beck (1978); Anderson, (1985); Sumita et al., (1985); Antinucci & Visalberghi, (1986); Visalberghi, (1987); Visalberghi & Trinca, (1989); Tokida et al., (1994); Zuberbühler et al., (1996); Nakamichi, (1999); Tebbich et al., (2001); Hayashi et al., (2005); Taylor et al., (2007); Bartolini et al., (2007); Yamamoto et al., (2008); Marshall-Pescini & Whiten, (2008); Geissmann, (2009); Hirata et al., (2009); Smith et al., (2011); Overington et al., (2011); Biro et al., (2013) and the studies presented in chapters IV & V.

introduction and Tomasello, 1999; Damerius et al., 2015). In a study on the effect of exposure to humans on captive orangutans, Damerius et al., (2015; 2017) found that increased levels of human orientation (measured using the human orientation index, HOI) led to a cascade of after-effects, including reduced neophobia and increased exploratory behaviours, which ultimately led to higher performance in experimental problem-solving tasks. As the orphanage group experiences a much more frequent exposure to both familiar and unfamiliar humans, it could be expected that this group would be successful in reinnovating the target pounding action. Yet, despite their increased levels of exposure to humans compared to the other groups, only one behaviour similar to stick pounding was observed, in which an individual inserted a stick into the apparatus, but did not follow-up with the target pounding action. This action only lasted 28 seconds and the individual was not successful in retrieving any of the food at the bottom of the apparatus. No other tool-use behaviours were observed (see results section above). There was a numerical difference in the total overall interaction time with the testing apparatus between the groups in the first and second pounding studies. However, as the testing apparatuses and the group compositions differed between the studies, a meaningful statistical analysis of this difference could not be carried out. Yet, the numerical differences in time spent interacting the apparatus may have influenced the reinnovation rates observed across the groups. Whilst DN might not have been motivated to interact with the apparatus due to her illness, the individuals in the orphanage might not have been as motivated as the other groups (and LJ) because their frequent contact with humans results in a much higher number of “treats” being given to these chimpanzees than in the other groups, therefore reducing their motivation to reinnovate a (potentially) relatively costly behaviour for a reward (the pear) that is not particularly appealing or unusual for them. Furthermore, alongside the differences in levels of social tolerance and motivation, other external factors not yet identified may have also played a role in limiting the interactions of the testing apparatus and subsequent reinnovation of the stick pounding behaviour (see also Bandini & Tennie, 2018 and the following chapter).

Crucially, however, four individuals (three in the first pounding study, and one in the second pounding study) across the two studies did reinnovate the target pounding behavioural form without prior experience or social information. Thus, it is likely that this behaviour is within the species ZLS. However, as the two pounding behavioural forms are classified as separate behaviours in the wild (see introduction), the results of the pounding experiments presented in this chapter only allow for a confident claim for the first experiment (replicating pestle pounding) being within the species' ZLS (as the double-case ZLS standard was met). On the other hand, only one individual reinnovated the target pounding action in the second experiment. Therefore, whilst it is very likely that the second type of pounding is within the species' ZLS as well (as it consists of the same target action), further testing is required before this claim can be made.

3.6 General Conclusion

In its current, strong formulation, the ZLS hypothesis makes a clear prediction: *every* wild-type non-human great ape behaviour should reappear in at least some subjects of the same species who are naïve to the behaviour in question when tested in Latent Solution test settings (Tennie et al. 2009; Henrich & Tennie, 2017). If this is the case, then human and chimpanzee cultures are ultimately founded on different underlying mechanisms. Over time, this dissimilarity leads to very different downstream effects: a restriction to behaviours drawn from the individually-bounded ZLS in chimpanzees versus the open-endedness of cumulative culture in humans (Tennie et al., 2009; although note that despite possessing extensive social learning abilities, human children seem to be surprisingly poor innovators, e.g., Beck et al., 2011; Nielsen 2013 but see also Reindl et al., 2016; Nelder et al., 2017). The results of the studies presented in this chapter provide further evidence for the ZLS approach and the growing body of literature that suggest that many primate tool-use behaviours are driven by individual learning mechanisms (see also chapter II). This data challenges the currently held view that great ape cultures depend on various forms of social learning (e.g., Kummer & Goodall, 1985; Boesch & Boesch 1991, Boesch, 1995; Whiten et al., 1999; Whiten et al., 2001; de Waal, 2001; Gruber et al., 2009; 2015; de Waal & Ferrari, 2011; Hopper 2016). A more parsimonious explanation for chimpanzee tool-use behaviours and the observed population differences observed in wild chimpanzees may be that whilst individual learning is sufficient to transfer the form of the behaviour, low-fidelity social learning facilitates the likelihood of reinnovation of the behaviour. As mentioned in the general introduction however, this does not mean that chimpanzee tool-use is genetic, in the sense that each behaviour has been directly selected for by natural selection. Instead, it may be that apes have specialised in enhanced individual learning, i.e., in innovations – and, at least for chimpanzees (Whiten et al., 1999; 2001) and orangutans (van Schaik et al., 2003), this is already well expressed by their varied use of tools in the wild (the other great apes showcase their skills, too, but do this more so in captivity). The unspecialised, low-fidelity social learning mechanisms that apes use are piggybacking on these innovative powers. In this synergy between individual and social learning, apes do not seem to be very special – indeed, social and individual learning is highly correlated across the primate range (Reader & Laland, 2001). Yet, in their absolute levels of complexity they can reach in this way (e.g., see the case of nut-cracking – but also the sheer number of different tool-uses that are thus enabled), great apes are exceptional animals (alongside some bird species; e.g., Weir & Kacelnik, 2006; Rutz et al., 2016).

Although there was clear evidence of individual reinnovation of the target behaviours in the scooping, picking and the first pounding experiment, one group in the first pounding experiment and two groups in the second pounding experiment did not reinnovate the target behaviour (thus not fulfilling the double-case ZLS standards for the second pounding experiment). The lack of reinnovation in these groups may have been due to low levels of motivation due to stress (at being separated from the rest of their social group), illness or over-exposure to “treat” foods. Another explanation for the lack of reinnovation in Group 3 in particular may be the observed lower levels of social tolerance observed in this group (Cronin et al., 2014). This study therefore also provides tentative support for the cultural intelligence theory, and suggests that more opportunities for social learning may also increase individual problem-solving capabilities (van Schaik & Pradhan, 2003; van Schaik, 2006; Hermann et al., 2007; Forss et al., 2016; Harrison & Whiten, in prep). Future studies should explore the effect of social tolerance on the reinnovation of novel tool-use behaviours across different captive groups of great apes.

In conclusion to this rather lengthy chapter, the studies discussed here present a picture of chimpanzee stick tool-use behaviour that is and can be reinnovated via individual learning, even in the absence of social information. This is consistent with the ZLS approach, and inconsistent with the current social learning hypothesis. However, these studies help bridge the gap between the two hypotheses by suggesting that although not essential, low-fidelity social learning does greatly facilitate the acquisition of these behavioural forms in naïve chimpanzees (thus increasing the frequency of the behaviour within populations). Indeed, it is possible that if a longer period of trail-and-error learning and/or exposure to low-fidelity social information had been provided, the individuals that did not reinnovate the pounding behaviour would have eventually expressed the target behavioural form (if their motivational levels also increased accordingly). Thus, rather than assuming, a priori, a strong (low or high-fidelity) social learning influence, future research should be carried out into the role of both individual and social learning for the acquisition of the remaining tool-use behaviours observed in wild chimpanzees (Whiten et al., 1999; 2001; Gruber et al., 2009; 2015).

3.6.1 Link to chapter IV

In this chapter, the results of four empirical studies on the individual learning abilities of chimpanzees were presented and discussed. Naïve, captive chimpanzees were found to spontaneously reinnovate three behavioural forms, thus suggesting that (at least these) stick tool-use behaviours are within the ZLS of chimpanzees. These studies focused on relatively simple stick tool-use behaviours and only in chimpanzees. The following chapter tests the ZLS of another primate species: long-tailed macaques, on a potentially more complex stone tool-use behaviour, to examine the learning mechanisms behind the acquisition of another, potentially more complex, tool-use form with a primate species that does not naturally use tools in the wild.

Chapter IV: Naïve, captive long-tailed macaques (Macaca fascicularis fascicularis) fail to individually and socially learn pound-hammering, a tool-use behaviour

This chapter is a slightly modified version of the (published) paper:

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For this chapter, the main text was slightly rearranged to allow for better readability. Minor modifications were made throughout the text to avoid redundancies, but otherwise the text is as published.

I am the primary author of this publication. The original idea for this study was developed in collaboration with Claudio Tennie. I was primarily responsible for the design of the studies and I carried out all data collection and analysis. Claudio Tennie contributed to authorship by providing feedback and editing versions of this paper leading to its publication.

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Chapter IV: Naïve, captive long-tailed macaques (Macaca fascicularis fascicularis) fail to individually and socially learn pound-hammering, a tool-use behaviour

4.1 Introduction

Long-tailed macaques (*Macaca fascicularis*) are commonly found throughout Southeast Asia and have been classified into ten different subspecies following genetic, anatomic and geographic differences (Bunlungsup et al., 2016). Studies have mostly focused on *Macaca fascicularis fascicularis (Mff)*, due to their widespread distribution in Southeast Asia. More recently, *Macaca fascicularis aurea (Mfa)* has received increased attention due to the scientific (re)discovery of complex stone-tool-use practices within some *Mfa* populations (Carpenter, 1887; Malaivijitnond et al., 2007; Gumert & Malavijitnond, 2012). *Macaca fascicularis* have a flexible diet that allows them to exploit several different encased food sources such as nuts and shelled marine prey (Gumert & Malavijitnond, 2012; Luncz et al., 2017). Four out of the eight currently observed populations of Burmese long-tailed macaques (*Mfa*), including one population of hybrid *Mfa x Mff* individuals (Bunlungsup et al., 2016), flexibly process shelled foods, such as rock oysters (*Saccostrea cucullata*), crustaceans, molluscs (e.g., gastropods and bivalves) and nuts, including sea almonds (*Terminalia catappa)* and oil palm nuts *(Elaeis guineensis;* Luncz et al., 2017) using various stone tools and techniques (Gumert & Malavijitnond, 2012, Bunlungsup et al., 2016). To open sessile rock oysters, *Mfa* individuals have been observed to adopt a more controlled “axe-hammering” technique, in which a small hammer stone is used to crack open attached valves (Gumert et al., 2009). Detached food sources, such as gastropods and sea almonds, are processed using another strategy, “pound-hammering”, in which the items are brought to an anvil (generally a large standing stone) and cracked open with a stone hammer (Gumert & Malavijitnond, 2012). These tool-use behaviours have been extensively recorded for some *Mfa* communities and despite the close spatial and genetic relationship between subspecies, no instances of using stones to crack open objects have been observed in the other subspecies of long-tailed macaques (Bunlungsup et al., 2016).

Although pound-hammering has been rigorously recorded for *Mfa* communities in the wild, very little is known about how the behaviours first emerge throughout *Mfa*, and why this behaviour is not practiced by *Mff*. Understanding how these tool-use behaviours originate across individuals may provide explanations as to why they are confined to only some populations and subspecies.

Several primate species use tools (Matsuzawa, 2008). However, to date, primate stone-tool-use has only been recorded in chimpanzees (Boesch et al., 1994), capuchins (Visalberghi, 1987, Ottoni & Mannu, 2001; Fragaszy, 2004; Proffitt et al., 2016) and long-tailed macaques (Carpenter, 1887; Malaivijitnond et al., 2007; Gumert & Malavijitnond, 2012). Until recently, most reports on wild (non-human) primate stone tool-use have been of stone hammers being used to crack open shelled food sources. The recent observation of wild bearded capuchins (*Sapajus libidinosus)* deliberately breaking stones – possibly in order to ingest powdered quartz and/or lichens (Proffitt et al., 2016), is an exception. Due to the similarities between stone tool-use techniques of extant non-human and human primates (Kortlandt, 1986), data from these studies may allow for inferences to be made on the techniques, behaviours and cognitive mechanism involved in the evolution of stone tool-use in the hominin record (Luncz et al., 2017).

The aim of the current study was to observe how one of these tool-use behaviours – pound-hammering – emerges, and in particular whether it’s overall behavioural *form* is the product of spontaneous individual learning and only its spread realised by various low-fidelity social learning mechanisms (i.e., to test whether pound-hammering is within the ZLS of *Mff*, following the protocol presented in the previous chapters of this thesis) or whether the behavioural form itself is and has to be socially learnt and transmitted (see Kummer & Goodall, 1985; Boesch & Boesch, 1991; Boesch, 1995; Whiten et al., 1999; Whiten et al., 2001; de Waal, 2001; de Waal & Ferrari, 2011; Gruber et al., 2015; Hopper, 2016). The current study focused only on the pound-hammering technique, which is arguably more complex than axe-hammering as it requires three interactive objects: stone tool, food source and substrate stone as an anvil (Matsuzawa, 1996). Conversely, the alternative technique, axe-hammering, involves only two objects: a stone and the attached food source.

To identify the mechanisms involved in the emergence of pound-hammering, the latent solutions testing methodology (LS test, Tennie & Hedwig, 2009) was applied to naïve *Mff* individuals, who had never seen the pound-hammering behaviour before. As pound-hammering did not develop spontaneously in the naïve *Mff* tested in this study, various levels of social information on the behaviour were provided to examine whether social information would facilitate the acquisition of the behaviour. Although this was not the case, and the *Mff* never developed pound-hammering, this study successfully applied a new testing methodology to identify the roles of various forms of individual and social learning mechanisms in the emergence of a novel tool-use behaviour. This testing methodology can be applied to all animal behaviours to identify the learning mechanisms involved, and can be used to experimentally test the ZLS hypothesis (Tennie et al., 2009). The results of this study with *Mff* and the novel testing methodology are presented in this chapter.

4.2 Methods

4.2.1 Latent Solutions testing methodology

The LS baseline condition, in which the only stimuli provided are the materials necessary for the behaviour to be performed, may not be sufficient to encourage the reinnovation of the target behaviour. One limiting factor is that subjects may not be motivated enough to express the behaviour (because, for example, they receive regular daily feeds). Thus, the first part of the updated LS testing methodology proposes a stepwise approach, in which the amount and type of information provided to subjects is gradually increased – though never includes demonstrations of the behavioural form. This allows for control over the amount and type of social learning provided in order to identify what conditions are required for the subjects to individually derive the target behavioural form[8]. In the previous published tests of the ZLS hypothesis and the studies presented in chapter III, only one condition, the LS baseline condition, was described, yet only the baseline condition proved *necessary* as the target behaviour was always reinnovated in this condition (Tennie et al., 2008; Allritz et al., 2013 Menzel et al., 2013; Reindl et al., 2016; Bandini & Tennie, 2017). The new, extended, LS testing methodology is described below.

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[8] The obvious downside to this method is that it may induce carry-over effects between conditions. However, here this was deemed a smaller disadvantage than the alternative option of having diminished sample sizes. Note that *any* order in which these LS test conditions are applied still allowed to test for the neccessity of observing the target behavioural form demonstrations for the expression of the behaviour in subjects, regardless of possible carry-over effects.

4.2.2 Results-dependency testing conditions

As action information is necessarily hierarchically placed above result information (Acerbi et al., 2011; Tennie et al., 2012), and most importantly, actions prescribe the behavioural form (i.e., the target) itself, target action information should, ideally, only be demonstrated at the very end of the sequence of conditions. Given several similar previous tests in the literature (carried out for different reasons; Caldwell & Millen, 2008; Reindl et al., 2017), the first set of conditions applied after the first LS baseline provide information on the end results of the behaviour (i.e., the physical static final environmental result of the behaviour). The first low-fidelity social learning condition used here involved a "*partial* end-state condition", in which only part of the environmental outcomes that typically would result from the target actions were demonstrated (but without actually demonstrating these actions). The following condition, the "results-dependency condition" tested for the reproduction of complete end-results (yet still without revealing the actions that were used to achieve this end-state). The final condition in the result-dependency test set involves an "object movement re-enactment condition", in which the relative movement of the objects involved (stone to nut) *as well as* the overall end-result are shown (yet, again, this condition does not involve an agent demonstrating action information; i.e., a so-called "ghost condition", Heyes et al., 1994; Hopper et al., 2008; Hopper, 2010). The object movement re-enactment condition therefore additionally reveals the sub-results and their relationship to each other, but still not the target actions. Note that, until this point, no target action demonstrations are provided. If the target behavioural form emerges in any of these conditions, these actions would have to be derived primarily through individual learning and their expression may only have been aided by low-fidelity social learning, as the crucial actions required for the behavioural form are not revealed.

4.2.3 Action-dependency testing conditions

If the target behaviour does not emerge in any of the LS test conditions, the next step is to provide demonstrations of the actions required for the behaviour (i.e., to demonstrate the full form of the behaviour, especially the actions, but also the results of the behaviour). Thus, the following conditions include full action demonstrations of the target actions, results (including the end state) and even the target goals of the behaviour in question (social learning conditions that enable action copying, potentially allowing for the copying of the full behavioural form itself) in order to assess whether the behaviour is a culture-dependent trait (i.e., action traits that cannot be reinnovated independently, Reindl et al., 2017). Only in cases where a behavioural form first does not emerge in the LS test conditions, but then later emerges in the action-dependency testing conditions, can the behaviour parsimoniously be considered to require social learning.

The updated LS – alongside the action-dependency testing – methodology therefore allows for the learning mechanisms involved in the emergence of a new behavioural form to be isolated and identified.

4.3 Pound-hammering test

Currently, the subspecies *Mfa* (the only subspecies that demonstrates pound-hammering in the wild, Bunlungsup et al., 2016) is not found in captivity. Thus, all tests were carried out with *Mff.* This subspecies was tested as they are very closely genetically related to *Mfa*, and in particular because the hybrids of *Mff* and *Mfa* have already been observed to use tools in similar ways to *Mfa* (Bunlungsup et al., 2016). By testing *Mff*, data would generate information on two levels: positive evidence for individual learning of actions (in the LS test) underlying pound-hammering in *Mff* would simultaneously show that the behavioural form is a latent solution for *Mff* and that high-fidelity social learning is unlikely to be necessary for wild *Mfa* to express the behaviour. The former is a possibility despite wild *Mff* not (yet) having been reported to show this behavioural form (also due to the “captivity effect”, described in chapter II; Tomasello & Call, 1997; van Schaik et al., 1998).

The updated LS testing methodology – alongside the action-dependency tests – were applied to two populations of *Mff* naïve to pound-hammering held at two wildlife parks in the UK (n=31, M_{age}=19.3, SD=4.3). Following the results of previous tests on the individual learning abilities of primates (e.g., great apes: Köhler, 1925; Nakamichi, 1999; Tennie et al., 2008; Allritz et al., 2013; Menzel et al., 2013; Reindl et al., 2016; Bandini & Tennie, 2017; Neadle et al., 2017; capuchin monkeys: Visalberghi, 1987; Waga et al., 2006; long-tailed macaques: Zuberbühler et al., 1996 and the studies presented in the previous chapters), pound-hammering was hypothesised to emerge in naïve individuals within the first baseline condition. As this was not the case, the series of test conditions according to the updated testing methodology were provided.

4.3.1 Statistical power for LS tests

As the ZLS hypothesis makes predictions on a species-wide level, it is essential that LS tests have the required statistical power to generalise data from samples to the whole species. Here the LS test methodology is updated with regard to this point. Note that the below is only applicable for test conditions in which the target behaviour does *not* occur (as any occurrence of the behaviour so far rendered these calculations obsolete).

According to Cohen (1988), statistical power of an experiment should aim to exceed 80% to allow for confident conclusions to be drawn from data sets. "Power" here refers to the probability of observing the target behaviour in at least one, or two, individuals. Following this guideline, LS tests *failing* to detect a target behaviour must exceed 80% power in order to confidently draw conclusions from a specific sample size (calculated below) to a species-wide level. Once the behaviour has been classified as relatively simple or complex (following the ZLS single or double-case standards; see general introduction), the required minimal sample size needed to confidently draw conclusions from the data can then be calculated (following Cohen's (1988) requirement of at least 80% power, see above). This calculation is carried out below, based on binomial cumulative distributions. To calculate the minimum sample size, the expected probability of individual reinnovation is also required. The ZLS hypothesis works under the assumption that, if the target behaviour is a latent solution, and the subject is motivated to engage with the situation, the probability of reinnovation in a given individual (i.e., outside high-fidelity social learning) must fall within a range that reaches from very high (100% - in case of latent solutions that may not even need to be harmonised by low-fidelity social learning in a population[9] to low (but not very low: in the current formulation of the ZLS hypothesis at least, the target behaviour should occur in independent naïve individuals with a probability that must substantially exceed zero (*van Schaik, pers. comm.*)). For current purposes, to

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[9] These would be behaviours that are hardwired, i.e., they would be close to the now out-dated concept of "instinct".

derive at minimally required sample sizes, only the lowest estimates of this probability must be defined. Given these considerations, and the fact that the empirically-derived rates of pure individual reinnovation so far seen in latent solution experiments were relatively high (Tennie et al., 2008 (83% reinnovation rate); Allritz et al., 2013 (at least 15%); Menzel et al., 2013 (at least 13%); Reindl et al., 2016 (80%); Bandini & Tennie, 2017 (at least 14%)), here a conservative standard of an (at least) 10% probability of pure individual reinnovation is proposed (this being a low, but not very low, reinnovation rate already takes into account the higher levels of motivation, and hence increased reinnovation rates in captivity due to the captivity effect; van Schaik et al., 1998). Thus, within both the single-case and the double-case ZLS standard, a 10% probability of reinnovation is applied. Given that both standards differ in the number of minimum reinnovations (one vs. two), they require a different sample size each to reach a power of 80%. Calculating this sample size shows that, to reach a power of 80%, the single-case standard requires a sample size of at least 16 subjects, and a sample size of at least 29 subjects in the double-case standard. The minimum sample size is calculated using a binomial cumulative distribution (once the required reinnovation rate and the probability of reinnovation is established; see Appendix IV for extended calculations):

$$F(k;n,p) = \Pr(X \leq k) = \sum_{i=0}^{n} \binom{n}{i} p^{i} (1-p)^{n-1}$$

As this study examined the origins of pound-hammering, a relatively complex multi-step tool-use behaviour (Carpenter, 1887; Malaivijitnond et al., 2007; Gumert & Malavijitnond, 2012; Tan, 2017) the single-case ZLS standard was applied. The sample size (*n*=31) therefore exceeded both the single-case and the double-case ZLS standards' requirements.

4.4 Materials

4.4.1 Subjects

Two adult female long-tailed macaques (*Macaca fascicularis fascicularis*) held at Shepreth Wildlife Park, Cambridge, UK (*n*=2, M_{age}=22, SD=2.3) and 29 long-tailed macaques (*Macaca fascicularis fascisularis)* held at Curraghs Wildlife Park in the Isle of Man, UK, participated in this study (*n*=29, M_{age}=16.7; SD= 5.6; 17 females; all captive-born). The first test was carried out at Shepreth Wildlife Park. The subjects were mother, Tina and daughter, Tammy. Tina was originally purchased by a private individual, and was donated to Shepreth Wildlife Park in January 1991. Tammy was born in captivity and reared by her mother at Shepreth Wildlife Park. Testing was carried out in November 2015 by EB. As both individuals lived almost exclusively (expect for Tina's first year) at Shepreth Wildlife Park, it was possible to control for their past experience with similar tasks (see below). The second test was carried out at Curraghs Wildlife Park. This group of long-tailed macaques (n=29) consisted of individuals ranging from infants (born in September/November 2015) to older adults (M_{age}=16.7) of both sexes.

All the keepers at both institutions filled out a questionnaire on the previous experiences of the subjects of any tasks that resembled the one presented in this study. The questionnaire was followed-up with interviews by EB with the keepers, in order to fully understand the previous knowledge of the individuals (see also chapter III). The keepers from both parks reported that although the subjects receive nuts occasionally, at Shepreth Wildlife Park, these were always unshelled (and therefore do not require any processing) and at Curraghs Wildlife park the animals were occasionally provided with shelled nuts, which they can easily crack with their teeth, or for the larger nuts (coconuts), the macaques cracked them by dropping them from the trees and hanging support structure in their indoor and outdoor enclosures onto the ground of their enclosure. No other shelled foods were ever included in the subjects' diets. Furthermore, the keepers reported that they never demonstrated the cracking action required to open nuts at either park, and that the animals were never involved in experiments or enrichment exercises that required tools to crack open objects. Although stones are found in the outdoor enclosures of both parks, the keepers confirmed that they have never observed the animals using the stones to crack open any objects. Thus, it was concluded that the subjects were naïve to pound-hammering before testing.

4.5 Procedure

4.5.1 Shepreth Wildlife Park

The subjects at Shepreth Wildlife Park were provided with the relevant stone tools and food sources to enable pound-hammering (see Fig. 1). Tools consisted of four stones ranging in mass following Gumert & Malavijitnond's (2013) findings on tool mass selection according to food type: X (40-60g), S (90-100g), M (150-200g) and L (400-1000g). Despite large standing stones being available in the enclosure, an anvil stone (with one, large, flat surface and nooks) was also provided (2000g). The stones and anvil were placed near the fence in the outdoor enclosure by the keepers before allowing the subjects back in. On the first two days of testing, raw, live clams (*Mollusca: Bivalvia*) were placed inside the enclosure by the keepers. Neither subject showed interest in the clams, therefore the clams were replaced by hard nuts: encased unroasted macadamia nuts (*Macadamia integrifolia*) thereafter (all the subjects showed an interest in these nuts).

Fig. 1: The four stones ranging from X to L placed inside the subjects' enclosure (photograph by EB).

The keepers placed the items in the outdoor enclosure before the subject was allowed into the area. The two subjects were kept separately whilst testing to control for social learning effects in case one individual expressed the behaviour spontaneously. Each testing session lasted 30 minutes and was filmed with a handheld Sony HDR-CX330E handycam. Over 35 hours of observational data were collected from Shepreth Wildlife Park.

4.5.2 Curraghs Wildlife Park

The same procedure as at Shepreth Wildlife Park, other than the differences described below, was carried out at Curraghs Wildlife Park with 29 subjects between March-June 2016. As the first two individuals at Shepreth Wildlife Park did not show an interest in the clams, the Curraghs Wildlife Park macaques were immediately provided with macadamia nuts. Furthermore, the same sea almonds (sourced from Thailand) that wild *Mfa* process in Thailand (Gumert et al., 2009; Falótico et al., 2017) were included alongside the macadamia nuts. 15 macadamia nuts and seven sea almonds were provided in each testing session. The individuals at Curraghs Wildlife Park could not be individually separated so were tested as a group. All subjects from Shepreth Wildlife Park and Curraghs Wildlife Park have free access to their indoor and outdoor enclosures. Although all the 29 individuals from Curraghs Wildlife Park were in one group, there were two semi-independent social groups within this group. Around 80 hours of video data were recorded at Curraghs Wildlife Park. All subjects participated in five testing sessions (30 minutes each) per condition (see below) over a period of six weeks.

