EXPERIMENTAL STUDIES OF BEHAVIOURAL FLEXIBILITY AND CULTURAL TRANSMISSION IN CHIMPANZEES AND CHILDREN

Rachel Anne Harrison

A Thesis Submitted for the Degree of PhD at the University of St Andrews



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Experimental studies of behavioural flexibility and cultural transmission in chimpanzees and children

Rachel Anne Harrison



This thesis is submitted in partial fulfilment for the degree of

Doctor of Philosophy (PhD)

at the

University of St Andrews

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Abstract

In this thesis, I explore two subjects of importance to the study of cultural evolution and cumulative culture; behavioural flexibility in chimpanzees, and social transmission in human children. In Chapter 1, I give an overview of current literature on the cognitive requirements of cumulative culture, with a focus on behavioural flexibility as a capacity which facilitates cumulative culture. I also explore a current discussion in the field of cultural evolution; namely the debate between "standard" and cultural attraction-based approaches to the study of cultural evolution. Chapter 2 is an experimental investigation of the capacity of chimpanzees to respond flexibly to a changing foraging task. This study found that chimpanzees did alter their behaviour, but to a limited degree. In Chapter 3 I provide the same artificial foraging task to two further groups of chimpanzees, at a sanctuary in Zambia. This study again found that chimpanzees altered their behaviour in response to task constraints, but also found a significant difference in performance between the two groups tested. Chapter 4 explores one potential factor which may contribute to these group differences; social tolerance. Data on social tolerance from all three groups of chimpanzees is presented. In Chapter 5, I turn to another key factor in the study of culture and also address the cultural attraction approach, by conducting a transmission chain study of four- to eightyear-old human children, comparing the transmission of a symbolic and non-symbolic image. I found that neither image was reliably transmitted along transmission chains. Finally, in Chapter 6, I discuss the findings of the thesis, and suggest that future work considers multiple demographic groups, whether this means the inclusion of multiple groups of apes in studies of non-human primate cognition, or the consideration of how cultural behaviours might be transformed when transmitted by human children rather than adults.

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Chapter 1: Introduction

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1.1 Cumulative culture

Culture has been defined as "group-typical behaviour patterns shared by members of a community that rely on socially learned and transmitted information" (Laland & Hoppitt, 2003, pp.151). This definition incorporates both observable behaviour (the "group-typical behaviour patterns") and unobservable 'socially transmitted information'. While including 'information' might seem to make this definition difficult to apply, its inclusion allows cultural traits to include instances in which an individual learns that a behaviour has a certain outcome when applied in a specific context, for example. In such cases, while a behaviour itself may not be socially acquired, its pattern and prevalence of use within a group may still rely upon this socially learned information (as Ramsey, 2013, emphasises, this still excludes instances in which information is passed between individuals without influencing behaviour). A wide variety of species are claimed to possess culture in some form, from cetaceans (Rendell & Whitehead, 2001) to New Caledonian crows (Corvus moneduloides; Hunt & Gray, 2003), as well as a range of primate species including chimpanzees (Pan troglodytes; Whiten et al., 1999), orangutans (Pongo pygmaeus; van Schaik et al., 2003), gorillas (Gorilla gorilla gorilla and Gorilla beringei beringei; Robbins et al., 2016), and capuchin monkeys (Cebus capucinus; Perry et al., 2003).

There has been much debate over the use of the term 'culture' in relation to current nonhuman evidence (Galef, 1992; Tuttle, 2001; Premack & Hauser, 2006). Tuttle argues that symbolic representation of ideas, beliefs and meaning is the *sine qua non* of culture, and that as there is, as yet, little evidence of this in non-humans, the term 'culture' should not be applied, while Galef (1992) and Premack and Hauser (2006) argue culture is not present in non-human animals because traditions are not transmitted via imitation or pedagogy. Premack and Hauser (2006) additionally argue that non-human traditions, such as hand-clasp grooming in chimpanzees, or lobtail fishing in humpback whales (*Megaptera novaeangliae*), are 'trivial', with no 'social consequences', and should therefore be distinguished from human culture. Much of this debate is driven by the definitions of culture to which authors subscribe, and there have been many debates and disagreements over the definitions in their 'culture' (Byrne et al., 2004), with Kroeber and Kluckhohn listing 164 definitions in their 1952 survey of culture concepts. Sterelny (2009) argues that definitions of culture are hypothesis-choosing, and can direct the focus of future research. Laland and Janik (2006) suggest that a broad definition of culture, inclusive of non-human evidence, is most likely to stimulate investigation. Throughout this thesis, the definition (above) offered by Laland and Hoppitt (2003) will be followed, as it allows for the comparison of human and non-human cultures. Whatever definition is used, however, it is clear that human culture is unique in its complexity and diversity.

A key contributing factor to the unique complexity of human culture is its cumulative nature (Tomasello, Kruger & Ratner, 1993; Richerson & Boyd, 2005; Tennie, Call, & Tomasello, 2009; Dean et al., 2014). Cumulative culture is the process whereby individuals modify socially learnt behaviours, and these modifications to the behaviour are retained in the population, in a process sometimes referred to as 'ratcheting' as modifications are retained with minimal loss or backward slippage (Tomasello, 1994; Tennie et al., 2009). Cumulative culture is distinct from cultural change, and from the accumulation of novel behaviours in a population's behavioural repertoire, in that it describes a process of repeated modification and transmission of traits, with these cultural traits increasing in their complexity, efficiency, or adaptiveness (Dean et al., 2014; Mesoudi & Thornton, 2018). This cumulative process allows the development, over time and transmission episodes, of behaviours and technologies more complex than any one individual could invent within their lifetime.

While conceptually useful, the 'ratchet' analogy is not perfect, as it implies that cultural traits undergoing cumulative cultural evolution will progress in only one direction (increased complexity or efficiency) apparently without constraint. Mesoudi (2011) demonstrates with mathematical modelling that cultures may reach a point at which the cost of acquiring the culture's cumulated knowledge is so high, and so time-consuming, that no innovation following this acquisition is possible. Furthermore, the very capacities thought to allow this cumulative process to occur (a tendency to socially acquire common behaviours in the population to which the individuals belongs) have been implicated in the spread of maladaptive behaviours (Boyd, Richerson & Henrich, 2011). There are also multiple human populations in which technological loss has been documented, indicating that there are certain conditions (such as a reduced population size, or the loss of key knowledgeable individuals) in which the metaphorical ratchet can 'slip', so then no longer truly functions as

a ratchet (Henrich, 2004; Boyd et al., 2011). The ratchet metaphor has also been criticised on the grounds that it implicitly emphasises a certain characteristic of cumulative culture (namely, the social learning processes that prevent modifications from being lost, and so prevent the 'ratchet' from 'slipping'), at the exclusion of the innovative modification that is also critical to the process (Whiten, Horner & Marshall-Pescini, 2003; Charbonneau, 2015).

Definitions of cumulative culture have incorporated multiple dimensions along which a behaviour can progress as cumulation occurs; while there is a lack of consensus in the field as to what types of change are critical in identifying cumulative culture (Wilks & Blakey, 2018), generally behaviours have been expected to become more complex or more efficient as modifications are transmitted and retained over generations (Dean et al., 2014). Mesoudi and Thornton (2018) state that modifications to behaviour in cumulative culture should result in an enhancement of "some measure of performance, which is a proxy for inclusive genetic and/or cultural fitness" (2018, pp.2). Mesoudi and Thornton's (2018) criterion of improvements to fitness seems to fit with previous ideas of increased efficiency, and indeed they state that increased energy efficiency can be assumed to translate into higher inclusive fitness. However, Mesoudi and Thornton (2018) also note the difficulty of assessing fitness in post- demographic transition human populations, where they suggest 'cultural fitness', the maximisation of wealth or social status, might be a better measure. Although Mesoudi and Thornton (2018) only include improved *fitness*, which seems closely linked to efficiency, as a core criterion in their definition of cumulative culture, they also list 'extended criteria', which may not be present in all cases of cumulative culture, some of which (functionally dependent traits, in which innovations are contingent upon one another, and recombination, in which separate traits are combined) appear closely related to complexity. Given the obvious difficulties in assessing and isolating the fitness impacts of behavioural variants, efficiency seems a good proxy measure for this core criterion put forward by Mesoudi and Thornton (2018), while large increases in complexity may indicate that a behaviour meets some of their extended criteria for cumulative culture.

In order to study cumulative culture, it is necessary to have a means of measuring in what way a behaviour is changing. There are operational challenges in measuring both complexity and efficiency. Complexity is perhaps more easily measured, and can be quantified, at least when dealing with technological artefacts, by techno-units (the number of physically distinct structures that form a finished tool: Oswalt, 1976) or by procedural-units (the number of manufacturing steps required to produce a tool: Perreault et al., 2013). However, these approaches have limitations; a tool may comprise only one techno-unit but be the result of a complex manufacturing process, such as a stone prismatic blade. Tools may require the same number of procedural-units to manufacture, but the skill required to carry out these procedures may differ. Complexity of behaviour (rather than technology) can be assessed by counting the repertoire of actions that form a behaviour, or by examining the length of the sequence of actions that forms a behaviour (Byrne, Corp & Byrne, 2001). However, these measures of complexity suffer the problem of 'lumping and splitting'; with some behaviours, it may be difficult to reliably split units that comprise the behaviour (for example, if a behaviour is repeated five times to achieve the desired result, should this be counted as five units, or one unit?). As Byrne (2007) notes, this approach also does not take into account the potential complexity of hierarchical subroutines within a behaviour.

Efficiency may also be difficult to operationalise. While it could potentially be quantified quite easily, by measuring the amount of time, or the cost, of achieving a goal using a certain behaviour, this requires that the goal is apparent to the researcher. For behaviours related to foraging (for example, nut cracking in wild chimpanzees, Pan troglodytes verus, Günther & Boesch, 1993; termite fishing in wild chimpanzees, Pan troglodytes schweinfurthii, McGrew & Marchant, 1999), this is achievable (although it requires detailed data), but for behaviours which have an unclear goal, or achieve multiple goals, measuring efficiency may be difficult. For example, Lindenfors, Envall, Isaksson and Enquist (2015) found that European cooking recipes increased in complexity (in terms of the number of steps, separate partial processes, methods and ingredients) between the years 1200 and 1999. The authors suggest that efficiency of these recipes also increased, as the recipes incorporated more semimanufactured ingredients (prepared ingredients containing one or more raw products) over time. However, how does one measure the efficiency of a recipe? Would an efficient recipe contain the fewest ingredients and processes for the highest calorific or nutritional pay-off, or for the best flavour, or for the most impressive dish? Measuring efficiency in this case surely depends upon the goal of the person cooking the meal, which may not be obvious to the researcher.

There are operational difficulties associated with both of these potential measures of cumulative culture, efficiency and complexity, and both are relevant to key questions regarding cumulative culture. Increases in efficiency help to demonstrate the adaptive advantage of cumulated behaviours (showing that these behaviours allow individuals to achieve greater pay-offs at lower costs, and likely meeting Mesoudi and Thornton's 2018 core criterion of increasing fitness), while increases in complexity are central to one of the main benchmarks of cumulative culture; that behaviours should reach complexity beyond that which an individual could achieve in their lifetime. This remains a useful way of identifying behaviours which are likely to be the result of a process of multiple individuals modifying and transmitting the behaviour, thereby detecting instances in which a cumulative process is likely to have occurred.

<u>1.1.1 Cumulative culture in humans</u>

There is no debate over the presence of cumulative culture in our species (for examples, see Basalla, 1988; Price, 1963) and so studies investigating the phenomenon in humans tend to focus upon the underlying processes, which remain poorly understood (Dean et al., 2014). One approach to studying cumulative culture empirically is through transmission chain experiments. These studies, in which each participant acts as a model for the next, allow researchers to approximate the transmission of behaviours across artificial 'generations' of participants, allowing the study of the transmission and modification of behaviours. Linear transmission chains require each participant to be the demonstrator for the next, resulting in a chain of 'generations' of participants, and simulating vertical transmission (Mesoudi & Whiten, 2008). While these linear transmission chains approximate vertical transmission (for example, transmission of a behaviour from parent to child), transmission chain studies are necessarily simplifications of real-world scenarios (in which an individual might have multiple potential demonstrators to learn from, and in which multiple generations might be available to observe), they do allow examination of the ways in which cultural traits are transformed by repeated transmission. Alternatively, researchers have used replacement chains, in which participants attempt a task as a group, and are replaced one-by-one by new participants, each new participant representing a new 'generation'. This process results in a chain of groups, members of which overlap with one another, and allows exploration of transmission dynamics within a group (Mesoudi & Whiten, 2008). While linear transmission

chains can be considered analogous to parent-offspring social transmission, replacement chains instead approximate instances of changing group membership, such as a community undergoing births, deaths, and migration. Like linear transmission chains, replacement chains also necessarily simplify a complex, real-world, social situation in order to allow empirical study of the processes underlying social transmission. Miton and Charbonneau (2018) highlight a number of limitations regarding the use of transmission chain studies to investigate cumulative culture, one of which is the simplicity of the tasks used, relative to the complex ecological problems solved by real human societies, and they also argue that asocial control conditions tend to disadvantage participants by allowing too little working time for a meaningful comparison to be made between asocial and social conditions. Despite these limitations, transmission chain studies have made it possible to study the processes involved in large-scale, multi-generational cultural phenomena in the lab.

These methods have been used extensively by Caldwell and colleagues to investigate cumulative culture (Caldwell & Millen 2008; Caldwell & Millen, 2009; Caldwell & Millen, 2010a; Caldwell & Millen, 2010b). Participants were asked to complete a simple task such as building a tower from spaghetti and modelling clay, or folding a paper aeroplane. Participants had the opportunity to observe members of previous generations completing the task, or to observe the products of previous generations' efforts. These studies have demonstrated that cumulative improvement can occur over generations of participants in the absence of opportunities for imitative learning, driven by emulation alone (Caldwell & Millen, 2009), and that the opportunity to observe a greater number of models did not result in more rapid improvement across generations (Caldwell & Millen, 2010a). They have also shown that increasing the uncertainty of the pay-off of individual innovation in a task (by delaying measurement of a constructed tower until it had been moved and stood in front of a desk fan, thus preventing participants from estimating their success as they constructed their tower) encouraged copying and suppressed cumulative improvement (Caldwell & Millen, 2010b). The finding that high-fidelity copying may not be necessary for cumulative improvement has been replicated in another transmission chain study in which participants were tasked with constructing baskets to carry rice (Zwirner & Thornton, 2015). However, in all of these studies, the items that participants were tasked with constructing were arguably easy to reverse engineer (for example, the places in which a paper aeroplane has been folded can easily be observed). This may have made the items amenable to transmission via emulation

(in which only the end-product is seen), as the end-product contained visible clues as to how it was constructed. High-fidelity copying, with the opportunity to observe the process whereby an object is made (imitation), or to receive direct instruction on how to make the object (teaching), might be necessary for cumulative culture when complex, causally-opaque, objects are being made. Indeed, a study in which participants had to manufacture an item which was functionally opaque (the item's functional features were not visible in its final form) found that cumulative improvement only occurred when participants had the opportunity to observe the item being manufactured (i.e. had the opportunity to imitate) (Wasielewski, 2014). A study in which participants in transmission chains, each chain starting with a trained stone-knapper, were required to make Oldowan-style stone flakes found that without verbal teaching, performance fell to floor levels (Morgan et al., 2015), though the task of making these artefacts appears to have been too challenging for any cumulative improvement to occur within the experiment. Participants were also given only a maximum of 20 minutes to work on the stone-knapping, which seems unlikely to be sufficient time for any level of proficiency to be acquired (especially given evidence that decades of knapping experience are required in order for individuals to be able to predict and control the shape of flakes produced; Nonaka, Bril and Rein, 2010).

Transmission chain studies have also been conducted with children, finding that when chains were seeded with an inefficient method for solving a task, children innovated better methods and transmitted these methods along the chain, but chains seeded with a relatively efficient solution did not improve upon it, and so did not surpass the inventive potential of an individual (Tennie et al., 2014). Flynn (2008) found that when transmission chains were seeded with a sequence of behaviours performed to open a puzzle box, some of which were 'irrelevant actions', children parsed out the irrelevant actions, with the third child in the chain onwards performing significantly fewer irrelevant actions than the first child in the chain. Behaviours therefore increased in efficiency as they were passed along transmission chains in Flynn's study – while many transmission chain studies mentioned previously use an increase in performance as evidence of cumulative improvement across experimental generations, increasing efficiency is also included in many definitions of cumulative culture (Tomasello, 1994; Enquist, Ghirlanda & Eriksson, 2011). Rather than using a transmission chain design, McGuigan et al. (2017) provided groups of children with a three-tiered puzzle box, in which extracting rewards became increasingly challenging, but rewards were also of higher-value,

as children progressed from the first to the third tier. This study demonstrated that progress on the task improved across testing sessions (with initial solutions occurring at the first level of the task, and solutions to the two further levels increasing over time), the progress on both an individual and group level appeared cumulative (with children using techniques which built upon those they had previously discovered), and that children attempting the task in a group setting were more likely to reach the third tier than children in an asocial control. Though this study does not have the advantage of a transmission chain design of multiple 'generations' of participants (therefore making it more challenging to demonstrate that children met a key criteria of cumulative culture – that behaviours are modified and built upon by multiple individuals over time), the authors demonstrate that in the majority of cases, the child inventing the first solution on a tier was a different child than the inventor of the first solution on the previous tier.