4.5.3 Conditions

Subjects were tested across different conditions sequentially (see introduction).

4.5.3.1 Baseline condition (original LS baseline method): this first condition tested for unprompted, spontaneous individual innovation of the behaviour –without the help of any type of social learning. The stones were placed inside the enclosure before allowing the subjects in. No demonstrations were provided. To ensure that the subjects would not reject the nuts, a keeper at Shepreth Wildlife Park consumed store-bought unshelled macadamia nuts in front of the subject whilst handing them similar, unshelled macadamia nuts. This process was repeated five times in total per individual. Both subjects ate the five nuts provided, thus confirming that this was a desirable food source. As the subjects at Curraghs Wildlife Park had received and eaten unshelled nuts (including macadamia nuts) in the past, they were provided with the shelled macadamia and sea almonds without keeper-facilitation. All groups of long-tailed macaques received five 30 minute sessions in total.

4.5.3.2 Results-dependency testing conditions

4.5.3.2.1 Partial end-state condition: In the first demonstration condition, the subjects were provided with 15 macadamia nuts that had already been partially opened in the lab, outside of the view of the subjects (Fig. 2). The nuts were still in their shells, but one side was shaved off to allow for the nut inside to be clearly seen, ensuring that the subjects were aware that the edible nut was inside the shell. Thus, this condition, whilst providing information that the macadamia shells contain edible kernels, did not provide information about hammer usage, or hammer effects (i.e., about the condition of nuts that have been hammered). A further 15 shelled macadamia nuts were provided for the Shepreth Wildlife Park subjects and 15 shelled macadamia nuts and seven shelled sea almonds were provided alongside the shaved-demonstration nuts at Curraghs Wildlife Park. Macadamia nuts were always used for the demonstrations. 15 macadamia nuts were provided in all conditions for both groups, alongside seven sea almonds in the Curraghs Wildlife Park group. As the subjects were never successful with cracking any nuts, the number of nuts in the enclosure increased with each condition (as 15 new macadamia nuts and seven sea almonds were introduced into the enclosure in each trial).

Fig.2: Macadamia nuts with one side-shaved off as used in the partial end-state condition (Photograph by EB).

4.5.3.2.2 End-state condition: The next demonstration involved cracking nuts outside of the view of the subjects, and placing them back inside their shells. This allowed the subjects to see again that edible nuts were inside the shells, but did not provide information on the hammering action required for the nuts to be opened. Here, subjects were able to remove the nut from the cracked and loose shells to consume the kernel. 15 cracked macadamia nuts were placed inside the enclosure alongside the same number of shelled nuts as in the previous condition (15 macadamias and seven sea almonds).

4.5.3.2.3 Object movement demonstration condition: The third demonstration involved an object movement demonstration condition, in which the environmental result of the shell cracking was demonstrated alongside the movements required to crack the nut, but without an active agent carrying out any actions which could be copied (technically this was simultaneously both an object movement demonstration and end-state condition). A pulley-system was devised with a stone (size M) attached to a string and draped over a branch of a tree standing in front of the outside area of the enclosure, between the protective barrier separating visitors from the enclosure. The tree was visible to the subjects when in their outdoor enclosure (Fig. 3). A macadamia nut in its shell was placed on top of the stone anvil and the string to which the stone was tied was released, allowing the stone to fall (from an approximate height of 50cm) on top of the nut, cracking it open. The open nut was then handed to the subjects through the mesh. Demonstrations were repeatedly carried out for approx. 15 minutes. Each demonstration lasted between five and 10 seconds (from the release of the stone to the nut-cracking). After each demonstration, the cracked nut was handed to the subjects through the mesh and the usual number of shelled macadamia and sea almonds were added (15 macadamias and seven sea almonds).

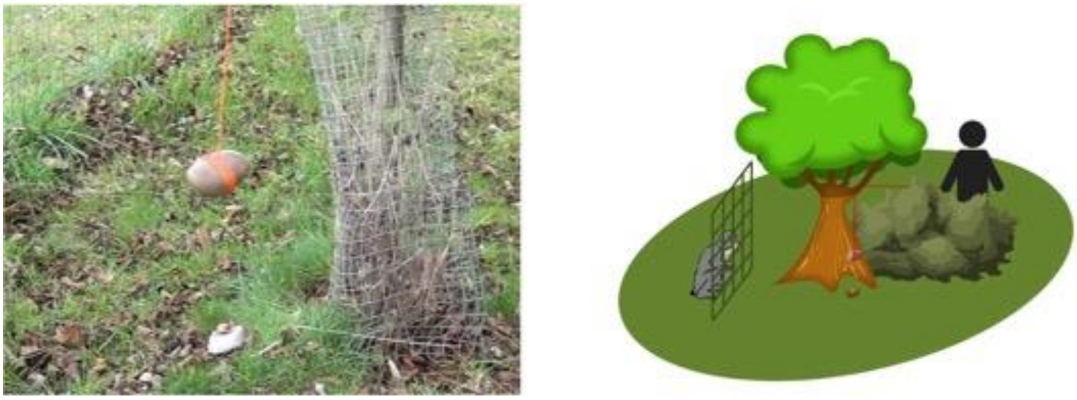

Fig.3: Photograph (right; by EB) and diagram (left; by D. Neadle) of the pulley system used to demonstrate the cracking action of the stones.

4.5.3.3 Action-dependency testing conditions

4.5.3.3.1 Full demonstration condition: A full demonstration (containing both copy-able pound-hammering actions and the accompanying results (including end results) of stone movement and object cracking) was provided by the keeper (AP) at Shepreth Wildlife Park and by the researcher (EB) at Curraghs Wildlife Park. Before each trial in the full demonstration condition, the demonstrator positioned themselves in front of the subjects, and placed a macadamia nut on the anvil and used one of the stones (size S or M) to crack open the nut. The opened nut was then handed to the subjects. Once the individual had consumed the nut, another full demonstration was provided. At Shepreth Wildlife Park, each individual was exposed to three demonstrations before being provided 15 shelled macadamia nuts. At Curraghs Wildlife Park, demonstrations were provided continuously for approx. 15 minutes before each trial. Each demonstration lasted between 10-25 seconds. Subjects were then provided with the usual number of shelled macadamia nuts and sea almonds after the demonstrations (15 macadamias and seven sea almonds).

4.5.3.3.2 Full subspecies conspecific demonstration video condition: To control for the effect of heterospecifics providing the demonstration, videos of wild long-tailed macaques (*Mfa*) provided by field-researchers (*L.Luncz & M.Gumert)* and taken from online sources, pound-hammering both nuts (sea almonds) and oysters were shown to the subjects before each trial. Videos were played on loop on a Samsung galaxy Gt-p5110 tablet (833x870mm; 800x1280 pixels) for 15 minutes. The video lasted 28 seconds in total and contained six cracking episodes per video. Subjects were then provided with the usual number of shelled macadamia nuts and sea almonds (15 macadamias and seven sea almonds).

It was not possible in this study to individually train subjects to show the behaviour and act as a demonstrator for the rest of the group (due to local restrictions at the testing institution and time constraints). However, this condition (in which a live conspecific provides a demonstration of the full behaviour to the rest of the group) would provide a valuable further condition to examine the role of high-fidelity social learning in the development of the target behaviour, and should be carried out in addition to the social learning conditions described above in future, if testing conditions allow.

After all the conditions were carried out, keepers continued to include shelled macadamia nuts in with the subjects' usual daily feed for a subsequent six week period to control for whether a longer period of individual trail-and-error learning might be required for the behaviour to emerge. Keepers reported back to EB with the results of observations during this extended testing period.

4.5.3.4 Ethical statement

All participation was voluntary and subjects continued with their normal feeding routine during testing. Subjects have access to water *ad libitum* and access to both outdoor and indoor enclosures, and were never food or water deprived during testing. This project was granted ethical approval by The University of Birmingham AWERB committee (reference UOB 31213) and by the host zoos following SSSMZP, EAZA, BIAZA and WAZA protocols on animal research and welfare.

4.5.3.5 Coding

All videos were coded following testing. Length of time spent manipulating the nuts was recorded, alongside seven different manipulation-types: *carry/hold, gnaw, sniff, hit/drop, roll/rub on hard substrate, roll/rub in hands* (see supplementary CD for a video clip of *roll/rub on substrate* and *roll/rub in hands), masturbate*. See tables 1 and 2 below for a description of each category. All analysis was run in R version 3.4.1 (2017-06-30).

Table 1: Behaviours coded and their descriptions

Method	Description
Carry/hold	Individual manipulating the nuts either standing or sitting still, or whilst moving around the enclosures.
Gnaw	Individual uses their teeth to bite and try to crack the nut, or when the nut is inserted into the mouth.
Sniff	Nut is sniffed
Hit/Drop	Nut is either hit with the hand or fist, or dropped from above.
Roll/Rub on hard substrate	Nut is rolled or rubbed with the palms on a hard surface, such as the ground, log or stone.
Roll/Rub in hands	Nut is rolled or rubbed in between the two hands.
Masturbate	Nut is used to masturbate

Single manipulation types and combinations were coded. Since the subjects at Curraghs Wildlife Park were tested in their groups, there were several occasions of manipulations being interrupted by external factors (the individuals at Shepreth Wildlife Park were tested individually, so did not experience interruptions from other individuals). Therefore, context of manipulation was coded only for Curraghs Wildlife Park. Context was coded as: *antagonistic behaviour*, *groom*, *sex* and *noise*. See table two for a description of the contexts.

Table 2: Descriptions of the contexts of nut manipulations for Curraghs Wildlife Park

Method	Description
Antagonistic behaviour	Individual manipulating the nut either received an aggressive action or another individual came too close and the manipulating subject performed an aggressive act towards the other macaque.
Groom	Individual manipulating the nut is interrupted by another individual initiating a grooming session.
Sex	Individual manipulating the nut is interrupted by a sexual advance by another individual
Noise	Individual manipulating the nut is interrupted by an external or internal noise.

For the conditions in which demonstrations were provided (object movement demonstration, full demonstration condition and full subspecies conspecific video demonstration condition) all data (including that from Shepreth Wildlife Park) was coded for the eye-gaze (i.e., where the individual was looking, see below) of the subjects during demonstrations, as a measure of attention. However, assessing the eye-gaze of subjects from the videos proved to be difficult due to the fact that the subjects at Curraghs Wildlife Park did not have IDs and could not be individually identified. Furthermore, at both parks, subjects had access to the whole enclosure during testing and moved around continuously during demonstrations, making it difficult to track which individuals had seen the demonstrations before, and how long each individual watched the demonstration. This was especially pronounced at Curraghs Wildlife Park where the individuals were tested as one group. Therefore, only clear cases of directed eye-gaze towards the demonstration (i.e., looking towards the stone falling on the nut in the object-movement demonstration; looking towards the researcher or keeper during the full action demonstration or towards the screen during the full subspecies conspecific video demonstration) were coded. An individual was recorded as observing the demonstration when their head (regardless of the direction of the body) was directed towards the demonstration (see supplementary information in the provided CD for a clip of an instance coded as eye-gaze). As mentioned, the individuals at Curraghs Wildlife Park do not have IDs and cannot be individually identified; therefore eye-gaze was coded as instances rather than by individuals. As assessing the direction of subject's eye-gaze could not always be measured confidently (due to the issues mentioned above), very stringent requirements were applied for the eye-gaze coding. These strict requirements may have resulted in fewer individuals being coded for eye-gaze towards the demonstration than in reality. Similarly, some of the individuals who watched the whole demonstrations may have been excluded from the dataset because they did not fit all the requirements for eye-gaze. However, the strict instructions for this set of coding were established in order to avoid false positives.

4.5.3.6 Reliability Coding

20% of all the testing videos were second-coded by a blind coder (*M.Bandini*), according to all the behavioural categories outlined in the previous section. Videos for inter-rater reliability coding were selected following the procedure outlined by *D.Neadle* and described in the previous chapter (chapter III).

4.6 Results

4.6.1 Interrater reliability

There was a strong and substantial agreement between coders for all the behavioural categories, (Length of time manipulating nuts: Cohen’s Kappa; *k*=0.72; Manipulation types; *k*=0.81; Context of manipulation; *k*=0.78). 20% of the videos were also second-coded for eye gazing and there was a substantial agreement between coders, *k*=0.71.

4.6.2 Experimental results

None of the subjects in this study used the stones to crack the nuts in any of the conditions. Thus, the captive long-tailed macaques (*Mff*) neither individually reinnovated pound-hammering, nor did they socially learn to do so. The subjects were not successful in cracking the nuts using other methods, either. Despite the fact that they were never successful, the interest in the nuts and motivation to open the nuts remained high throughout all testing sessions, demonstrated by a consistent manipulation of nuts across testing sessions. Over 105 hours of observational data was collected from both Shepreth Wildlife Park and Curraghs Wildlife Park combined, and in 89% of each testing session at least one subject was manipulating nuts. Manipulation bouts lasted between two seconds and eight minutes. Mean interaction time with the nuts was 00.38 seconds (SD=1.23).

Seven different manipulations of the nuts were observed: *carry/hold, gnaw, sniff, hit/drop, roll/rub on hard substrate (ground, log or stone), roll/rub in hands* and, on one occasion, using a macadamia nut to *masturbate* (see methods section for full descriptions of each behaviour). Single manipulation of the nuts was recorded in 44.7% of bouts and combination was recorded in 42.1% of bouts. The use of three different manipulation types was recorded in 10.5% of bouts, whilst using four different types was observed in 2.6% of cases. The most common single manipulation was *"gnaw"* (57.4%) followed by *"carry/hold"* (18.5%), "*roll/rub in hands*" (7.4%), "*sniff*" (3.7%) "*roll/rub on hard substrate*" (3.7%), "*hit/drop* (3.7%), "*masturbate*" (1.9%). The most commonly used combination of manipulation types was "*gnaw & sniff"* (25%), followed by "*carry/hold & gnaw"* (17.8%), "*gnaw, roll/rub in hands, roll/rub on substrate"* (14.3%), "*roll/rub in hands & gnaw"* (14.3%), *"carry/hold & sniff"* (7.5%), *"roll/rub in hands & gnaw"* (3.6%), *"carry/hold, gnaw, roll/rub in hands"* (3.6%), *"carry/hold, rub/roll in hands, roll/rub on substrate, hit/drop"* (3.6%), "*rub/roll, carry/hold, hit/drop"* (3.6%), "*carry/hold & rub/roll in hands"* (3.6%).

At Curraghs Wildlife Park, subjects were tested in a group setting, and the videos were coded for interruptions. Interruptions were frequently due to antagonistic behaviour between individuals. In 48% of manipulations of the nut there was an instance of distraction. Distractions were coded as *antagonistic behaviour, groom, sex* and *noise*: the most common interruption was due to *antagonistic behaviour* (88%), followed by *sex* (6.9%), *groom* (6.8%) and *noise* (6.8%). The mean length of an interruption was 8 seconds (SD=2.33). In 34.5% of cases the nut was lost (either stolen by another individual or left behind) as a result of the interruption.

Stones were rarely manipulated throughout the whole experiment. Instances in which a stone was manipulated at the same time as the nut were coded, and in only 9.8% of cases the stones were manipulated at the same time as the nuts. Of these cases, 44% of times the stone was used as a surface to roll the nut on, and in all the remaining cases, the stone was simply held in the free hand or rolled around the enclosure. Only two instances of stone manipulation independently of nut manipulation were recorded, and both involved the stones being moved to investigate the area underneath the stone.

Despite the high levels of motivation (see above) none of the subjects used the stones provided to crack the nuts – or even to attempt to crack the nuts – in either the baseline or any of the social learning conditions. The subjects continued to be unsuccessful during the additional six weeks at the end of testing when the keepers at Curraghs Wildlife Park provided the nuts alongside the subject’s regular feed.

4.6.3 Eye-gaze

Overall, low levels of attention were recorded during all three demonstrations. Subjects only watched on average 2.2% of the whole demonstration session (which lasted 15 minutes in each demonstration condition). However, when assessing the mean time watching each individual demonstration, subjects watched a higher percentage of the demonstration. The object movement demonstration lasted on average 7.5 seconds (SD=4.3), of which individuals watched on average 13.3% of each demonstration. Full demonstration lasted on average 18 seconds (SD=19.4), of which subjects watched 25.9% of each demonstration. Each video in the full subspecies conspecific video demonstration was 28 seconds long, with subjects watching 9.1% of the videos. Two individuals could be confidently considered to have watched a full demonstration. The first was Tina (F, 25 years), in Shepreth Wildlife Park, who watched one whole full demonstration of the keeper using a stone to crack open a nut. The second instance occurred during the video demonstration in which an individual (M, unknown age) at Curraghs Wildlife Park watched all 28 seconds of the subspecies conspecific video demonstration (as the video contained six instances of pound-hammering by different individuals, thus this subject can be considered to have watched six demonstrations of the target behaviour). Therefore at least two individuals, one from each park, watched one full demonstration.

4.7 Discussion

Despite ample individual learning opportunities as well as various social learning demonstrations (including the demonstration of underlying actions), pound-hammering did not appear in any of the tested captive *Mff*. The *Mff* macaques in this study did not spontaneously develop pound-hammering individually, but also did not socially learn the behaviour with the help of any of the available social learning mechanisms that the new conditions allowed for (i.e., across the partial end-state condition, end-state condition, object movement re-enactment condition, full demonstration condition and the full subspecies conspecific demonstration video condition; see introduction). The sample (*n*=31) of this study exceeded the power requirements for both the single and the double-case ZLS standards, allowing for conclusions to be drawn on a species-level from our negative findings. Thus, this data suggests that pound-hammering is not a latent solution for *Mff*. This however raises the question of why the behaviour did not emerge in either the individual or social learning conditions provided in this study.

4.7.1 Possible explanations for the lack of pound-hammering in Mff

4.7.1.2 Genetic predispositions

One explanation as to why the behaviour did not emerge in naïve *Mff* is that there may be a genetic component to the behaviour that is only found in *Mfa*. This may explain why the behaviour is present in wild *Mfa* but absent (so far) in *Mff*. It may be that *Mfa* have a genetic predisposition for enhanced individual learning and, subsequently, some forms of social learning relevant for the expression of pound-hammering. As the underlying mechanisms for individual and social learning are likely based on associated mechanisms (Reader & Laland, 2001; van Schaik & Pradhan, 2003; Heyes, 2012), one potential explanation for the presence of this behaviour in wild *Mfa* and not in *Mff* (in wild and captive *Mff* populations, such as the one tested here), may be that the two subspecies have differing levels of individual learning abilities and motivation to attend to socially mediated information.

Based on the assumption that individual and social learning had an interdependent evolutionary path (van Schaik & Pradhan, 2003; see also Reader & Laland, 2001), it would seem likely that species that are better at individual learning should therefore also be more attentive to social information. The captive *Mff* in this study demonstrated very low levels of attention to all the social demonstrations provided. Despite the range of social demonstrations, the subjects only watched a maximum of 25% of a demonstration (in the full demonstration condition), and it could only be confirmed for two individuals that they watched a whole demonstration (note however, as mentioned above, that it may be that more individuals watched a whole demonstration but might have been excluded by the conservative requirements set for these data). Thus it may be that *Mff* are relatively uninterested in socially mediated information, and, as a result, are also less likely to individually or socially learn the behaviour (overall low levels of attention to social demonstrations were also found in marmosets; a study on the attention of marmosets to knowledgeable demonstrators manipulating a problem-solving task found that individuals only attended to the demonstrator for a median of 6 seconds; Range & Huber, 2007). Indeed, a recent study on two different subspecies of otters also found differences between the subspecies in their levels of attention to socially mediated information (Ladds et al., 2017). However, this study did not directly test the role of genetics in pound-hammering in *Mfa*, and in the absence of data on the levels of attention to social information by wild *Mfa*, it is currently impossible to assess whether a distinct difference in the levels of individual and social learning does indeed exist between the subspecies. Yet, a possible genetic component to the behaviour may provide one explanation as to why wild *Mff* do not show the behaviour, but a population of hybrids of *Mff* and *Mfa* in the wild practice pound-hammering.

Although the *Mff* showed overall levels of low attention to the demonstrations, it is important to note that at least two individuals watched at least one full demonstration. One individual, Tina, watched a full human demonstration and one individual from Curraghs Wildlife Park watched the subspecies conspecific video demonstration in full (thus this individual watched six demonstrations of the target pounding behaviour). Therefore, at least two individuals attended to all the social information – including the actions – required to crack open the nuts using stones. Subsequently, it is likely that if the behaviour required social information to be expressed in the naïve macaques, at least the two individuals that attended to the full demonstrations should have been equipped with the knowledge necessary to reinnovate pound-hammering. Yet, the behaviour still did not emerge, suggesting that either a longer exposure to social information is required for the behaviour to develop, or, more likely, that social information may not be sufficient to encourage the reinnovation of pound-hammering – potentially due to a lack of motivation to use the information, and/or to a lack of imitative ability.

4.7.1.3 Sensitive learning periods

An alternative explanation for the lack of reinnovation of the target behaviour observed in this study may be that a sensitive period for the acquisition of this behaviour exists early in ontogeny (Tebbich et al., 2001; Biro et al., 2003; Tennie et al., 2010; Tan, 2017). Indeed, Tan (2017) found that wild juvenile *Mfa x Mff* hybrids only begin practicing pound-hammering and axe-hammering at around three years of age. The period before the acquisition of this behaviour consists of extensive play and manipulation bouts with the stones and nuts involved in the later behaviour (Tan, 2017). Tan (2017) concludes that this extended period of manipulation of the objects is required for the full behaviour to emerge in adulthood. A similar finding was reported for juvenile chimpanzees, who may only acquire nut-cracking after a sensitive period in which they manipulate the materials of the behaviour between the ages of 3-5 years, and an extensive trial-and-error learning period between 8-14 years in which they perfect the technique (Biro et al., 2003). Although the subjects in this study ranged from infants to older adults and all ages were represented, it is possible that a longer period of manipulation of the stones and the nuts whilst in the sensitive learning period is required for the behaviour to emerge (note that this does not rule out individual learning, as an extended period of independent learning may be required before an individual reaches the solution; Tennie et al., 2009). Here all the materials were placed in the subjects’ enclosures and daily feed for a total period of four months, with no reports of the behaviour emerging even after this extended exposure to the nuts. However it might be that up to three years of exposure to the materials is required before the behaviour develops (Tan et al., 2017). Thus, the absence of the materials within this extended sensitive learning period might have limited the development of pound-hammering observed in this study.

4.7.1.4 Motivation levels

It might also be that the individuals were not motivated enough to solve the task, but this seems an unlikely for this subject sample as the levels of manipulation of the nuts remained high throughout the whole testing period (and keepers reported that the macaques continued to try to open the nuts even after testing). Yet, it is possible that the two Shepreth Wildlife Park *Mff* individuals’ rejection of clams (provided in the first test) reflects a general dislike of molluscs in this subspecies, which may be one of the factors limiting the emergence of pound-hammering in both wild *Mff* and our captive population. Pound-hammering is observed primarily in coastal areas in which *Mfa* have access to marine shelled foods, which they consume more than other encased food sources, such as nuts (Gumert et al., 2009). Indeed, observations of wild *Mfa* cracking nuts have only recently increased, perhaps also as a response to the increase of palm oil monocultures in their environment (Falótico et al., 2017; Luncz et al., 2017). Thus, it could be that pound-hammering emerged primarily to exploit marine encased food sources and was only after then generalised to cracking nuts (*M.Gumert, pers. comm*). Thus, if *Mff* are not interested in cracking open molluscs and are not motivated enough to open encased nuts, as they have access to other resources, they may have not developed the tool-use abilities to exploit any encased food sources**.** This explanation seems more likely than one that suggests that *Mff* cannot use tools at all, as both captive and wild long-tailed macaques have already been found to spontaneously show tool-use behaviours. For example, Zuberbühler et al., (1996) describe the spontaneous emergence of a raking behaviour to retrieve out of reach apples from outside the enclosure in one *Mff* individual (suggesting this to be an individually learnt behaviour, although note that this single observation does not fulfil the double-case ZLS standard required of relatively less complex behaviours), and there have been other observations of sporadic tool-use in wild *Mff* (Wheatley, 1988; Wantabe et al., 2007), including one potential observation of stone tool-use (Fuentes et al., 2005). Thus, it seems that long-tailed macaques are likely to at least possess the motivation and capability to spontaneously learn some tool-use behaviours, making the absence of pound-hammering in this study all the more surprising. However, it may be that the cognitive requirements for multi-step stone tool-use behaviours, such as pound-hammering, are different to those required for more general tool-use, and that although *Mff* can spontaneously express simple tool-use behaviours, more complex stone tool behaviours are at the limits of their learning abilities.

4.7.1.5 Pre-existing techniques

Another possible explanation for the lack of emergence of this behaviour in the naïve macaques is that once a strategy to retrieve a specific resource is acquired, it might negatively impact the emergence of related strategies in that individual. For example, as discussed in chapter II, if an individual has already learnt to use a specific tool or technique to retrieve honey from a tree, this pre-existing strategy may hinder the individual's ability or motivation to innovate a different method to retrieve the same food source (e.g., Hrubesch et al., 2009; Tennie & Hopper, 2011). A relative inflexibility in switching methods (and/or lack of motivation to do so) may have also played a role in the current study. Before testing, the macaques only received shelled nut types which they could crack open with their teeth or by dropping them from elevated surfaces (e.g., coconuts; see methods section. Interestingly, this dropping technique was only observed in 3.7% of manipulations with the macadamia nuts and sea almonds, perhaps due to the fact that it was never successful with the testing nuts used here). The most commonly observed manipulation type recorded across both groups of macaques in this study was the "gnaw" manipulation (57.4%), which involved the individuals trying to crack the nuts open with their teeth. As this gnawing strategy worked in the past with other types of nuts, it may be that the macaques were not able to switch to a new technique, even if gnawing became inefficient (impossible as a solution) in the current study.

The macaques were also observed adopting a "rolling" manipulation, in which the individuals would roll or rub the nut between their hands or on a hard substrate, such as a rock or piece of wood (this occurred in 7.4% and 3.7% of manipulation events respectively). Rolling or rubbing the nuts never resulted in the opening of a nut. However, this rolling behaviour has also been observed in wild Balinese *Mff*, who rub objects such as seeds, empty shells (coconut and snail shells), peanuts, sweet potatoes, rocks and insects such as caterpillars and worms between their hands before eating or abandoning the object (Wheatley, 1988). The rolling of food sources in the wild *Mff* has no apparent purpose, as is it does not seem to help with the opening of the food source (if it is encased) and is often carried out also with inedible objects (such as rocks and shells) or already dead animals (such as the caterpillars and worms; Wheatley, 1988). Therefore, in addition to the gnawing behaviour, it might be that these two behaviours (both seemingly latent solutions, given the patterns of reinnovation across subspecies and habitats) negatively impact the exploration of hammering strategies.

4.7.1.6 The role of social learning in the emergence of latent solutions

Given the widespread occurrence of diverse low-fidelity social learning mechanisms across animal species (Reader & Laland, 2003), is reasonable to assume that *Mfa* behaviours observed in the wild are also influenced by social learning (at least in increasing the *frequency* of some behaviours; see also Bandini & Tennie, 2017). However, in the captive population of *Mff* tested here, social information was not sufficient to elicit the emergence of the target pound-hammering behaviour. This is not the first study to find that social learning did not encourage the reinnovation of a behaviour in individuals who did not spontaneously express it in the first place. In their study on tool-use in naïve woodpecker finches, Tebbich et al. (2001) found that all of the juvenile naïve finches in their sample reinnovated a wild tool-use behaviour (the behaviour involved using twigs to retrieve beetle larvae from an artificial tree trunk) without social learning. On the other hand, some of the adults in their group did not reinnovate the target behaviour and exposing these adult finches to tool-using models did not increase their likelihood of reinnovation of the behaviour either (thus perhaps suggesting that a sensitive learning period may exist for the acquisition of this behaviour, see above). Similarly, Visalberghi (1987) observed two capuchins (*Cebus apella*) spontaneously cracking nuts. The behaviour did not emerge in the rest of the group, despite the tests being carried out in a group setting (with all ages represented), allowing for ample opportunities for the rest of the group to observe the two nut-cracking capuchins and thus for social learning to take place. Kenward et al., (2005) ran a study in which they found that two juvenile hand-raised New Caledonian crows that had never been exposed to tools or demonstrations on tool-making, spontaneously made twig tools to retrieve food from a crevice. Two other crows, also hand-raised, were provided with full action demonstrations on how to make the tools, but the authors found no difference in tool-oriented behaviours between the naïve crows and the ones that had received demonstrations (Kenward et al., 2005; see also the studies described above in the individual learning database; chapter II). Thus, it seems that, similarly to what was found in the current study, social learning might not always be the key to release (or even copy) the behaviour, even in behaviours that can be, and are, reinnovated.

It might be argued that human demonstrators are not efficient models for non-human animals (de Waal, 1998), and that perhaps the reason why the behaviour was not socially facilitated in the human full demonstration condition might have been because the subjects in this study did not recognise the human demonstrators as efficient social learning models. However, evidence for the view that only conspecifics are valuable demonstrators is limited (e.g., see Tennie et al., 2012, in which the actions of a novel behaviour were not copied even when they were demonstrated by a conspecific, and see also the results of ghost demonstrations in which chimpanzees expressed the target behaviour even when the actions of the behaviour were provided without any demonstrator; e.g., Hopper et al., 2008; Hopper, 2010). Yet, to control for this potential confound, (video) demonstrations from subspecies conspecifics were provided in this study. Although video demonstrations are not as effective as live conspecific demonstrations (Hopper et al., 2010), previous studies have found that video demonstrations can influence the behaviour of observers (e.g., see Hopper et al., 2012; Gunhold et al., 2014). Due to local restrictions at the testing institutions, the fact that *Mfa* are not currently found in captivity and that the *Mff* in this sample never showed the behaviour, or even precursors of the behaviour, it was impossible to train a live conspecific demonstrator in this behaviour (and even if *Mfa* individuals did exist in captivity, a demonstrator of a different subspecies into the *Mff* group would have to be introduced), thus videos of unfamiliar *Mfa* conspecifics showing the pound-hammering behaviour were provided. The videos were, however, the least-watched demonstrations (9.1% of each video was watched) and the behaviour did not emerge after this condition either, suggesting that having subspecies conspecifics demonstrate the behaviour did not have an effect on the likelihood of reinnovation of the behaviour. Future studies should focus on attempting to train *Mff* individuals to provide live demonstrations of the actions required for pound-hammering to the rest of their group, to observe whether this type of demonstration helps release the behaviour (however, given the results of the social learning demonstrations provided in this study, this seems unlikely).

The outstanding question on how pound-hammering emerges in wild *Mfa* communities therefore remains. The *Mff* subjects in this study did not spontaneously use tools to crack open the nuts, but nor did they learn the behaviour from various demonstrations (including demonstrations from other long-tailed macaques, and demonstrations of the underlying behavioural form). Whilst the reasons behind the lack of tool-use in the captive *Mff* remain inconclusive, this chapter provides a new methodological approach, including a method to calculate the minimum sample sizes required, to examine the learning mechanisms behind the development of tool-use behaviours that can be applied across animal species. By providing both an asocial baseline and several levels of social learning conditions, the roles of each learning mechanisms can be identified in the emergence of novel behaviours. This methodology can also be used to experimentally test the zone of latent solutions (ZLS) hypothesis. The results of this study do not, however, support the ZLS hypothesis, as the naïve *Mff* did not individually learn the behavioural form. Yet the macaques also did not socially learn the behaviour. Thus, the roles of genetic predispositions, sensitive learning periods, levels of motivation and pre-existing techniques in the emergence of pound-hammering should be further investigated in both subspecies of long-tailed macaques.

4.8 Conclusion

Although tool-use in primates is a highly researched area, research into long-tailed macaque tool-use has been only recently begun. Pound-hammering in long-tailed macaques is comparable in complexity to behaviours in other primates, including great apes; such as nut-cracking in chimpanzees (*Pan troglodytes*; Sugiyama & Koman, 1979; Boesch & Boesch, 1990; Matsuzawa, 1994) and capuchins (*Cebus apella*; de Moura & Lee, 2004; Fragaszy et al, 2004; Mannu & Ottoni, 2009). The use of stone tools to process food sources might also have been an important feature of early human (*Homo sapiens sapiens*) settlers in marine environments (Gumert & Malaivijitnond, 2012). Prehistoric modern humans also consumed many of the same food sources as modern long-tailed macaques do today, most likely using stone tools and similar techniques to extract the organisms (Marean et al., 2007; Jerardino, 2010). Therefore, understanding how this behaviour emerges in modern long-tailed macaques may provide some insight into the mechanisms behind the emergence of this behaviour in both human and non-human primates.

Furthermore, this study suggests that not all primate tool-use behaviours are as easily reinnovated as the stick tool-use behaviours described in the previous chapter. Indeed, it provides further evidence for the view that some behaviours, such as nut-cracking across primate species, may be at the limit of individual learning. More complex behaviours, such as this one, may impose higher cognitive loads on individuals (e.g., in terms of executive functions such as planning, inhibition, sequencing, and decision making and working memory; Haidle, 2010) and therefore require more complex cognitive processes to be reinnovated. Further testing on this particular behaviour is required to assess the cognition behind more complex primate behaviours.

4.8.1 Link to chapter V

The macaques in this study did not reinnovate the target pound-hammering behaviour, nor did they socially learn it. Some of the reasons behind the lack of reinnovation observed in this study were explored and potential limits to the individual learning abilities of non-human primates were discussed. As long-tailed macaques do not possess the natural tool-use repertoires observed in great apes, it was hypothesised that chimpanzees, who have already been found to spontaneously reinnovate some stick tool-use behaviours (see chapter III), and who have an extensive tool-use repertoire in the wild, would be able to reinnovate a similarly complex stone tool-use behaviour (contra the findings presented in this chapter). To explore this question and to provide new comparative data for the study of early hominin tool-use, naïve chimpanzees were tested on their stone knapping abilities following the extended LS testing methodology presented in the current chapter.

Chapter V: Investigating the manufacture and use of stone flakes by naïve chimpanzees

"The ability to make and use simple stone tools is a primitive behavioural capacity that may have been "discovered" numerous times"
- Westergaard & Suomi (1994, 5)

5.1 Introduction

The emergence of stone tools in the hominin archaeological record has been heralded as one of the turning points in human culture, marking a critical leap in both the cognitive and motor abilities of early hominins (Toth & Schick, 2009; Stout & Kreisheh, 2015). Despite a large body of research into the evolution of material culture in the hominin record, the current understanding of early stone tools is consistently being challenged by new findings. Until recently, it was thought that Oldowan assemblages (≈ 2.5 Mya), attributed to *Homo habilis*, constituted the first stone tools made by hominins. However, a recent excavation in West Turkana, Kenya, uncovered new stone tools, potentially pushing the emergence of material culture back to ≈3.3 million years ago (Harmand et al., 2015). These new "Lomwekian" stone tools would predate the Oldowan assemblages by over 700,000 years, suggesting, in this case, that rather than being a distinguishing feature of the *Homo* lineage, stone flakes were most likely already being made and used by *Kenyanthropos platyops* (Harmand et al., 2015). However, the Lomweki assemblage is still a relatively new finding, and some have argued that the excavation methods and interpretations adopted by Harmand and her team (2015) do not allow for confident interpretations on the dates of these tools (e.g., Dominguez-Rodrigo & Alcalà, 2016). Thus, as further research is still required into the new Lomweki assemblage, this chapter will only discuss the Oldowan industrial complex (these tools will be referred to throughout this chapter as "early stone tools").

Alongside potential changes to the chronology of early stone tools, recent theoretical advancements have challenged some of the preconceived notions on the required cognition behind early stone tool industries. The current (and long-standing) accepted view for early stone tools seems to be one that defines them as cultural products (McNabb et al., 2004; Gamble & Porr, 2005; Lycett & Gowlett, 2008; Shipton, 2010;

Goren-Inbarm 2011; Whiten et al., 2003; 2011; see also Rein et al., 2013 and Stout & Kreisheh, 2015 for an overview of these studies), making them culture dependent traits (CDTs; see general introduction and Reindl et al., 2017). Although authors may differ on some of the smaller details, most of the past and current literature assumes that early stone tools required the same high-fidelity learning mechanisms that are widespread in modern human culture: "*The relative simplicity and duration of the knapping processes from the early technocomplexes, such as the Oldowan, may indicate learning by direct observation*" (Lombao et al., 2017, 9; and see references above). Yet, similarly to the case for chimpanzee tool-use (Whiten et al., 1999; 2001; Tennie et al., 2009; Bandini & Tennie, 2017), the *need* for high-fidelity social learning for the acquisition of some of these stone tools is controversial.

5.1.1 The Oldowan technocomplex

Oldowan assemblages are characterised by cores that have been knapped to make sharp-edges flakes (most likely to be used as cutting tools; Kuman & Clark, 2000). The Oldowan technocomplex is dated to ≈2.6 to 1.7 million years ago (although note that Oldowan-type tools are also found in later assemblages) and the same forms of tools are found across Africa throughout this period (Kuman & Clark, 2000). One of the distinguishing features of Oldowan assemblages is the similarity observed in the form (i.e., the physical characteristics) of the tools used across hominin species in a wide spatiotemporal distance (Richerson & Boyd, 2005). This stasis in variability has been argued by some to be maintained via high-fidelity social learning and that, consequently, early stone tools were CDTs (e.g., Shipton, 2010; Stout et al., 2010; 2015; Morgan et al., 2015). Although there were early critics of the cultural claim for Oldowan tools (Foley, 1987; Richerson & Boyd, 2005), an alternative approach to explaining the emergence, continuity, and lack of perceived change in the form of these tools, independent from culture, has only recently started gaining momentum (Tennie et al., 2016; 2017). Richerson & Boyd (2005) first argued against the cultural approach for early stone tools, citing the "*bewildering*" temporal and geographic stability of these tools as inconsistent with cultural transmission models, which instead predict rapid change (and copying errors; Kempe et al., 2012) driving cultural objects. Indeed, if Oldowan tools were being socially acquired and transmitted across individuals following a cumulative process, one would expect to see more rapid changes in the form of the tools and a gradual increase in variance and complexity (Foley, 1987; Richerson & Boyd, 2005; Kempe et al., 2012; Tennie et al., 2016). The stasis observed in Oldowan assemblages is reminiscent of chimpanzee tool-use behaviours, which also reappear, to the best of our current knowledge, in the same form across space and time (Whiten et al., 1999; 2001; Tennie et al., 2009; Bandini & Tennie, 2017). It may be, therefore, that Oldowan tools, similarly to what has been argued for chimpanzee behaviours, are also consistent with the ZLS account (Tennie et al., 2009; 2016; 2017). If this were the case, rather than assuming that high-fidelity social learning was required for the acquisition of Oldowan tools, a more parsimonious interpretation would be that individual learning drove the simplest forms of these tools. Thus, similarly to the chimpanzee case, early hominins may have been able to individually reinnovate the form of Oldowan tools (when in the appropriate ecological circumstances) without *requiring* social learning. Moreover, low-fidelity social learning increased the frequency of the tools within and across populations and also influenced the small details of the behaviour, such as the choice of raw material used (Tennie et al., 2009; 2016; 2017).

Thus, there continues to be debate over whether early stone tools were the first products of cumulative culture or whether they were individually derived (a similar cultural argument has been made for the later Acheulean and Levallois industrial complexes, but only Oldowan-type stone tools were tested in this study, so the focus of this chapter will remain on these assemblages; but see O’Brien, 1981; Kohn & Mithen, 1999; Wynn, 1990; Vuaghan, 2001; Bar-Josef & Belfer-Cohen, 2001; Samson, 2006; Le Tensorer, 2006; Lycett, 2008; Shipton, 2010; Iovita & McPherron, 2011; Wynn, 2011; Beyene et al., 2013; Adler et al., 2014; Corbey et al., 2016; Tennie et al., 2016; 2017 and Hosfield et al., 2018 for some of the arguments made on these later assemblages). In order to begin examining these two alternative hypotheses, experimental tests are required. Although many such tests have been already conducted, most of these were with modern humans, who may not be ideal models for early hominins as we differ with regards to our anatomical build, motivations, cognition and genetic background from early hominins (Tennie et al., 2016; 2017). Instead, through cognitive cladistics, better models for the cognition of early hominins might be other primate species, who most likely posses a similar cognition and anatomy to early hominins (Sayers & Lovejoy, 2008).

5.1.2 Non-human primate stone tool-use

Although there is (currently) no evidence for the *intentional* shaping of stone tools in wild primates, several species of primates proficiently *use* stone tools across various contexts (see previous chapter). The most common stone tool-use behaviour recorded for various species of monkeys and chimpanzees is nut-cracking. Wild chimpanzees, predominantly across Western Africa, use stone or wood hammers and anvils to crack open five different types of nuts from around three years of age (Inoue-Nakamura et al., 1997; Biro et al., 2003). As these chimpanzees use at least two different tools and a set of steps to crack nuts, this behaviour is considered one of the most complex tool-use behaviours observed in wild non-human animals (Biro et al., 2003). Chimpanzee nut-cracking has been compared to early hominin stone knapping, as both behaviours require more than one tool and a step-wise approach to achieve the end result (alongside a similar "hitting" action; Whiten et al., 2009). A further similarity between chimpanzee nut-cracking and hominin flaking is the existence of a perceived nut-cracking "Movius" line[10] equivalent in Africa, which divides the nut-cracking chimpanzees in West Africa from the chimpanzees in East and South Africa who, until recently, were never observed to crack nuts, despite the local availability of both nuts and hammers (McGrew, 1996; Biro et al., 2003). The presence of nut-cracking at some sites, and its absence at others (despite no differences in ecology thus far detected) has been cited as evidence for the view that nut-cracking is a cultural behaviour that *requires* social information to emerge in naïve individuals (similarly to what has been suggested for early stone tools; Whiten et al., 1999). However, recently, Morgan et al. (2006) reported the first observation of chimpanzees nut-cracking in Cameroon, 1,700km away from the N'Zo-Sassandra river in Côte D'Ivoire, which had been proposed as the divider between nut-cracking chimpanzees and other populations. Therefore, similarly to the case of the Movius line for early hominins, nut-cracking was eventually identified (albeit in a lower frequency) in

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[10] The Movius line is a theoretical line that runs across northern India to delineate a perceived absence of Acheulean handaxes for most of the Pleistocene record under the Movius line area (Movius, 1948). This phenomenon has been cited as evidence for the cultural nature of Acheulean handaxes (e.g., Mithen, 1999). However, handaxes have now been found under the Movius line, in the Bosin Basin (Yamei et al., 2000), falsifying the Movius line concept. Indeed, a more parsimonious explanation for the general lack of handaxes under the Movius line (as, for now, Bosin Basin remains the only site with handaxes; Yamei et al., 2000) is that the behaviour (or the genes for the behaviour; Corbey et al., 2016) may have remained dormant until the raw material became available once again (Yamei et al., 2000; Corbey et al., 2016; Tennie et al., 2016), and in the meanwhile, alternative materials were used to make similar tools (Bar-Yosef & Belfer-Cohen, 2013).

communities that were previously hypothesised to not possess the cultural knowledge to crack nuts.

Despite being perceived as a complex tool-use behaviour, chimpanzees are not the only primates that crack nuts in the wild. Capuchins in Brazil (e.g., *Sapajus libidinosus,* Fragaszy et al., 2004, *Cebus apella,* Ottoni & Mannu, 2001) also habitually use hammerstones and anvils to crack nuts[11]. Recently nut-cracking was also (re)discovered in long-tailed macaques (*Macaca fascicularis aurea*), who use various pounding techniques to crack open nuts in the Andaman region of Thailand (Luncz et al., 2017; although, as described in the previous chapter, only one subspecies of long-tailed macaques has been found to crack nuts using tools; Bandini & Tennie, 2018). Thus, this complex tool-use behaviour is not only present in chimpanzees, but it is also observed across species of monkeys who have not been suggested to possess high-fidelity social learning skills (Visalberghi, 1987; Ottoni & Mannu, 2001; Fragaszy et al., 2004).

A by-product of nut-cracking in wild primates is that, although there is no evidence for intentional production of stone tools, occasionally stone flakes, indistinguishable to those made by early hominins, are found in the debris of nut-cracking sites across species. Mercander et al., (2002; 2007) describe how chimpanzees during nut-cracking bouts in Taï Forest, Côte d'Ivoire, unintentionally produce flakes from the hammerstones they use to pound the nuts. After comparing the flakes made by chimpanzees when nut-cracking to the flakes found in the earliest Oldowan assemblages, the authors conclude: "*the stone by-products of chimpanzee nut-cracking fall within the size spectrum and morphological parameters observed in a subset of the earliest known hominin technological repertoires"* (Mercander et al., 2002, 1455). Brazilian capuchins have also recently been observed to unintentionally make stone flakes similar to the ones found in the archaeological record (Proffitt et al., 2016). These capuchins practice a behaviour known as stone-on-stone (SoS) percussion, in which a smaller stone hammer is used to strike larger stationary standing stones (see also chapter II). The forceful striking of the hammerstone onto

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[11] Alongside various other stone tool behaviours, including digging for tubers and other hard-to-reach foods, other foraging behaviours, threat and sexual displays (Falótico et al., 2017) and the use of stone hammers to intentionally break standing stones; Proffit et al., 2016).

the standing stone sometimes creates small sharp-edged flakes, indistinguishable to the ones found in the hominin Oldowan archaeological record (according to Proffitt et al., 2016). Despite the rare, and unintentional, occurrence of flakes made by other animals, these tools are never used or intentionally made. Yet, the fact that flakes *can* be made by other primates suggests that their absence in animal tool-use repertoires might be due to a lack of need and/or motivation to use stone tools in the wild, rather than the lack of cognitive ability. Indeed, the teeth of most primates, especially chimpanzees, are sharp and strong enough to fulfil all the cutting needs of currently living wild primates (Toth & Schick, 1994).

5.1.3 Early tests on ape stone knapping

To test whether primates have the cognitive capacities to make and use stone tools, several experimental tests on captive subjects have been carried out. One of the first studies with this aim was carried out by Wright (1972), who tested a male captive orangutan (*P. pygmaeus)* named Abang on his stone knapping abilities (see also: https://www.youtube.com/watch?v=3exAOxSKYCE&feature=youtu.be). Abang was provided with all the materials needed for stone knapping: hammerstones, cores and a rewarded puzzle box that was sealed by a rope. The only way to access the reward inside the box was to cut the rope that sealed the door shut using a sharp cutting tool, such as a flake (Wright, 1972). Before testing, Wright (1972) demonstrated for Abang how to detach a flake from a core using a stone cobble as a hammer. Wright (1972) then used the flakes he made in front of Abang to cut a rope that sealed shut the door of the testing apparatus to retrieve the reward. After the first successful trial (in his tenth testing session) in which Abang made a flake by hitting a hammerstone against the core which lay on the ground and then used it independently to cut the rope of the testing apparatus, Wright (1972) concluded the experiment suggesting that modern orangutans demonstrate the motor and cognitive abilities for the stone knapping process, thus making it likely that early australopithecines (who had a similar anatomical structure to modern orangutans) also possessed the appropriate skills to make stone tools. Although Wright's (1972) pioneer study into the knapping abilities of a non-human ape provided one of the first comparative studies into the evolution of material culture in hominins, limited conclusions can be drawn from this data. Firstly, Abang, although naïve to stone knapping before Wright's (1972) study, had been trained in other behaviours beforehand and had been exposed to extensive human contact (Wright, 1972). Furthermore, Abang was always provided with demonstrations on how to make and use a flake before he was allowed to freely manipulate the materials, thus not rendering him naïve to the actions required for this behaviour. Indeed, Wright (1972, 300) acknowledges this shortcoming as well, writing: "*In retrospect it would clearly have been more informative had we been less helpful to Abang"*. Thus, conclusions cannot be drawn on the learning mechanisms behind the acquisition of stone knapping in apes (as Abang was not given the opportunity to individually learn the behaviour before social information was provided) or on what wild orangutans are capable of without any human training or exposure.

However, Wright's (1972) pilot study inspired further research into the stone knapping skills of other great apes, and was followed by Toth and colleagues (1993) who tested Kanzi, an adult male Bonobo (*Pan paniscus*) on his knapping abilities after human demonstrations (see general introduction for further discussion on Kanzi's enculturation). Toth et al., (1993) used a similar testing apparatus to Wright's (1972) original study, and so Kanzi was provided with stone cores, hammerstones, and a metal box with a hinged rear door that was also sealed by a rope. In the first phase of the study, the demonstrator fractured a core using a hand-held bipolar knapping technique (a hypothesised stone knapping technique for early hominins; Toth et al., 1993), making a flake in front of Kanzi. The demonstrator then used the flake to cut through the rope to open the apparatus and retrieve the reward (Toth et al., 1993). After the first few demonstrations, Kanzi picked up one of the flakes made by the demonstrator and used it to cut the rope and open the apparatus independently. In the second phase of the experiment, Kanzi was again provided with all the stone materials, but no useable flakes, and verbally encouraged to make the flakes himself to open up the box. This phase involved a long process of trail-and-error learning that was concluded, after 25 testing sessions, with Kanzi successfully producing flakes similar to those observed in Oldowan assemblages (according to Toth et al., 1993). The authors conclude that Kanzi: "*made significant and rather startling progress in his stone-tool making, rapidly acquiring many of the basic skills required to produce sharp-edged cutting tools from stone cores*" (Toth et al. 1993, 89). Yet, Toth et al., (1993, 1999) also acknowledge that there were some differences between Kanzi's preferred method of knapping and that hypothesised for

Oldowan hominins, most prominently in that Kanzi never seemed to perfect the amount of force needed and exhibited *“a relatively low degree of technological finesse*”, compared to modern human knappers (Toth et al. 1993, 89). Furthermore, Kanzi never used the demonstrated bipolar knapping technique to make flakes, but instead developed a new technique (not shown to him by the demonstrators) in which he threw a core onto the hard surface of his enclosure or against another one of the provided cores to make flakes (Schick et al., 2009). This new technique quickly became Kanzi’s preferred one, despite efforts to teach him to use the bipolar knapping method. Kanzi’s new technique of throwing a core against the other provided cores or hammerstones is comparable to the stone-on-stone (SoS) behaviour observed in wild bearded capuchin monkeys in Brazil that also produces flakes, according to Proffitt et al., (2016), identical to the ones associated with early hominins. Indeed, projectile reduction techniques, such as the one used by Kanzi and the wild capuchins in Brazil, have recently been demonstrated to be the most efficient ways to reduce cores and produce flakes, almost as expedient as bipolar knapping (Putt, 2015). Thus, the method demonstrated by Kanzi and the capuchins in Brazil could be a precursor technique (as it is considered to be less sophisticated, and potentially more dangerous, than bipolar flaking) to bipolar flaking, and one potentially also used by early hominins (Putt, 2015). Although this method remained Kanzi’s preferred technique to exploit cores, in a follow-up study, and after extensive training, Roffman et al., (2012) report that Kanzi did eventually start also using bipolar flaking techniques to make his stone tools.

Similarly to the limitations discussed for Wright’s (1972) study, the work carried out with Kanzi can only provide information on what enculturated apes can do after extensive training and demonstration in the target stone knapping behaviour. Thus, conclusions cannot be drawn on the individual learning of stone knapping by the apes from a naïve state. So far, only *one* study on stone knapping in non-human primates neither trained the subjects, nor provided demonstrations on the stone knapping process before testing. Westergaard & Suomi (1994) gave naïve, captive, unenculturated tufted capuchins (*Cebus apella*) cores, hammerstones and a large stationary stone anvil to examine whether they would spontaneously make flakes without any social information and without a clear motivation to make these tools. The monkeys were tested in their social group, and six out of eleven capuchins in the group spontaneously made flakes during the first seven trials (Westergaard & Suomi, 1994). The capuchins made flakes using three techniques: 1) striking a hammerstone against the large stationary stone anvil that had been provided by the researchers (displaying a similar technique to wild capuchins; Proffitt et al., 2016, and to Kanzi's preferred technique; Toth et al., 1993), 2) positioning a core on a perch and then hitting it with one of the hammerstones and, 3) striking together stones in each hand (a method roughly similar to the bipolar knapping technique hypothesised for early hominins; Toth et al., 1993). All of the six capuchins used the first method (SoS percussion; Proffitt et al., 2016), four used the second technique, and only two individuals used the bipolar knapping method (Westergaard & Suomi, 1994). The flakes made by the capuchins were comparable to those found in Oldowan archaeological assemblages (according to Westergaard & Suomi, 1994). It is important to note here that the captive capuchins spontaneously made flakes even though there was no clear need for them. In a follow-up experiment, the authors investigated whether the capuchins could spontaneously *use* the flakes they made, if they were motivated to do so. As in the first experiment, no demonstrations of how to use the flakes as cutting tools were provided, but a puzzle box was placed within the enclosure. The puzzle box consisted of a plastic container with a square opening on top. The opening of the puzzle box was sealed by an acetate covering that had to be cut to access the reward inside (Westergaard & Suomi, 1994). By the tenth testing session, three naïve capuchins used the flakes as cutting tools to retrieve the reward from the puzzle box, and two more capuchins went on to use the flakes as tools after testing (Westergaard & Suomi, 1994). The capuchins cut open the apparatus either by pressing the flake against the acetate cover and carrying out a cutting action to pierce through the covering, or by using the flake in conjunction with a hammerstone, in a hammer and chisel fashion (Westergaard & Suomi, 1994). This study demonstrates that naïve monkeys can spontaneously make stone flakes similar to those found in Oldowan assemblages, and use them for cutting purposes, without requiring social learning.