Related paradigms, also based upon the transmission chain design, have used tasks which do not require adult participants to construct physical artefacts, but instead examine the transmission of virtual tasks. Derex, Godelle and Raymond (2013) found that participants tasked with building a virtual fishing-net who had access to step-by-step instructions from the previous participant in the chain outperformed those who had access only to the final net produced by a previous participant or had to construct successive nets with no information from others. The effect of group size (access to a larger number of social models) upon cultural complexity has also been examined using virtual rather than physical tasks (Derex, Beugin, Godelle & Raymond, 2013), finding that participants in larger groups made improvements in a simple task (building a virtual arrowhead), and avoided loss of performance on a complex task (building a virtual fishing net). In this study, task complexity was quantified as the number of steps required to complete the task. As in Morgan et al. (2015), the task appears to have been too complex for participants to improve upon performance. Larger groups also maintained the inclusion of both tasks across 15 trials, rather than specialising as a group to one task or the other, which the authors equate to cultural diversity (the accumulation of distinct cultural traits within a population) and suggest this could be a prerequisite for the emergence of division of labour, as it may lead to groups containing individuals that specialise in certain cultural traits (Derex et al., 2013). Groups of participants, with access to social information from one another, have been shown to be able to produce virtual artefacts more complex than an individual is able to create in the same

amount of time (Derex & Boyd, 2015). In a study of real-world (though computer-based) behaviour, Miu, Gulley, Laland and Rendell (2018) studied the entries submitted to computer coding competitions, finding that scores (based upon code effectiveness, speed and complexity) increased over time, indicating cumulative improvement. Participants in these competitions could view the entries submitted by other coders, and Miu et al. (2018) found that copying was common, with the majority of submissions sharing over 90% of their code with the current leader, indicating that participants selectively copied the highest scoring code. The majority of improvements were made by 'tweaking' (making minor modifications to) the highest-scoring code, and cultural diversity decreased over time. Studies such as these, conducted in a species known to possess cumulative culture, can shed light upon the cognitive abilities required for cumulative culture to emerge.

<u>1.1.2</u> Cumulative culture in non-humans

In considering potential evidence of cumulative culture in non-human animals, it is beneficial to consider the criteria an observed behaviour should meet to be considered cumulative. particularly in cases in which the progression of a behaviour, over time and generations, has not been observed. A behaviour must be 'cultural', in that it is socially acquired, and should have reached a level of complexity beyond that which an individual could invent alone (Tennie et al., 2009). A behaviour can be 'cultural' and maintained in a population via social learning but still be inventable by individuals; for example, Hobaiter et al. (2014) found that moss-sponging behaviour spread through a group of chimpanzees via social learning, but this behaviour was also independently invented by some individuals. In such cases, social learning may maintain behaviours by reducing the cost of acquisition for individuals if social learning is less costly than individual exploration and innovation. For this reason, the criterion that a behaviour should be too complex for an individual to invent alone is a useful rule of thumb for determining whether extant behaviours are likely to be the product of a process of repeated modification and transmission by multiple individuals over generations. Boesch (2003) puts forward three behaviours observed in wild chimpanzees which he argues should be considered as potential evidence of cumulative culture; nut-cracking (which may have progressed from hitting nuts against tree trunks, to using hammer stones, and additionally anvil stones and additional stones to stabilise the anvil, observed in Bossou), parasite manipulation (placing removed parasites on a leaf and then folding and cutting it, observed in Mahale, or placing them on an assembled pile of leaves, observed in Gombe) and well-digging (which may have progressed from digging in dry river beds, to digging near running water or algae-choked water, and finally incorporating the use of leaf-sponges to retrieve water from deep wells, seen in Semliki). Similarly, based upon examination of tools manufactured by wild New Caledonian crows, Hunt and Gray (2003) argue that Pandanus leaf tools have diversified through cumulative changes to an earlier type, progressively incorporating the cutting of more steps into the tool. Most recently, Schofield, McGrew, Takahashi and Hirata (2018) have presented an assessment of the changes over time in Japanese macaque (*Macaca fuscata*) food-washing behaviour at Koshima, suggesting that these behaviours appear to have increased in both complexity and efficiency over the 60+ years for which this population has been studied.

These examples remain controversial as potential examples of cumulative culture in nonhumans, largely due to the assumptions they require around the social transmission of these behaviours, whether the behaviours are truly cumulative progressions or unconnected innovations, and whether they represent greater complexity than an individual could achieve alone. However, studies such as Hobaiter et al. (2014) demonstrate that it is possible to observe the transmission and spread of novel behaviours in wild chimpanzee communities, confirming that behaviours are transmitted socially in this species in the wild. If chimpanzees possess the capacity for cumulative culture, in the future, studies like this could capture the emergence and spread of behaviours which meet the criteria for cumulative culture. Investigation of the capacity of New Caledonian crows to socially learn a solution to an artificial foraging task found that crows socially acquired information about the context of the task (namely, the locus to act upon), but did not imitate the actions they had observed (Logan et al., 2016). Further investigation of New Caledonian crows' ability to learn socially, perhaps by copying the physical form of tools encountered, rather than the action-sequence used to manufacture them, will shed further light on whether it is likely that the tool manufacturing behaviour argued by Hunt and Gray (2003) to be the result of cumulative culture is indeed socially learnt. Archaeological approaches may also play a role in revealing the ways in which non-human primate tool use has changed over time, and indicate whether any extant behaviours are the result of a cumulative process of gradual change and modification over generations (Haslam et al., 2009; Haslam, 2012; Haslam et al., 2017; Proffitt et al., in press), though this would of course be limited to behaviours which leave a lasting trace in the archaeological record, such as nut cracking. Researchers have also

investigated whether behaviours observed in wild chimpanzees and New Caledonian crows are inventable by naïve, captive chimpanzees and crows (Bluff et al., 2007; Bandini & Tennie, 2017). These studies could provide an indication of whether any extant wild behaviours go beyond the level of complexity achievable by a single animal; in the case of the Japanese macaque food washing behaviours (Schofield et al., 2018), this approach could be used to investigate whether the behaviours observed in the wild population could be reached by naïve individuals, without the need for social information, and crucially, without the need for the repeated, sequential episodes of modification and transmission which occur in cumulative culture (Mesoudi & Thornton, 2018).

Experimental studies have also been conducted to examine the capacity for cumulative culture in non-human animals, primarily in chimpanzees. Marshall-Pescini and Whiten (2008) found that chimpanzees did not socially learn a tool-based foraging technique which cumulatively built upon a technique they already knew. Dean et al. (2012) provided captive chimpanzees, capuchins (Sapajus apella), and three- to four-year-old human children with an artificial foraging task with three progressive solutions, each of which incorporated the previous solution. While this task does not fully reflect cumulative culture, as it was not provided over successive generations, and any process of modification and transmission could not be repeated, it does provide an insight into the socio-cognitive factors which contribute to cumulative culture. Only one chimpanzee reached the third, most complex solution, even with the addition of trained demonstrators, and no capuchin reached the third solution. In comparison, 15 children, from five experimental groups, reached this solution. Children were significantly more likely to engage in teaching, imitation, and prosocial behaviours such as donating rewards to others, and the authors argue that these social behaviours are likely to contribute to the human capacity for cumulative culture. One criticism of Dean et al.'s approach is the limitation inherent in drawing conclusions about the cognitive abilities necessary for cumulative culture based upon the behaviour of humans alone – humans may differ cognitively from other species in a variety of ways, not all of which may be relevant to their success in cumulative tasks (Kurzban & Barrett, 2012). However, the within-species findings that children who received higher amounts of instruction (teaching), showed higher levels of imitation, and showed higher levels of prosociality, progressed further in the task, supports the assertion that these abilities contribute to cumulative culture, and are not simply between-species differences that

happened to coincide with better performance in a cumulative task. An experiment examining the ability of children to solve the task used by Dean et al. (2012) individually, without social input, indicates that while social behaviours may have facilitated children's success in Dean et al.'s study, a substantial number of children are capable of reaching the third, most complex, solution asocially (Reindl, Gwilliams, Dean, Kendal & Tennie, 2017). As each progressive solution to the task built upon the previous stages, the fact that children could reach the most complex stage without social information raises the possibility that studies like this could give the illusion of cumulative culture without in fact relying on cumulative cultural processes. Vale et al. (2017) studied the capacity of captive chimpanzees to socially learn a complex foraging behaviour built upon previously acquired, comparatively simple behaviours. Chimpanzees were more likely to acquire the complex behaviour (unbending a tube so that liquid could be sucked through it, unscrewing a valve on the tube to allow liquid through, and finally sucking liquid through the tube), if they had previous experience using straws to retrieve the liquid, demonstrating that the complex method built upon simpler behaviour. While an asocial control group did not succeed in inventing the complex behaviour (suggesting it may meet the criteria of being beyond the capacity of an individual to invent), the behaviour did emerge in a group in which it was not seeded by a trained demonstrator. The authors argue that this may have been through a combination of social learning of component behaviours and individual invention, but cannot exclude the possibility that the behaviour is within an individual chimpanzee's ability to invent.

As in the study of human cultural transmission, transmission chain designs have also been used to study the capacity of non-humans to show cumulative improvement across multiple episodes of transmission. Adapting a classic transmission chain design used in human studies, Sasaki and Biro (2017) examined the efficiency of homing pigeon (*Columba livia*) flight routes. Pigeons in a replacement transmission chain (each pigeon after the first flying the route 12 times paired with an experienced bird, before acting as the experienced partner with the next, naïve, pigeon) outperformed pigeons in control groups (flying the route 60 times either alone or in fixed pairs) in terms of route efficiency. Routes were also more similar in successive generations within transmission chains than between transmission chains, indicating that routes in the transmission chains were socially transferred. The authors argue that presenting animals with the same problem repeatedly can elicit a cumulative improved

efficiency was demonstrated, no increase in complexity was observed, and that the nature of the task and existence of an optimum route distinguishes the problem from many tackled by human cumulative culture.

Also using an adapted transmission chain design, Claidiere, Smith, Kirby and Fagot (2014) presented Guinea baboons (*Papio papio*) with a touch-screen task in which in order to earn a reward they were required to memorize and attempt to reproduce a pattern of coloured squares on a 4x4 grid. Each baboon's response pattern on the grid was then the model pattern for the next baboon. There was a progressive increase in performance (copying accuracy) across generations of transmission, and structure in the form of tetromino patterns emerged in the patterns input by baboons. Baboons were more likely to successfully replicate the model pattern if it was a tetromino pattern. The authors argue this demonstrates crucial aspects of cumulative culture; an increase in performance, the emergence of structure, and lineage specificity. However, as in Sasaki and Biro (2017), while there was an apparent improvement in efficiency, via the emergence of structure in the patterns, there was no apparent increase in complexity. Both studies used tasks in which only a single behaviour could be improved, up to an optimum point, in contrast with examples of human cumulative culture, which is openended and incorporates numerous behaviours which may be recombined (Charbonneau, 2016).

1.1.3 Cognitive requirements of cumulative culture

Many of the studies discussed previously have examined the cognitive abilities which may be required to support cumulative culture. Broadly, it seems likely that three main abilities are required. Firstly, a species must be capable of transmitting and learning information socially. The type of social learning required in order to support cumulative culture is a subject of debate, with some authors arguing that only high fidelity social learning will allow the development of cumulative culture (Boyd & Richerson, 1985; Tomasello et al., 1993), whilst others suggest that cumulative culture may be possible based upon lower-fidelity forms of social learning (Caldwell & Millen, 2009; Zwirner & Thornton, 2015; Logan et al., 2016). Connected to this potential requirement for high-fidelity social learning is the presence of prosocial tendencies, such as the tendency to share rewards (Dean et al., 2012), or sociability in tolerating others observing ones' behaviour (Pradhan, Tennie & van Schaik, 2012) that

may promote high-fidelity social learning. The second ability required in order for cumulative culture to develop is behavioural flexibility; that is, members of the species must be capable of flexibly altering their behaviour (both in order to learn novel behaviours and to modify these behaviours). Finally, a species must be capable of innovating both novel behaviours and novel alterations to learnt behaviours. These three abilities work in concert to support cumulative culture – an individual innovates an improvement to a behaviour or tradition, and this improvement is passed on via social learning to other group members. In order for both the alteration to the behaviour to occur on an individual level in the innovator, and then for other group members to adopt this alteration, individuals in the species must be capable of flexibly altering their behaviour. If a species does not possess cumulative culture, it seems likely to be due to a deficit in one or more of these three abilities.

Behavioural flexibility, the ability to alter behaviour based upon environmental feedback and to inhibit previously successful behaviours, allows organisms to adapt their behaviour to suit changing or novel environments and supports problem solving (Griffin & Guez, 2014; Sol, Timmermans & Lefebvre, 2002). Behavioural flexibility is distinct from innovation (defined by Reader & Laland 2003, pp.14, as "A process that results in new or modified learned behaviour and that introduces novel behavioural variants into a population's repertoire") as it involves inhibiting previously successful behaviours and can include the acquisition of novel, socially learned behaviours (Wright et al., 2010). It is also thought to be a key ability supporting the evolution of cumulative culture (Dean et al., 2014). Cumulative culture relies upon the repeated modification and transmission of known behaviours (Tennie et al., 2009; Mesoudi & Thornton, 2018) and therefore necessitates flexibility in both the process of innovative modification by some individuals, and in the acquisition by others of the improved behaviours that result (as in a cumulative process, these improved behaviours replace previous versions already in the population's repertoire). As outlined by Charbonneau (2015), an ability to innovate entirely novel behaviours 'from scratch' alone is not sufficient to support cumulative culture, which instead requires an ability to modify known behaviours. As evidence for cumulative culture in our closest living relative, the chimpanzee, is limited (Dean et al., 2014; Whiten, 2017), behavioural flexibility, along with innovation and social learning, should be considered and investigated as a potential limiting factor for cumulative culture.

1.1.4 Population factors facilitating cumulative culture

In addition to the cognitive requirements of cumulative culture described above, demographic factors are likely to facilitate cumulative culture. Derex et al. (2013) found that when players completed virtual tasks in larger groups, more improvements were made to cultural traits, and greater cultural diversity was maintained. This experimental finding is supported by evidence from real human populations; Henrich (2004) describes cultural loss in Tasmania and demonstrates through modelling that smaller populations are more vulnerable to cultural loss through small copying errors, while Kline and Boyd (2010) found that in Oceanic island populations, population size positively correlates with both the number of marine foraging tools, and the complexity of these tools in terms of techno-units. However, the relationship between population size and cultural complexity may be more nuanced than these findings suggest. Acerbi, Kendal and Tehrani (2017) found a negative relationship between population size and the complexity of folktales (as measured by the number of motifs in a narrative), though larger populations tended to have a greater number of distinct folktales. This could be due to increased pressure for memorability in larger populations, as folktales must be learnable by larger numbers of individuals, but the authors also suggest that the effect of demographic factors upon cultural complexity and cultural transmission may be domainspecific, with some types of behaviour more susceptible to loss through copying error (eg. technology in Henrich's 2004 Tasmanian model) than others (such as folktales, where individuals may be able to easily reproduce relevant features – see discussion of cultural attractor theory later in this chapter).

It is not only the size of a population that may facilitate or constrain cumulative culture, but also its structure. Derex and Boyd (2016) presented participants with a virtual task in which different ingredients could be combined to make a remedy for an illness, with optimum combinations producing new ingredients, and combinations of these new ingredients scoring more highly. Partially-connected groups (groups of six participants, split into three separate dyads, with occasional transfer between dyads) scored more highly than fully-connected groups (groups of six participant seeing all group-members results after each trial). This was due to greater exploration in partially-connected groups, resulting in greater diversity of solutions, while fully-connected groups tended to converge on one solution. Similarly, modelling has shown that frequent migration between groups increases

the cultural repertoire of groups, and can drive cultural change (Creanza, Kolodny & Feldman, 2017). Derex, Perreault and Boyd (2018) suggest from modelling evidence that there is an optimum intermediate level of population connectedness; that fully-connected populations can maintain cultural traits, but lack the variation and diversity to innovate complex cultural traits (with innovation in this model operationalised as combining existing traits), while poorly-connected populations have high diversity of cultural traits, but cannot maintain complex traits due to a small effective group size (each learner has a limited number of potential models, and the risk of inaccurate transmission increases with fewer models, resulting in cultural loss). While the cognitive requirements described previously are crucial for cumulative culture to emerge, population factors such as group size and population connectedness appear critical for cumulative culture to be maintained.

1.2 Behavioural flexibility

1.2.1 Defining and measuring behavioural flexibility

Behavioural flexibility is defined throughout this thesis as the ability to alter behaviour based upon environmental feedback and to inhibit previously successful behaviours (Logan, 2016a; Griffin & Guez, 2014). It has been argued to be a key ability supporting the evolution of cumulative culture (Dean et al. 2014). However, behavioural flexibility has been argued to be an ill-defined concept (Coppens, de Boer & Koolhaas, 2010), to the extent that Audet and Lefebvre (2017) argue that the term be avoided altogether. Griffin and Guez (2014) suggest that behavioural flexibility is likely to encompass a range of abilities, including the ability to inhibit a previously rewarded behaviour, to invent novel behaviour, and to perform an existing behaviour in a novel context. This description would suggest that behavioural flexibility includes capacities commonly described as innovation (inventing novel behaviour, and performing existing behaviour in a novel context is the definition of innovation according to Kummer and Goodall, 1985), but in addition includes the ability to inhibit previously rewarded behaviour. Logan (2016b) suggests that behavioural flexibility is an independent trait that can facilitate innovation. Mikhalevich, Powell and Logan (2017) describe behavioural flexibility as a special case of behavioural plasticity (plasticity being the capacity to modify behaviour in response to environmental input), in which an organism can modify "the rules governing behavioural expression, and thus the behaviours themselves"

(Mikhalevich, Powell & Logan, 2017, pp.4). The lack of consensus over an appropriate definition for behavioural flexibility, and the likelihood that as a concept it encompasses a collection of abilities, is perhaps best illustrated by the range of measures used as indicators of behavioural flexibility.

One means of assessing a species' behavioural flexibility seen in the literature is through the measurement of innovation rate (Sol et al., 2002; Nikolakakis, Sol & Lefebvre, 2003; Sol & Lefebvre, 2000; Lefebvre, Whittle, Lascaris & Finkelstein, 1997; Lefebvre, Reader & Sol, 2004) or the number of behavioural variants in a population (Wright et al., 2010) as proxy measures of flexibility. This approach has found relationships between behavioural flexibility (innovation rate) and invasion success (Sol & Lefebvre, 2000; Sol et al., 2002), forebrain size (Lefebvre et al., 1997; Lefebvre et al., 2004) and species richness (Nikolakakis et al., 2003). This measure is perhaps better thought of as repertoire flexibility (following Ramsey, Bastian & van Schaik, 2007), and may be difficult to reconcile with alternative measures also purporting to measure behavioural flexibility, as behavioural flexibility may not always lead to increased innovativeness, at either an individual or species level (Griffin, Guez, Lermite & Patience 2013; Logan, 2016a; Logan 2016b).

Tebbich, Griffin, Peschl and Sterelny (2016) include behavioural flexibility as a facilitating factor in their framework of animal innovation, suggesting that a propensity to switch between foraging techniques and strategies increases an organism's breadth of interactions with an unexploited resource, and so facilitates innovation, but is only one of a range of capacities that can increase the variety of interactions an organism has with novel problems (the others including the breadth of the organism's existing behavioural repertoire, its motivation to interact with novel opportunities, and its morphology). Logan (2016a, 2016b) found that despite performing well in experimental tests of behavioural flexibility (a reversal learning test in which subjects learned to associate food with one of two colours, which were then reversed, and an Aesop's fable water displacement test with changing parameters, Logan, 2016a), great-tailed grackles (*Quiscalus mexicanus*) did not succeed in innovating solutions to novel problems (Logan, 2016b). Griffin et al. (2013) found that Indian mynas (*Sturnus tristis*) that successfully solved novel extractive foraging tasks more quickly were slow to flexibly respond to changing contingencies in a serial reversal learning task, again suggesting that behavioural flexibility (as measured by reversal learning tasks) is dissociated

from innovation propensity. In this case, mynas that solved the innovation tasks more quickly also formed more rapid initial associations in the reversal learning task, but then were slower to reverse these when contingencies changed. While behavioural flexibility may be a mechanism that facilitates innovation (Griffin & Guez, 2014), these studies indicate that the relationship between the two may not be direct, and their findings suggest that the two abilities should be considered separately. One conceptual distinction between behavioural flexibility and innovation is that an organism can behave flexibly without exhibiting any novel behaviour; flexibility only requires inhibiting a previously rewarded response and applying an alternative behaviour, while innovation requires expanding the behavioural repertoire.

Behavioural flexibility (sometimes termed cognitive flexibility in the experimental literature, Audet & Lefebvre, 2017) has been tested experimentally in a range of species, both in the wild and captivity, frequently by employing experimental paradigms in which animals must respond to a change in task parameters. Reversal learning paradigms are frequently used, in which animals are trained to one association and then in the test phase, reward contingencies are reversed. For example, Manrique & Call (2015) trained great apes (chimpanzees, bonobos - Pan paniscus, orangutans - Pongo abelii, and gorillas - Gorilla gorilla) to open a container by pulling a handle to either the left or right, and then in the test phase, the container, which previously only opened when the handle was pulled in one direction, now only opened when the handle was pulled in the opposite direction. In this type of task, an animal must inhibit a previously rewarded response in order to be successful in the test phase. The speed at which an animal reverses its response preference in reversal learning experiments can be used as a measure of behavioural flexibility (Logan, 2016a), as can the frequency of errors during the test phase (Manrique & Call, 2015). Reversal learning paradigms are perhaps most common in neuroscience research (de Bruin et al., 1994; Homberg et al., 2007; Schoenbaum, Roesch, Salnaker & Takahashi, 2009) and are also used in comparative psychology (Rumbaugh & McQueeney, 1963; Rumbaugh, 1971; Bond, Kamil & Balda, 2007; Boogert, Monceau & Lefebvre, 2010; Liu, Day, Summers & Burmeister, 2016).

Additionally, behavioural flexibility has been measured via set-shifting paradigms. Perhaps the most famous paradigm for measuring set-shifting is the Wisconsin Card Sorting Test (Grant & Berg, 1948), in which human participants are asked to match cards, without being
informed of the rules by which they must sort them. Cards can be matched by colour, shape or number (eg. a card showing two green stars could be matched with cards showing any number or colour of star symbols, or any card also showing two symbols, or any card showing any number of green symbols). Participants are told whether their card selected to match the model card is correct or incorrect, and must infer the sorting rule from this information. The correct 'dimension' (colour, number, or shape) by which to sort cards is then changed after the participant has made a number (e.g. ten) of correct responses (Mountain & Snow, 1993). The ability to perform well on this task develops with age, with 10-year-old children performing at a level comparable to adults in terms of the number of categories successfully sorted and the number of perseverative errors made (Chelune & Baer, 1986).

The Wisconsin Card Sorting Test has been adapted for use with non-humans, and tests of this type are commonly referred to as intradimensional/extradimensional (ID/ED) tasks, in reference to the attentional shifts that must be made by subjects – intradimensional shifts are functionally similar to the reversal learning paradigms described previously, as subjects are trained to respond to one stimulus (for example, an odour) in a two-choice discrimination, and the reward contingency changes such that the correct response is to the previously unrewarded stimulus (the previously incorrect odour). As this shift occurs within one perceptual dimension (odour), it is referred to as an intradimensional shift. Extradimensional shifts occur when a subject has been trained to discriminate and respond to one perceptual dimension (eg. odour), and the reward contingency changes such that another perceptual dimension now indicates reward (eg. the texture of the digging medium in which a reward is buried) (Shepp & Eimas, 1964; Roberts, Robbins & Everitt, 1988; Roberts et al., 1994; McAlonan & Brown, 2003). Research indicates that the neurological bases of reversal learning and extradimensional set-shifting are dissociated, with lesions to the orbital prefrontal cortex impairing performance on reversal learning paradigms but not extradimensional set-shifting (Dias, Robbins & Roberts, 1996; McAlonan & Brown, 2003).

Multi-access box or extractive foraging task paradigms are another approach that has been used to assess behavioural flexibility in non-humans (Auersperg et al., 2011; Lehner, Burkart & van Schaik, 2011; Manrique, Völter & Call, 2013; Richter, Hochner & Kuba, 2016; Davis et al., 2016). In these studies, animals can access food rewards by solving a physical problem

(for example, reaching through a hole to retrieve a reward, Manrique et al., 2013; or pulling a string attached to the food reward, Auersperg et al., 2011), but once attained, this initial solution is rendered ineffective. Animals must then acquire a novel solution, or modify the previously successful solution, in order to continue to retrieve rewards. Such measures appear to call upon some of the abilities described by Griffin and Guez (2014) as components of behavioural flexibility; abandoning previously rewarded behaviours, and applying novel behaviour in response to novel conditions. Conceptually, there are clear similarities between this approach and classic reversal learning paradigms; once a rewarding behaviour is attained, reward contingencies are altered such that previously rewarded behaviour must be inhibited and novel behaviour displayed in order to attain a reward. However, Audet and Lefebvre (2017) argue that the direct relationship between cue and reward in a reversal task, and the sudden and repeated changes in a cue's predictive value that characterize reversal and setshifting tasks, are not reflected in extractive foraging tasks in captivity or problem-solving in the wild. Therefore, despite the surface-level conceptual similarity between these approaches to measuring behavioural flexibility, it is possible that these tasks are measuring different processes.

Token exchange paradigms have also been used as a means of assessing behavioural flexibility in chimpanzees (Hopper, Schapiro, Lambeth & Brosnan, 2011; van Leeuwen et al., 2013; Hopper, Kurtycz, Ross & Bonnie, 2015; van Leeuwen & Call, 2017). In these studies, chimpanzees are trained to exchange tokens with an experimenter for food rewards of different value – low value rewards being less-preferred foods. Different token exchange locations can also be offered. Both van Leeuwen et al. (2013) and Hopper et al. (2015) explored the capacity of chimpanzees to exchange tokens at novel locations, having been trained and rewarded at a previous location. van Leeuwen et al. (2013) found that chimpanzees previously trained to exchange tokens at one location remained faithful to their trained location in the face of a majority of the group trained to an alternative location and receiving equal reward, but did change their behaviour and exchange at an alternative location for a higher value reward. Similarly, Hopper et al. (2015) found chimpanzees trained to exchange tokens for different value food rewards at different locations in their enclosure were able to flexibly switch between locations when the reward value at locations changed, and explored novel locations despite receiving low-value rewards at a known location.

Studies have also explored the capacity of chimpanzees to select novel token types for exchange, despite training to exchange a known token type. Hopper et al. (2011) found that chimpanzees continued to primarily exchange a token type, initially demonstrated by a group member, that yielded a low value reward, despite the opportunity to exchange a different token type for a far higher value reward. van Leeuwen and Call (2017) trained chimpanzees to exchange one token type for a low value reward, and did not expose them to alternative token types or to alternative food rewards. These chimpanzees were then exposed to a demonstrator chimpanzee that exchanged a different token type, and received either a highervalue food reward or the same, low-value, reward as the observer. Chimpanzees primarily continued to exchange the token type they had been trained on, but those that did change their behaviour were more likely to copy the demonstrator if the demonstrator had received a highvalue food. Vale et al. (2017) found that chimpanzees with prior experience of exchanging one token type for a low value reward showed some inclination to explore an alternative, high value reward token when given the opportunity, but that this was not affected by observing a social model. The authors suggest this reflects a strategy of 'proportional reservation', in which individuals copy only to the extent that they are dissatisfied with their current pay-off.

While token exchange paradigms allow easy experimental control of reward value, and control for any intrinsic preference for certain techniques (eg. a preference for 'poking' a stick into a device to retrieve a reward rather than 'lifting' a barrier to retrieve the reward, Hopper et al., 2007), they do not require animals to acquire novel forms of behaviour, and so may be less challenging than multi-access box or artificial foraging paradigms. It may also be telling that two studies in which chimpanzees had only to alter the location at which they exchanged tokens, and not the token type they exchanged (van Leeuwen et al., 2013; Hopper et al., 2015), found more evidence of behavioural flexibility than those in which chimpanzees were instead required to exchange alternative token types (Hopper et al., 2011; van Leeuwen & Call, 2017; though see also Vale et al., 2017).

Observing the behaviour of animals outwith controlled experiments may also provide an insight into the flexibility of such species. The modification of known tool behaviours in chimpanzees indicates a capacity for behavioural flexibility; for example, an individual in Bossou was observed firstly applying a tool and technique generally used for ant-dipping on the ground to ant-fishing in trees, and later using tools of a length better suited to ant-fishing

in trees (Yamamoto, Yamakoshi, Humle & Matsuzawa, 2008). Although the relationship between innovation and behavioural flexibility remains unclear (Griffin et al., 2013; Griffin & Guez, 2014; Logan, 2016b), the observation of innovative tool use in wild chimpanzees, such as crafting sponges from moss rather than leaves (Hobaiter et al., 2014), or the diverse novel behaviours documented by Nishida, Matsusaka and McGrew (2009), could also be interpreted as evidence for behavioural flexibility.

The behaviour of migrating female chimpanzees is also indicative of a capacity for flexibility; in a case study of one immigrant female Luncz and Boesch (2014) found that her hammer tool selection for nut cracking changed to match the behaviour of her new group, and in the second year after her migration her pattern of tool selection was statistically indistinguishable from that of her new group. While only a case study, the authors note that the pattern of hammer selection differs in three neighbouring groups at Tai, with one group preferentially choosing stone hammers throughout the season, while the neighbouring two groups move from stone to wooden hammers as the nut season progresses and nuts dry out, becoming easier to crack (Luncz, Mundry & Boesch, 2012). If females migrating between groups maintained their initial preference in hammer selection, this group difference would not remain stable. The authors also show that males (which are philopatric) and females in these groups show equal levels of similarity to the group behaviour, again indicating that immigrant females likely adjust their behaviour to match that of the group. This was further supported by an archaeological study in Tai showing that the tool selection pattern of the natal group of four immigrant females differed from that of the group into which they migrated, while their tool selection in their new group matched the group's existing tool selection pattern (Luncz, Wittig & Boesch, 2015). Immigrant females appear to adjust their behaviour to match their new group despite differences in efficiency between the groups' nutcracking strategies, driven by differences in efficiency between hammer materials and the physical power used while nut-cracking (Luncz, Sirianni, Mundry & Boesch, 2018). While the mechanism behind this is unclear, with Luncz and Boesch (2014) and Luncz et al. (2018) suggesting conformist social learning, the modification of behaviour shown by immigrant females is a good example of behavioural flexibility in wild chimpanzees. Notably in this case, it does not involve the acquisition or innovation of novel behaviour, as immigrants are believed to have experience using both stone and wooden hammers (Luncz, Wittig & Boesch, 2015, though see also Luncz et al., 2018, which suggests a difference in technique between

groups that immigrants may also acquire), but rather a change in frequency that seems to reflect immigrant females adjusting the rules governing their behaviour, and crucially, abandoning the tool selection strategy they had followed in their natal group. Neighbouring chimpanzee communities which maintain differences in their cultural behaviour despite female migration (eg. Kalinzu: Koops, Schöning, Isaji & Hashimoto, 2015; Bossou and Nimba: Humle, 2016) could provide valuable data on behavioural flexibility in wild chimpanzees, as well as an opportunity to investigate conformist social learning.

1.2.2 Behavioural flexibility in non-human primates

Multiple studies have measured behavioural flexibility, either with this as an explicit aim or incidentally, in non-human primates, resulting in divergent conclusions regarding the capacity for behavioural flexibility, in chimpanzees especially.

Some of the literature indicates that chimpanzees tend to be conservative (unwilling / unable to alter their behaviour) when completing foraging-based tasks (Hrubesch, Preuschoft & van Schaik, 2009; Marshall-Pescini & Whiten, 2008; Hopper et al., 2011; Gruber et al., 2011; van Leeuwen & Call, 2017). Marshall-Pescini and Whiten (2008) found that, having acquired a technique for completing an artificial foraging task ('dipping' a stick tool through a trap door to retrieve honey from within a small box), chimpanzees failed to 'upgrade' to a more complex, human-demonstrated alternative technique (probing with a stick tool to move a bolt, allowing a larger trap door to be opened and a mixture of honey and peanuts to be retrieved). This alternative technique yielded greater rewards, but chimpanzees failed to acquire it despite having the opportunity to observe over 200 demonstrations. Hrubesch et al. (2009) presented chimpanzees with a task in which food rewards placed on a wooden board outside their enclosure could be retrieved using a stick tool, or by shaking the board. When the board was reinforced to prevent the shaking strategy, chimpanzees who had used this approach continued to attempt it despite its complete lack of utility. Hopper et al. (2011) used a tokenexchange paradigm, and found that chimpanzees continued to primarily exchange a token type, initially demonstrated by a group member, that yielded a low value reward, despite the opportunity to exchange a different token type for a far higher value reward. It should be noted that although this behaviour pattern can be described as 'conservative', the authors argue that conformity is a more parsimonious explanation for these results. This raises an

important point; that a finding of 'conservatism' in a study may be due to factors other than a lack of capacity for behavioural flexibility. Dean et al. (2014) argue that conservatism as a mechanism and an outcome should be separated, as a conservative outcome (like that of Hopper et al., 2011) can be the result of conformity or an inability to copy in proportion to payoffs. In another token exchange study, van Leeuwen and Call (2017) found that chimpanzees trained to exchange one token type for a low-value reward, did not tend to switch token type after observing another chimpanzee exchange an alternative token for a higher-value reward (though individuals who did switch, on around 40% of trials, were more likely to do so if they had observed a conspecific receiving a higher-value reward rather than a reward of the same value).