The stone tool-use repertoires of wild primates and the experimental findings with captive (albeit enculturated, except for the capuchins; Westergaard & Suomi, 1994) primates suggest that other animals possess the required cognitive and anatomical abilities to make and use flakes in similar ways to early hominins. However, to draw insight into the learning mechanisms behind early stone tools in both human and non-human primates, chimpanzees (one of our closest living relatives and one of the species with the most extensive tool-use repertoires; Whiten, 2015) should be tested on their stone knapping abilities, following the LS testing methodology outlined in the previous chapters of this thesis (and following recommendations by Pradhan et al., 2012). Thus, the aim of the study presented in this chapter was to provide naïve chimpanzees with all the materials necessary for stone knapping to observe whether they would spontaneously make *and* use flakes comparable to those found in the archaeological record (see below). As stone knapping is a complex behaviour, only one reinnovation of the process was required to provide evidence for the individual learning approach (thus the single-case ZLS standard was applied here, and the sample size *n*=52 met and surpassed the minimal sample size for this standard and the double-case standard as calculated in Bandini & Tennie, 2018).

By providing naïve chimpanzees with all the materials of stone knapping, it was hypothesised, based on previous LS studies with chimpanzees (see chapter III) and based on the results of studies with other primates (Wright, 1972; Toth et al., 1993; Westergaard & Suomi, 1994), that the chimpanzees in this study would be able to make and use flakes *without* requiring demonstrations, i.e., in the absence of any social learning. As this was not found to be the case here (see below), the social learning conditions described in the previous chapter were carried out in this study as well.

5.2 Materials and Methods

5.2.1 Subjects

Subjects were housed at Chimfunshi Wildlife Orphanage in Zambia, Africa (12^{o}23'S, 29^{o}32' E; see Appendix I). Chimfunshi was founded in the 1980s and is now over 4500-hectare large and one of the largest chimpanzee sanctuaries globally (Ron & McGrew, 1988). There are currently six groups of chimpanzees at Chimfunshi. Each group is housed separately in enclosures that measure between 17 and 77 hectares each. Subjects for this study were part of the “escape artists” group (*n*=4; M_{age}=29.5, SD=13.5) and Group 2 (*n*=48; M_{age}=17.6; SD=10). The “escape artists” group consists of: Milla, Cleo, Chiffon, and Colin (see table 1). The “escape artists” are the only chimpanzees that can be tested individually in Chimfunshi. These four individuals were placed in a separate enclosure from the rest of the chimpanzees at Chimfunshi as they gained a reputation for escaping the larger enclosures of groups 1-4 (hence the name "escape artists"). These chimpanzees live in a seven-hectare enclosure that consists of one outdoor area and four indoor management areas. The escape artists spend the day primarily in the outdoor enclosure, and sleep in the inside management rooms. Subjects receive two daily feeds between 11.30 and 12.30 and between 14.30 and 16.30. Group 2 live in semi-wild conditions in fenced woodlands (Ron & McGrew, 1988). The chimpanzees in Group 2 live outdoors and only enter the enclosed areas for their daily feeds, and have water available *ad libitum* throughout their enclosures (see Appendix I for demographic information on Group 2 and table 1 below for information on the escape artists group).

Table 1: Demographic information on the subjects in the escape artists (EA) group

Group	Name	Sex	Approx. DoB	Origin	Rearing
EA	Chiffon	Male	01.01.2000	Wild	Mother
EA	Cleo	Female	01.01.1983	Wild	Hand
EA	Colin	Male	05.10.1988	Captive	Mother
EA	Milla	Female	01.01.1972	Wild	Hand

5.2.2 Escape artist chimpanzees

One point of interest on the subjects in the escape artists group is the fact that Milla experienced extensive exposure to humans before coming to Chimfunshi. Milla was retrieved from a bar in Chingola (approx. 80km from Chimfunshi), where she was used as entertainment for patrons. Cleo was also hand-raised, but did not receive the same level of human contact as Milla. Chiffon was wild-born and mother-raised and Colin is Cleo's son, and so was born and mother-reared by Cleo in captivity. Milla and Cleo's higher exposure to human contact may have had an effect on their cognition (Pope et al., 2018) that could, in turn, have influenced their performance in this study (e.g., Milla's previous experience in the bar may have made her more likely to reinnovate the behaviour as she had pre-existing experience with cutting tools such as knives). Thus, these exceptional circumstances were kept in consideration during testing and subsequent analysis for Milla and Cleo. As the escape artists were the only group at Chimfunshi in which the chimpanzees can be separated and tested individually, this group was included in the study even if the background of two of the subjects was not ideal for the testing conditions. Due to Milla and Cleo's rearing histories, another group, Group 2, was also included in the testing sample, in order to incorporate chimpanzees that had a more stable and, likely, a more ecologically-valid background and current living situation (all the chimpanzees in Group 2 would be considered "*enriched captive apes*"; Henrich & Tennie, 2017). As the chimpanzees in Group 2 cannot be tested individually, they were tested in their social group.

5.2.3 Ethical statement

The research was approved by the University of Birmingham research board (reference UOB 31213), in line with the requirements for testing of animals in the UK and internationally. The project was also approved by CRAB (Chimfunshi Research Advisory Board) for the chimpanzees at Chimfunshi Wildlife Orphanage. All participation in the study was voluntary, and the escape artists, who were tested individually, entered the testing room of their own accord, and were allowed to leave if they showed visible signs of distress from being separated from the rest of their group. In Group 2, the testing apparatus was placed in the indoor feeding area, and the doors were left open so as to allow free access in and out of the testing room at all times during testing. Subjects were not food or water-deprived, and continued with their regular feeding routine during the study. Subjects have access to water *ad libitum*.

5.3 Materials

5.3.1 Testing Apparatus

The testing apparatus used in this study was modelled on the earlier version described in Wright (1972) and Toth et al., (1993) and consisted of two boxes secured to a wooden board (see Fig. 1 & 2). Box one (length/width/height in cm): 36cm x 15cm x 17.2cm; Box two (reward box): 26cm x 17.3cm x 17.3cm. The reward box had a clear Plexiglas window at the top that allowed for the reward inside to be visible to the chimpanzees (measuring 5cm x 16cm). The door of the reward box was pulled shut by a rope that ran through the inside, exited through a hole in the opposite end where it was accessible for approx. 5cm before running into a hole in box one. The rope was then secured in box one to a clamp that could be tightened to ensure that the rope was taut. Thus, the rope was only accessible in the area between the two boxes, and had to be cut here to allow the door of box one to open (see Fig. 1 & 2). The rope was a brown twisted cord hemp rope, approx. 2mm thick. This type of rope was selected as it was found to be (after pilot testing by EB) strong enough to withstand most attempts at removal without a tool, but could be cut using a knife or flake. Collectively, the apparatus weighed approx. 21kg (including the board). The apparatus was transported to Chimfunshi as two separate boxes, and then combined at the site by fastening the boxes to the wooden board with screws (the board measured 55.5cm x 75cm; distance of the puzzle box to the edge of the board: 21cm to the sides; 4cm to the front and back). The reward placed inside the apparatus included peanuts and dog biscuits, two of the Chimfunshi chimpanzees' favoured treat foods used during training sessions (*T.Calvi, pers.comm*). The reward was placed directly under the glass so that the subjects could clearly see the food through the window. The rope was then secured to a screw inside box one using a bowline knot, and passed through the reward box, where it was tied to the door again using a bowline knot.

Fig. 1: Colin (M, 18yo, escape artists group) manipulating the testing apparatus outside his enclosure (photograph by EB).

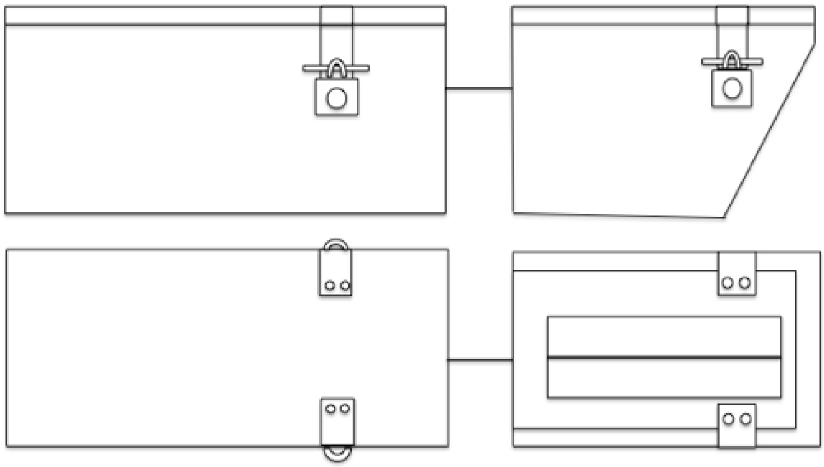

Fig. 2: Schematic drawing of the testing apparatus (Left: Box one; Right: Reward box. Drawing courtesy of A. Motes-Rodrigo).

5.3.2 Hammerstones

Hammerstones were collected prior to testing at various seaside locations around the UK and shipped to Chimfunshi alongside the cores. The hammerstones were selected based on the size and shape of the ones most commonly found in archaeological assemblages. Three ovoid hammerstones were included in each testing session, weighing between 500 and 1000g. Each subject received one small, medium and large hammer stone per testing session (Fig. 3).

Fig. 3: Hammerstones provided during testing. From left to right: small, medium and large hammerstones (photo by EB).

5.3.3 Cores

Retouched Norfolk Chert cores were provided to the subjects alongside the three hammerstones. As raw material, unretouched cores were purchased from a provider (Needham Chalks) in the UK and then retouched by *W. B. Archer* and EB at the University of Birmingham. The cores were modified to display: "*angle variability between ~90 degrees and ~30-40 degrees, and we aimed to produce either (1) 3 separate surfaces - with varying angles - from which flakes could potentially be struck from each specimen or (2) a continuous edge around the perimeter of the core with continuously varying angles between the above mentioned parameters*" (*W.B. Archer, pers. comm*). Overall, 50 cores were modified following this procedure to ensure a reliable source of test cores. The cores were numbered and weighed, ensuring that each core weighed min. 500g and max. 1500g. Each core was then scanned using the Artec Spider structured light scanner and images were combined in the 3D program MeshLab. The cores were then all packed separately and shipped to Chimfunshi (see Fig. 4 & Fig. 5). Subjects received one core per testing session, and overall 30 cores were used during the testing sessions.

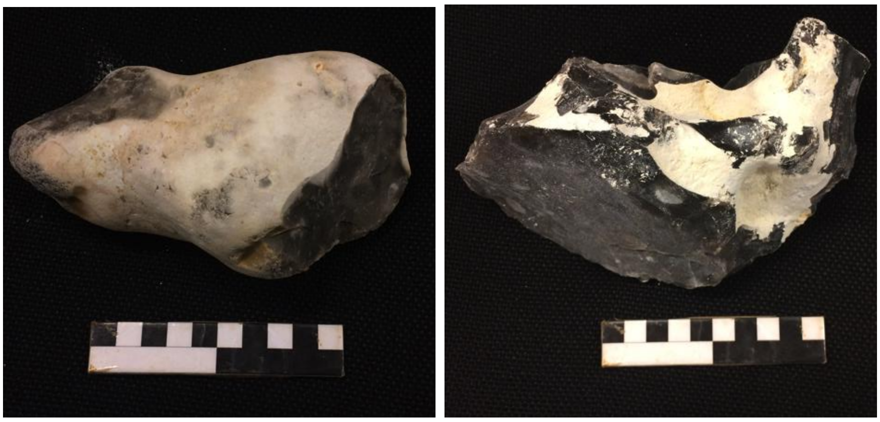

Fig. 4 & 5: from the left: unretouched core and retouched "test core" on the right (photo by EB).

5.4 Testing procedure

Each individual testing session with the escape artists lasted 20 minutes and group tests lasted 30 minutes. The escape artists participated in three individual tests per condition (see below for descriptions of the testing conditions) after which a group test was carried out. Subjects in Group 2 were tested twice per condition, in their normal group setting for 30 minutes per condition. The testing apparatus was set-up before the individuals were allowed into the testing area. The hammerstones and cores were placed near to the testing apparatus, on the side of the puzzle box. In the escape artists group, the testing apparatus was placed on a ledge directly outside of the indoor enclosure (see Fig. 1 above). The puzzle box was fastened to the mesh using black zip wires, which were secured around the locks of the puzzle box and then tied to the bars of the mesh. In the demonstration conditions, the apparatus was kept on the same ledge when testing Chiffon and Milla, and placed on a wooden table (approx. 80cm high) at around one meter distance from the enclosure when testing Cleo and Colin (due to personal safety concerns with these two individuals). The apparatus was also placed on the ledge outside of Group two’s indoor enclosure (and secured with black zip wires to the mesh). The door between Group two’s outdoor and the indoor enclosure was left open to allow for any individual to enter or exit the testing area, as these individuals were tested in their social group. During demonstrations in Group 2, the apparatus was placed on a separate table (approx. 80cm high) at around half a meter from the ledge. Subjects participated in the following conditions (carried out sequentially, see below for further description of each condition): *baseline condition, rope-cutting demonstration condition, soft-rope condition, flake demonstration condition, flake exchange condition, object movement re-enactment condition, stone-drop condition, full demonstration condition*. Testing was carried out by EB between June-August 2016.

5.4.1 Testing conditions

5.4.1.2 Baseline condition: This condition allowed for the individual reinnovation of the flake manufacture and use process (see previous chapter). Therefore, no social information on how to make or handle flakes, or how to cut the rope to open the puzzle box, was provided. Group 2 participated in two baseline tests in their social group, whilst the escape artists participated in three individual tests and one group test (see above; this was the case for all conditions, unless stated otherwise below).

5.4.1.3 Results-dependency conditions

5.4.1.3.1 Rope-cutting demonstration condition: This condition provided information on the result of cutting the rope to open the door, but not on the use of *flakes* to cut the rope, or how to make a flake. Instead, a regular kitchen knife (approx. 26cm long) was used to demonstrate the cutting actions of the rope and subsequent door opening. The demonstrator (EB) either stood near the ledge where the apparatus was placed (for the chimpanzees who were comfortable with having close contact with humans: Milla and Chiffon) or stood one meter away with the apparatus set up on a wooden table at approx. a height of 80cm (when testing Cleo, Colin and Group 2). Once the attention of the subject was attracted (e.g., by calling their name), the demonstrator (EB) slowly cut the rope with the knife and then allowed the subject to eat the reward inside (for Milla and Chiffon) or handed the reward to the subject (to Cleo, Colin and the subjects in Group 2). The box was then rebaited and placed on the ledge, next to the hammerstones and cores. The escape artists then had 20 minutes to manipulate the apparatus, and Group 2 had 30 minutes (the length of the testing sessions remained consistent across all the subsequent conditions).

5.4.1.3.2 Soft-rope condition: Due to the fact that interaction levels with the testing apparatus in the escape artists group seemed to decrease across testing conditions (see results section below); perhaps partly due to the fact that none of the subjects had been successful so far with retrieving the reward, a soft-rope condition was run. In this condition, the rope was left loose (the rope still keep the door to the reward box closed, but only loosely so). If the rope was pulled with the appropriate amount of force, the door to the reward box would open, allowing access to the food inside. By ensuring that the door could be opened (and the food accessed) without having to cut the rope, the aim was to increase the chimpanzees' levels of motivation to interact with the apparatus across the following tests. The hammerstones and core were still provided next to the testing apparatus, even if they were not needed in this condition. The levels of manipulation seemed to remain consistent in Group 2 (see data below), and to avoid potential conflict around reward retrieval between subjects (as Group 2 was tested in their social group), the subjects in Group 2 did not participate in the soft-rope condition. Similarly, only individual tests were carried out with the escape artists in this condition.

5.4.1.3.3 Flake no demonstration condition: In this condition, a premade flake (measuring approx. 12cm x 9cm x 4cm made using a bipolar knapping method by EB out of the view of the subjects) was provided to the subjects, but without any demonstrations on how to make *or* use the flake. The pre-made flake was placed in the enclosure, next to the hammerstones, core and puzzle box before the subjects were allowed into the testing area. Once the subjects entered the testing area, the normal testing period was carried out (i.e., 20minutes for the escape artists when tested individually, and 30minutes in their group testing conditions, and 30minutes for Group 2 in their social group testing conditions).

5.4.1.3.4 Flake demonstration condition: This condition provided information on how to cut the rope using a flake (without providing any information on how to *make* a flake). A pre-made flake (measuring approx. 12cm x 9cm x 4cm made using a bipolar knapping method by EB out of the view of the subjects) was used to cut the rope in front of the subjects. Similarly to the knife condition, the demonstrator either cut the rope using the flake whilst the puzzle box was on the ledge in front of the mesh (with Chiffon and Mila), or on a table approx. one meter away from the mesh when testing Colin, Cleo and Group 2. Once the puzzle box was opened, the subjects were allowed to eat the reward (either directly from the puzzle box, or the reward was handed over by EB). The reward box was then rebaited and placed back on the ledge, alongside the core and the hammerstones. The flake used to cut the rope was *also* placed in the enclosure, next to the hammerstones and core to observe whether the chimpanzees would *use* this flake to cut the rope as demonstrated.

5.4.1.3.5 Flake exchange condition (this condition was not carried-out with the long-tailed macaques in the previous chapter as it was not applicable[12]): As none of the subjects made or used flakes in the previous conditions (see data in results section below), this condition was provided in order to increase the *value* of the flakes, thus encouraging the chimpanzees to make their own flakes (even if only to be exchanged for food). Thus, three pre-made flakes measuring approx. 12cm x 9cm x 4cm (made by EB out of the view of the subjects) were placed in the enclosure next to the testing apparatus, hammerstones and core before the chimpanzees entered the area. The

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[12] The aim of this condition was to increase the chimpanzees' recognition of the value of flakes, and therefore encourage them to make flakes to open the testing apparatus. This condition (or similar, as the study in the previous chapter did not involve making a tool, but soley using one) was not required, as the macaques' motivation to manipulate the materials of the study remained high during testing. Therefore, this is an additional condition in the results-dependency testing conditions that was not applied in the macaque study (chapter IV & Bandini & Tennie, 2018).

escape artists were already familiar with trading practices, and regularly handed objects from inside their enclosure to their keepers in return for rewards (*T.Calvi, pers.comm*). Once the subject entered the testing area, EB pointed to one of the flakes, signalling for it to be handed to EB. Once the subject returned the flake, EB cut open the apparatus in front of the subject and allowed them to retrieve the reward. Colin and Cleo were familiar with (gently) throwing objects over to the keepers for exchanges, so the flakes were thrown over to EB, and the reward was thrown back in return. The apparatus was then rebaited, and another flake was requested. This process was repeated three times per subject (and in all exchanges the subjects always traded the flakes for the bait). Once all three pre-made flakes had been traded, the apparatus was rebaited and placed back on the ledge, alongside the core and hammerstones, but no flakes were provided. This condition was only carried out with the escape artists as the subjects in Group 2 are not familiar with the exchange procedure, and it was deemed too dangerous to attempt to exchange objects with them. Therefore, only the escape artists participated in this condition. Each of these subjects participated individually in three sessions and in one group test in which the exchange process was carried out with any individual that participated.

5.4.1.3.6 Object movement re-enactment condition: In this condition, subjects could observe how a stone dropping onto the core made a flake, but not the bodily actions of using a hammerstone to strike the core (i.e., they were not shown the actions of an arm holding a hammerstone and hitting a core). For this demonstration condition, a pulley-system was developed in which a large hammerstone (weighing approx. 1,000g) was attached to a rope. The core was then placed on a small box approx. 5cm from a metal mesh barrier, right under where the stone was hanging by the rope. The demonstrator (EB) hid behind the barrier, and once the chimpanzee’s attention was gained by another researcher (*L.Oña*) calling their name, the rope was released from the top of the barrier and the stone was dropped (from a height of around 50cm) on to the core, hitting the core on an angle. This procedure was repeated until a flake was made (on average, the stone was dropped three times before a flake was made). The produced flake was then retrieved by EB and used to cut open the rope in front of the subject. The reward was then passed to the subject by EB; and the puzzle box was rebaited and placed back on the ledge, next to the hammerstones and core.

5.4.1.4 Action-dependency conditions

5.4.1.4.1 Stone-drop demonstration condition: The aim of this condition was to further demonstrate the end product of dropping a stone onto core, this time with an agent carrying out the actions of dropping a stone from above. In this condition, the end product of the dropping action: the production of a flake, alongside a main component of the behaviour: the hammerstone hitting the core, were both demonstrated. However, the hypothesised early hominin bipolar knapping technique was still not revealed. To demonstrate these components of the behaviour, EB stood in front of the enclosure and the core was placed on the ground, in front of EB. Once the attention of the subject had been gained (e.g., by calling their name), the stone was dropped from a height of approx. 1.30m, falling on the core. This procedure was repeated until a flake was produced (on average the hammerstone was dropped twice before a flake was made). The produced flake was then retrieved and used to open the puzzle box and the reward was passed to the subjects. The apparatus was then rebaited and placed on the ledge next to the hammerstones and core.

5.4.1.4.2 Full demonstration condition: In the final demonstration condition, all the actions, goals and results of the bipolar stone knapping technique were demonstrated. If the manufacture of a flake is possible in apes (which it is, at least in enculturated orangutans and bonobos, see above) and if it *does* indeed require social learning, the behaviour should emerge in this condition – as it provides the same conditions in which Abang (Wright, 1972) and Kanzi (Toth et al., 1993) made and used flakes. The demonstration was carried out as follows (for all individuals in the escape artists group): EB baited the puzzle box and placed it on the same wooden table as used in previous conditions in front of the enclosure alongside a core and hammerstone. EB then attempted to open the door of the apparatus by pulling on it with exaggerated motions and making frustrated facial expressions (this act mimicked the inefficient method used by all of the subjects; see results section below). EB then manipulated the rope with her fingers and moved over to the core and hammerstone. Sitting in front of the enclosure, and near to the puzzle box, EB then proceeded to make a flake by striking the core at an angle (held in the left hand) with the hammerstone (held in the right hand). Once a flake was produced, EB used it to the cut the rope and open the door of the puzzle box. The reward was then passed to the subject, and the apparatus was rebaited and placed on the ledge. The hammerstones and core were placed alongside the apparatus. Only the escape artists were tested in this demonstration condition due to time constraints. Also due to time constraints, each escape artist participated in only two testing sessions, and one final group test.

5.4.2 Coding of behaviours

For each test, the recorded video was coded after testing. The video was coded for any manipulation of the testing apparatus. Fourteen different types of manipulation of the testing apparatus were identified. Each time the hammerstones and/or the core were manipulated was also recorded (see table 1 for the behaviours recorded and their detailed descriptions). 25% of the videos were second-coded following the same ethogram as EB (see below, table 2, including the behavioural forms included in the “other manipulations” and “stone manipulation” categories, see results section below) by a naïve coder (*M.Bandini*) who was not familiar with the aim or hypothesis of the study, in order to assess the interrater reliability of the data. The videos for interrater reliability were selected following the procedure designed and described by *D. Neadle* (see also previous chapters). The second coders observations were then compared to EB’s using a Cohen’s Kappa calculation (in R version 3.4.1).

5.4.2.1 Analysis

A non-parametric Mann-Kendall test (as the data was not normally distributed) was used to assess whether there was a monotonic upwards or downwards trend in the levels of manipulation of the testing apparatus over time across conditions and a Wilcoxon signed rank test (also a non-parametric test) was used to test whether there were any significant differences in time spent manipulating the rope and hammerstone and cores across the conditions. All analysis was run in R version 3.4.1 (2017-06-30).

5.5 Results

Table 2: Behaviours demonstrated by the subjects during testing and descriptions

Behaviour	Description
Manipulate Door	Manipulates the door of the testing apparatus with either the hands or feet, both hands and feet or with the mouth
Manipulate Locks	Manipulates the locks of the testing apparatus with either the hands or feet, both hands and feet or with the mouth
Manipulate Rope	Manipulates the rope with the hands, fingers or mouth
Manipulate Screws	Manipulates the screws of the testing apparatus with the hands or mouth, or combination of hands and mouth
Tool Door	Manipulates the doors of the puzzle box using a tool (e.g., one of the provided hammerstones or core)
Tool Locks	Manipulates the locks of the puzzle box using a tool (e.g., one of the provided hammerstones or core)

Tool Rope	Manipulates the rope using a tool (e.g., one of the provided hammerstones or a core)
Knock	Knocks on the apparatus with the knuckles
Shake	Shakes the testing apparatus violently with the hands or the feet, or a combination of hands and feet (Behaviour usually results in a very loud noise)
Multiple Manipulations	Individual uses a series of manipulations in rapid succession
Other	Individual manipulates the apparatus in a different way as described above
Stone Manipulation	Individual manipulates the hammerstones or core with mouth, fingers or hand
Pull Towards	Puzzle box is pulled towards the mesh between the subject and the apparatus
Push Away	Puzzle box is pushed away from the mesh between the subject and the apparatus

5.5.1 Reliability coding

The naïve coder watched 25% of the videos across all testing conditions and coded all the behaviours described in the previous table. Substantial agreement (Cohen, 1968) was found between coders, k =0.68.