In wild chimpanzees in the Budongo Forest, Gruber et al. (2011) found that individuals did not acquire a novel tool behaviour when provided with scaffolding towards it in the form of a stick already inserted into a tree cavity baited with honey, a configuration designed to demonstrate the affordances of the stick tool to the chimpanzees. A subset of these Budongo chimpanzees studied by Gruber et al. (2011) manufactured leaf-sponges to attempt to retrieve the honey, while others simply attempted to use their hands. Gruber (2016) argues, based upon a definition of 'conservatism' as "a failure to adopt a behavioural alternative over a known behaviour in the same task context" (Hrubesch, 2009; Gruber, 2016), that individuals who attempted to use their hands to reach the honey, rather than a tool, should not be considered conservative, as they did not have a known task solution to abandon in favour of stick-use – rather, they failed to discover any effective solution to the task. Additionally, the leaf-spongers can be considered conservative (by the definition followed by Gruber) only if the honey-dipping task is considered to be the same task context as water acquisition, for which leaf sponges are generally used in the Budongo community (Gruber, 2016).

It could be argued that, having mastered one technique, even if it is only minimally rewarding, it is not worthwhile for chimpanzees to expend cognitive resources 'upgrading' to a more efficient technique (as in Marshall-Pescini and Whiten, 2008). However, the finding of Hrubesch et al. (2009) provides an example in which there is no obvious benefit to chimpanzees' conservative behaviour, as their conservatism in this task meant they did not succeed in retrieving the reward. It is unclear whether, having mastered one technique to solve such a task, chimpanzees are unable or unwilling to learn new techniques, or whether

chimpanzees are unable to inhibit a previously learnt response to a task and thus produce an initial behaviour repeatedly.

These studies, of both wild and captive chimpanzees, seem to indicate that chimpanzees are often not only unwilling or unable to acquire new behaviours in order to retrieve greater rewards (Marshall-Pescini & Whiten, 2008; Hopper et al., 2011; van Leeuwen & Call, 2017), but can also be unwilling or unable to do so in order to retrieve any reward at all (Hrubesch et al., 2009). However, they also highlight some of the limitations of this field of research; namely, vague definitions for behavioural flexibility and its absence ('conservatism') and the potential for findings of apparent conservatism in chimpanzees to be due to factors other than their capacity for behavioural flexibility. One particularly relevant point is whether some instances of conservatism could be due to chimpanzees satisficing; continuing to apply suboptimal behaviour rather than changing strategy, because the reward they receive for persisting is satisfactory (or 'good enough') (Simon, 1956). This could apply to studies in which a less efficient, or less rewarding technique remained accessible to chimpanzees, and they did not switch to more efficient or more rewarding options (eg. Marshall-Pescini & Whiten, 2008; Hopper et al., 2011; van Leeuwen & Call, 2017; Vale et al., 2017). However, Dean et al. (2012) found no evidence of satisficing in their cumulative artificial foraging task; chimpanzees continued to manipulate moving pieces of the task related to the second- and third-stage solutions at the same rate after they had achieved the first-stage solution (so, continued to explore the rest of the task after finding a way to retrieve low value rewards).

Further research indicates that non-human primates may be capable of a greater degree of behavioural flexibility than these previous studies suggest. Yamamoto, Humle, and Tanaka (2013) found that, when presented with a tube containing juice, chimpanzees that initially solved the task by 'dipping' a straw into the tube (an inefficient solution) were able to swap to the more efficient 'straw-sucking' technique following exposure to a conspecific who performed this behaviour. Both behaviours were already part of the studied chimpanzees' behavioural repertoire, and both were argued to be equally cognitively challenging, which may have allowed individuals to learn them more easily following their initial experience of an alternative technique (Yamamoto et al., 2013). The fact that three of the five chimpanzees that 'dipped' initially stopped participating during the first stage of the task (before observing the alternative technique and altering their behaviour) may also suggest that these individuals

were unsatisfied with the results of their chosen technique, and may thus have been more willing to alter their behaviour (Yamamoto et al., 2013). As both techniques are described by the authors as being part of the chimpanzees' behavioural repertoire, it must be noted that individuals who swapped to the more efficient technique did not necessarily have to learn this technique, but simply had to apply it to the situation at hand.

Manrique et al. (2013) presented four species of great ape with a task in which, once discovered, solutions were made to be obsolete. The task had three stages, with the number of possible solutions diminishing at each stage, and only one solution available in the final stage. The task therefore required participants to switch flexibly between solutions each time the task was altered, and potentially to desist from utilising a technique that had previously been successful. Chimpanzees, bonobos and gorillas succeeded in solving all three stages of the task, indicating that these species were capable of altering their behaviour in response to changing task conditions. Orangutans failed to solve the final stage of the task, and four out of seven orangutans used the same technique in all three stages of the task (which was effective in stages 1 and 2 but ineffective in stage 3). For many participants, the transitions between solutions were quick, indicating both that they discovered the successful solution quickly, and that they were able to stop using the previously successful response.

Although orangutans performed poorly relative to other great ape species in Manrique et al.'s task (2013), there is evidence of behavioural flexibility in orangutans also. Lehner et al. (2011) presented a changing tool-based foraging task to captive orangutans (*Pongo abelii*), in which a liquid reward could be retrieved from a tube using a variety of tool materials. The authors altered the diameter of the tube and the range of materials available to the orangutans during the study, restricting the solutions available. This study found that when faced with a tool-based foraging task in which available solutions were restricted over time, orangutans were able to flexibly alter their behaviour. Orangutans in this study used a variety of tool techniques within stages (i.e. unprompted by alterations to the task) and also responded to task alteration by changing their responses (though, unlike the Manrique et al., 2013, study, the changes in response were more gradual, with orangutans still attempting to use solutions which had worked previously after they had been rendered ineffective). Unlike the chimpanzees in Yamamoto et al. (2013), orangutans had to invent novel techniques in order to successfully solve the task.

Davis et al. (2016) found that chimpanzees presented with an artificial foraging task were able to relinquish a highly inefficient task solution in favour of a more efficient solution when provided with demonstrations of the efficient solution by a conspecific or human demonstrator. Vale et al. (2017) found that following the removal of simple tools that could be used to acquire juice in a dipping task, chimpanzees began to use complex tools that required modification (unscrewing a valve so a tube could be used as a 'straw' to suck up juice). Davis et al. (2016) argue that such flexibility may be more apparent in situations in which there is a large difference in efficiency between two technique options (with a relatively highly inefficient solution more likely to be relinquished). This may suggest chimpanzees use a 'copy-if-dissatisfied' strategy when given the opportunity to socially acquire more efficient solutions to problems (Laland 2004). If so, behavioural flexibility in such studies may only be apparent when the original solution is rendered highly inefficient and dissatisfying, or entirely impossible. The findings of Lehner et al. (2011) and Manrique et al. (2013) may, in light of this, imply that great apes also employ an 'explore-ifdissatisfied' strategy when given the opportunity to achieve improved solutions to problems without the benefit of an existing competent model. Many studies in which great apes show behavioural flexibility employ paradigms in which solutions are rendered impossible or highly dissatisfying, again raising the question of the role satisficing might play in limiting chimpanzees' apparent behavioural flexibility in experimental conditions. However, chimpanzees have also shown a lack of flexibility in response to tasks in which there is a large disparity in reward quality (Hrubesch et al., 2009; Hopper et al., 2011; van Leeuwen & Call, 2017), and satisficing has not been found to affect motivation in one artificial foraging task (Dean et al., 2012).

The existing experimental evidence regarding behavioural flexibility in chimpanzees is thus divergent (though observations in the wild indicate chimpanzees can and do behave flexibly there, Luncz and Boesch, 2014), and further research is required to shed light upon the situations in which chimpanzees may be able and motivated to abandon known techniques in favour of novel ones. Such studies can have significant implications for comparative research on cumulative culture; if chimpanzees are found to have the ability to behave flexibly under certain conditions, such conditions might also promote the emergence of cumulative technology. The capacity of chimpanzees to respond flexibly to changes in task constraints is explored experimentally in Chapters 2 and 3 of this thesis, following the paradigm used by

Lehner et al. (2011), and the potential influence of group-level social tolerance upon performance on this task is examined in Chapter 4.

1.3 Cultural attraction

1.3.1 The cultural attraction debate

The majority of the research relating to culture and cumulative culture discussed thus far has been conducted under the umbrella of the 'standard approach' to cultural evolution (Acerbi & Mesoudi, 2015). This approach is based upon the assumption that cultural evolution (the transmission and transformation of cultural information) can be conceptualised as an evolutionary process, similar, though not identical, to genetic evolution. Culture is predicted to evolve in a manner consistent with key Darwinian principles set out in The Origin of Species; that traits exhibit variation, differ in their survival and reproduction, and are transmitted from one organism to another (Boyd & Richerson, 1985; Mesoudi, Whiten & Laland, 2004, 2006; Acerbi & Mesoudi, 2015; Whiten, 2017). This approach informs the manner in which studies are designed, the hypotheses generated and the questions asked. For example, the standard approach places social learning at the heart of culture; the presence of social learning is critical in defining behaviours as cultural (Laland & Hoppitt, 2003), and investigation of the potential presence of culture in non-human animals has often relied upon the 'method of exclusion' (Hoppitt & Laland, 2013); excluding genetic and environmental explanations for group differences in behaviour (leaving social learning as the most parsimonious explanation for variation in behaviour between groups) (Whiten et al., 1999; Rendell & Whitehead, 2001; van Schaik et al., 2003; Krützen et al., 2005; though see also Tennie et al., 2009; Reindl, Bandini & Tennie, 2018, for arguments that cultural behaviours in non-humans are primarily maintained by individual learning). The emphasis the standard approach places upon the transmission of behaviours has encouraged research focused upon the capacity of non-human animals to engage in high-fidelity social learning (for example, learning the exact motor-pattern of a behaviour from another individual via imitation, Tennie et al., 2009; Dean et al., 2014) (Whiten et al., 1996; Whiten, Horner & de Waal, 2005; Tennie, Call & Tomasello, 2006; Whiten et al., 2007), with some authors arguing that a lack of capacity for high-fidelity social learning is what distinguishes human cumulative culture from the cultural behaviour of other species (Tennie et al., 2009). There is evidence that highfidelity social learning is critical for cumulative culture to emerge; Lewis and Laland (2012) demonstrate through mathematical modelling that high-fidelity, accurate, social transmission is key in allowing cultural traits to persist in a population for long enough to allow modification and recombination to occur (leading to cumulation). While lower-fidelity transmission processes such as emulation learning can generate stable traditions (for example, Biro et al., 2003, suggest nut-cracking in wild chimpanzees is learnt via emulation), Tennie et al. (2009) argue that acquiring behaviour via emulation and other social learning mechanisms (such as stimulus or local enhancement) limits the complexity of behaviour achievable, as individuals must 'reinvent the wheel' and partially rely upon their individual problem solving abilities when acquiring the behaviour. Empirical transmission chain studies (discussed earlier in this chapter) have also indicated that high-fidelity social transmission may be critical for cultural traits to cumulatively improve, with Wasielewski (2014) showing that groups in which a structure-building technique could be imitated showed successive improvement, while groups reliant on emulation did not, while Morgan et al. (2015) found that without verbal teaching performance on a stone-knapping task fell to floor levels. Miu, Gulley, Laland and Rendell (2018) found that in a computer coding tournament in which participants could view previous entries, participants copied one another extensively (here, copying entails reproducing exactly another participant's line of code, and so is high-fidelity social transmission though it takes place via computer rather than directly), with most entries showing a similarity of over 90% with the highest-scoring entry at the time of submission. Cumulative improvements were achieved most frequently by participants making small 'tweaks' to the code, while primarily copying the code of previous entries. Although Miu et al.'s study was a computerised task, and so does not shed light on the importance of direct interpersonal social learning, it demonstrates the role that high-fidelity social learning (copying) can play in real-world human cumulative culture.

In contrast, the cultural attraction approach put forward by Sperber and colleagues (Sperber, 1996), suggests that the stability of cultural behaviour is due not to high-fidelity copying but to cognitive biases that are common to group members. Rather than being 'replicated' in a manner comparable with genetic information, cultural behaviours are reproduced by each individual learner, and in being reproduced are subject to the cognitive biases of that individual, as well as historical or ecological factors (Claidiere, Scott-Phillips & Sperber, 2014). If group members have the same cognitive biases, and are subject to the same

historical and ecological factors, they are likely to produce similar behaviours. This results in a tendency for cultural behaviours to transform non-randomly toward a range of types called cultural attractors (Driscoll, 2011; Claidiere et al., 2014; Scott-Phillips, Blancke & Heintz, 2018). For example, Norenzayan, Atran, Faulkner and Schaller (2006) found that folktales are most memorable if they include mostly intuitive concepts (concepts that concur with intuitive theories of biology, physics and mind) along with a minority of counterintuitive concepts (concepts that are inconsistent with expectations, for example: the pumpkin coach in Cinderella). In a cultural attraction framework, folktales which do not match this template are predicted to not be remembered or reproduced, or to be transformed in reconstruction to incorporate minimally counter-intuitive concepts. The transmission of behaviour at an individual level is not assumed to be high-fidelity (Acerbi & Mesoudi, 2015). The key questions raised by this approach would be what the psychological, biological and ecological factors of attraction which affect the probability of cultural behaviours transforming and propagating are (Scott-Phillips et al., 2018); Acerbi & Mesoudi (2015) suggest that the two approaches do not conflict so much as promote a focus on different aspects of cultural evolution, though Scott-Phillips (2017) argues that in fact, the two approaches suggest that stability (and therefore its opposite, change) in culture arises through entirely different mechanisms.

The cultural attraction theory also has implications for our approach to the study of nonhuman culture; rather than focusing upon the capacity of other species for high-fidelity copying, the key question becomes *why* certain behaviours are more readily reconstructed by a species, and so remain stable in a population despite individuals reconstructing them (Scott-Phillips, 2017). Scott-Phillips (2017) suggests that examination of the 'Zone of Latent Solutions' (ZLS), put forward by Tennie et al. (2009) as the basis of non-human primate traditions may represent the first step in answering this question. The ZLS hypothesis predicts that product copying, or emulation, is the form of social transmission by which behaviours spread in great apes, with individuals using their individual physical problem solving skills at each step of transmission. Solutions are latent in that each ape has the capacity to independently invent the behaviour, and so when such behaviour appears to spread socially, the behaviour was merely dormant until observation of a demonstration prompted reinvention by the observer (Tennie & Hedwig, 2009). It should be noted, however, that the ZLS was proposed as a restriction upon non-human primate culture that humans have overcome via high-fidelity social learning (ie. human culture is not restricted to behaviours inventable by an individual thanks to a capacity to imitate others), and so there is a theoretical mismatch between the ZLS argument and Scott-Phillips' cultural attraction account of human culture.

Studying the factors, cognitive or otherwise, that underlie the production of latent solution behaviours could indicate why some behaviours are more easily reproducible than others, as Scott-Phillips (2017) suggests. Reindl, Bandini and Tennie (2018) argue that the production of latent behaviours depends upon genetic, environmental, and social factors (with captive chimpanzees kept in environmentally or socially deprived conditions predicted to be less likely to produce these behaviours). Bandini and Tennie (2017) tested the ZLS hypothesis by providing captive chimpanzees with a task designed to approximate the context of algaescooping (a tool-use behaviour observed in wild chimpanzees, Humle, Yamakoshi & Matsuzawa, 2011, which the captive chimpanzees had not performed in the past), and found that two of 14 individuals tested produced the behaviour. The authors take this as evidence that algae-scooping is within the chimpanzee ZLS, as no social demonstration was required to elicit the behaviour in these two individuals. While only a limited number of the chimpanzees tested performed the target behaviour, Bandini and Tennie (2017) argue that this is sufficient to logically demonstrate that social learning is not necessary for this behaviour to emerge in chimpanzees. However, further work could examine the factors that led to only these two individuals producing the behaviour; individual differences such as causal reasoning ability, motivation, or neophilia could all have contributed. Furthermore, what factors might bias chimpanzees towards the stick tool form of algae-scooping observed by Bandini and Tennie (2017)? The captive chimpanzees tested had previous experience of stick tool use, though not for this specific purpose, and only sticks were provided in the experimental set-up. Had additional potential tool materials been provided, or populations of chimpanzees with no stick tool experience been tested, this type of study could indicate whether chimpanzees are biased towards stick tool use over other potential tools (though the mechanism and function of such a bias would still be unexplained).