5.5.2 Experimental results

None of the subjects in either the escape artists group or Group 2 in this study made a flake from the materials provided in any of the testing conditions, including the social learning conditions. Overall very low levels of interaction with the testing apparatus were recorded across both groups of chimpanzees. Out of the total 30 hours of testing in both single and group testing sessions, subjects spent only 4:40:08 of those testing hours manipulating the apparatus (15.6%). Interaction with the testing apparatus decreased numerically across the conditions, perhaps due to frustration at the lack of success experienced by the chimpanzees. However, the difference between interaction times across conditions was not significant (Mann-Kendall; z = -0.55141, n = 1036, p-value = 0.5814), suggesting that the subjects maintained their low levels of motivation from the start of testing to the end, despite the soft-rope condition (introduced to increase motivation), and even after trade of the flakes was introduced as a factor. The chimpanzees in the escape artists group varied in how long they spent manipulating the apparatus (this could not be calculated for the chimpanzees in Group 2 as the IDs of each individual were not known, and as the chimpanzees were tested as a group, interaction times could not be determined with confidence). Colin spent the longest time manipulating the testing apparatus (30.1% of the total testing period of this subject was spent manipulating the apparatus), followed by Milla (24.5%), Cleo (17.6%) and lastly Chiffon (8.6%).

5.5.2.1 Attempted flake-use

Although none of the subjects made flakes, one individual (in the escape artists group, Chiffon) did attempt to *use* one of the pre-made flakes to cut the rope of the apparatus on three occasions during the first, second and third trial of the flake demonstration condition (see supplementary CD for a video clip of one of Chiffon’s attempts during his third trial in the flake demonstration condition, and see also Fig. 6). In his attempts, Chiffon first picked-up one of the pre-made flakes that had been provided, then placed it on the rope of the puzzle box and carried-out a cutting motion with the flake on the rope. Unfortunately, Chiffon was unsuccessful in all three of his attempts to use the flake to cut the rope (making these "failed attempts"; more on this below), and did not damage the rope. These attempts may have failed because Chiffon did not persist long enough with trying to cut the rope with the flake to damage the rope (first attempt lasted 3secs, second attempt lasted 4secs and the last attempt lasted 10secs). If Chiffon had continued cutting the rope with the flake for longer, he may have been successful in opening the puzzle box. Chiffon did not show any other similar cutting behaviours in any of the remaining testing conditions.

Fig. 6: Chiffon attempting to use one of the pre-made flakes to cut the rope in the third trial of the flake demonstration condition (photograph by EB).

During the second trial of the flake-exchange condition, Cleo was also observed attempting to cut the rope. However, Cleo used the whole core for this failed attempt (attempt lasted 15secs). The core was too thick to fit in the space in between the two boxes (this was intentionally so to avoid allowing the chimpanzees to use the whole core instead of making a flake) and therefore Cleo's attempts were also unsuccessful. Other than Chiffon's attempts to cut the rope with one of the pre-made flakes, no other individual was observed using the flakes to cut the rope. Thus, similarly to the findings of the previous chapter, the chimpanzees in this study did not express the target behavioural form in any of the individual or social learning conditions provided.

5.5.2.2 Manipulations of the testing apparatus

Fourteen different manipulation types by the chimpanzees in this study were observed during testing (see table 2 above). Subjects across both groups and all conditions spent the longest time practicing the *manipulate door* behaviour (37.7% of the time spent manipulating the apparatus was coded as *manipulate door;* see Fig.7 below). This was followed by *shake* (14.4%), *manipulate rope* (10.5%), *stone manipulate* (6.9%), *manipulate lock* (6.7%), *multiple manipulations* (5.9%), *other* (4.5%*), tool door* (3.4%), *pull towards* (2.7%), *knock* (1.7%), *screw manipulate* (1.6%), *tool lock* (1.6%), *push away* (1.5%) *tool rope* (0.9%).

Fig. 7: Milla showing the door manipulation behaviour (photograph by EB).

Subjects also seemed to vary in their individual preferred manipulation types. See table 3 below for an overview of the time spent practicing the different manipulation types of each individual across all conditions. *Manipulate door* was the most common manipulation type for all the individuals, except for Colin, whose preferred manipulation was *shake* (see section below on alternative methods to open the apparatus for a further explanation of this behaviour). Indeed, the *shake* manipulation was almost only recorded for Colin. *Manipulate rope* was the second highest manipulation type for Milla and Cleo, whilst *manipulate rope* was observed rarely by Colin throughout the testing conditions, only being recorded in 1% of his testing sessions.

Table 3: percentage of time spent using the different manipulation types per individual (see table A5-1 in Appendix VI in for the same data but in number of occurrences)

	Chiffon		Cleo		Colin		Milla	
Manip.	Time (mm:ss)	%	Time (mm:ss)	%	Time (mm:ss)	%	Time (mm:ss)	%
Knock	00:07	0%	00:00	0%	02:21	3%	02:01	2%
Manipulate Door	13:20	47%	17:37	40%	27:07	31%	36:38	45%
Manipulate Lock	01:38	6%	05:18	12%	02:15	3%	06:33	8%
Manipulate Rope	04:18	15%	05:52	13%	00:47	1%	17:18	21%
Manipulate Screws	00:00	0%	01:50	4%	00:19	0%	02:17	3%
Multiple Manipulation	01:13	4%	03:05	7%	01:08	1%	03:07	4%
Other	00:00	0%	02:09	5%	00:20	0%	04:42	6%
Pull Towards	00:00	0%	01:34	4%	01:50	2%	00:13	0%
Push Away	01:26	5%	01:53	4%	00:00	0%	00:00	0%
Shake	00:00	0%	00:12	0%	39:44	46%	00:00	0%
Stone Manipulation	04:43	17%	02:47	6%	08:04	9%	01:49	2%
Tool Door	00:39	2%	00:05	0%	02:29	3%	05:22	7%
Tool Lock	00:00	0%	00:07	0%	00:30	1%	01:00	1%
Tool Rope	00:57	3%	01:16	3%	00:00	0%	00:16	0%

5.5.2.3 Other Manipulations

Manipulations coded as “other” included: manipulating the wooden platform on the bottom of the testing apparatus, manipulating the wires fastening the testing apparatus to the mesh (this was the most common “other” manipulation; 68%), peering into the window where the reward was located and turning the apparatus upside down. See table 4 below for the percentage of each manipulation across all individuals and conditions.

Table 4: Percentage of time spent practicing "other" manipulations (see table A5-2 in Appendix VI for the same data in number of occurrences)

Manipulation	Time (mm:ss)	%
Change orientation	01:37	13%
Manipulate wire	08:39	68%
Manipulate wood	01:07	9%
Peer into window	01:20	10%

5.5.2.4 Manipulations across conditions

The most commonly used manipulation by all the subjects varied across conditions. See table 5 below for an overview of the different manipulations of the testing apparatus and stones across individuals and conditions. As can be seen in the following table (table 5), manipulation of the door and lock are the most common manipulation types across conditions. Manipulation of the rope did seem to increase across conditions: starting from a maximum of 8% in the baseline condition, to 48% of manipulations in the final full demonstration condition, however this was not a significant difference (Wilcoxon signed rank test; V = 2, p-value = 0.375).

Furthermore, the numerical increase in manipulations of the rope may have simply been a product of extended exposure to the testing apparatus (as there are only a limited amount of manipulations possible).

Table 5: Occurrences and percentages of manipulations per individual across conditions. Condition name is in bold.

Manipulation & Occurrences

Individual & Condition	Knock		Manipulate Door		Manipulate Lock		Manipulate Rope		Manipulate Screws		Multiple Manipulation		Other		Pull Towards		Push Away		Shake		Stone Manipulation		Tool Door		Tool Lock		Tool Rope	
Baseline Test	**11**	**5%**	**33**	**16%**	**39**	**18%**	**13**	**6%**	**10**	**5%**	**17**	**8%**	**9**	**4%**	**7**	**3%**	**8**	**4%**	**36**	**17%**	**20**	**9%**	**3**	**1%**	**5**	**2%**	**0**	**0%**
Chiffon	2	8%	2	8%	9	36%	2	8%	0	0%	2	8%	0	0%	0	0%	7	28%	0	0%	0	0%	1	4%	0	0%	0	0%
Cleo	0	0%	10	19%	15	28%	4	7%	4	7%	7	13%	7	13%	3	6%	1	2%	0	0%	2	4%	0	0%	1	2%	0	0%
Colin	4	4%	13	14%	8	8%	4	4%	3	3%	5	5%	2	2%	4	4%	0	0%	36	38%	15	16%	0	0%	1	1%	0	0%
Milla	5	14%	8	22%	7	19%	3	8%	3	8%	3	8%	0	0%	0	0%	0	0%	0	0%	3	8%	2	5%	3	8%	0	0%
Rope-Cutting Demonstration	**5**	**4%**	**34**	**27%**	**12**	**9%**	**8**	**6%**	**1**	**1%**	**1**	**1%**	**7**	**6%**	**4**	**3%**	**3**	**2%**	**27**	**21%**	**19**	**15%**	**5**	**4%**	**1**	**1%**	**0**	**0%**
Chiffon	0	0%	1	7%	1	7%	1	7%	0	0%	0	0%	0	0%	0	0%	1	7%	0	0%	10	71%	0	0%	0	0%	0	0%
Cleo	0	0%	3	21%	2	14%	0	0%	0	0%	1	7%	0	0%	0	0%	2	14%	1	7%	5	36%	0	0%	0	0%	0	0%
Colin	2	3%	16	26%	5	8%	0	0%	0	0%	0	0%	0	0%	4	6%	0	0%	26	42%	3	5%	5	8%	1	2%	0	0%
Milla	3	8%	14	38%	4	11%	7	19%	1	3%	0	0%	7	19%	0	0%	0	0%	0	0%	1	3%	0	0%	0	0%	0	0%
Soft Rope Condition	**0**	**0%**	**27**	**39%**	**8**	**11%**	**6**	**9%**	**1**	**1%**	**2**	**3%**	**1**	**1%**	**2**	**3%**	**3**	**4%**	**5**	**7%**	**9**	**13%**	**6**	**9%**	**0**	**0%**	**0**	**0%**
Chiffon	0	0%	4	40%	1	10%	1	10%	0	0%	1	10%	0	0%	0	0%	1	10%	0	0%	2	20%	0	0%	0	0%	0	0%
Cleo	0	0%	11	34%	6	19%	5	16%	1	3%	1	3%	0	0%	0	0%	2	6%	0	0%	6	19%	0	0%	0	0%	0	0%
Colin	0	0%	8	40%	0	0%	0	0%	0	0%	0	0%	0	0%	2	10%	0	0%	5	25%	0	0%	5	25%	0	0%	0	0%
Milla	0	0%	4	50%	1	13%	0	0%	0	0%	0	0%	1	13%	0	0%	0	0%	0	0%	1	13%	1	13%	0	0%	0	0%
Flake No Demo Condition	**3**	**5%**	**26**	**42%**	**6**	**10%**	**5**	**8%**	**1**	**2%**	**1**	**2%**	**0**	**0%**	**2**	**3%**	**0**	**0%**	**9**	**15%**	**9**	**15%**	**0**	**0%**	**0**	**0%**	**0**	**0%**
Chiffon	0	0%	2	50%	2	50%	0	0%	0	0%	0	0%	0	0%	0	0%	0	0%	0	0%	0	0%	0	0%	0	0%	0	0%
Cleo	0	0%	2	11%	4	21%	4	21%	1	5%	0	0%	0	0%	1	5%	0	0%	0	0%	7	37%	0	0%	0	0%	0	0%
Colin	3	8%	21	57%	0	0%	1	3%	0	0%	0	0%	0	0%	1	3%	0	0%	9	24%	2	5%	0	0%	0	0%	0	0%

Milla	0	0%	1	50%	0	0%	0	0%	0	0%	1	50%	0	0%	0	0%	0	0%	0	0%	0	0%	0	0%	0	0%	0	0%
Flake Demo Condition	**7**	**4%**	**65**	**38%**	**13**	**8%**	**31**	**18%**	**0**	**0%**	**3**	**2%**	**0**	**0%**	**3**	**2%**	**6**	**3%**	**28**	**16%**	**9**	**5%**	**3**	**2%**	**0**	**0%**	**5**	**3%**
Chiffon	0	0%	13	35%	2	5%	14	38%	0	0%	0	0%	0	0%	0	0%	1	3%	0	0%	0	0%	2	5%	0	0%	5	14%
Cleo	0	0%	7	44%	0	0%	1	6%	0	0%	1	6%	0	0%	1	6%	5	31%	0	0%	1	6%	0	0%	0	0%	0	0%
Colin	7	8%	31	37%	4	5%	5	6%	0	0%	1	1%	0	0%	2	2%	0	0%	28	33%	5	6%	1	1%	0	0%	0	0%
Milla	0	0%	14	39%	7	19%	11	31%	0	0%	1	3%	0	0%	0	0%	0	0%	0	0%	3	8%	0	0%	0	0%	0	0%
Flake Exchange Condition	**5**	**5%**	**48**	**48%**	**6**	**6%**	**26**	**26%**	**5**	**5%**	**4**	**4%**	**0**	**0%**	**0**	**0%**	**1**	**1%**	**0**	**0%**	**2**	**2%**	**1**	**1%**	**0**	**0%**	**3**	**3%**
Chiffon	0	0%	19	56%	0	0%	12	35%	0	0%	0	0%	0	0%	0	0%	0	0%	0	0%	1	3%	0	0%	0	0%	2	6%
Cleo	0	0%	5	26%	1	5%	7	37%	3	16%	1	5%	0	0%	0	0%	1	5%	0	0%	1	5%	0	0%	0	0%	0	0%
Milla	5	10%	24	50%	5	10%	7	15%	2	4%	3	6%	0	0%	0	0%	0	0%	0	0%	0	0%	1	2%	0	0%	1	2%
Object Movement Re-enactment	**0**	**0%**	**19**	**40%**	**2**	**4%**	**8**	**17%**	**0**	**0%**	**1**	**2%**	**0**	**0%**	**0**	**0%**	**2**	**4%**	**0**	**0%**	**14**	**30%**	**1**	**2%**	**0**	**0%**	**0**	**0%**
Chiffon	0	0%	3	43%	0	0%	1	14%	0	0%	1	14%	0	0%	0	0%	1	14%	0	0%	1	14%	0	0%	0	0%	0	0%
Cleo	0	0%	3	50%	0	0%	1	17%	0	0%	0	0%	0	0%	0	0%	1	17%	0	0%	1	17%	0	0%	0	0%	0	0%
Colin	0	0%	0	0%	0	0%	0	0%	0	0%	0	0%	0	0%	0	0%	0	0%	0	0%	10	100%	0	0%	0	0%	0	0%
Milla	0	0%	13	54%	2	8%	6	25%	0	0%	0	0%	0	0%	0	0%	0	0%	0	0%	2	8%	1	4%	0	0%	0	0%
Stone Drop Demonstration	**0**	**0%**	**20**	**35%**	**3**	**5%**	**13**	**23%**	**0**	**0%**	**1**	**2%**	**0**	**0%**	**1**	**2%**	**0**	**0%**	**0**	**0%**	**7**	**12%**	**11**	**19%**	**1**	**2%**	**0**	**0%**
Chiffon	0	0%	2	40%	0	0%	2	40%	0	0%	0	0%	0	0%	0	0%	0	0%	0	0%	1	20%	0	0%	0	0%	0	0%
Cleo	0	0%	1	100%	0	0%	0	0%	0	0%	0	0%	0	0%	0	0%	0	0%	0	0%	0	0%	0	0%	0	0%	0	0%
Colin	0	0%	0	0%	0	0%	0	0%	0	0%	0	0%	0	0%	0	0%	0	0%	0	0%	5	100%	0	0%	0	0%	0	0%
Milla	0	0%	17	37%	3	7%	11	24%	0	0%	1	2%	0	0%	1	2%	0	0%	0	0%	1	2%	11	24%	1	2%	0	0%
Full Demonstration	**0**	**0%**	**35**	**30%**	**3**	**3%**	**47**	**40%**	**1**	**1%**	**1**	**1%**	**0**	**0%**	**3**	**3%**	**5**	**4%**	**6**	**5%**	**9**	**8%**	**2**	**2%**	**0**	**0%**	**5**	**4%**
Chiffon	0	0%	2	18%	0	0%	5	45%	0	0%	0	0%	0	0%	0	0%	1	9%	0	0%	3	27%	0	0%	0	0%	0	0%
Cleo	0	0%	16	28%	1	2%	26	46%	1	2%	1	2%	0	0%	2	4%	4	7%	0	0%	0	0%	1	2%	0	0%	5	9%
Colin	0	0%	2	13%	2	13%	0	0%	0	0%	0	0%	0	0%	1	6%	0	0%	6	38%	5	31%	0	0%	0	0%	0	0%
Milla	0	0%	15	45%	0	0%	16	48%	0	0%	0	0%	0	0%	0	0%	0	0%	0	0%	1	3%	1	3%	0	0%	0	0%

5.5.2.5 Individual and group testing

Numerical differences were recorded between the occurrences of manipulation types individuals (from the escape artists group) showed when tested individually and when they were tested in a group. As there were only six group tests in total (with the escape artists), and the chimpanzees were tested in a group setting on different days to when they were tested on their own, these observed differences could not be tested statistically and could have simply been the product of other, unaccounted for, external factors (but see table 6 below for numerical occurrences). One observed difference between manipulations in the individual versus the group setting was that when tested individually, the most common manipulation for Colin was *shake* (46% of his manipulations were *shake* when tested alone), yet there were no instances of the *shake* behaviour in the group test by Colin, or any other individual. *Manipulate door* remained high for both Chiffon and Milla in both individual and group testing sessions, but was never recorded for Cleo in the group test, although she did show this behaviour when she was tested alone. Overall, numerically, fewer manipulation types were observed in the group test than in when the subjects were tested individually (however, again, these differences may have simply been the product of external factors as testing conditions were not always the same between individual and group testing session; see above).

Table 6: Time spent practicing manipulation types when subjects were tested in a group setting (see table A5-3 in Appendix VI for the same data in occurrences)

	Chiffon		Cleo		Colin		Milla	
Manipulation	Time (mm:ss)	%	Time (mm:ss)	%	Time (mm:ss)	%	Time (mm:ss)	%
Knock	00:00	0%	00:00	0%	00:05	3%	00:08	1%
Manipulate Door	00:47	48%	00:00	0%	01:42	52%	04:13	29%
Manipulate Lock	00:12	12%	00:00	0%	00:00	0%	01:43	12%
Manipulate Rope	00:00	0%	00:00	0%	00:00	0%	00:43	5%
Manipulate Screws	00:00	0%	00:00	0%	00:00	0%	00:00	0%
Multiple Manipulation	00:23	23%	00:19	100%	00:10	5%	00:08	1%
Other	00:04	4%	00:00	0%	00:09	5%	03:15	22%
Pull Towards	00:00	0%	00:00	0%	00:58	29%	00:12	1%
Push Away	00:00	0%	00:00	0%	00:00	0%	00:14	2%
Shake	00:00	0%	00:00	0%	00:00	0%	00:00	0%
Stone Manipulation	00:00	0%	00:00	0%	00:00	0%	00:41	5%
Tool Door	00:00	0%	00:00	0%	00:13	7%	00:50	6%

Tool Lock	00:12	12%	00:00	0%	00:00	0%	02:36	18%
Tool Rope	00:00	0%	00:00	0%	00:00	0%	00:00	0%

5.5.2.6 Group 2

The chimpanzees in Group 2 spent (numerically), on average, less time manipulating the testing apparatus than the escape artists. Again, this numerical difference could not be investigated statistically as the individuals in Group 2 were tested in their social groups, whilst the escape artists participated in both individual and (a different number of) group tests, thus not making the data between the two groups comparable for statistical testing. See table 7 below for the cumulative time spent of all the individuals in Group 2 manipulating the testing apparatus.

Table 7: Time spent practicing the manipulation types in Group 2 (see table A5-4 in Appendix VI for the same data but in occurrences)

Manipulation	Time (mm:ss)	%
Push Away	00:40	3%
Manipulate Door	04:13	21%
Manipulate Lock	01:04	5%
Manipulate Rope	00:23	2%
Manipulate screws	00:00	0%
Multiple Manipulation	07:00	35%
Stone Manipulation	01:16	6%
Knock	00:08	1%
Shake	00:27	2%
Other	02:04	10%
Pull Towards	02:40	13%
Tool Door	00:00	0%
Tool Rope	00:00	0%
Tool Lock	00:00	0%

5.5.2.7 Manipulations of the hammerstones, core and flakes

Stone manipulation events consisted of: *knock hammerstones or core with knuckles, sniff hammerstone or core, lick or bite hammerstone or core, touch hammerstone or core, drag hammerstone or core across the mesh of the enclosure, hit hammerstone or core on the ledge, throw hammerstone or core out of the enclosure, spin on hammerstone, wave hammerstone or core in the air, move hammerstone or core* and *throw hammerstone or core in the air during display* (see table 8 for the percentage time spent practicing each of these manipulations; and see the provided CD for video clips of Chiffon showing the *throw hammerstone or core in the air during display* manipulation and Colin showing the *hit hammerstone or core on ledge* and *spin* manipulations). Any stone manipulation that was directed towards the testing apparatus was coded as "*tool door*", "*tool lock*" or "*tool rope*" (see above). It was hypothesised that the manipulation of the hammerstones and core would increase after the demonstration conditions (this can even happen due to widespread social learning mechanisms such as stimulus enhancement). However, no significant difference was found between the number of instances of hammerstone and core manipulation across the conditions (Wilcoxon signed rank test; V = 7, p-value = 0.625).

Table 8: Time spent practicing the different manipulations of the hammerstones and core (see table A5-5 in Appendix VI for the same data but in number of occurrences)

Manipulation	Time (mm:ss)	%
Display	02:49	15%
Drag across mesh	02:54	15%
Hit on ledge	01:54	10%
Knock	01:47	9%
Lick or Bite	01:00	5%
Move	00:43	4%
Sniff	02:09	11%
Spin	00:32	3%
Throw	03:44	19%
Touch	01:03	5%
Wave	00:45	4%

5.5.2.8 Alternative methods to open the testing apparatus

Although the chimpanzees never cut the rope that sealed the door of the testing apparatus, Colin, Cleo and Milla were occasionally successful in opening the door using other methods. As a by-product of Colin's *shake* behaviour, the screw holding the rope taut would, on occasion, become unattached, loosening the rope (this occurred four times across all the testing conditions). Once the rope was no longer taut, Colin was able to forcefully pull open the door, retrieving the reward. Cleo and Milla were both successful in opening the door without cutting the rope once in four and three testing sessions respectively. Both subjects opened the door by picking at the rope with their fingers throughout the whole 20 minute testing session, loosening the rope until it was not tight anymore (therefore losing its strength) and then they could pull the door of the reward box open. Chiffon never attempted any of these alternative methods, nor did the subjects in Group 2.

5.6 Discussion

Despite an extended period of interaction with the testing apparatus and several low and high-fidelity social learning conditions (including a full demonstration of the stone knapping behaviour) none of the chimpanzees tested in this study made, or even attempted to make, a stone flake to open the apparatus. One chimpanzee, Chiffon, did attempt to use a pre-made flake to cut the rope, but was unsuccessful in all of his attempts. These findings are inconsistent with those of previous studies with other species of non-human primates (e.g., Wright, 1972; Toth et al., 1993; Westergaard & Suomi, 1994) and do not support the initial hypothesis that chimpanzees would *spontaneously* make flakes (in the baseline condition). Potential explanations for the lack of reinnovation of the stone knapping process in this study are discussed below.

5.6.1 Limitations of the testing apparatus

One possible limitation of this study, which may have hindered the chimpanzees' ability to reinnovate the target behaviour, is that the testing apparatus used here might have been too cognitively opaque for the chimpanzees. The apparatus was modelled on those used by Wright (1972) and Toth et al., (1993) for their subjects. However, the subjects in these earlier studies were immediately shown by the researchers that the rope had to be cut (and how to cut it using a flake) to open the door of the reward box. On the other hand, no demonstrations on how to cut the rope were provided to the chimpanzees before the social learning conditions in the current study. Thus, the subjects in this study were required to individually learn the opening mechanism of the puzzle box (at least in the first LS baseline condition, in later conditions the purpose of the rope and the opening mechanism was demonstrated by EB). Furthermore, the fact that the puzzle box consisted of two different boxes, one of which served no clear purpose to the subjects (as it only contained the screw to tighten the rope), may have resulted in the overall testing apparatus being too cognitively opaque for the chimpanzees. Indeed, an extended learning period seemed to be necessary for the subjects of this study to make the connection between the door of the reward box and the rope, as it was only after three conditions (one individual learning and two demonstration conditions, in which the rope was cut in front of the subjects), in the flake demonstration condition that Chiffon attempted to sever the rope with a pre-made flake. Furthermore, rope manipulations stayed low throughout the conditions (see results section) and manipulations of the rope only increased numerically, but not statistically, in the later conditions (after repeated demonstrations by EB on how to cut the rope to open the puzzle box). These findings suggests that the purpose of the rope was not immediately clear to the subjects, and that perhaps a longer overall testing period may have been required (the current study was carried out daily over eight weeks) for the subjects to fully understand that the rope had to be removed to open the door, after which they could start exploring methods to do so.

Additionally, it is possible that the Plexiglas viewing pane on the top section of the reward box may have been too narrow for the subjects to gain a clear view of the food, potentially reducing their motivation to manipulate the apparatus (although see also Boysen & Berntson, (1995) and Wood & Whiten, (2017) who both report that chimpanzees (*Pan troglodytes*), capuchins (*Sapajus apella*) and children (*Homo sapiens*) performed worse in a cognitive test when the reward was visible than when the reward was out of view, suggesting that being able to see a reward is not always conductive to performance). To correct the potential limitations of the testing apparatus used here, an alternative apparatus, modelled on that used by Westergaard & Suomi, (1994), will be used in future follow-up tests. The new apparatus consists of a Plexiglas "drum", in which the sides of the drum are fully transparent, so that the food rewarded inside is clearly visible, and the top of the drum is made of silicone, which can only be cut open using a sharp object (see Fig. 8. This new, amended, apparatus is currently being used by *A. Motes-Rodrigo* in follow-up studies with chimpanzees and the other great ape species). This alternative testing apparatus is less cognitively taxing and may be more naturalistic for the apes.

Fig. 8: 'Drum' testing apparatus used in follow-up studies by A.Motes-Rodrigo (photograph by EB).

5.6.2 Motivation levels

The overall difficulty of the puzzle box used in this study may have also contributed to the perceived low levels of motivation by the subjects to participate in the task. Whilst in the initial individual testing conditions all subjects spent at least 30% of the testing session manipulating the apparatus, the levels of interaction numerically decreased across the conditions (although this was not statistically significant; see above). The observed lack of motivation could be related to the difficulty of the task and the subjects' subsequent lack of success. Indeed, the fact that none of the chimpanzees were successful in gaining the reward whilst interacting with the puzzle box (other than Milla, Cleo and Colin who on occasion managed to open the box using one of the alternative methods, see results section) may have also discouraged further interaction with the apparatus (see also Englemann et al., 2017).