There are a variety of limitations to the cultural attraction approach to culture. While examining the ways in which cultural behaviours are transformed during the transmission process, and the factors which may lead to some types of transformation occurring more frequently than others is a useful goal, there are elements of cultural evolution that are challenging to explain within a purely cultural attractionist framework. Acerbi and Mesoudi (2015) suggest that transmission fidelity may differ between different behavioural domains, with technology highlighted as a domain in which high-fidelity transmission may be particularly important, especially in cases where the technology is causally opaque, or relies upon the performance of a set sequence of actions, deviation from which will render the technology unusable. Acerbi, Tennie and Nunn (2011) describe smooth and peaked search spaces, in which a target behaviour may be a single peak in the landscape of potential behaviours, and individual learning would require the learner to fully explore the landscape in order to discover the target behaviour. Smooth search spaces still contain an optimum 'peak' behaviour, but it is surrounded by slightly less rewarding behaviours, meaning that an individual learner can obtain a reward through trial-and-error, and that through this trial-anderror they can receive feedback on the relative success of different behaviours. Acerbi et al.'s (2011) model showed that high-fidelity transmission was particularly important for search spaces with narrow peaks, while smooth search spaces were amenable to individual learning (reconstruction). The idea of a continuum of behaviours, for which replication vs reconstruction may be relatively more or less important, suggests that there may be domains of behaviour for which cultural attraction theory cannot adequately explain stability.

In addition, it is difficult to explain the apparent prevalence of high-fidelity social learning in humans given the assertion of Scott-Phillips et al. (2018) that "the cognitive mechanisms producing social transmission... do not in general aim at high-fidelity copying as such". Within this framework it is therefore challenging to explain the prevalence of overimitation in humans (apparently indiscriminate imitation extending to the reproduction of irrelevant actions; Lyons, Young & Keil, 2007). Both children (Horner & Whiten, 2005; McGuigan, Whiten, Flynn & Horner, 2007; Nielsen, Mushin, Tomaselli & Whiten, 2014; Clay & Tennie, 2018) and adults (McGuigan, Makison & Whiten, 2011; Berl & Hewlett, 2015; Whiten et al., 2016) are susceptible to overimitation, and it occurs not only when a task is causally opaque (when such indiscriminate imitation is rational) but also when a task is causally transparent (and so it is clearly visible that irrelevant actions have no causal effect) (Whiten et al., 2016). The suggestion that high-fidelity transmission is not responsible for cultural stability appears at odds with these findings that imitation in humans can, at times, be indiscriminate. Scott-Phillips et al. (2018) also state that cultural attraction theory does not aim to explain human

adaptation, or to examine the adaptiveness of cultural behaviours. The lack of importance placed upon adaptiveness in the cultural attraction approach makes it poorly suited for those interested in examining how and why a capacity for culture evolved, from a comparative perspective. Acerbi and Mesoudi (2015) suggest that purely replicative and purely transformative processes in cultural transmission are at two ends of a continuum, and the standard approach to cultural evolution includes 'guided variation' (the biased transformation of cultural traits during transmission) as a means of understanding transformative processes. On this basis, the benefit of a cultural attraction approach appears limited to simply placing stronger emphasis upon transformative processes, which can still be done within the existing framework of the standard approach.

1.3.2 Empirical studies of cultural attraction

Studies of cultural transmission following the standard approach to cultural evolution were described earlier in this chapter. Empirical studies have also been undertaken following the cultural attraction framework, often using transmission chain paradigms to examine the ways in which information is transformed during transmission. Recent work explicitly following a cultural attraction approach to the study of cultural transmission is discussed below, though of course further studies conducted following the standard approach to cultural evolution are relevant to the debate. For example, Tamariz and Kirby (2014) demonstrated that storing graphical patterns in memory results in compression and simplification of images across transmission chains in humans, while Claidiere et al. (2014) found that tetromino patterns (geometric shapes composed of four squares connected orthogonally) emerged in grid patterns more reproducible. Stubbersfield, Tehrani and Flynn (2015) found that urban legends containing social and survival information were recalled with greater accuracy than control material. These studies demonstrate the impact of cognitive biases upon transmission of cultural information, but do not explicitly follow a cultural attractors approach.

Scott-Phillips (2017) drew upon a thought experiment first proposed by Sperber (2000) and conducted a transmission chain experiment contrasting reconstruction and replication in the transmission of images of the letters 'ABC'. One seeded image (the 'Attractor') was the letters 'ABC', while the other (the 'Non-attractor') was the component lines of the letters

'ABC' rearranged so it bore no resemblance to the letters or any other symbol. Participants were asked to either view and memorise the model image and then attempt to reproduce it, or to trace over it. Scott-Phillips conducted no quantitative analyses, but argued that the 'ABC' image was reproduced faithfully under both copying conditions, while the jumbled lines were reproduced faithfully in only the tracing condition. From this result, Scott-Phillips argued that high-fidelity copying does not, alone, explain cultural stability in humans (as the 'Non-attractor' image was not faithfully reproduced). This study is somewhat limited in terms of analysis of the results (though Scott-Phillips' aim is simply to illustrate the relative importance of replication vs reconstruction in cultural transmission). It is also unclear the extent to which Scott-Phillips' replication condition (in which participants simply traced over the image) is a fair interpretation of the standard approach's posited high-fidelity transmission mechanisms. Had Scott-Phillips instead employed a design more similar to that of Tamariz and Kirby (2014), in which some participants were able to continue looking at the target image while drawing, this might have been a better analogy for the process of high-fidelity transmission.

Miton, Claidiere and Mercier (2015) examined the practice of bloodletting using a cultural attraction framework, firstly reviewing anthropological data on the practice, then conducting transmission chain experiments in order to investigate the success of stories involving bloodletting. Bloodletting (the practice of cutting a patient and allowing blood to flow in order to cure an illness) was found to be a cross-culturally recurrent practice, observed in human cultures worldwide, and is therefore likely to have emerged independently in these cultures. In transmission chains conducted with participants resident in the USA, stories involving bloodletting were more likely to be successfully transmitted along a chain than stories involving ritual prayer or emetic plant eating. A further transmission chain study found that in chains seeded with a story in which a protagonist accidentally cuts themselves, intentional bloodletting was introduced to the story by participants in five of 32 chains, while a causal link between the cut and recovery from an illness was added to the story in 15 of 48 chains in which this causal link was absent in the seeded story. The authors suggest that this finding supports an explanation of the prevalence of bloodletting in disparate human cultures as the product of universal cognitive mechanisms, perhaps related to disgust and naïve or folk biology (intuitive causal theories of biology, including the idea that good and bad things going in and out of the body effect health, Inagaki and Hatano, 2004). While the participants

recruited in Miton et al.'s (2015) study may well have possessed more nuanced knowledge of biology than these intuitive theories, the study indicates that stories which fit with these intuitions may be more likely to propagate than those which are counter-intuitive.

Xu, Dowman and Griffiths (2013) examined the role of cognitive biases in colour naming, using a transmission chain design. English-speaking participants were shown colours labelled using novel terms, and then asked to generalize those terms to other colours. Between two and six colour terms were presented to the participants, forcing them to categorise colours differently than the 11 basic colour categories in the English language. Each participant's responses were used to train the next participant in the chain. Resulting systems of categorizing colours converged towards forms consistent with the world colour survey, suggesting that learning and perceptual biases in humans may account for similarities between systems of colour terms across languages.

Examination of historical trends in cultural behaviours have also been interpreted within a cultural attraction framework; for example, Morin (2013) demonstrated that European portraiture underwent a change in the Renaissance in that the proportion of portraits in which the subject gazes directly out at the viewer increased gradually and remained prevalent for centuries. This is argued to be due to an innate attentional bias towards faces which gaze directly at us.

Studies explicitly examining the role of replication versus reconstruction in cultural transmission in relation to the cultural attraction debate are few, and so in Chapter 5 I conduct the thought experiment proposed by Sperber (2000) with an under-explored demographic; human children.

1.4 Thesis outline

The literature discussed in this chapter raises many questions. A major question in the field of cultural evolution is whether any other species has the capacity for cumulative culture. Given the very limited evidence for cumulative culture in chimpanzees, a species which demonstrates some of the apparent prerequisites for cumulative culture (such as socially transmitted cultural traditions and a propensity to innovate), I have explored chimpanzees'

ability to behave flexibly, by providing groups of captive chimpanzees with artificial foraging tasks in which the constraints of the task change over time. The current evidence for behavioural flexibility in chimpanzees is mixed, and so one aim of this thesis was to extend the existing literature on chimpanzee behavioural flexibility, using an experimental paradigm already shown to be effective in orangutans (Lehner et al., 2011). In the work described in Chapter 3 I investigated the capacity of chimpanzees to respond flexibly to a changing artificial foraging task requiring tool use, based upon the task used with orangutans by Lehner et al. (2011). I incorporated the provision of limited scaffolding towards a novel tool technique into the study design, which allowed exploration of how chimpanzees learn from physical artefacts, a means of social learning suggested to be important for the maintenance of cultural traditions in wild chimpanzees (Tennie et al., 2009; Fragaszy et al., 2013). In the research described in Chapter 4 I extended this study to two further groups of chimpanzees at a second, very different facility in Africa. The response of these two groups allowed exploration of group differences in response to the task, and adds further data to the debate over chimpanzee behavioural flexibility. In Chapter 5, I examine the levels of social tolerance in the two groups of chimpanzees involved in the study of **Chapter 4**, using observations of social behaviour at the foraging task, and relate these findings to the results of the behavioural flexibility task. Examining group differences in behavioural flexibility, and relating these to social factors such as social tolerance may provide some context for the current inconsistencies in the literature on chimpanzee behavioural flexibility.

Within this thesis, I was also keen to engage with broader debates in the field of cultural evolution, and to this end, in the work described in **Chapter 6**, I expanded the scope of my studies by conducting a transmission chain experiment with four- to eight-year-old children, based upon the thought experiment proposed by Sperber (2000) which was explored to a limited extent by Scott-Phillips (2017). This study aimed to explore the relative importance of replication and reconstruction in cultural transmission, and makes a novel contribution to the literature by examining how drawings are transmitted and transformed by children.

Finally, in **Chapter 7**, the relevance of my findings to the study of culture in both human and non-human primates is discussed, particularly the importance of including multiple groups and demographics in studies of cognition and behaviour. I make suggestions for future work to build upon the findings of this thesis.

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Chapter 2: General Methods

Chapter 2: General methods

2.1 Summary

In this chapter, I introduce the study sites and participants included in the studies presented in this thesis. I also describe methods and statistical approaches that are shared in multiple empirical chapters of the thesis. Methods specific to Chapters 3, 4, 5, or 6 will be described in the relevant chapters.

2.2 Study sites and participants: Chimpanzees

2.2.1 RZSS Edinburgh Zoo – Budongo Trail facility

Data collection for Chapter 3 was conducted at the Royal Zoological Society of Scotland's (RZSS) Edinburgh Zoo, Scotland, UK. Edinburgh Zoo housed 18 chimpanzees (Pan troglodytes) in the Budongo Trail facility at the time of data collection. Budongo Trail is an exhibit consisting of three interconnected 'pods' (indoor enclosures) measuring 12 x 12 x 14m, along with an outdoor enclosure measuring 1832 m^2 (Schel et al., 2012). The pods have different lighting levels, flooring materials and temperatures, and both indoor and outdoor enclosures have climbing frames, platforms and ledges. Tunnels connect the enclosures, and chimpanzees are free to move between them as they choose unless individual pods are being cleaned (Schel et al., 2012). Chimpanzees are fed multiple times a day at irregular intervals and have access to water ad libitum. In addition to these four 'on-show' areas (the three pods and the outdoor enclosure) that can be viewed by the visiting public, there is an 'off-show' bedding area measuring approximately 21 m² (E. Herrelko, PhD thesis). This bedding area is connected by overhead tunnels and ladders to the facility's two research pods, a dedicated research area, on show to the public, to which the chimpanzees have access only for the purpose of cognitive and behavioural research. These research pods measure approximately 26 m^2 in total (both pods combined). Figure 1 shows the layout of the research pods. A research office is connected to the research pods by 'test windows' measuring 48 x 90 cm, and these windows are fitted with removable mesh and Perspex slides, allowing tasks to be presented via these windows to chimpanzees in the research pods.

Chimpanzees at Edinburgh Zoo receive regular enrichment in the form of simple artificial foraging tasks provided by their keepers, some of which encourage the use of stick tools.

The group was composed of 18 individuals (see Table 1 for details), and was formed by merging two sub-groups in 2010 (Schel et al., 2013); long-term residents of the zoo, prior to

2010 ('Edinburgh' chimpanzees), and others introduced in 2010 ('Beekse Bergen' chimpanzees), each numbering nine individuals. Chimpanzees at Edinburgh Zoo at the time of data collection were primarily captive-born, though rearing history (mother vs human-raised) differed amongst the captive-born individuals. The 'Beekse Bergen' subgroup had a history of laboratory-housing and lived in a zoo environment for the first time in 2007, before moving to Edinburgh Zoo in 2010. All individuals in the long-term 'Edinburgh' sub-group, except for wild-born individuals, had lived only in zoo environments.



Figure 1. Diagram of Budongo Trail research pods and research office, not to scale.

Table 1.

Individual	Sex	Year of birth (age at time of testing)	Age category*	Mother (if present in group)	Origin (wild or captive born)	Rearing					
Edinburgh Subgroup (N=9)											
Qafzeh	М	1992 (22)	Adult	Emma	Captive	Mother					
Kindia	М	1997 (17)	Adult		Captive	Mother					
Liberius	М	1999 (15)	Subadult	Lucy	Captive	Mother					
David	М	1975 (39)	Adult		Captive	Mother					
Louis	М	1976 (38)	Adult		Wild	Likely hand-raised					
Lucy	F	1976 (38)	Adult		Captive	Mother					
Kilimi	F	1993 (21)	Adult		Captive	Mother					
Cindy	F	1964 (50)	Adult		Wild	Likely hand-raised					
Emma	F	1981 (33)	Adult		Captive	Mother					
Beekse Bergen Subgroup (N=9)											
Paul	М	1993 (21)	Adult		Captive	Hand-raised					
Pearl	F	1969 (45)	Adult		Wild	Likely hand-raised					
Sofie	F	1981 (33)	Adult		Captive	Hand-raised					
Lianne	F	1989 (25)	Adult		Captive	Mother					
Heleen	F	1991 (23)	Adult		Captive	Mother					
Edith	F	1996 (18)	Adult	Eva	Captive	Mother					
Eva	F	1980 (34)	Adult		Captive	Hand-raised					
Frek	М	1993 (21)	Adult		Captive	Hand-raised					
Rene	М	1993 (21)	Adult		Captive	Hand-raised					

Demographic and Rearing Information of the Chimpanzees at Edinburgh Zoo

*Age categories following Reynolds (2005), with behavioural characteristics considered in addition to age in years.

2.2.2 The Chimfunshi Wildlife Orphanage Trust, Zambia

Data collection for **Chapters 4 and 5** was conducted at the Chimfunshi Wildlife Orphanage (CWO) in northern Zambia. The sanctuary was founded in 1983 by David and Sheila Siddle, after an injured chimpanzee was brought to their farm, and has grown substantially since. At the time of the study, the main site at CWO housed 98 chimpanzees (*Pan troglodytes*) in five separate social groups. Four of these groups live in large, *miombo* woodland enclosures, with group sizes ranging from 10 to 48 individuals, and all four groups contain both males and females, and infants, juveniles and adults. Enclosures at CWO are bounded by electric fencing and range in size from 19 - 77 hectares (Cronin, West & Ross, 2016). An aerial view of the site is provided in Figure 2. A fifth group (four individuals known as the 'escape artists') live in a barred enclosure due to their reputation for escaping from the larger woodland enclosures. The groups were formed over time by adding incoming chimpanzees to existing groups until staff judged the group to be large enough or balanced in terms of sex and age. No new chimpanzees had been added to these groups for at least ten years at the time of data collection.



Figure 2: Aerial view of the Chimfunshi Wildlife Orphanage, imagery dated to 12/05/2013. The fence lines of the four woodland enclosures can be seen and the four groups resident in them are indicated by number. Groups 3 and 4 participated in the study presented in this thesis. Map data: Google, CNES / Astrium.