The soft-rope condition, in which the testing apparatus was loosely sealed with a slack rope that allowed the chimpanzees to pull open the door and retrieve the reward, was an attempt to counteract the observed low levels of motivation. Although the subjects in the escape artist group did show a slight numerical increase in levels of manipulation in the conditions after the soft-rope condition, this was not statistically significant. The low levels of motivation remained even after the demonstration conditions. Indeed, despite the multiple demonstrations of the rope being cut with a flake, only Chiffon eventually attempted to use a flake (and only in the later conditions), and even then was unsuccessful in cutting the rope in all of his attempts. In all attempts, Chiffon only made a couple of cutting actions (lasting 3, 4 and 10seconds each; see results section) on the rope, without damaging it, before placing the flake down and moving away from the testing area. Chiffon's failure may have discouraged him from trying to use a flake again. However, it is of note that Chiffon's attempts to use the flake occurred only after the demonstration conditions in which EB used a flake to cut open the rope (i.e., after the flake demonstration condition). The fact that only Chiffon attempted to use a flake after these demonstrations however further suggests that the demonstrations may not have been seen as effective learning opportunities by the other chimpanzees (see general introduction). The new apparatus described above may provide one potential solution to the low levels of motivation observed here, as perhaps having a clearer view of the reward, and a an overall less cognitively taxing and more naturalistic apparatus may increase the subjects' motivation to solve the task. This remains to be tested.

5.6.3 Pre-existing techniques

One interesting aspect of Milla's background knowledge is that, due to her early exposure to humans, Milla had experience with standard kitchen knives, and had been observed multiple times cutting food with a knife when she was kept at the bar (before she was rescued and brought to Chimfunshi; *T. Calvi, pers. comm*). Therefore, Milla already had some experience of the properties and functions of cutting tools. Yet Milla never attempted to use a flake to cut the puzzle box's rope (whilst Chiffon, who, to the best of our knowledge, did not have experience of cutting tools, did try to use the flakes to cut the rope). Milla's apparent inability to transfer her knowledge of cutting tools (knives) to flakes may have been due to some level of behavioural conservatism (a reluctance to acquire and explore novel behaviours; Harrison & Whiten, 2018). This phenomenon, alongside functional fixedness (the reluctance to innovate a novel use for a tool with which an animal already has experience; Hanus et al., 2011; Harrison & Whiten, 2018), has been observed in chimpanzees, amongst other non-human apes (Marshall-Pescini & Whiten, 2008; Hanus et al., 2011; Bonnie et al., 2012; Harrison & Whiten, 2018; but see also Manrique et al., 2013). Milla may have associated knives, and only knives, with cutting tasks, and therefore might not have been able to view flakes as valuable alternative cutting tools. Additionally, it is possible that Milla only considered food as a substance that required cutting, but did not transfer this knowledge (that objects can be cut) to the rope. Thus, Milla's previous experience with cutting tools and tasks may have obstructed her ability to reinnovate the stone knapping process and use of flakes. This does not, however, explain why flakes were not made or used by any of the other chimpanzees (who did not have experience of cutting tools), even when the context of the study was changed (when the general trading value of the flakes was introduced in the *flake exchange condition*).

5.6.4 Sensitive learning periods

As discussed for the long-tailed macaques (*Mff)* in the previous chapter (Bandini & Tennie, 2018), it is possible that, if the chimpanzees in this study had been exposed to flakes during a sensitive learning period in ontogeny, they may have recognised their value as cutting tools earlier on in the study. In turn, this knowledge may have motivated the chimpanzees to make their own flakes when needed to open the puzzle box. Although Milla and Cleo had some experience of man-made objects (including Milla's experience with knives; see above), none of the chimpanzees in this study had encountered flakes before this study. On the other hand, early hominin children were, most likely, naturally surrounded by the products of knapping whilst growing-up, including discarded flakes, and this exposure early in ontogeny may have helped reinnovate (or, if the alternative hypothesis is correct, socially learn) the knapping process – perhaps via end-state emulation (Reindl et al., 2017). Group 2 did include five juvenile chimpanzees (between the ages of 3-7 years) however these individuals rarely came into the testing room, and most likely a much longer exposure to flakes would be required for the juvenile chimpanzees to appreciate their function. Future follow-up studies on stone knapping in primates should introduce flakes and stone cores to chimpanzees (and other great apes) at a younger age (the youngest individuals in this study were 3 years old at the time of testing), to examine whether this experience increases the likelihood of reinnovation in adulthood (as may also be the case for *Mfa* x *Mff* hybrids; Tan et al., 2017).

5.6.5 Knapping may not be within chimpanzees' ZLS

Finally, it could be that the chimpanzees did not make or use flakes in this study simply because stone knapping may not be within chimpanzees' ZLS. Thus, it could be that unenculturated chimpanzees are not capable of individually reinnovating, or socially learning, early hominin stone knapping. Although it is indeed possible that knapping is not in chimpanzees ZLS, this possibility is surprising when taking into consideration the fact that naïve capuchin monkeys, who are phylogenetically more distant to humans than chimpanzees, spontaneously reinnovated the manufacture and use of flakes in similar circumstances as the ones presented in this study (Westergaard & Suomi, 1994). However, stone knapping could have evolved separately in the two primate lineages, and therefore it is possible that capuchins can spontaneously make flakes, whilst chimpanzees cannot. Indeed, whilst chimpanzees may have a larger overall tool-use repertoire than capuchins, both wild and captive capuchins demonstrate more stone tool-use behaviours within their repertoires than chimpanzees. So far, wild chimpanzees have only been recorded nut-cracking with stone tools, whilst capuchins demonstrate a wide range of stone tool-use behaviours (Ottoni & Mannu, 2001; Proffitt et al., 2016). Therefore, capuchins may possess the cognitive requirements to flexibly use stone tools in a more efficient and varied manner than chimpanzees. This hypothesis remains to be tested.

Yet, if stone knapping is not within chimpanzees' ZLS, and if the alternative approach is correct and chimpanzees do require social information to acquire this behaviour (Whiten et al., 1999; 2001; 2003; 2011; Gruber et al., 2015 and for early hominin stone tools; McNabb et al., 2004; Gamble & Porr, 2005; Lycett & Gowlett, 2008; Shipton, 2010; Goren-Inbarm

2011), the behaviour should have emerged in either the low-fidelity social learning conditions in which the results and goals of the behaviour were demonstrated, or in the high-fidelity social learning condition, in which the full goals, actions and results of the behaviour were demonstrated, as was the case for Abang the orangutan (Wright, 1972) and Kanzi, the bonobo (Toth et al., 1993). However, the fundamental difference between this study and the previous studies with great apes (Wright, 1972 and Toth et al., 1993) is that, in this study, unenculturated apes were tested (with the possible exception of Milla and Cleo; see above). As discussed in the general introduction, after extensive training and demonstrations, enculturated apes may be able to copy behaviours that are outside of the ZLS of their species. Indeed, it seems likely that this was the case for both Abang and Kanzi, who acquired the behaviour after extensive training by their human carers in this, and other, human tasks (Wright, 1972; Toth et al., 1993). Conversely, in this study, the target behaviour did not emerge after any of the social learning conditions. This finding is in line with the ZLS hypothesis, which argues that primates can only acquire behaviours that they could individually reinnovate in the first place. Thus, whilst this study did not provide evidence for the ZLS account of stone knapping in apes, it also failed to provide evidence for the alternative social learning hypothesis.

5.7 Conclusion

Further testing on the emergence of stone knapping in non-human primates is still required, as this study remains inconclusive on the learning mechanisms behind this behaviour (however note that the minimum sample sizes for both the single and double-case ZLS standards required to draw conclusions from negative findings were met and surpassed in this study; Bandini & Tennie, 2018). Future directions for research include retesting naïve, captive chimpanzees following the method described in this chapter, but controlling for the additional factors mentioned above (e.g., the relatively cognitively opaque nature of the testing apparatus and overall low levels of motivation to interact with the testing apparatus). Testing chimpanzees with multiple, more naturalistic, less cognitively opaque apparatuses might yield different results to the ones presented here (indeed, this task is currently being carried-out by *A.Motes-Rodrigo*).

Although this study did not provide conclusive support for either the ZLS or the social learning hypotheses for early stone tools, this research contributes to the debate over whether chimpanzees are capable of socially learning behaviours outside of their ZLS. The strong formulation of the ZLS hypothesis predicts that individuals are not able to learn behaviours that are outside their zone of latent solutions, and, as discussed in the introduction, the evidence for action-copying is very rare in enculturated apes, and, so far absent for unenculturated apes (Tennie et al., 2009). If it was to be confirmed that stone knapping is beyond chimpanzees' ZLS, even after controlling for the influencing factors (see above), then this study would provide further support for the view that chimpanzees cannot individually or socially acquire behaviours that are outside of their individual learning abilities.

Chapter VI: General Discussion

6.1 Summary and discussion

This thesis investigated the individual learning abilities of primates in relation to their material culture. Chapter I provided the theoretical background to the thesis, including a brief history and overview of the current state of the individual and social learning field in primates. The general introduction discussed some of the theoretical and methodological limitations of the current approaches to examining the acquisition of behavioural forms in primates (e.g., “the method of exclusion” Whiten et al., 1999; 2001; Perry, 2001; van Schaik et al., 2003; Santorelli et al., 2011; Robbins et al., 2016). Although these methods have many commendable points, it was argued that they cannot truly identify cultural behaviours (as currently defined), as they fail to rigorously control for factors other than social learning in the acquisition of behavioural forms in primates. Factors such as the environment and genetics cannot be fully excluded from playing an important role in creating and sustaining wild primate behaviours through observational studies alone. Thus, although the method of exclusion can document (to some degree) wild behavioural repertoires, it cannot (alone) identify the mechanisms behind the emergence of these repertoires within and across populations (Laland & Janik, 2006).

The ZLS hypothesis (Tennie et al., 2009) introduced in the first chapter provides an alternative theoretical and methodological approach to explaining primate (including human) tool-use. The ZLS hypothesis fills the phylogenetic gap left open by Vygotsky’s (1978) ZAD/ZPD concepts, by providing a baseline for the ZAD concept and by extending these concepts to make species-wide claims (Reindl et al., in press). The ZLS favours an individual reinnovation approach to explaining animal tool-use, in which all animals have their own species-specific range of behaviours that each individual is technically capable of reinnovating without *requiring* social learning. As for the role of culture in the ZLS account, low-fidelity social learning plays an important part in increasing the frequency of these behaviours within populations, creating the observed differences in behavioural repertoires (e.g., in chimpanzees; Whiten et al., 1999; 2001; through socially mediated serial reinnovations; Bandini & Tennie, 2017). The ZLS approach combined with aspects of the current null social learning hypothesis currently provides the most parsimonious explanation for the behavioural repertoires of primates by combining the roles of individual and low-fidelity social learning to explain the emergence and sustenance of primate behavioural forms.

The ZLS hypothesis therefore constitutes the theoretical background for the empirical studies presented in chapters III-V of this thesis.

Chapter II presented a systematic literature review of the role of individual learning in tool-use across animal species (including non primate species). The review included observational accounts of the emergence of tool-use behaviours in wild, semi-wild and habituated animals, and experimental studies in which behavioural forms were reinnovated (in some cases encouraging reinnovation was the aim of the study, in others the reinnovation was a by-product of the experimental set-up). To the best of our knowledge, this is one of the first literature reviews on the individual learning of tool-use behaviours across animal species (but see also Reader & Laland, 2001). Currently, over 100 studies are included in the resulting database, demonstrating the extent of individual learning of material culture in the animal kingdom and contributing to the growing literature on innovation in animals (Laland & Reader, 2001). This chapter highlights the importance of including baseline conditions in experimental tool-use studies to allow for the occurrence of spontaneous reinnovations of the target behaviour before social information is introduced. The chapter concludes suggesting that it is likely that animals, and in particular, primates, have been underestimated in their ability to individually learn their tool-use behaviours. Further investigation into this field will, most likely, reveal many more animal tool-use behaviours that can emerge in the absence of social information.

6.1.2 Testing the ZLS in chimpanzees

Köhler (1925) argued that it is essential to identify the individual learning abilities of each animal species in order to fully understand what they are capable of when social information is available. The studies in chapter III followed Köhler's (1925) recommendations by providing naïve, captive, unenculturated chimpanzees with the materials of three wild behavioural forms (scooping, picking, and pounding) and no social information on the actions involved. Some have argued that these behavioural forms have to rely on social learning (e.g., Whiten et al., 1999; 2001; Byrne, 2003; de Waal & Ferrari, 2011, i.e., they are CDTs; Reindl et al., 2017). Contra these claims (but consistent with Köhler's (1925) predictions), the naïve chimpanzees tested in these studies spontaneously reinnovated the target behaviours in the absence of social information. The results of these studies demonstrate that various forms of chimpanzee stick tool-use can indeed be reinnovated through individual learning. Thus, it seems that at least the behavioural forms of scooping, picking and pounding are within chimpanzees' ZLS. As emphasised throughout chapter III however, although this data supports the view that individual learning is sufficient to catalyse the form of these behaviours, low-fidelity social learning facilitates the acquisition of the target behaviour across connected individuals, thus increasing the frequency of the behaviours within wild populations (the latent solutions (LS) studies presented in chapter III do not, however, explicitly test for increases in frequency of the behaviour, but drawing from the vast literature on the low-fidelity social learning abilities of chimpanzees (e.g., Whiten et al., 2004), it seems likely that these forms of social learning play an important role in the relative frequencies of chimpanzee behaviours).

6.1.2.1 The latent solutions testing methodology

Whilst the asocial testing conditions carried out in LS tests (in which subjects do not have access to any social information of the behaviour prior to testing) are required in order for the roles of individual and social learning to be isolated, some may argue that these conditions do not fully represent the natural learning contexts of wild chimpanzees (e.g., see comments by the anonymous reviewer in Bandini & Tennie, 2017). Indeed, it is only in rare situations that wild chimpanzees (other than the first innovator of a behaviour) confront new problems without other individuals around them, or in the complete absence of social cues. Thus, the LS tests carried out in chapter III were designed to identify what chimpanzees are *technically* capable of reinnovating in, to a certain extent, "artificial" conditions, in which they do not have access to any type of social information on the behavioural form being investigated. However, the chimpanzees in these studies were not tested in a social "vacuum", as the fact that the materials to solve the problem (e.g., sticks) were placed in the enclosure alongside the testing apparatus provided some social cues on the solution of the task. Therefore, the LS testing conditions recreate those of chimpanzees in the wild, when, for example, they encounter the debris of another individual's reinnovation. In these cases, even when there is no model demonstrating the behaviour, the tools and debris left by the innovator in the vicinity of the problem space will facilitate the reinnovation of the behaviour by the rest of the group (this phenomenon is particularly enhanced in ground-dwelling species, such as primates; Meulman et al., 2012). Indeed, even the first innovator may encounter slightly scaffolded conditions due to the stochastic nature of object sorting, which may lead to the materials of a behaviour, by chance, being found in the vicinity of the problem space (encountering this situation may, in turn, increase the first individual's likelihood of innovating or reinnovating the behaviour). Thus, LS testing conditions recreate the conditions encountered by chimpanzees *after* the first innovation of a behaviour, or the rare cases in which, by chance, an innovator comes across the appropriate materials in the relevant problem space.

Three out of the total 39 chimpanzee "*putative cultural behaviours"* were tested in chapter III (as reported by Whiten et al., 1999; 2001), and all three behavioural forms were found to be in the ZLS of naïve chimpanzees. Future studies should continue testing the remaining behaviours on Whiten et al.s' (1999; 2001) list of "cultural" behaviours, following the LS testing methodology, to examine whether these behaviours can also be reinnovated or whether any of these prove to require social learning to emerge (based on the results presented in chapter III, however, it seems unlikely that any of the stick tool-use behaviours will be found to require social learning). Previous experimental tests on the ZLS have already found several behavioural forms, including non-tool-use behaviours, which were reinnovated by naïve subjects across great ape species. For example, Tennie et al., (2008) demonstrated that captive naïve gorillas could spontaneously reinnovate the same program-level patterns of nettle feeding as observed in wild gorillas (which had previously been suggested to be acquired via high-fidelity social learning mechanisms; Byrne et al., 2003). Similarly, Neadle et al., (2017) provided naïve, captive gorillas with dirty apples to examine whether they would clean them without requiring social information beforehand. As predicted, the naïve gorillas did indeed clean the apples before eating them, similarly to wild gorillas, without social learning (Neadle et al., 2017). Allritz et al., (2013), Menzel et al., (2013) and Reindl et al., (2016) describe similar findings with different species of great apes (including human children; Reindl et al., 2016), when provided with the materials of the target behaviours and no social information on the actions involved. Thus, the studies in chapter III presented in this thesis add three more behavioural forms to the growing list of behaviours that can be reinnovated by primates through individual learning.

6.1.3 Pound-hammering in long-tailed macaques

Chapter IV shifts to testing another primate species: long-tailed macaques (*Macaca fascicularis fascicularis; Mff)*, contributing new data to the investigation of *stone* tool-use in long-tailed macaques (Carpenter, 1887; Gumert et al., 2009; Luncz et al., 2017). These macaques constitute an especially promising species for the discovery of new tool-use repertoires outside of chimpanzees, as another subspecies, (*Macaca fascicularis aurea; Mfa)*, has been observed using stone tools and two different methods (pound-hammering and axe-hammering) to crack open encased foods in the same area as *Mff* (*Mff* and *Mfa* inhabit the same geographical area; Gumert et al., 2009). The aim of the study in chapter IV was to investigate the emergence of pound-hammering in naïve, captive *Mff* (as *Mfa* are not currently found in captivity) following the LS testing methodology. It was hypothesised that naïve *Mff* would be able to reinnovate the same behavioural form of pound-hammering as wild *Mfa*. When the behaviour did not emerge in the individual learning baseline condition, a series of social learning conditions were carried-out (see below). Despite providing full demonstrations of the behaviour, the subjects did not reinnovate the target pound-hammering behaviour.

This chapter introduced and discussed a new systematic and extended LS testing methodology, which allows for the identification of the level (if any) of social learning required for a behaviour to emerge if it is not reinnovated in the baseline condition. Chapter IV also introduced a novel statistical measure (via cumulative binomial distributions) to determine the sample sizes required to confidently generalise negative findings from a study sample to the entire species (see Appendix IV for full calculations). The new methodological advances presented in this chapter contribute two important extensions to the original LS testing methodology (see Tennie & Hedwig, 2009), which allow for clear conclusions to be drawn from LS studies even when the target behaviour is *not* reinnovated in the baseline condition (all this was published in Bandini & Tennie, 2018).

Furthermore, possible explanations for the observed lack of reinnovation of pound-hammering by *Mff* were discussed in chapter IV. The role of genetics in the emergence of this behaviour was considered, as this is consistent with data from wild populations in which only *Mfa* and hybrid *Mff* x *Mfa* populations have (so far) been observed pound-hammering. It was argued that *Mfa* might possess some genetic predispositions for the learning mechanisms associated with this form of tool-use. This does not, however, imply that pound-hammering is genetically "encoded" for (see also Moore, 2013), but rather that adaptations for the acquisition from and attention to social information may have been selected for in the *Mfa* lineage. As social and individual learning are most likely based on associated mechanisms (Heyes, 2012), *Mfa* individuals may be more likely to pay attention to low-fidelity social cues for tool-use behaviours and subsequently possess enhanced individual learning abilities compared to the other subspecies (Bandini & Tennie, 2018). It may also be that mere (genetically predisposed) food preferences influence the acquisition of tool-use and foraging behaviours. For example, both wild and captive *Mff* seem to dislike clams and other marine foods. Thus, if pound-hammering emerged specifically to exploit marine encased foods (and only afterwards was generalised to other food sources, such as nuts), *Mff*'s' distaste for marine foods may have obstructed their ability to acquire or express the ability to use stone tools.

The differences in tool-use abilities between subspecies of long-tailed macaques emphasises the importance of examining the role of genetics in the acquisition of behavioural forms (see also Langergraber et al., 2010; Ladds et al., 2017). If behavioural predispositions can vary between subspecies, it is also possible that the ZLS, which has until now been suggested to vary across species but remain consistent within species, may have to be reinterpreted to reflect the possibility that subspecies have different behaviours within their ZLS. If this is found to be the case, we should no longer expect, for example, any *Pan troglodytes* to spontaneously reinnovate behaviours that are within the ZLS of *Pan troglodytes schweinfurthii*. Future studies should continue testing for the role of genetics in the differences in the acquisition of behaviours and learning mechanisms between subspecies (e.g., Ladds et al., 2017; Bandini & Tennie, 2018).

Further explanations for the lack of reinnovation by *Mff* included the absence of a sensitive learning period in which individuals had access to the materials of the behaviour. The exposure to the materials during a sensitive learning period early in ontogeny might be required for the behaviour to emerge later in life. This suggestion is consistent with early evidence from wild *Mfa x Mff* hybrids, in which juveniles who played with nuts and stones in their infancy were more likely to acquire pound-hammering as adults (Tan, 2017). The possibility that manipulation of the materials during a sensitive learning period influences the later reinnovation of associated behaviours raises some important questions for the ZLS. For example, it could be that previous experience has an effect on the number of behaviours within an individual's ZLS (thus implying that not all individuals in a species have the same ZLS). Alternatively, it could be that the ZLS remains stable across individuals, but previous experience increases (or decreases) the likelihood of reinnovating these behaviours. Personally, the second case seems more likely for unenculturated primates, as the same behavioural forms seem to appear across unconnected individuals (e.g., see the studies presented in chapter II and III). On the other hand, enculturated primates may be able to acquire behaviours outside of their species' ZLS (which would move enculturated apes from the ZLS-only category, in which they are restricted to only acquiring behaviours that they could individually reinnovate themselves, to the ZLS-plus category, alongside humans, who can acquire behavioural forms beyond their individual learning abilities through high-fidelity social learning; see general introduction and Reindl et al., in press; Tennie et al., submitted). Indeed, enculturated apes have been found to perform "better" in cognitive test batteries (Schick et al., 2009), pay more attention to actions performed by their counterparts (Kano et al., 2018), and may even be able to copy actions (Toth et al., 1993; Schick et al., 2009), abilities which seem to be beyond the individual learning reach of their unenculturated conspecifics. Following this line of enquiry, it would be worthwhile to continue exploring the impact of human exposure and training on the cognition and behaviour of great apes (e.g., van Schaik et al., 1998; Pope et al., 2018). Early investigations suggest that human experience and training have long-lasting effects on the cognition of non-human primates (Hermann et al., 2007; Damerius et al., 2015; Forss et al., 2016; Pope et al., 2018; Kano et al., 2018). If these findings can be further substantiated across species, and it is found that *only* enculturated primates, reared in species-atypical conditions (Bjorklund, 2018), can copy behaviours outside of their individual learning abilities, then the interesting question for the understanding of our own cultural evolution would shift from identifying what behaviours chimpanzees can reinnovate (as all the behaviours we currently see in wild, unenculturated, chimpanzees logically must be individually learnt), to understanding which experiences, and what level of these experiences (alongside training, exposure, and motivation) are required before non-human primates can learn to copy behaviours outside of their natural repertoires. The answer(s) to this question will further our understanding on the conditions that were in place when high-fidelity social learning, and our reliance on these forms of social learning, first emerged in the hominin lineage.

However, previous experience might not always have a *positive* effect on the reinnovation of behaviours. Pre-existing strategies with the materials of a behaviour may actually *hinder* the reinnovation of alternative behaviours in non-human primates (e.g., see Tennie & Hopper, 2011). One of the most common manipulations of the nuts observed by the *Mff* in chapter IV was a rolling/rubbing movement, either between the hands or against a hard substrate. This behaviour has also been observed in other species of wild macaques (Wheatley, 1988), suggesting that it is a common manipulation for macaques. The existence of this strategy with encased foods may have, in essence, blocked the exploration of alternative behaviours with the provided nuts, hindering the reinnovation of pound-hammering. This phenomenon, also referred to as "functional fixedness", has been identified in chimpanzees as well (Hrubesch et al., 2009; Hanus et al., 2011; Vale et al., 2016; Harrison & Whiten, 2018), and, as discussed in chapter II; may constitute a significant obstacle for innovations in non-human primates.

6.1.4 Testing for stone knapping in chimpanzees

Chapter V presented the results of an empirical comparative study into early hominin and extant chimpanzee stone tool culture. Similarly to the cultural claims made for some chimpanzee behaviours (Whiten et al., 1999; 2001), early hominin stone tools have also been argued to be acquired via social learning (McNabb et al., 2004; Gamble & Porr, 2005; Lycett & Gowlett, 2008; Shipton, 2010; Goren-Inbarm 2011; Whiten et al., 2003; 2011), yet, the evidence for this view is also tenuous (Boyd & Richerson, 2005; Corbey et al., 2016; Tennie et al., 2016; 2017). Studies on stone knapping in non-human primates have, so far, excluded chimpanzees and only one study (with capuchins; Westergaard & Suomi, 1994) allowed individuals to explore the task without providing them with any social information beforehand (i.e., only one study, so far, has carried out a LS test on stone knapping).

To fill this gap in the literature, naïve chimpanzees at Chimfunshi Wildlife Sanctuary (Zambia, Africa) were tested on their ability to make and use stone tools, following the extended LS testing methodology introduced and developed in chapter IV. Due to the spontaneous reinnovation of stone knapping by captive capuchins (Westergaard & Suomi, 1994), it was hypothesised that the chimpanzees, when motivated to make flakes, would spontaneously reinnovate the same stone knapping process. Despite ample opportunities to individually and socially learn the behaviour, the chimpanzees never made a flake (similarly to the results of the pound-hammering study with the long-tailed macaques in the previous chapter). One individual, Chiffon, did attempt to *use* one of the provided pre-made flakes to access the bait, but was never successful. As in the previous chapter, potential explanations for the lack of reinnovation of stone knapping by the chimpanzees were explored. The complexity of the apparatus, alongside the frustration at not being able to access the reward, were cited as possible explanations for the subjects' consistently low levels of motivation to interact with the testing apparatus (which may, in turn, may have prevented the chimpanzees from reinnovating the solution of making a flake to open the puzzle box). Furthermore, similarly to the previous chapter, it was hypothesised that a sensitive learning period during ontogeny, in which the chimpanzees had an extended period to familiarise themselves with the materials of the behaviour, might have been required before stone knapping could be reinnovated. All the chimpanzees included in this study had experience of stones, but perhaps a more specific experience of the task itself (of the apparatus and even of flakes) during this sensitive learning period might have been required for the reinnovation of stone knapping. Indeed, a longer period of exposure to the testing apparatus may have helped the chimpanzees grasp the mechanism behind opening the puzzle box (i.e., cutting the rope which kept the door to the reward box closed), which may have been too cognitively opaque for the subjects. One solution to the limitations of this study, and to increase the chimpanzees' general motivation to interact with the testing apparatus and the stones, is to use a simpler apparatus in future studies. A less cognitively taxing design would allow the subjects to focus more on finding a way to open the apparatus, rather than on understanding the mechanisms behind the puzzle box itself (indeed, a new, simpler apparatus is currently being used in follow-up studies on stone knapping with chimpanzees and other great apes by *A.Motes-Rodrigo*).

Thus, similarly to the results of chapter IV, this study was inconclusive with regards to the role of individual and social learning in the acquisition of stone knapping. The chimpanzees did not reinnovate the behaviour, but they also did not socially acquire it, suggesting that, as for *Mff*, chimpanzees do not automatically reinnovate or copy this behaviour. Although follow-up studies are still required, these preliminary findings strongly suggest that social learning is not the key to release stone knapping in chimpanzees, as the behaviour was not acquired in any of the social learning conditions (and the sample size met and exceeded the requirements of the single-case and the double-case ZLS standards). It is therefore possible that the earliest hominin stone tools (e.g., Oldowan tools; and potentially the new Lomweki tools; Harmand et al., 2005) were reinnovated in a similar way to other chimpanzee tool-use behaviours: primarily through individual learning, but facilitated by low-fidelity forms of social learning (e.g., Tennie et al., 2016; 2017). To continue examining this prediction, naïve chimpanzees should be tested following the suggestions outlined in chapter V.

6.1.5 Culture in primates

The empirical work presented in this thesis provides a mixed picture of the acquisition of tool-use by non-human primates. At least three stick tool-use behaviours were found to be within the individual learning capabilities of chimpanzees, and so these (and likely similar) tool-use behaviours can be reinnovated by naïve chimpanzees without social learning. However, two tool-use behavioural forms did not emerge via individual or social learning in chimpanzees or macaques. Perhaps the physical properties of the tools involved render a behaviour harder or easier to reinnovate (e.g., both studies on pound-hammering and stone knapping involved stone tools), or perhaps more likely, the inherent complexity of the behaviour (e.g., the higher number of cognitive and physical steps involved) might prohibit the individual's learning reach. Other, interacting, factors such as genetics, environment, developmental age, motivation, limitations of the testing conditions and pre-existing strategies may all play an important role in encouraging or limiting the reinnovation of behaviours, and future directions for research should focus on investigating the role of each of these factors in primate tool-use (Bandini & Tennie, 2018).

The results from the empirical chapters (chapters III-V) support the view that if a behaviour can be individually reinnovated, social learning is not required, and that if it is not individually learnt (as in the case of pound-hammering and stone knapping), it cannot, seemingly, be socially learnt either. These findings suggest that the role of social learning in primate tool-use may have been over estimated, and that the emphasis placed on the *necessity* of social learning in many definitions of animal culture has been misplaced (e.g., Whiten et al., 1999; 2001; Perry, 2001; van Schaik et al., 2003; de Waal & Ferrari, 2011; Gruber et al., 2015; Robbins et al., 2016). Thus, rather than making social learning a prerequisite for (non-human) cultural behaviours, cultural behaviours should be those that can be individually reinnovated, but social learning influences the variance of the behaviour observed in the majority of the population (thus excluding behaviours that come about spontaneously and involuntarily, such as yawning). Following this definition, non-human animals would have a "soft" form of culture (Neadle et al., 2017). The ZLS approach would predict that most (if not all) chimpanzee behavioural forms fall into this category (Tennie et al., 2009; Reindl et al., in press). However, it seems possible that some behaviours, such as nut-cracking in chimpanzees, are at the limits of their individual learning abilities, as this particular behaviour has only been (so far) reinnovated by few individuals without social learning (e.g., Marshall-Pescini & Whiten, 2008; Hirata et al., 2009). If the emphasis on social learning for culture is shifted from behaviours *resting* on it, to social learning having *at least* some influence on the emergence of behavioural forms across individuals (Reindl et al., in press; Neadle et al., 2017), then a soft form of culture is possible and, indeed, seems to be the case for chimpanzee and other animal behaviours (Neadle et al., 2017). The difference between human and non-human culture may then simply lie on the degree of reliance on social learning for the acquisition of these cultures (i.e., whether any non-human animal traits can be described as culture-dependent traits as in human culture; Reindl et al., 2017). Future studies should continue investigating whether animal tool-use is, or could ever be, cumulative as modern human culture is. Although some tentative cases of cumulative culture in animals have been made (Sasaki & Biro, 2016; Vale et al., 2017; Schofield et al., 2017), these are still rare cases in the non-human animal kingdom. Furthermore, cumulative culture has been argued to rest on high-fidelity social learning (Tomasello, 1986; Tennie et al., 2009; although see also Caldwell & Millen, 2008 and Reindl et al., 2017), and evidence for the ability to acquire knowledge via high-fidelity social learning by (unenculturated) non-human primates is still tenuous and heavily debated (see general introduction for an overview, and Whiten et al., 1999; 2001; Tennie et al., 2009; Bandini & Tennie, 2017; Vale et al., 2017). Thus, it seems likely that the ability to create and sustain cumulative culture may indeed be the distinguishing feature of human culture (Tennie et al., 2009; Dean et al., 2012).

6.2 Limitations and possible objections

This section will address some of the limitations and potential objections to the studies presented in this thesis.

6.2.1 Small sample sizes

One potential limitation of the studies presented in chapter III is that only a maximum of four individuals (in the picking study; although see the limitations section of this study in chapter III) reinnovated the target behaviour in each study. In ideal testing conditions, the subjects in these studies would have been tested individually (out of view from each other) to allow for even more *independent* reinnovations. However, most zoological institutions do not allow their animals to be separated, so the majority of the subjects in chapter III were tested in their social groups. Due to the testing conditions, only the first reinnovation of the target behaviour could be confidently attributed to individual learning, as social learning could not be excluded for subsequent reinnovations. Thus, the amount of data that could be extrapolated from these tests was limited, and although chimpanzees other than the first reinnovators were observed (by EB) showing the target behaviour, their data was not included in the results. One solution to this problem is to test the same behaviour across multiple groups and/or multiple zoos, and indeed this was done with the picking study, where chimpanzees at Twycross zoo and il Bioparco di Roma were tested. However, other than the clear logistic and financial demands of organising testing at multiple institutions, the subjects' previous experience was also a restrictive factor. As all the behaviours examined in chapter III involved stick tool-use behaviours and most captive chimpanzees are regularly provided with enrichment exercises that require sticks as tools, finding a population that was still naïve to the target behaviours proved difficult and significantly restricted the number of subjects and testing institutions at which these studies could be carried out.

Although a higher number of reinnovations for each behaviour would have perhaps been more convincing for sceptics of the ZLS approach, the (relatively) small sample sizes in these studies do not inherently present a problem for the theoretical approach. The ZLS works on the standard assumption that just one or two (depending on whether the behavioural form fits the single or double-case ZLS standard; Bandini & Tennie, 2017) independent reinnovations are enough to draw the logical conclusions that all individuals of a species are technically capable of reinnovating the same behavioural form, when in the appropriate context. All the studies in chapter III, other than the second pounding experiment, fulfilled the double-case ZLS standard (requiring at least two reinnovations of the target behavioural form by two independent individuals), rendering further reinnovations unnecessary to draw the conclusion that these behaviours are most likely in the ZLS of the species.

6.2.2 Previous experience

As discussed in the preceding section, the role of previous experience on the reinnovation of novel behaviours presents a valuable direction for further exploration. Indeed, one reviewer of the scooping manuscript (Bandini & Tennie, 2017) argued that because the subjects in this study already possessed stick-tool skills before testing, they were no longer naïve to the scooping task. Yet, due to the nature of life in captivity (e.g., regular access to enrichment tasks and research studies), most (if not all) captive chimpanzees possess some form of tool-use experience, most often with sticks. However, again, this does not constitute a problem for the interpretations presented in chapter III, as the subjects were not being tested on whether they could spontaneously use sticks *in general* as tools. Rather, the chimpanzees were tested on their individual reinnovation abilities of the target *behavioural form* with the stick-tools (i.e., the actions involved, such as “scooping”). Thus, even if the subjects had experience of general and other tool-use forms, but *not* of the *target* behavioural form, they were still considered naïve to the task at hand – given the focus on explaining the appearance of the target behavioural form (to make a concrete example of this logic in humans, just because person A speaks English, and perhaps even another language (hypothetically, lets say they also speak Italian and some French), this does not necessarily then mean that person A is automatically capable of speaking another language (for example, hypothetically, German), without actively trying to speak German. Thus, just because person A is capable of speaking one or more languages, this experience alone does not make them less naïve to a completely new language (Unfortunately I can personally confirm this logic).

This approach is not unique to the ZLS. Fieldwork reports follow the same logic: each chimpanzee behaviour is classified separately, even when these behaviours involve the same tools, and indeed often even the same underlying actions (e.g., see the case of “algae scooping” and “algae fishing” in wild chimpanzees which have recently been described as two different behaviours, despite the fact that both behaviours involve the same tool, food source and action, with the only difference between the two behaviours being the length of the stick used; Boesch et al., 2016). Therefore, the existence of general tool-use knowledge does not necessarily imply that the subject will have any knowledge on the actions required for the target behavioural forms, and therefore does not preclude subjects from being naïve to the task at hand (but see discussion above on how pre-existing strategies can aid or hinder reinnovations of related behaviours indirectly).

6.2.3 Context of behaviours

It could be further argued that a potential limitation to this empirical work, as a result of testing captive individuals, is that these studies only focus on the reinnovation of the isolated behavioural forms, rather than the whole context of the behaviour. Indeed, the LS tests presented in chapters III-V did not include the steps that occur in the wild before and after tools have been used. This is because the captive subjects were already provided with the materials of the target behaviour, potentially eliminating some of the build-up steps to the behaviour (for example, the monkey hunting phase of wild marrow picking was not replicated in the picking study). As some reviewers have noted, these testing conditions may therefore provide “scaffolded” conditions over those available to wild chimpanzees (see discussion of this above). However, the cultural claim for these behaviours rests primarily on the tool-use component of the behavioural form (Whiten et al., 1999; 2001), rather than the surrounding steps or the context of the behaviour. In the case of picking, for example, it is possible that low-fidelity social learning mechanisms, such as stimulus enhancement, help naïve chimpanzees understand that bone marrow is edible. Although this remains to be tested, it is possible that some aspects of the behaviours tested in chapter III are affected, to a greater extent on social rather than on individual learning. This hypothesis was not tested in the current studies, and is not under debate here. However, when the cultural-dependency claim for the tool-use aspect of picking was tested, the same behavioural form as in the wild was reinnovated by captive chimpanzees, demonstrating that, the crux of the behaviour: the tool-use aspect, does not necessarily require social learning, contra previous claims (Boesch & Boesch, 1991; Whiten et al., 1999; 2001)

6.2.4 Generalising from captive subjects to wild animals

Lastly, as all the empirical work in this thesis was carried out with captive and semi-wild individuals, it could be argued that the subjects already possessed enhanced cognitive and behavioural repertoires from their increased levels of exposure and interaction with humans (which, although limited, is greater than that of most wild primates,). Indeed, this is a possibility (see the captivity effect phenomenon; van Schaik et al., 1998). However, the extent of the captivity effect on the ZLS is yet to be determined (see above), and rather than increasing the number of behaviours within the individual's ZLS, since the same behavioural forms seem to reappear in both wild and captive individuals, it is more likely that the captivity effect simply increases the likelihood of reinnovating behaviours within the species' ZLS. Currently, it seems that only enculturated primates are able to learn behaviours outside of their ZLS (see general introduction), and none of the subjects included in these studies would be categorised as enculturated (the only potential exceptions to this would be Milla and Cleo, who lived for some time amongst humans before coming to Chimfunshi, but who, nevertheless, failed to reinnovate the target behaviour). Thus, the findings presented in chapter III can be generalised to chimpanzees as a species, as the subjects in these studies were not trained in or demonstrated the behavioural forms before testing. The same conclusion can be drawn for the negative findings in chapters IV & V, as both studies tested sample sizes that fulfilled (and surpassed) the minimum requirements for the single-case and double-case ZLS standards, which allow for conclusions to be drawn on the species from studies in which the target behaviour was not reinnovated (Bandini & Tennie, 2018).

6.3. Directions for future work

Rather than presenting a complete picture of the learning mechanisms behind primate tool-use, the aim of this thesis was to provide a theoretical and methodological approach to continue testing the emergence of primate material culture. The first step towards this goal is to continue testing the 39 (now 36) chimpanzee "cultural" behaviours identified by Whiten et al., (1999; 2001), alongside the cultural behaviours of other primates (e.g., Perry, 2001; van Schaik et al., 2003; Santorelli et al., 2011; Robbins et al., 2016). A research effort led by *D.Neadle* is currently investigating the individual learning abilities of other genera of great apes, following the methodology presented in this thesis (the behavioural forms of scooping and picking have already been tested in naïve bonobos, orangutans and gorillas; Bandini et al., in prep; Neadle et al., in prep). Following the data presented in chapter III, it is likely that most chimpanzee (and potentially other great ape) stick tool-use behaviours can be reinnovated by naïve subjects when presented with the appropriate materials.

As mentioned above, one potential exception to this prediction is the behavioural form of nut-cracking, which might be at the limit of individual reinnovation in primates. Thus, a particularly interesting line of research would be to investigate the origins of nut-cracking with naïve chimpanzees following the LS testing methodology. So far, most tests on nut-cracking in captive chimpanzees have neglected the need for a clear asocial baseline condition in which subjects are allowed to manipulate the materials without any social information (e.g., see Marshall-Pescini & Whiten, 2008; Hirata et al., 2009). On the other hand, previous studies with captive naïve capuchins did provide these baselines, resulting in the naïve capuchins reinnovating the same behavioural form of nut-cracking as their wild counterparts, without social learning (e.g., Visalberghi, 1987). Thus, it is possible that if chimpanzees were provided with a long enough baseline condition, they would also reinnovate the behaviour without social information, contra current claims on the acquisition of nut-cracking (e.g., Whiten et al., (1999, 3): "*The only major difference between the western and eastern populations (of chimpanzees) is that nut- cracking occurs in the west; although the fact that this behaviour terminates abruptly at the Sassandra-N'Zo river within the range of the verus sub-species shows it is culturally, rather than genetically, transmitted"*). Furthermore, as the studies in chapter IV and V were inconclusive on the mechanisms behind the reinnovation of pound-hammering and stone knapping (although note that in both cases the minimal sample sizes for the single-case ZLS standard to draw conclusions on the abilities of the species were met, and surpassed; Bandini & Tennie, 2018), follow-up studies on these behaviours, and other stone tool behaviours in primates, should be carried out following the recommendations for improvements made in the previous two chapters.

A further noteworthy line of research would be to compare the ZLS of human and non-human primates. This would involve extending the work initiated by Reindl et al., (2016), in which 11 behaviours were found to be in modern human childrens' ZLS (therefore likely also in the ZLS of our last common ancestor with great apes; Reindl et al., 2016). Questions remain on which *other* behaviours great apes share and whether humans have a larger ZLS than other great apes. To investigate these questions, a test battery involving the same behavioural forms for all the great apes could be provided to naïve subjects following the LS methodology presented in this thesis.

Furthermore, as discussed above, the effect of previous experience on the reinnovation of behaviours remains an open question. Recent studies have found that pre-existing knowledge can both encourage (e.g., Ottoni et al., 2005; Tan, 2017), have no effect (Laumer et al., 2017) or even limit (Hrubesch et al., 2009; Tennie & Hopper, 2011; Harrison & Whiten, 2018) the subsequent reinnovation of a target behaviour. Currently, few studies have attempted to experimentally test the role of previous experience on reinnovation rates of novel behaviours (Price et al., 2016). However, this line of enquiry would provide valuable insight on the conditions behind the emergence of human and non-human culture. More data is also required on sensitive learning periods and their effect on the later acquisition of related tool-use behaviours. By testing two groups of subjects, one in which the materials of the target behaviour are only provided in adulthood, and one in which naïve juveniles are already provided with the materials of a target behavioural form and allowed to manipulate these objects for an extended testing period (e.g., through an extended asocial baseline condition), it might be possible to examine whether this experience increases the likelihood of reinnovating the behavioural form later in life. Observational studies in the wild can also provide insight on the role of previous experience and sensitive learning periods in the acquisition of tool-use behaviours. For example, Perry (2009) tracked the emergence of food acquisition methods in wild capuchin monkeys over seven years and found that, after exploring several different (equally efficient) exploitation methods across the years, the capuchins seemed to settle on the technique they had practiced most often in infancy (Perry, 2009). Similarly, Tan (2017) tracked the number of manipulations of stones and nuts by juvenile *Mfa* x *Mff* hybrids, and found that previous experience with the materials of pound and axe-hammering seemed to increase the likelihood of showing these behavioural forms in adulthood.

It is now clear that enculturated primates are capable of expressing and/or learning behaviours beyond those of their wild counterparts. Investigating how, and in what conditions (i.e., what level of enculturation is required), this occurs would provide invaluable insight on how much great apes can learn through extensive human training, and whether they are currently, or ever will be, capable of high-fidelity social learning and of creating and sustaining culture-dependent traits across generations. Finally, this thesis focused only on the tool-use aspect of primate behaviour. Studying the learning mechanisms behind other aspects of primate behaviour, in particular gestures and vocalisations, would provide a more comprehensive view of primate behaviour (e.g., Liebal & Oña, 2018).

6.4 Conclusion

This thesis presents a collection of theoretical and empirical work on the individual learning abilities of primates in relation to their material culture, with a particular focus on our closest living relatives, chimpanzees. Whilst the literature review in chapter II and the empirical studies with chimpanzees in chapter III suggest that animals, across many species, are capable of consistently reinnovating tool-use solutions to novel problems, the following chapters (IV and V) demonstrated that these learning mechanisms have limits, which may only be overcome through high-fidelity social learning and cumulative culture (e.g., see Vygotsky's (1978) ZAD and ZPD concepts). Drawing from these findings, it seems likely that individual learning works in conjunction with low-fidelity social learning to support and facilitate the acquisition and sustenance of the rich behavioural repertoires observed across both wild and captive animals – cultures based on increases in frequencies of latent solutions. However, some behaviours may be impossible to acquire for the species in question, and even individual and social learning combined may not be enough to encourage the reinnovation of these more complex behaviours. Thus, other factors, many of which remain to be identified (e.g., environmental influences, genetic predispositions, previous experience, developmental stage and motivation level, to name a few) may limit the acquisition of a behaviour, even when the learning conditions are optimal. Future studies into each of these factors, alongside the learning mechanisms involved in the reinnovation of tool-use behaviours, will likely generate fruitful and exciting contributions to our ever-growing understanding of animal culture.

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Appendix I: Information on the study site Chimfunshi Wildlife Trust

Table A1-1: Demographic information on the chimpanzees at Chimfunshi Wildlife Trust (Courtesy of *T.Calvi*)

Group	Name	Sex	Approx.DoB	Origin	Rearing	Species	Subspecies
1	BJ	Female	07/02/2007	Captive	Mother	*Pan troglodytes*	
1	Bob	Male	04/18/2001	Captive	Mother	*Pan troglodytes*	*schweinfurthii*
1	Booboo	Male	01/01/1982	Wild	Hand	*Pan troglodytes*	*schweinfurthii*
1	Brenda	Female	08/12/1995	Captive	Mother	*Pan troglodytes*	*schweinfurthii*
1	Chrissy	Female	12/14/2006	Captive	Mother	*Pan troglodytes*	
1	Genny	Female	02/19/1997	Captive	Mother	*Pan troglodytes*	*schweinfurthii*
1	Gerald	Male	04/14/2002	Captive	Mother	*Pan troglodytes*	
1	Girly	Female	01/01/1982	Wild	Hand	*Pan troglodytes*	*schweinfurthii*
1	Gonzaga	Male	04/05/2008	Captive	Mother	*Pan troglodytes*	
1	Ilse	Female	05/07/2002	Captive	Mother	*Pan*	

1	Ian	Male	01/25/2015	Captive	Mother	*Pan troglodytes*	
1	Ingrid	Female	01/10/1991	Captive	Mother	*Pan troglodytes*	*schweinfurthii*
1	Innocentia	Female	01/10/2007	Captive	Mother	*Pan troglodytes*	
1	Ireen	Female	11/02/2011	Captive	Mother	*Pan troglodytes*	
1	Josephine	Female	01/01/1983	Wild	Hand	*Pan troglodytes*	*schweinfurthii*
1	Pal	Male	01/01/1981	Wild	Hand	*Pan troglodytes*	*schweinfurthii*
1	Rachel	Female	06/28/2012	Captive	Mother	*Pan troglodytes*	
1	Regina	Female	12/21/2006	Captive	Mother	*Pan troglodytes*	
1	Renata	Female	01/10/1997	Captive	Mother	*Pan troglodytes*	*schweinfurthii*
1	Rita	Female	01/01/1983	Wild	Hand	*Pan troglodytes*	*schweinfurthii*
1	Rusty	Male	10/14/2006	Captive	Mother	*Pan troglodytes*	
1	Tara	Male	01/01/1983	Wild	Hand	*Pan troglodytes*	*schweinfurthii*
1	Tobar	Male	01/01/1982	Wild	Hand	*Pan troglodytes*	*verus*
2	Carol	Female	12/06/1996	Captive	Mother	*Pan troglodytes*	

2	Charity	Female	08/13/2007	Captive	Mother	*Pan troglodytes*	
2	Chitalu	Female	01/01/2014	Captive	Mother	*Pan troglodytes*	
2	Claire	Female	05/15/2002	Captive	Mother	*Pan troglodytes*	
2	Coco	Female	01/01/1985	Wild	Hand	*Pan troglodytes*	*schweinfurthii*
2	Daisy	Female	10/17/2004	Captive	Mother	*Pan troglodytes*	
2	Danny	Male	04/23/2012	Captive	Mother	*Pan troglodytes*	
2	Darwin	Male	03/27/2007	Captive	Mother	*Pan troglodytes*	
2	David	Male	09/12/2001	Captive	Mother	*Pan troglodytes*	
2	Debbie	Female	12/11/2015	Captive	Mother	*Pan troglodytes*	
2	Diana	Female	01/01/1991	Wild	Hand	*Pan troglodytes*	*schweinfurthii*
2	Diz	Female	10/12/2007	Captive	Mother	*Pan troglodytes*	
2	Dolly	Female	10/28/1996	Captive	Mother	*Pan troglodytes*	*schweinfurthii*
2	Donna	Female	01/01/1984	Wild	Hand	*Pan troglodytes*	*schweinfurthii*
2	Dora	Female	01/01/1989	Wild	Hand	*Pan troglodytes*	*schweinfurthii*

2	Doug	Male	01/19/2003	Captive	Mother	*Pan troglodytes*	
2	Little Jack	Male	03/22/2012	Captive	Mother	*Pan troglodytes*	
2	Little Jane	Female	01/01/1985	Wild	Mother	*Pan troglodytes*	*schweinfurthii*
2	Little Jenkins	Male	02/19/2007	Captive	Mother	*Pan troglodytes*	
2	Little Jones	Male	09/16/2010	Captive	Mother	*Pan troglodytes*	
2	Little Judy	Female	05/16/1995	Captive	Mother	*Pan troglodytes*	
2	Long John	Male	11/07/2006	Captive	Mother	*Pan troglodytes*	
2	Maggie	Female	01/01/1986	Wild	Mother	*Pan troglodytes*	*schweinfurthii*
2	Martin	Male	04/14/2012	Captive	Mother	*Pan troglodytes*	
2	Mary	Female	09/04/2005	Captive	Mother	*Pan troglodytes*	
2	Mavis	Female	01/10/2013	Captive	Mother	*Pan troglodytes*	
2	Max	Male	08/29/2006	Captive	Mother	*Pan troglodytes*	
2	Maxine	Female	05/19/2001	Captive	Mother	*Pan troglodytes*	
2	May	Female	12/20/2012	Captive	Mother	*Pan troglodytes*	

2	Masya	Female	01/01/1991	Wild	Hand	*Pan troglodytes*	*schweinfurthii*
2	Mikey	Male	01/01/1988	Wild	Hand	*Pan troglodytes*	*schweinfurthii*
2	Misha	Female	01/01/1988	Wild	Hand	*Pan troglodytes*	*schweinfurthii*
2	Moyo	Male	08/15/2007	Captive	Mother	*Pan troglodytes*	
2	Nikkie	Female	11/12/1997	Captive	Mother	*Pan troglodytes*	*schweinfurthii*
2	Nina	Female	03/21/2003	Captive	Mother	*Pan troglodytes*	
2	Noel	Female	01/01/1977	Wild	Hand	*Pan troglodytes*	*schweinfurthii*
2	Pan	Male	01/01/1989	Wild	Hand	*Pan troglodytes*	*schweinfurthii*
2	Pippa	Female	01/01/1989	Wild	Hand	*Pan troglodytes*	*schweinfurthii*
2	Taylor	Female	09/16/2004	Captive	Mother	*Pan troglodytes*	
2	Tess	Female	08/26/1998	Captive	Mother	*Pan troglodytes*	
2	Tina	Female	05/10/2015	Captive	Mother	*Pan troglodytes*	
2	Tilly	Female	01/24/2001	Captive	Mother	*Pan troglodytes*	