The woodland in the enclosures includes multiple plant species known to provide a food source to wild chimpanzees, and CWO chimpanzees have been observed consuming several of these species (Ron & McGrew, 1988). The woodland also contains termite mounds, though there are no reports of chimpanzees engaging in termite fishing. The chimpanzees live outdoors, including sleeping outdoors at night, and enter an indoor holding area for a twohour feeding period between 11:30 – 13:30 each day, with water available ad libitum in their enclosures at all times. Chimpanzees in the four main groups do not receive behavioural enrichment (the fifth, 'escape artist', group do receive regular enrichment). Contraception has been administered to female chimpanzees at CWO opportunistically, and as a result there is a mix of reproductive status at CWO (Cronin et al., 2016). Fewer than 50% of the chimpanzees housed at CWO at the time of data collection were wild-born, the remainder thus being sanctuary-born. The majority of sanctuary-born chimpanzees at CWO were raised by their mothers within their social groups, with infants being removed from their group only for veterinary care, when necessary. Wild-born chimpanzees at CWO were generally orphaned by the pet trade, and likely suffered physical and psychological trauma prior to their arrival at CWO. While research at CWO has examined the effect of being orphaned upon social behaviour (van Leeuwen, Mulenga & Chidester, 2014), and has assessed the welfare of mothers vs non-mothers (Cronin, West & Ross, 2016), the potential effect of early trauma upon wild-born individuals at CWO has not been examined. Potential stress-indicators such as excessive self-grooming or stereotypical behaviour were rare during my observations. Only two of the five groups (Group 3 and Group 4) were included in data collection, and the details of the individuals in these groups are provided in Table 2. Unlike Edinburgh Zoo, CWO did not have a dedicated research area or enclosure. Apparatus for tasks presented to chimpanzees at CWO were therefore attached to the outer boundary of their woodland enclosure, next to their indoor holding facility (see Figures 3 and 4; for photographs of the task in place see Chapter 4).

Table 2.

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Individual	Sex	Y ear of birth	Age	Mother (if present	Origin (wild	Rearing
		(age at time of	category*	in group)	or captive	
		testing)			born)	
Group 3 (N=1	(0)					
Brian	М	1994 (21)	Adult		Wild	Hand-raised
Clement	М	1993 (22)	Adult		Wild	Hand-raised
Bussy	М	2004 (11)	Subadult	Barbie	Captive	Mother
Buffy	F	1985 (30)	Adult		Wild	Hand-raised
Roxy	F	1995 (20)	Adult		Wild	Hand-raised
ET	F	1995 (20)	Adult		Wild	Hand-raised
Barbie	F	1995 (20)	Adult		Wild	Hand-raised
Bruce	М	2009 (5)	Juvenile	Barbie	Captive	Mother
Lods	F	2010 (5)	Juvenile		Captive	Mother
Brent	F	2014 (1)	Infant	Barbie	Captive	Mother
Group 4 (N=1	2)					
Commander	М	2001 (14)	Adult		Wild	Hand-raised
Val	М	2000 (15)	Adult		Wild	Hand-raised
Nicky	М	1991 (24)	Adult		Wild	Hand-raised
Sinkie	М	1994 (21)	Adult		Wild	Hand-raised
Bobby	М	1993 (22)	Adult		Wild	Hand-raised
Kit	М	2005 (10)	Subadult	Kambo	Captive	Mother
Jack	М	2008 (7)	Juvenile	Mother deceased	Captive	Mother
Kathy	F	1999 (16)	Adult		Wild	Hand-raised
Kambo	F	1996 (19)	Adult		Wild	Hand-raised
Miracle	F	2000 (15)	Adult		Captive	Hand-raised
Kenny	М	2011 (4)	Infant	Kambo	Captive	Mother
Jewel	М	2013 (2)	Infant	Mother deceased	Captive	Hand-raised
				Kathy (adoptive		
				mother)		

Demographic and Rearing Information of the Chimpanzees Tested at CWO

*Age categories following Reynolds (2005), with behavioural characteristics considered in addition to age in years.



Figure 3. Diagram of CWO task presentation area. Not to scale.



Figure 4. Photograph of the CWO task presentation area. The indoor facility is highlighted in grey, the mesh gate area in orange, and the electrified fence line in black.

2.3 Study sites and participants: Children

Children were recruited for participation in the experiment presented in this thesis (**Chapter 6**) at three locations: the Budongo Trail facility at Edinburgh Zoo, the Dundee Science Centre, and a university open day event at the University of St Andrews. In all three sites, families were approached while visiting the location and both parent and child were asked if they would be interested in participating in research. Those who expressed an interest were provided with an information sheet detailing the rationale of the study, any potential risks involved in participation, and data protection information. Parents were then asked to formally consent to their child taking part.

At both Edinburgh Zoo and the Dundee Science Centre, children who took part in the study were shown to a quiet area of the museum with their parents (in Edinburgh Zoo, this was a quiet area of the Budongo Trail facility, and at the Dundee Science Centre, this was a quiet area of a mobile demonstration trailer normally used for science communication). At the University of St Andrews, children who took part in the study were taken to the Baby and Child Lab in the School of Psychology and Neuroscience with their parents, where a room was set aside for data collection.

2.4 Data collection

Data collection methods that are relevant to two or more experimental chapters are detailed in this section. Data collection methods that are specific to only one chapter are detailed in the methods section of the relevant chapter. The methods used in my study with child participants will be described in Chapter 6, along with the study itself.

2.4.1 Chimpanzee studies

All experimental sessions were recorded using a Sony CX240E Full HD Camcorder. This recorded chimpanzees' responses to the task, while the experimenter narrated chimpanzees' actions as well as their identity and the presence of other individuals in the task area. The camera was placed behind the task at both Edinburgh Zoo and CWO (see Figure 4), providing a clear view of actions carried out at the task apparatus.



Figure 4. Screenshots of the video recordings of the chimpanzee studies, taken at Edinburgh Zoo (top) and CWO (bottom).

While the same apparatus was used in both Edinburgh Zoo and CWO, there were methodological differences in its presentation between the two sites. For this reason, the task will be described in the methods section of Chapters 3 and 4, but I will briefly describe the physical parameters of the task here, as the same apparatus was used at both sites. Following the methods used by Lehner, Burkart and van Schaik (2011) in their study of orangutan behavioural flexibility and innovation, I used an artificial foraging task composed of a polycarbonate tube from which chimpanzees could retrieve diluted juice using either tools or their hands. Two widths of tube were used. The first, 'wide', tube measured 30cm tall with a 10cm diameter. The second, 'narrow', tube also measured 30cm tall but had a 5cm diameter (Figure 5).



Figure 5. The dimensions of the polycarbonate tubes that composed the artificial foraging task provided to chimpanzees in Chapters 3 and 4. To scale.

At both Edinburgh Zoo and CWO, these tubes were presented sequentially (the 'wide' tube first, followed by the 'narrow' tube), and were presented within the chimpanzees' enclosures (further details of presentation are provided in the relevant chapters). The tube could be refilled using a funnel and rubber pipe from outside the chimpanzees' enclosures, allowing me to re-bait the tube without interrupting data collection, though at both sites this could only be done when chimpanzees moved away from task as otherwise they could seize the funnel and rubber pipe. A valve at the base of the tube could be released in order to empty the tube at the end of experimental sessions.

2.5 Statistical analyses

Data in all experimental chapters of this thesis were analysed in R (version 3.2.2, R Core Team, 2015) and RStudio (version 0.99.893, RStudio Team, 2015). Where appropriate, I used generalised linear mixed models with Laplace approximations (GLMM), via the function glmer in the R statistics package lme4 (Bates, Maechler, Bolker & Walker, 2012). Where appropriate, for analyses in which repeated measures had been taken from multiple individuals, these GLMMs were fitted as full random slope models (for discussion on the benefits of fitting random slopes as well as random intercepts, see Schielzeth & Forstmeier, 2009). In order to assess whether GLMMs containing relevant predictor variables were a better fit to the data than a null model containing only random effects, likelihood ratio tests were conducted to compare full and null models, using the function anova in R. While many of the core analyses presented in this thesis were applied where appropriate, and these are reported in the relevant chapters.

2.6 Ethical approval

Ethical approval for each of the studies reported in this thesis was received from the University of St Andrews School of Psychology and Neuroscience Ethics Committee (letters of approval are presented in Appendix E). In addition, the study presented in **Chapter 3** was approved by the Budongo Trail Research Committee, and the study presented in **Chapters 4 and 5** was approved by the Chimfunshi Research Advisory Board. Research with chimpanzees was conducted in accordance with the guidelines of the Association for the Study of Animal Behaviour.

Chapter 3: Chimpanzees (*Pan troglodytes*) show limited behavioural flexibility in response to a changing foraging task requiring tool use

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Chapter 3: Chimpanzees (*Pan troglodytes*) show limited behavioural flexibility in response to a changing foraging task requiring tool use

Abstract

Behavioural flexibility, the ability to alter behaviour in response to environmental feedback, and to relinquish previously successful solutions to problems, is a crucial ability in allowing organisms to adapt to novel environments and environmental change; it is essential to cumulative cultural change. To explore this ability in chimpanzees, 18 individuals (*Pan troglodytes*) were presented with an artificial foraging task consisting of a tube partially filled with juice that could be reached by hand or retrieved using tool materials to hand. Effective solutions were then restricted in the second phase of the study by narrowing the diameter of the tube, necessitating the abandonment of previously successful solutions. Chimpanzees showed limited behavioural flexibility in comparison to some previous studies, increasing their use of effective techniques, but also continuing to attempt solutions that had been rendered ineffective. This adds to a literature reporting divergent evidence for flexibility (the ability to alter behaviour in response to environmental feedback, and to relinquish previously successful solutions to problems) versus conservatism (a reluctance or inability to explore or adopt novel solutions to problems when a solution is already known) in apes.

3.1 Introduction

Behavioural flexibility, the ability to alter behaviour based upon environmental feedback and to inhibit previously successful behaviours, is an ability that allows organisms to adapt their behaviour to suit changing or novel environments and supports problem solving by allowing individuals to adapt their behaviour to success or failure at a problem (Sol, Timmermans & Lefebvre 2002; Griffin & Guez 2014; Chow, Lea & Leaver 2016; Audet & Lefebvre 2017). Behavioural flexibility can also describe the capacity for, and interest in, continuing to acquire novel solutions to an unchanging problem for which a solution is already known (Lehner, Burkart & van Schaik 2011), though most experimental explorations of behavioural flexibility incorporate changes in task parameters (and therefore changes in environmental feedback). Whilst innovation (defined by Reader and Laland, 2003, pp.14, as "A process that results in new or modified learned behaviour and that introduces novel behavioural variants into a population's repertoire") has been suggested to be a component of behavioural flexibility (Lehner et al. 2011), we also consider the acquisition of novel behaviours via social learning to constitute flexible behaviour (Wright et al. 2010), and indeed the application of known behaviours to a novel problem. Behavioural flexibility is thought to be a key ability supporting the evolution of cumulative culture (Dean et al. 2014). With culture defined as "group-typical behaviour patterns shared by members of a community that rely on socially learned and transmitted information" (Laland & Hoppitt 2003, pp.151), cumulative culture is the process whereby these socially learnt behaviours are modified and the modifications are retained, resulting in behaviours and technologies more complex than an individual could invent within their lifetime (Tomasello 1994; Tennie, Call & Tomasello 2009). As cumulative culture relies upon the modification of known behaviours it necessitates flexibility in both the process of innovation by some individuals, and in the acquisition by others of the improved behaviours that result.

3.1.1 Behavioural flexibility and cumulative culture

Evidence for cumulative culture in our closest living relative, the chimpanzee, is limited and controversial (Dean et al. 2014; Whiten 2017), with Boesch (2003) highlighting three behaviours observed in wild chimpanzees (nut-cracking incorporating additional stones to stabilise the anvil, parasite manipulation in which parasites are placed on a leaf which is then folded and cut, and well-digging incorporating the use of leaf-sponges to retrieve water from deep wells) as potential evidence of cumulative culture, whilst Sanz, Call and Morgan (2009)
describe apparent improvements made to termite fishing tools by chimpanzees in the Goualougo Triangle, Republic of Congo. However, such interpretations require assumptions to be made regarding the social transmission of these behaviours, whether they represent greater complexity than that achievable by an individual alone, and indeed whether they are the result of cumulative progressions rather than unconnected innovations (which might be better described as 'accumulation'; Dean et al. 2014). With such limited evidence of cumulative culture in chimpanzees, investigation of the abilities required to support cumulative culture is required. We suggest that behavioural flexibility, along with innovation and social learning, should be considered and investigated as a potential limiting factor for cumulative culture. These three capacities are expected to work in concert to support cumulative culture - an individual innovates an improvement to a behaviour or tradition, and this improvement is passed on via social learning to other group members. As cumulative culture requires the modification of known behaviours, flexibility is required in both the innovator, to modify a behaviour within their repertoire, and in the group members socially acquiring this modified behaviour (that, in a process of cumulation, is expected to replace a known behaviour which previously served the same purpose). As outlined by Charbonneau (2015), an ability to innovate entirely novel behaviours 'from scratch' alone is not sufficient to support cumulative culture, which instead requires an ability to modify known behaviours. High-fidelity social transmission is believed to be critical in supporting cumulative culture, as it prevents backwards 'slippage' or the loss of modifications to behaviours (Tennie et al. 2009; Lewis & Laland 2012). However, somewhat paradoxically, at least some individuals in a population must also be capable of modifying behaviours, having acquired them via highfidelity social learning.

3.1.2 Measuring behavioural flexibility

Behavioural flexibility has been assessed at a species level via the proxy measure of innovation frequency (for example, Lefebvre et al. 1997; Lefebvre, Reader & Sol 2004, for avian comparisons), and innovation has been considered a component of behavioural flexibility (Lehner et al. 2011; Audet & Lefebvre 2017). This makes the assumption that behavioural flexibility leads to increased innovativeness, which may not always be the case at either an individual or species level (Griffin et al. 2013; Logan 2016). Behavioural flexibility in response to environmental change has been tested directly in a range of species, both in the wild and captivity, frequently by employing experimental paradigms in which animals must

respond to a change in task parameters, such as reversal learning (Bond, Kamil & Balda 2007; Boogert, Monceau & Lefebvre 2010; Manrique & Call, 2015; Liu et al.2016) or multiaccess puzzle box tests (Auersperg et al. 2011; Lehner et al.2011; Manrique, Völter & Call 2013; Richter, Hochner & Kuba 2016).

Both intra- and interspecific differences in flexibility have been found using these experimental techniques. Individual differences in behavioural flexibility within species have been shown in animals as diverse as octopuses, pigs and mice (Benus et al. 1990; Richter et al. 2016; Bolhuis et al.2004), as well as in wild chimpanzees and sanctuary-housed orangutans (Gruber 2016). Such inter-individual differences within species are perhaps not surprising, given potential differences between individuals in terms of task motivation, cognitive ability, and personality (the latter having been shown to impact performance on problem solving tasks in chimpanzees; Massen et al., 2013). In the context of cumulative culture, an understanding of which individuals are most capable of behavioural flexibility, and investigation of any other traits that might co-occur with behavioural flexibility on an individual level, may allow predictions to be made regarding which individuals or demographics are likely to contribute to the modification of behaviours in a population's repertoire.

In addition, interspecific differences in behavioural flexibility have been demonstrated in both corvids and great apes (Bond et al. 2007; Manrique et al. 2013), and investigation of these interspecific differences allows exploration of hypotheses regarding the evolution of behavioural flexibility. Bond et al. (2007) argue that behavioural flexibility may be more apparent in species with highly complex social systems, in order to cope with rapidly fluctuating social contexts, and found that pinyon jays, a highly social species, had lower error rates on a serial reversal learning tasks than Clark's nutcrackers (a relatively solitary species with specialised spatial memory supporting caching behaviour) and western (California) scrub jays (a generalist species in terms of both ecology and social behaviour). Continued investigation of species' abilities to behave flexibly will allow investigation of the evolutionary pressures that lead to high behavioural flexibility, and will also allow investigation of other cognitive abilities that may co-evolve with behavioural flexibility. For example, it has also been shown that pinyon jays outperform Clark's nutcrackers on social learning tasks (Templeton, Kamil & Balda 1999). Given that a suite of abilities is likely required to support cumulative culture (Dean et al. 2014), an understanding of why

component abilities may emerge, and whether they share common evolutionary origins, is likely to enhance our understanding of the evolution of cumulative culture.