2	Tom	Male	02/25/2015	Captive	Mother	*Pan troglodytes*	
2	Toni	Female	01/23/2003	Captive	Mother	*Pan troglodytes*	
2	Trixie	Female	01/01/1990	Wild-born	Hand-raised	*Pan troglodytes*	*schweinfurthii*
2	Violet	Female	01/01/1991	Wild	Hand	*Pan troglodytes*	*schweinfurthii*
2	Vis	Male	04/05/2004	Captive	Mother	*Pan troglodytes*	
2	Zsabu	Male	01/01/1990	Wild	Hand	*Pan troglodytes*	*schweinfurthii*
3	Barbie	Female	01/01/1995	Wild	Hand	*Pan troglodytes*	*schweinfurthii*
3	Brent	Female	01/03/2014	Captive	Mother	*Pan troglodytes*	
3	Brian	Male	01/01/1994	Wild	Hand	*Pan troglodytes*	*schweinfurthii*
3	Bruce	Male	12/21/2009	Captive	Mother	*Pan troglodytes*	
3	Buffy	Female	01/01/1985	Wild	Hand	*Pan troglodytes*	*schweinfurthii*
3	Bussy	Male	06/23/2004	Captive	Mother	*Pan troglodytes*	
3	Clement	Male	01/01/1993	Wild	Hand	*Pan troglodytes*	*schweinfurthii*
3	E.T	Female	01/01/1995	Wild	Hand	*Pan*	*schweinfurthii*

						troglodytes	
3	Lods	Female	06/01/2010	Captive	Mother	*Pan troglodytes*	
3	Roxy	Female	01/01/1995	Wild	Hand	*Pan troglodytes*	*schweinfurthii*
4	Bobby	Male	01/01/1993	Wild	Hand	*Pan troglodytes*	*schweinfurthii*
4	Commander	Male	01/01/2001	Wild	Mother	*Pan troglodytes*	*schweinfurthii*
4	Jack	Male	04/16/2008	Captive	Mother	*Pan troglodytes*	
4	Jewel	Male	05/19/2013	Captive	Hand	*Pan troglodytes*	
4	Kambo	Female	01/01/1996	Wild	Hand	*Pan troglodytes*	*schweinfurthii*
4	Kathy	Female	01/01/1999	Wild	Mother	*Pan troglodytes*	conflicting results
4	Kenny	Male	05/25/2011	Captive	Mother	*Pan troglodytes*	
4	Kit	Male	01/12/2005	Captive	Mother	*Pan troglodytes*	
4	Miracle	Female	07/13/2000	Captive	Hand	*Pan troglodytes*	*schweinfurthii*
4	Nicky	Male	01/01/1991	Wild	Mother	*Pan troglodytes*	*schweinfurthii*
4	Sinkie	Male	01/01/1994	Wild	Hand	*Pan troglodytes*	*schweinfurthii*

Fig. A1-1: Aerial map of Zambia with the location of Chimfunshi marked with a star (Google maps. Chimfunshi Wildlife Orphanage. Retrieved from: https://www.google.com/maps/@-13.0982159,26.0996825,1231752m/data=!3m1!1e3)

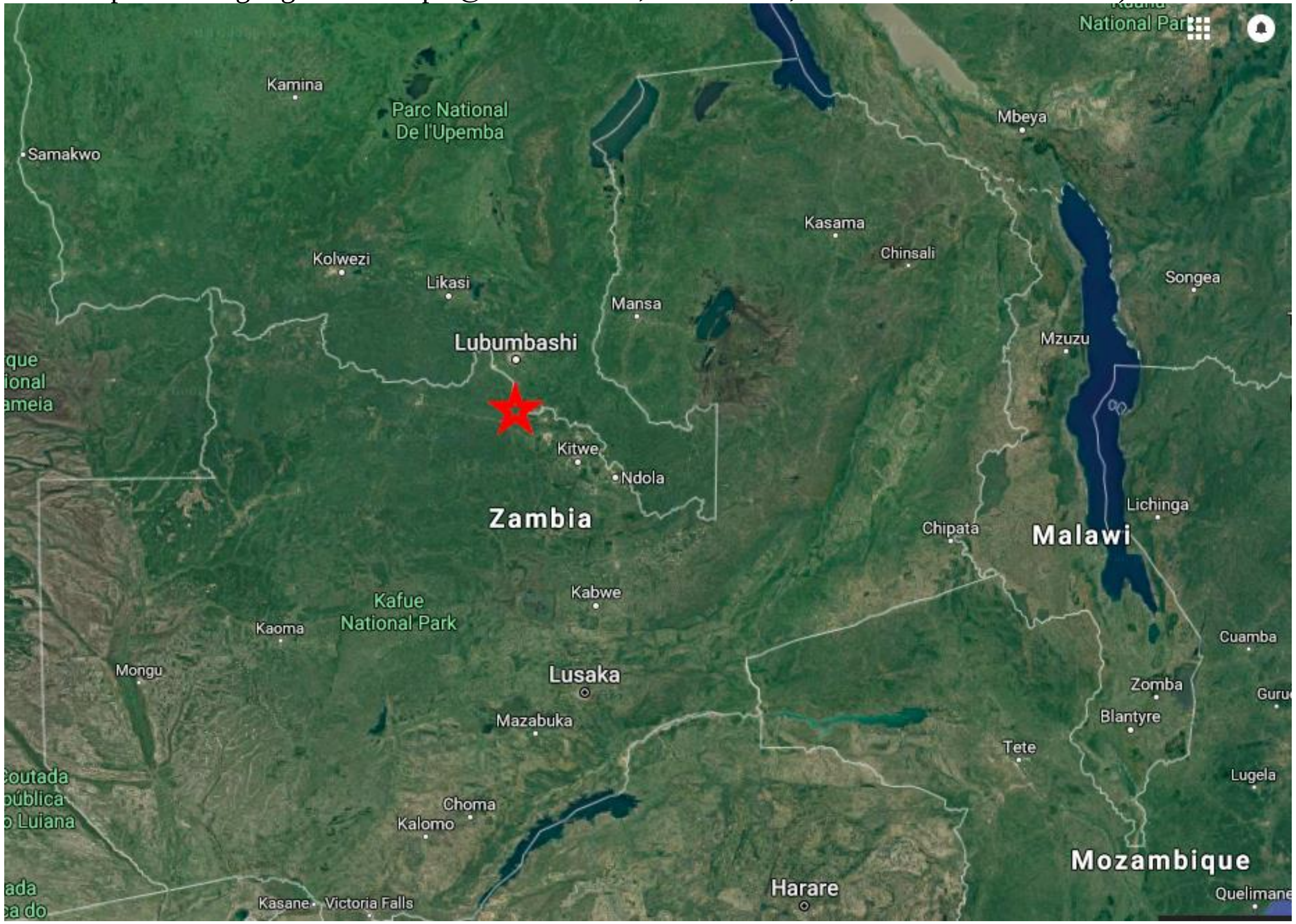

Fig A1-2: Aerial map of Chimfunshi with enclosures 1-4 marked (Google maps. 2016. Chimfunshi Wildlife Orphanage. Courtesy of *R.Harrison*. Numbers added by EB).

Appendix II: Demographic information on the chimpanzees at Twycross Zoo, UK & Il Bioparco di Roma, Italy

Table A2-1: Demographic information on the chimpanzees at Twycross Zoo, UK

Group	Name	Sex	Approx. DoB	Origin	Rearing	Species
1	William	M	30/06/82	Captive	Captive	*Pan troglodytes*
1	Holly	F	27/12/82	Captive	Captive	*Pan troglodytes*
1	Peter	M	09/07/92	Captive	Captive	*Pan troglodytes*
1	Tommy	M	30/01/95	Captive	Captive	*Pan troglodytes*
1	Samantha	F	01/01/80	Wild	Wild	*Pan troglodytes*
2	Rosie	F	30/04/76	Captive	Captive	*Pan troglodytes*
2	Charlotte	F	28/09/78	Captive	Captive	*Pan troglodytes*
2	Jambo	M	09/06/82	Captive	Captive	*Pan troglodytes*
2	Flyn	M	25/10/86	Captive	Captive	*Pan troglodytes*
2	Victoria	F	18/08/90	Captive	Captive	*Pan troglodytes*
2	Jomar	M	28/12/90	Captive	Captive	*Pan troglodytes*
2	Tuli	F	10/08/07	Captive	Captive	*Pan troglodytes*
2	Mongo	M	13/08/94	Captive	Captive	*Pan troglodytes*
2	Genet	F	25/05/95	Captive	Captive	*Pan troglodytes*
2	Tojo	F	17/06/77	Wild	Wild	*Pan troglodytes*
2	Josie	F	20/02/88	Captive	Captive	*Pan troglodytes*
2	Coco	F	01/01/65	Wild	Wild	*Pan troglodytes*

2	Noddy	F	14/12/71	Wild	Wild	*Pan troglodytes*
2	Kibali	M	05/12/03	Captive	Captive	*Pan troglodytes*

Table A2-2: Demographic information on the chimpanzees at il Bioparco di Roma, Italy

Name	**Sex**	**Approx. DoB**	**Origin**	**Rearing**	**Species**
Bingo	M	01.01.1990	Captive born	Unknown	*Pan troglodytes*
Susy	F	01.01.1981	Captive born	Unknown	*Pan troglodytes*
Edy	F	01.01.1992	Captive born	Unknown	*Pan troglodytes*
Pippy	F	01.01.1976	Captive born	Unknown	*Pan troglodytes*

Appendix III: Definitions of terminology used throughout the thesis

Tool-use: "*The external employment of an unattached or manipulable attached environmental object to alter more efficiently the form, position, or condition of another object, another organism, or the user itself, when the user holds and directly manipulates the tool during or prior to use and is responsible for the proper and effective orientation of the tool*" (Schumaker et al., 2011). Importantly, even though the authors mention "*manipulable attached environmental objects*', they exclude the use of body parts, such as horns or tails.

Innovation: Throughout the thesis, novel behaviours are referred to as "innovations" (Reader & Laland, 2003). Despite growing interest in this field, one definition of the term "innovation" is still lacking. Whilst there are differences in the focus (whether on an individual or population level) of innovations (see Bandini & Harrison, in prep, for a review), in the following innovation is defined following Reader & Laland (2003), in which an innovation is: "*a process that results in new or modified learned behaviour and that introduces novel behavioural variants into a population's repertoire".* Crucially, the authors clarify that "*population repertoire is not meant to imply that all individuals in a population will necessarily acquire the novel behaviour, but rather that at least one individual in the population will behave in a manner not previously seen"* (Reader & Laland, 2003).

Low-Fidelity social learning mechanisms

Local enhancement: *When exposure to the demonstrator animal or its products (e.g. scent cues, excavations) draws the observer's attention to the stimuli with which the demonstrator was interacting* (Thorpe, 1965; as described in Heyes, 1994).

Stimulus enhancement: *When the demonstrator's behaviour (i) increases the probability that the observer will be exposed… to certain stimuli, and (ii) the stimuli in question are not only those tokens with which the demonstrator interacts, but all token stimuli of the same physical type* (Spence, 1937; as described in Heyes, 1994).

Emulation: in emulation learning, according to Tomasello (1998), animals are: "*learning about the environment, not about behaviour*". Thus, in emulative learning processes, observers learn about the results of a behaviour, rather than the actions or details of the behaviour itself (Tomasello et al., 1987; Horner & Whiten, 2005). It is important to note here that the classification of emulation as a low-fidelity social learning mechanisms is still debated, as recent studies with modern humans have demonstrated that some forms of culture-dependent traits can be transmitted via emulation alone (Caldwell and Millen, 2008; Reindl et al., 2017). If this is indeed the case, then emulation may have to be classified as a high-fidelity social learning mechanism, or the current theory that cumulative culture requires high-fidelity social learning will have to be revisited.

High-fidelity social learning mechanisms

Imitation: Contrary to emulation, through imitation, an observer learns about the actions and the details of the target behaviour. Whiten and Ham (1992) define imitation as a: "*process whereby one individual copies some part of the form of an action from another*".

Teaching: A broad definition of teaching is "*Behavior with the intent to facilitate learning in another*" (Pearson, 1989). However, similarly to the concept of culture, teaching has also been defined in stricter and broader ways. See Kline (2015) for an overview of the different definitions.

These are the terms that are most frequently referred to throughout the thesis, but in no means constitute an exhaustive list of all the learning mechanisms described in the literature. For an overview of the terminology, see also Carpenter & Call (2002).

Appendix IV: Binomial Cumulative Distribution Formula as referred to in chapter IV

$$F(k;n,p) = \Pr(X \leq k) = \sum_{i=0}^{n} \binom{n}{i} p^{i}(1-p)^{n-1}$$

in which: $\binom{n}{i}$= n!/i!(n-i)!

To figure out the probability of two or more inventions, first the likelihood of 0 inventions, and then 1 invention has to be calculated. Adding the two, and subtracting the sum from 1, the likelihood of 2 or more inventions can be found.

F(k;n;p)=what follows is a function where k;n;p =Pr(X<-k)= probability of invention (X) is minus, or equal to k, and:

$\binom{n}{i}$= n!/i!(n-i)!

For the case of 31 macaques (sample size) and 0.10 reinvention probability, first the likelihood of zero reinventions is calculated:

$\sum_{i=0}^{1} \binom{n}{1}$in which (n)=is the floor

Pr (X=k)=(31!/(0!(31-0!))) $(.10^{0}(1-.10)^{31-1})$ + (31!/(1!(31-1!))) $(.10^{1}(1-.10)^{31-1})$

Zero equation first:

n!/i!(n-i)! = 31!/0!(31-0)! , where 0! Is always = 1
31!/1(31-0)! = **1**

So,
$(1).10^{0}\ (1-.10)^{31-1} = (1)\ 1\ (1-.10)^{30}$ = **0.0424**

So,
0.0424 + (31!/(1!(31-1!))) $(.10^{1}(1-.10)^{31-1})$
n!/i!(n-i)!=31!/1!(31-1)! = 31!/1!(30)! = 31!/(30)! = 31
$31\ (.10^{1})\ (1-.10)^{30} = 31\ (.10)\ (1-.10)^{30}$ = **0.1314**

So, 0.0424 + 0.1314 = **0.1738**
And the likelihood of two or more inventions is: 1-0.1738 = **0.8262**

Table A4-1: Minimum sample sizes for each of the ZLS standards

	Double-Case ZLS	Single-Case ZLS
0.10 reinnovation probability (80% power)	**Min. *n*= 29** (Power for *n*=28: 78.4)	**Min. *n*= 16** (Power for *n*=15: 79.4)

Appendix V: Example of the behaviour questionnaire provided to keepers to establish the past experience of the subjects tested in chapters III-V (in collaboration with D.Neadle)

Claudio Tennie Research Group's animal behaviour questionnaire

Please indicate on the scales below if you have ever seen the behaviour described in the great apes *in your care* (if so, then please give details). Please note that we are not asking for behaviour seen in great apes elsewhere. This questionnaire only involves apes under your current care.

Please indicate to the best of your knowledge in the space provided, the species, name, age, frequency, date and context of the behaviour; for example in the following way:

Example statement: "I observed Francine (gorilla F/around 32Y old at that time), once (around Winter 2015) attempting to use a light stone to hammer open a wooden puzzle box, but her attempt failed. I have not observed her (or the other gorillas in our care today) act in any similar behaviour before or after."

Please also take care to note any *modifications* to objects; for example in the following way:

Example statement: "I have seen Francine (gorilla F/ca. 32Y old at the time) once (ca Spring 2011) bite the end of a stick and which became sharpened as a result before using it to get raisins out of a hole inaccessible by her fingers. I have not observed her (or the other gorillas in our care today) act in any similar behaviour before or after."

If relevant behaviours have been witnessed in the context of an earlier scientific study please specify the respective study (as much information as possible please, e.g. name/research question; University; name of researchers or research group). Please also report cases in your animals that you have not seen yourself but which you have heard or read about. In such cases, please report this too, for example in the following way:

Example statement: "I was told by XX/I once read in a keeper report that ..."

In all cases, please give as much detail as possible.

Please answer these questions alone; it is important to us that the answers are based on your own experience or that which you yourself have read or have been told (please specify these cases as shown above).

Explanation for tick-boxes:

Seen by me: I have seen the behaviour described in one or more (please specify how many and which) individuals, within the group that is the target of this questionnaire.

Seen by another: I have heard/read that another person has seen the behaviour described in one or more (please specify how many and which) individuals, within the group that is the target of this questionnaire.

Never seen, to my knowledge: Behaviour has never been witnessed, to my knowledge, within the group that is the target of this questionnaire.

Unknown/Unsure: I am unaware that the behaviour has ever been witnessed in the group that is the target of this questionnaire; but this may simply be due to a lack of relevant opportunities to witness the behaviour e.g. if you have only worked with these animals for a few weeks.

Chimpanzees

Using one object to bang on, or hit, another object or substrate

Usually, this means the use of a hard object to bang on or hit another object (or substrate). This may be with the aim to crack or break open the latter object, or to remove pieces of a substrate. Here, we are interested in *any* hammer-like behaviours, regardless of the targets involved.

Seen by me	Seen by another	Never seen, to my knowledge	Unknown/Unsure
☐	☐	☐	☐

If you answered "seen by me" or "seen by another" please give details below.

Comments: Please include species, name(s), age(s) at the time. Please also include in each case: frequencies (Once? Rarely? Often?), rough date(s), details, such as what type of "hammer object" and what type of "target object/substrate" - and what limb used (hand? Foot?) - regarding the behaviour. Please include context, description and anything else you consider important as well. Continue overleaf if necessary

Appendix VI: Supplementary tables for Chapter V

Table A5-1: Number and percentage of occurrence of each manipulation types per individual

Manipulation	Chiffon		Cleo		Colin		Milla	
	Occurrences	%	Occurrences	%	Occurrences	%	Occurrences	%
Knock	2	1%	0	0%	16	5%	13	5%
Manipulate Door	48	33%	58	27%	91	28%	110	41%
Manipulate Lock	15	10%	29	13%	19	6%	29	11%
Manipulate Rope	38	26%	48	22%	10	3%	61	23%
Manipulate Screws	0	0%	10	5%	3	1%	6	2%
Multiple Manipulation	4	3%	12	6%	6	2%	9	3%
Other	0	0%	7	3%	2	1%	8	3%
Pull Towards	0	0%	7	3%	14	4%	1	0%
Push Away	12	8%	16	7%	0	0%	0	0%
Shake	0	0%	1	0%	110	33%	0	0%
Stone Manipulation	18	12%	23	11%	45	14%	12	4%
Tool Door	3	2%	1	0%	11	3%	17	6%

Tool Lock	0	0%	1	0%	2	1%	4	1%
Tool Rope	7	5%	5	2%	0	0%	1	0%

Table A5-2: Number and percentage of total occurrences of “other” manipulations

Manipulation	Occurrences	%
Change orientation	7	23%
Manipulate wire	17	55%
Manipulate wood	4	13%
Peer into window	3	10%

Table A5-3: Number and percentage of manipulation types per individual when tested in a group setting

	Chiffon		Cleo		Colin		Milla	
Manipulation	Occurrences	%	Occurrences	%	Occurrences	%	Occurrences	%
Knock	00:00	0%	00:00	0%	00:00	8%	00:00	2%
Manipulate Door	00:00	29%	00:00	0%	00:00	31%	00:00	22%
Manipulate Lock	00:00	29%	00:00	0%	00:00	0%	00:00	20%
Manipulate Rope	00:00	0%	00:00	0%	00:00	0%	00:00	14%
Manipulate Screws	00:00	0%	00:00	0%	00:00	0%	00:00	0%
Multiple Manipulation	00:00	14%	00:00	100%	00:00	8%	00:00	2%

Other	00:00	14%	00:00	0%	00:00	8%	00:00	12%
Pull Towards	00:00	0%	00:00	0%	00:00	38%	00:00	2%
Push Away	00:00	0%	00:00	0%	00:00	0%	00:00	2%
Shake	00:00	0%	00:00	0%	00:00	0%	00:00	0%
Stone Manipulation	00:00	0%	00:00	0%	00:00	0%	00:00	6%
Tool Door	00:00	0%	00:00	0%	00:00	8%	00:00	6%
Tool Lock	00:00	14%	00:00	0%	00:00	0%	00:00	12%
Tool Rope	00:00	0%	00:00	0%	00:00	0%	00:00	0%

Table A5-4: Number and percentage of total occurrences of manipulation types in Group two

Manipulation	Occurrences	%
Push Away	5	6%
Manipulate Door	10	12%
Manipulate Lock	6	7%
Manipulate Rope	6	7%
Manipulate screws	0	0%
Multiple Manipulation	15	19%
Stone Manipulation	12	15%
Knock	3	4%
Shake	2	2%
Other	6	7%
Pull Towards	16	20%
Tool Door	0	0%
Tool Rope	0	0%
Tool Lock	0	0%

Table A5-5: Number and percentage of total occurrences of stone manipulations

Manipulation	Occurrences	%
Display	9	8%
Drag across mesh	3	3%
Hit on ledge	8	7%
Knock	18	16%
Lick & Bite	4	4%
Move	1	1%
Sniff	22	19%
Spin	2	2%
Throw	33	29%
Touch	10	9%
Wave	3	3%

Appendix VI: Curriculum vitae

Elisa Bandini

Email: elisa-bandini@hotmail.it

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72072
Tübingen, Germany

Education

September 2014-Present: Archaeology PhD candidate at the The University of Tübingen, Germany.

April 2013: Successfully completed a ten-week accredited online course provided by Duke University, USA, on Human Evolutionary Genetics.

2012- 2013: Achieved an MSc with Distinction in Human Osteoarchaeology from the University of Edinburgh, UK.

2009 – 2012: Achieved a First Division Second Class Honours BA in Archaeology from the University of Bristol, UK.

Work Experience

October 2014-October 2018: Research Assistant at The University of Birmingham and the University of Tübingen, Germany.

June 2015-June 2016: Collecting and analysing observational data for a collaborative project with Twycross Zoo to improve their Great Ape enclosures.

October 2015-March 2017: Presented research at several Open Days of The University of Birmingham for prospective students and parents.

May-August 2014: Worked at the annual international Flower Festival in Rome.

August 2011: Interned at the Natural History Museum in Oslo, Norway for five weeks. Worked in the laboratories cleaning, re-assembling and preparing Jurassic fossils for exhibition.

June 2011: Interned at the Italian Consulate Office in Oslo, Norway.

Teaching Experience

January 2018: Invited as a guest lecturer at The University of Tübingen to give a 2hr lecture on the evolution of culture and cognition in early humans.

November 2017: Invited as a guest lecturer at The University of Birmingham to give a 2hr lecture on social learning in animals, and presented a seminar to postgraduate Psychology and Animal Behaviour students.

April-June 2017: Teaching Assistant for the postgraduate course “Cognitive Evolution”.

January 2016-2017: Teaching Assistant for the postgraduate course “Transferable Skills”

September 2016-April 2017: Teaching Assistant for the undergraduate course “Research Methods”

September 2016-January 2017: Teaching Assistant for the third-year course “Cultural Evolution and Cognition”. Presented a 2hr lecture on methodologies for testing cultural evolution in human and non-human subjects.

June 2015-June 2016: Co-supervised four undergraduate students working towards their third-year dissertation and one MSc student.

October – December 2015: Teaching Assistant for the “Primate Anatomy” course in the Department of Biosciences.

February 2015/2016: Teaching Assistant for the “Developmental Psychology” course at The University of Birmingham.

Conference and Workshop Organisation

May 2017: Organised a third Culture Conference (two days) with the title: “Innovation in cultural systems: an interdisciplinary meeting”. Was awarded three bursaries amounting to £5000.

June 2016: Organised a second “Culture Conference” (two days) examining “When and How does Cumulative Culture emerge?”. Was awarded two bursaries amounting to £3000.

May 2015: Organised a highly successful one-day interdisciplinary conference at The University of Birmingham titled: “The Origins and Transmissions of Culture”. Was awarded two bursaries (two times £1, 500) to organise the conference.

January-October 2017: Participated in several outreach days at ThinkTank Science Museum in Birmingham, presenting research to the general public.

November 2014: Part of a committee to organise and staff the Social Sciences Fair at the central library in Birmingham.

Conference Participation

July 2018: Invited Keynote speaker at the Culture Conference (now organised by The University of Stirling, UK).

September 2017: Presented research talk at the ESHE conference in Leiden, Netherlands.

September 2017: Presented research talk at the inaugural Cultural Evolution Society Meeting in Jena, Germany.

February 2017: Presented a talk on Women in Science at The University of Birmingham, UK.

August 2016: Presented research poster at IPS conference in Chicago, USA.

January 2016: Presented research poster at ASAB conference in Durham, UK.

December 2015: Presented research poster at the PSGB conference in London, UK.

September 2015: Presented research poster at the ESHE conference at The British Museum in London, UK.

August 2015: Presented research talk at the annual Biosciences conference at The University of Birmingham, UK.

June 2015: Presented research poster at The School of Mind and Thought conference at The University of Berlin, Germany.

April 2015: Presented research at The University of Birmingham research event. Was awarded “Best Poster” prize and “Best Presentation” award.

March 2015: Presented research poster at the ASAB conference in Durham, UK.

September 2013: Presented MSc research poster at the annual BABAO conference in York, UK.

Publications & Grants

May 2018: Awarded a Leakey Foundation Research Grant to carry-out fieldwork in Serra da Capivara National Park, Brazil, as PI of an independent project.

Bandini E & Tennie C. 2018. Naïve, captive long-tailed macaques (*Macaca fascicularis fascicularis*) fail to individually and socially learn pound-hammering, a tool-use behaviour. *R. Soc. open sci.* 5: 171826. http://dx.doi.org/10.1098/rsos.171826

Bandini E & Tennie C. 2017. Spontaneous reoccurrence of “scooping”, a wild tool-use behaviour, in naïve chimpanzees. PeerJ 5, e3814.

Reindl E, Bandini E, Tennie, C. The zone of latent solutions and its relation to the classics: Vygotsky and Köhler. In: Di Paolo LD, D’Almeida AFA, Vincenzo FD, eds. Social cognition in non-human primates and early Homo. Berlin: Springer, in press.

Review work

Ad-hoc reviewer for Ethology (June 2018)
Ad-hoc reviewer for Behavioural Processes (April 2018)

Field Work Experience

June-August 2016: Research trip to Chimfunshi Wildlife Sanctuary, Zambia, Africa. Carried out studies on chimpanzee tool-use.

January-April 2016: Took several research trips to the Isle of Man, UK, to carry out research project on *Macaca fascicularis fascicularis*.

June 2012: Took part in the annual University of Bristol excavation at Berkley Castle. Promoted to supervisor and was responsible for keeping records of finds and contexts and overlooking and managing the first and second year students (four weeks).

May 2011: Participated in the University of Bristol's excavation at Berkley Castle in Somerset (three weeks).

July 2008- August 2010: Excavated each summer with the University of Bologna on an 11th century monastery in Ravenna, Italy. Learnt basic field techniques, digging processes and recording methods. Elected responsible for all the context sheets and recording of finds.

Volunteer Work

November 2015-March 2017: Volunteered with RunBirmingham, a charity that encourages people from the less affluent areas of Birmingham to start running. Worked as a running coach and a marshal at running events.

October 2014-March 2017: Volunteered at a Birmingham local charity: "Summerfield Stables" which teaches disabled children and young adults to ride and work with rescue horses. Taught lessons with the children, took care of the animals and acted as a volunteer coordinator.

February-March 2014: Volunteered at the orphanage "Tumani for Africa" in Arusha, Tanzania, for six weeks teaching English, taking care of the younger children and helping with running the orphanage.

April-November 2013: Interned at Learning at Archaeology Scotland, and travelled around primary and secondary schools in Scotland introducing the study of archaeology to the students.