Observation of the tool preferences of wild tool-using species also provides some indication of the flexibility of such species. Examination of the tool preferences of wild New Caledonian crows found strong, persistent local preferences in terms of the plant species from which their hook-tools are manufactured (St Clair et al. 2016), despite access to alternative plants, which are preferred, at another, nearby study site. This may indicate some level of individual conservatism (a reluctance to explore alternative solutions) in this species' tool manufacture, though the authors also point out that it shows that crows at one study site have either switched from a previous tool material, or acquired hooked stick tool-use relatively recently. Both scenarios would reflect flexibility, both on the part of initial innovators and any individuals that may have socially acquired this alternative behaviour. Study of individual crows' tool manufacture indicates multiple bending techniques and adjustments during manufacture, which would seem to indicate flexibility (Klump et al. 2015; Rutz et al. 2016). Wild chimpanzees have been observed to modify their tool-use behaviours, with an individual in Bossou being observed firstly applying a tool and technique generally used for ant-dipping on the ground to ant-fishing in trees, and later using tools of a length better suited to ant-fishing in trees (Yamamoto et al. 2008). Wild chimpanzees have also been observed to socially learn novel tool behaviours, such as crafting sponges from moss rather than leaves (Hobaiter et al. 2014). These observations of wild behaviour provide some insight into chimpanzees' capacity for behavioural flexibility.

3.1.3 Chimpanzees – behaviourally flexible or conservative?

In several studies, chimpanzees have been reported to be conservative, rather than flexible, in their approach to artificial foraging tasks, continuing to use a habitual solution despite the prospect of gaining a greater reward via behavioural change (Marshall-Pescini & Whiten 2008) or the habitual solution being made impossible or unrewarding (Hrubesch et al. 2009; Bonnie et al. 2012). Behavioural conservatism has also been reported in wild chimpanzees, with Gruber et al. (2009) finding that two different communities relied upon their respective habitual tool behaviours when faced with a novel artificial honey-dipping task, in one community failing to acquire the useful tool behaviour used by the other community even when scaffolded towards it (Gruber et al. 2011; Gruber 2016). Similarly, Cardoso and Ottoni (2016) found that providing two communities of wild bearded capuchin monkeys with a

dipping task resulted in only the group that already habitually used probing tools solving the task, again despite efforts to scaffold the non-probe-using group towards this behaviour. Chimpanzees may also continue to perform behaviours when these behaviours are no longer necessary, for example, continuing to avoid a non-functional trap in the inverted trap-tube problem (Povinelli 2000; though see also Mulcahy & Call 2006), although it should be noted that in paradigms in which continuing this behaviour is equally rewarding as ceasing to avoid the trap, adult humans also continue to avoid non-functional traps (Silva, Page & Silva 2005). Related to these findings of apparent conservatism or lack of flexibility in chimpanzees is the concept of 'functional fixedness': the inability to invent a novel use for a tool with which the animal already has experience (Hanus et al. 2011; Brosnan & Hopper 2014). Hanus et al. (2011) found that captive chimpanzees were more likely to solve the 'floating peanut' experiment (in which water must be added to a tube in order to raise a floating peanut to a level at which it can be reached) when a novel water dispenser was added to their enclosure. The authors suggest that the old dispenser had a fixed function for the animals, which prevented them from discovering it as a potential task solution.

By contrast, other recent studies have implied that under certain conditions, great apes may be capable of flexibly altering their behaviour in response to a changing task (Lehner et al. 2011; Manrique et al. 2013; Yamamoto, Humle & Tanaka 2013; Davis et al. 2016; Vale et al. 2017). In the studies of both Lehner et al. (2011), and Manrique et al. (2013), in order to successfully retrieve a reward, great apes had to not only flexibly alter their behaviour in response to changing tasks, but also develop novel methods of solving the foraging tasks that they were presented with. Lehner et al. (2011) found that orangutans were capable of inventing novel solutions to a task in which juice could be retrieved from a tube by dipping tool materials into the tube. When the width of the tube was narrowed, orangutans flexibly altered their behaviour, abandoning previously successful solutions and inventing novel solutions, some of which the authors argue are cumulative improvements upon previous solutions. It should be noted that although novel solutions were not experimentally seeded in the Lehner et al. study (2011), orangutans were tested under group conditions, and so potentially had access to social information. In a study testing all four nonhuman species of great ape, in which subjects were tested individually (eliminating the possibility of social learning), Manrique et al. (2013) found that all species were able to abandon previous solutions and invent novel solutions to a non-tool-based artificial foraging task in which solutions were rendered obsolete in three stages, though orangutans performed more poorly

than other species, only solving two stages. These studies demonstrate that great apes can be capable of flexibly altering their behaviour and relinquishing previously successful behaviours in order to solve changing artificial foraging tasks, without the benefit of experimentally-seeded solutions.

Studies have also shown that chimpanzees are able to socially acquire more efficient or more rewarding solutions to problems, having already mastered a less efficient solution. Yamamoto et al. (2013) found that chimpanzees provided with a task in which juice could be retrieved from within a tube via a small hole were capable of swapping from an inefficient 'dipping' technique to a more efficient 'straw-sucking' technique following observation of a conspecific employing the more efficient technique, while Vale et al. (2017) found that following the removal of simple tools that could be used to acquire juice in a dipping task, chimpanzees began to use complex tools that required modification (unscrewing a valve so a tube could be used as a 'straw' to suck up juice). Davis et al. (2016) found that chimpanzees were able to relinquish a highly inefficient task solution in favour of a more efficient solution when provided with demonstrations of the efficient solution by a conspecific or human demonstrator. The authors of the latter study argue that such flexibility may be more apparent in situations in which there is a large difference in efficiency between two technique options (with a relatively highly inefficient solution more likely to be relinquished). This may suggest chimpanzees use a 'copy-if-dissatisfied' strategy when given the opportunity to socially acquire more efficient solutions to problems (Laland 2004). If so, behavioural flexibility in such studies may be apparent only when the original solution is rendered highly inefficient and unsatisfying. The findings of Lehner et al. (2011) and Manrique et al. (2013) may, in light of this, imply that great apes also employ an 'explore-if-dissatisfied' strategy when given the opportunity to achieve improved solutions to problems without the benefit of an existing competent model.

3.2 Study aims

We aimed to investigate the capability of chimpanzees to alter their behaviour in response to an artificial foraging task in which viable solutions became restricted as time progressed, using a liquid-retrieval task comparable to that used by Lehner et al. (2011) with orangutans.

3.2.1 Behavioural flexibility

Chimpanzees were presented with the task as a group, and therefore had access to both individual and social information about the task and potential solutions. This means that individuals were not limited to what they themselves could invent in terms of task solutions, which we believe provides a more ecologically valid measure of behavioural flexibility, as this has been defined in the past as the continued acquisition of new solutions through either innovation or social learning (Lehner et al. 2011). If chimpanzees are able to respond flexibly to changes in task conditions (as shown by Manrique et al. 2013), we would predict individuals to increase their use of techniques that remain effective, and to decrease their use of techniques that have been rendered ineffective, in the face of task restrictions. Alternatively, if chimpanzees are behaviourally inflexible, we predict the continued use of ineffective techniques and no increase in the use of effective techniques. If chimpanzees follow an 'explore if dissatisfied' strategy, we would predict the emergence of novel techniques following the imposition of task restrictions, whilst a 'copy if dissatisfied' strategy would result in the acquisition of effective techniques by individuals other than the technique's innovator following the imposition of task restrictions.

3.2.2 Subgroups and the impact of developmental conditions

Chimpanzees were studied in Edinburgh Zoo, which houses a single community that originates from two separate subgroups; long-term residents of the zoo ('Edinburgh' chimpanzees), and others introduced in 2010 ('Beekse Bergen' chimpanzees). These subgroups are now well integrated socially (Schel et al. 2012; Watson et al. 2015) but have differing life histories, with the Beekse Bergen subgroup coming from a laboratory and first living in a zoo environment from 2007. The majority of chimpanzees in the Beekse Bergen subgroup were hand-reared in nurseries rather than mother-reared, whilst all captive-born chimpanzees in the Edinburgh subgroup were mother-reared. Both rearing history and housing have been found to impact problem solving ability (and other behaviour) in chimpanzees (Brent, Bloomsmith & Fisher 1995; Bloomsmith et al 2006; Morimura & Mori

2010; Vlamings, Hare & Call 2010), so this study also considers the impact of subgroup membership upon task performance. Members of the Beekse Bergen subgroup, with a history of laboratory-housing and including a number of hand-reared chimpanzees, were predicted to perform more poorly on the task than long-term zoo residents.

3.2.3 Scaffolding towards an effective solution

Learning through exposure to the artefacts of others' tool use is hypothesised to aid in the development of tool behaviour in wild populations (Tennie et al. 2009); however, previous experimental studies of chimpanzees (Gruber et al. 2011) and capuchin monkeys (Cardoso & Ottoni 2016) have not shown that providing scaffolding intended to approximate these artefacts (tool materials already inserted into a task, for example) leads to the acquisition of novel tool behaviours. By providing chimpanzees with limited exposure to scaffolding towards a novel tool technique in the final phase of our study, we examined whether chimpanzees could acquire novel tool behaviour through exposure to favourable affordances in the form of an effective tool material correctly inserted into the task, as might occur in the wild where proficient tool-users leave tools in place that novices may discover.

3.3 Methods

3.3.1 Ethical approval

The study received ethical approval from the University of St Andrews Animal Welfare and Ethics Committee, and was approved by the Budongo Trail Research Committee. Research was conducted in accordance with the guidelines of the Association for the Study of Animal Behaviour.

3.3.2 Subjects and study site

Subjects were 18 chimpanzees housed as one group in the Budongo Trail facility at Edinburgh Zoo (see Table 1 for details). The group is composed of two 'subgroups', long-term residents of the zoo ('Edinburgh' chimpanzees), and others introduced in 2010 ('Beekse Bergen' chimpanzees), each numbering nine individuals. The chimpanzees lived in three interconnecting indoor enclosures measuring 120m² each and one outdoor enclosure measuring 1832m², along with two research 'pods' (two connected rooms measuring 26.5m² in total) provided for cognitive research. Chimpanzees were fed six to eight scatter feeds

throughout the day at random times and locations, with water available ad libitum throughout the facility. The research pods were accessible via overhead tunnels from the chimpanzees' indoor enclosures, and activity within the pods could not be viewed by chimpanzees outside the pods. Our task was presented in one of these research pods, and chimpanzees had access to both pods during testing. Chimpanzees in the second research pod during testing had limited visual access to the task through an open slide door separating the pods, while individuals in the primary pod (in which the task was presented) generally had good visual access to the task. A maximum of seven chimpanzees were recorded as present in the primary pod during testing, with space for further individuals in the second pod. All chimpanzees had previous experience with artificial foraging tasks involving tool use, having been provided with the 'Panpipes' task (in which a stick tool is used to retrieve a grape from within the apparatus, see Whiten, Horner and de Waal, 2005, for details of the apparatus) and a foodraking task in which plastic stick tools could be used to retrieve out-of-reach rewards (see Price et al., 2009, for a similar task) (V West, unpublished master's thesis; R Harrison, unpublished master's thesis). In addition, chimpanzees had previous experience using a touchscreen device in the research pods (Wallace et al. 2017).

Table 1.

Demographic and Rearing Information of the Chimpanzees with Level of Participation in Current Study

Subgroup	Individual	Sex	Year of	Origin (wild or	Origin Rearing		Participation in current study		
			(age at time of testing)	captive born)		Wide	Narrow Tube	Narrow Scaffolded	
Edinburgh	Qafzeh	М	1992(22)	Captive	Mother	0	1	0	
	Kindia	М	1997(17)	Captive	Mother	14	4	1	
	Liberius	М	1999(15)	Captive	Mother	1	0	1	
	David	М	1975(39)	Captive	Mother	4	0	0	
	Louis	М	1976(38)	Wild		6	15	0	
	Lucy	F	1976(38)	Captive	Mother	11	2	0	
	Kilimi	F	1993(21)	Captive	Mother	175	103	87	
	Cindy	F	1964(50)	Wild		0	0	10	
	Emma	F	1981(33)	Captive	Mother	37	59	0	
Beekse Bergen	Paul	М	1993(21)	Captive	Hand- raised	0	0	0	
	Pearl	F	1969(45)	Wild		311	214	40	
	Sofie	F	1981(33)	Captive	Hand- raised	3	0	2	
	Lianne	F	1989(25)	Captive	Mother	0	0	0	
	Heleen	F	1991(23)	Captive	Mother	4	0	0	
	Edith	F	1996(18)	Captive	Mother	385	741	73	
	Eva	F	1980(34)	Captive	Hand-	311	21	4	
					raised				
	Frek	М	1993(21)	Captive	Hand- raised	125	80	11	
	Rene	М	1993(21)	Captive	Hand- raised	152	11	3	

Note: In addition to their own attempts, all individual with the exception of Cindy and Liberius were present in the research pods during another individual's attempt on at least on occasion.

3.3.3 Apparatus

Echoing the study of Lehner et al. (2011), we provided the chimpanzees with an artificial foraging task in which dilute Ribena juice could be retrieved from within transparent polycarbonate tubes, using either provided tool materials or hands. The task had two stages, for which two widths of tube were provided. The first ('wide') tube measured 30cm tall with a 10cm inner diameter (see Figure 1), and the second ('narrow') tube measured 30cm tall with a 5cm inner diameter. These tubes were presented in the research pods, bolted to a polycarbonate screen facing into the pod, and could be filled and emptied by the experimenter through holes in the screen. Alongside the tubes, chimpanzees were provided with a selection of tool materials comprising plain sticks (rigid sticks measuring approximately 40-50cm), straw bedding material, strips of cloth and 'wood wool'/'excelsior' (fine wood slivers typically provided as bedding material). Leafy sticks (a selection of browse generally provided to the chimpanzees by care staff for nesting and feeding, primarily eucalyptus - these leafy sticks were flexible and measured approximately 40-80cm) were available in the chimpanzees' enclosure throughout testing, and were placed in the research pod along with the other tool materials from the fifth hour of testing onwards. Chimpanzees were familiar with all tool materials, as straw, cloth, wood wool and browse were generally provided as nesting material, and sticks were readily available in their outdoor enclosure. All tool materials were placed into the research pods before chimpanzees were given access.

3.3.4 Procedure

The apparatus was presented during twice-daily research sessions facilitated by Edinburgh Zoo staff. These sessions lasted for 45-60 minutes. In the first stage of the study ('Wide Tube' phase), chimpanzees were provided with the wide tube, filled with diluted sugar free Ribena to a depth of around 7cm. This was presented alongside the aforementioned selection of tool materials, and in the 'Wide Tube' phase the juice could also be reached by hand. All provided tool materials could potentially be used to successfully retrieve juice from the task. The tube was baited with juice for ten sessions, each lasting between 45 and 60 minutes, with juice added by the experimenter to ensure a reward was present for the duration of each session. The tube was emptied of liquid by the researcher through a valve at the base at the end of each session, as removing the chimpanzees from the research pods was logistically unfeasible, and so the juice reward was removed in order to discourage further interaction with the tube outside of the twice-daily research session.

In the second stage of the study ('Narrow Tube' phase), chimpanzees were presented with the narrow tube, filled with juice to a depth of 7cm, along with the same selection of tool materials. Again, chimpanzees had access to the baited tube for ten 45-60 minute sessions. The narrow tube prevented chimpanzees from inserting their hands into the tube to gain juice, and also rendered attempts made using rigid, leafless sticks relatively unsuccessful, due to the ledge surrounding the panel to which the tube was attached. This ledge meant that rigid sticks inserted into the tube frequently hit the back of the tube and could be inserted no further, preventing them from reaching the juice. Leafy sticks remained functional. Absorbent materials (straw, cloth, and wood wool) could no longer be inserted and retrieved by hand.

In the third stage of testing ('Narrow Scaffolded' phase), chimpanzees were again presented with the narrow tube for ten 45-60 minute sessions, but at the start of each day of testing, prior to the chimpanzees having access to the research pods, a leafy stick was inserted into the tube, with its leaves in the juice. As multiple sessions were conducted on some testing days, with no access to the research pods to re-insert the stick following the start of the first session each day, this provided four sessions which began with a stick already inserted. Only the first individual to interact with the task on these four sessions encountered this scaffolding; however, their interactions with the scaffolding and their subsequent interactions with the task could be observed by other group members.

In the course of testing, on 12 occasions, two sessions occurred on the same day, and due to the impossibility of removing chimpanzees from the research pods between sessions, chimpanzees had access to the empty tube and remaining tool materials for approximately one hour between sessions. It was not possible to document any attempts made during this time as the researcher did not have access to the adjacent research office to film or observe behaviours in between sessions.





The 'wide' tube as presented to the chimpanzees within the research pod. The 'narrow' tube was presented in the same manner. The height of both tubes was 30cm, with the 'wide' tube diameter measuring 10cm and the 'narrow' tube diameter measuring 5cm.

3.3.5 Data collection and coding

Sessions were recorded using a Sony Handycam DCR-SX21 camera. This recorded chimpanzees' responses to the task, while the experimenter narrated chimpanzees' actions as well as the identity and presence of other individuals in the research pod. The video and narration were later coded together. The chimpanzee identity, tool material choice (hand, plain stick, wood wool, straw, or leafy stick), action (dip, retrieve, squash, drop), and success of individuals attempting the task were coded for each attempt. The presence of other individuals in the research pod was also coded for each attempt. Techniques were then classified as 'Always effective' and 'Partially effective' (Table 2), based upon their potential efficacy in narrow tube conditions. A second coder, blind to the experimental hypotheses,

coded 50 randomly selected attempts for tool material, technique (as listed in Table 2), and success. Narration of these attempts did not include narration of tool material, technique or success, and so the second coding was independent. Inter-observer reliability was calculated using Cohen's Kappa, revealing agreement for all variables (tool material K = 0.90, technique K = 0.87, success K = 0.95).

3.3.6 Data analysis

Data were analysed in R (version 3.2.2, R Core Team 2015) and RStudio (version 0.99.893, RStudio Team, 2015) using a generalised linear mixed model with a Laplace approximation (GLMM), using the function glmer in the R statistics package lme4 (Bates, Maechler & Bolker 2012). Analysing binomial data using GLMM is recommended by Jaeger (2008) and Bolker et al. (2009). The impact of predictor variables upon the number of 'Always effective' vs 'Partially effective' technique attempts in the 'Wide Tube' and 'Narrow Tube' phases was assessed for all individuals that made attempts in both the 'Wide' and 'Narrow' tube phases (N=10).

A full random slope model was fitted (for discussion on the benefits of fitting random slopes as well as random intercepts, see Schielzeth & Forstmeier 2009). The full model contained fixed effects for Phase ('Wide Tube' vs 'Narrow Tube') and Subgroup (Edinburgh vs Beekse Bergen), along with an interaction between the two and a random intercept and slope by Phase for each Individual (N=10). This full model was compared with a null model including only the random intercept and slope by Phase for each Individual. Both models were fitted using a binomial error structure, due to the binary nature of the response variable (Effectiveness), and a logit link function. A likelihood ratio test comparing the full and null models indicated that the full model was a significantly better fit ($\chi^2 = 8.65$, df = 3, p = .0343; dAIC = 2.7).

In addition, a full random slope GLMM was fitted to examine the likelihood of 'Always effective' vs 'Partially effective' across experimental sessions within the 'Narrow Tube' phase, in order to investigate any change in behaviour over time within this phase. The model contained a fixed effect for Session (the ten 45-60 minute sessions that comprised each phase), and a random intercept and slope by Session for each Individual that took part in the 'Narrow Tube' phase (N=11). As with the main analysis described above, this model was compared with a null model containing only the random effects, and a likelihood ratio test

indicated that the model containing a fixed effect for Session was no improvement upon a null model ($\chi^2 = 2.37$, df = 1, p = .1238; dAIC = 0.4).

3.4 Results

Sixteen of the eighteen chimpanzees interacted with the task during at least one of the three phases of testing (see Table 1 for frequency of participation for all individuals) In addition, sixteen of eighteen individuals were present in the research pod during another individual's attempt at the task on at least one occasion (with only Cindy and Liberius never having the opportunity to observe others at the task). Ten individuals attempted the task in both the 'Wide Tube' and 'Narrow Tube' phases. Seven individuals participated in all three phases (see Table 1). A total of 3,022 attempts were made across the three phases and 30 hours of testing. Seven techniques were used to successfully solve the task (see Table 2). Six of these techniques emerged in the 'Wide Tube' phase (and four of these six within the first testing session), with the remaining technique emerging in the 'Narrow Tube' phase. No novel techniques were observed in the 'Narrow Scaffolded' phase. Techniques involving the use of hands only and the use of plain, rigid sticks emerged first, within the first testing session. The use of leafy sticks emerged after several hours of exposure to the task (Table 2). Only one novel technique (wood wool retrieve) emerged in the 'Narrow Tube' phase, though some individuals performed techniques in this phase that were novel to them (though not novel to the group, and so potentially acquired socially) (Table 3).

3.4.1 Behavioural flexibility

In order to examine behavioural flexibility in the chimpanzees' response to the task restrictions imposed by the transition from the 'Wide Tube' to 'Narrow Tube' phase, the techniques described above were categorised as 'Always effective' or 'Partially effective' according to their potential efficacy across phases (see Table 2). Note that all techniques (see Table 2) were effective in the 'Wide Tube' phase, as the tube width allowed individuals to insert their hands into the tube, facilitating the use of a wide variety of techniques.

Techniques involving the insertion of a hand into the tube (i.e. *hand dip*) were classified as 'Partially effective', as insertion of the hand into the tube was made impossible by the width of the tube in the 'Narrow Tube' phase, though this technique could be successfully used in the 'Wide Tube' phases. Techniques reliant upon the insertion of a plain, rigid stick into the tube were also classified as 'Partially effective', as the overhang of the task presentation

window was such that these sticks could frequently no longer be inserted into the tube in the 'Narrow Tube' phase. Short rigid sticks could still successfully be dropped into the tube and retrieved by hand, and so the technique *stick drop* is categorised as 'Always effective'. For further discussion of this classification, see Supplemental Article S1.

Comparison of the use of 'Partially effective' and 'Always effective' techniques in the 'Wide Tube' and 'Narrow Tube' phases indicates the extent to which chimpanzees altered their behaviour in response to the change in task, and the extent to which they were able to set aside techniques that had been rendered impossible by the change in tube width. An increase in the use of 'Always effective' techniques in the 'Narrow Tube' phase compared with the 'Wide Tube' phase would indicate a flexible response to the task changes. The 'Narrow Scaffolded' phase is not included in these analyses, in order to exclude the possibility of the scaffolding impacting observed flexibility.

Table 2.

Techniques successfully used to solve the task

Technique	Description	Latency to first successful use from start of first testing session	Effective in 'Wide Tube' phase?	Maintained efficacy in 'Narrow Tube' phase?	Effective in all phases?
Hand dip	Dip hand directly into juice	00:00:35	Yes	No	Partially effective
Stick dip	Stick is dipped directly into the juice	00:00:43	Yes	No	Partially effective
Stick retrieve	Stick already in tube removed with hand	00:23:38	Yes	No	Partially effective
Stick drop	Drop stick into tube then retrieve by hand	00:21:16	Yes	Yes	Always effective
Leafy stick dip	Dip stick end of a leafy branch directly into the juice	02:47:23	Yes	Yes	Always effective
	(this differs from 'stick dip' only in the material) This				
	technique remained Effective in Narrow tube phases				
	due to the flexibility of the leafy sticks in comparison				
	to standard sticks				
Leaf squash	A leafy branch is inserted stick first, and the leaves are	05:56:26	Yes	Yes	Always effective
	then forced down into the tube into contact with the				
	juice				
	(Note: this technique was used successfully only once)				
Wood wool	Wood wool pushed part way into tube by a previous	11:43:12	Yes	No	Partially effective
retrieve	individual removed with hand				
	(Note: this technique was used successfully only once)				

Note: Dashed horizontal line indicates transition between the 'Wide Tube' and 'Narrow Tube' phases. The 'Narrow Tube'.phase began at 8:17:44 (the start of the 11th experimental session).





Individual chimpanzees' proportions are indicated by dots. Coloured horizontal bars show each subgroup's mean proportion. Black horizontal bars show overall mean proportion. Note that in the 'Narrow Tube' phase, the subgroup means and overall mean are the same.

The ten individuals that took part in both 'Wide' and 'Narrow' tube phases used 'Always effective' techniques for 58 of 1527 attempts in the 'Wide Tube' phase, increasing to 514 of 1250 attempts in the 'Narrow Tube' phase. On average, each individual used 'Always effective' techniques for a mean of 8.7% (SD = 15.6) attempts in the 'Wide Tube' phase, increasing to a mean of 24.2%% (SD = 19.4) of attempts in the 'Narrow Tube' phase (see Figure 2). Individual preferences in terms of specific techniques for the 10 individuals that took part in both 'Wide' and 'Narrow' tube phases are shown in Table 3.

Table 3.

The two most frequently used techniques of individuals that made attempts in both the 'Wide' and 'Narrow' tube phases. 'Always effective' techniques are shown in bold. An asterisk indicates that an individual used a technique for the first time within the 'Narrow' Tube phase (ie. that the technique was novel to them).

Subgroup	Individual	'Wide	Tube' phase	'Narrow Tube' phase		
		1 st preferred	2 nd preferred	1 st preferred	2 nd preferred	
		technique (no.	technique (no. of	technique (no.	technique (no. of	
		of attempts; %	attempts; % of	of attempts; %	attempts; % of	
		of attempts)	attempts)	of attempts)	attempts)	
Edinburgh	Kindia	Stick dip (6;	Leafy stick dip (6;	Stick dip (2;	Leafy stick dip (2;	
		43%)	43%)	50%)	50%)	
	Louis	Stick dip (6;		Stick dip (13;	*Leafy stick dip (2;	
		100%)		87%)	13%)	
	Lucy	Stick dip (7;	Hand dip (4; 36%)	Stick dip (2;		
		64%)		100%)		
	Kilimi	Stick dip (127;	Hand dip (33; 19%)	Stick dip (49;	Leafy stick dip (44;	
		73%)		48%)	43%)	
	Emma	Stick dip (19;	Hand dip (16; 43%)	Stick dip (38;	Hand dip (8; 14%) /	
		51%)		64%)	*Leafy stick dip (8;	
					14%)	
Beekse	Pearl	Hand dip (165;	Stick dip (134;	Stick dip (119;	Leafy stick dip (71;	
Bergen		53%)	43%)	56%)	33%)	
	Edith	Stick dip (320;	Hand dip (64; 17%)	Stick dip (364;	*Leafy stick dip	
		83%)		49%)	(294; 40%)	
	Eva	Stick dip (237;	Hand dip (61; 20%)	Stick dip (12;	Hand dip (5; 24%)	
		76%)		57%)		
	Frek	Hand dip (74;	Stick dip (27; 22%)	Stick dip (40;	Stick drop (23; 29%)	
		59%)		50%)		
	Rene	Hand dip (141;	Stick dip (7; 5%)	Hand dip (6;	Stick dip (3; 27%)	
		93%)		55%)		

Note: Percentages are rounded.

The full model (see Table 4) indicates that use of 'Always effective' tool techniques increased significantly in the 'Narrow Tube' phase (b = 2.93, p = .0013); in the 'Narrow Tube' phase, chimpanzees were 18.67 (Wald 95% CI [3.16, 110.47]) times more likely to use an 'Always effective' technique than in the 'Wide Tube' phase. This indicates a significant increase in 'Always effective' technique use in the 'Narrow tube' phase, and as we present a binomial GLMM, and each attempt made could only be 'Always effective' or 'Partially effective', an equivalent significant decrease in the use of 'Partially effective' techniques.

There was no significant effect of Subgroup (b = 1.57, p = .1631) upon the likelihood of an individual using 'Always effective' techniques in either Phase, and no significant interaction between Phase and Subgroup (b = -1.57, p = .2387), indicating that the two Subgroups did not respond significantly differently to the change in Phase. A likelihood ratio test indicated no significant difference between this full model (including the impact of Subgroup and an interaction with Phase) and a reduced model including only Phase ($\chi^2 = 1.52$, df = 2, p = .4676; dAIC = 2.4), and so we present the full model with all predictors here.

An additional analysis examining the impact of Session upon the likelihood of individuals using 'Always effective' techniques within the 'Narrow Tube' phase found that Session had no significant effect (b = 0.17, p = 0.077), indicating that individuals did not become more likely to use 'Always effective' techniques as time passed within the 'Narrow Tube' phase.

3.4.2 "Narrow Scaffolded" phase

Four individuals (Kindia, Edith, Frek, and Pearl) encountered the task with the scaffolded leafy stick solution in place. Of these individuals, only two (Edith and Pearl) put the leaves in their mouths to retrieve the reward. Frek and Kindia instead discarded the branch without retrieving any reward from it. These four individuals (Kindia, Edith, Frek, and Pearl) who encountered the leafy stick solution first-hand did not use the leafy stick solution (dipping the top, leafy part of the branch in, rather than the bare, stick end). It therefore appears that scaffolding the behaviour in this limited manner did not provide sufficient information for these chimpanzees to acquire a novel 'Always effective' solution to the task.

Table 4.

Results of full model GLMM on the effects of Phase, Subgroup and an interaction between the two, with random intercept and slope for Individual by Phase upon 'Always effective' technique use. Variance, standard deviation, and correlation for the random intercept and slope for Individual by Phase is provided.

Fixed effects	Estimate	[Wald 95% CI]	Std. Error	z value	<i>p</i> value	
Intercept (including 'Wide	-4.13	[-5.62, -2.64]	0.76			
Tube' phase and Beekse						
Bergen subgroup)						
Phase ('Narrow Tube')	2.93	[1.15, 4.70]	0.91	3.23	0.0013	**
Subgroup (Edinburgh)	1.57	[-0.63, 3.77]	1.12	1.40	0.1631	
Phase*Subgroup	-1.57	[-4.17, 1.04]	1.33	-1.18	0.2387	
Random effects	Variance		Std.	Correlation		
			Deviation			
Individual (Intercept)	2.46		1.57			
Slope by Phase	3.31		1.82		-0.87	

**=*p* < 0.01

3.5 Discussion

In this study, chimpanzees were found to be capable of responding with some flexibility to a changing task. However, although individuals significantly increased their use of 'Always effective' techniques in the 'Narrow Tube' phase, no individual that made more than one attempt used 'Always effective' techniques for a majority of their attempts. This indicates that chimpanzees' behavioural flexibility was limited by an inability to relinquish the previously successful solutions used in the 'Wide Tube' phase, which continued to comprise at least 50% of all individuals' attempts. Scaffolding provided to four individuals in an attempt to facilitate use of an 'Always effective' technique in the final 'Narrow Scaffolded' phase did not result in the use of this novel technique by this limited subsample of chimpanzees. Membership of subgroups with differential experiential histories did not have a

significant impact upon use of 'Always effective' techniques. The principal issues addressed by the study are discussed in turn below.

3.5.1 Behavioural flexibility

Chimpanzees did typically alter their behaviour in response to the change in task, using significantly more 'Always effective' techniques in the 'Narrow Tube' phase. However, no individual that made more than one attempt used 'Always effective' techniques for a majority of their attempts, in contrast with the findings of Manrique et al. (2013) in whose study chimpanzees successfully used an effective solution for the majority of attempts in the appropriate condition. Using a very similar task to the current study, Lehner et al. (2011) found that orangutans preferentially used efficient methods when task constraints rendered their previous preferences inefficient. Similarly, Davis et al. (2016) found that most chimpanzees used a novel, efficient solution for the majority of attempts when the efficiency of their previously known solution became very low, though this extent of switching was observed only in groups with a trained demonstrator using the efficient solution or with human demonstrations provided: in 'non-seeded' groups, only one individual switched to the efficient solution, but then used it for the majority of attempts. These comparisons with previous research indicate that whilst chimpanzees in this study showed behavioural flexibility (altered their behaviour), the flexibility was limited in comparison to several previous studies, thus concurring with some other previous studies of chimpanzees (Marshall-Pescini & Whiten 2008; Hrubesch et al. 2009; Bonnie et al. 2012). The finding also concurs to some extent with experimental studies of wild chimpanzees which have shown that individuals approach novel problems with culturally-informed known behaviours, which may limit the extent to which individuals perceive the affordances of alternative tools (Gruber et al. 2009, 2011). However, evidence from wild observations also shows that chimpanzees are capable of modifying tool behaviour (Yamamoto et al. 2008), and using novel materials to achieve known forms of tool use (Hobaiter et al. 2014), both of which indicate some level of behavioural flexibility in individual wild chimpanzees.

Regarding the 'explore-if-dissatisfied' strategy discussed previously, we found that only one novel technique emerged following the imposition of task constraints (see Table 2), and this technique was used successfully only once. This would seem to indicate that chimpanzees in the current study did not respond to the task changes by exploring the possibility of novel solutions, but rather altered the extent to which they employed known solutions. Three

individuals (Louis, Emma and Edith) used a technique that was novel to them in the 'Narrow Tube' phase for a considerable proportion of their attempts (see Table 3). The technique in question (*leafy stick dip*) was not novel on a group level, and so this may be the result of observational learning (perhaps indicating a 'copy-if-dissatisfied' strategy).

The relatively limited flexibility found in the current study could be due to differences in task demands between the present study and others reporting more flexibility. One possible explanation for the difference in the apparent level of flexibility seen in this study compared with Davis et al. (2016) is the presence in the Davis et al. (2016) study of social information provided by a trained, competent model. The scaffolding in the final 'Narrow Scaffolded' phase aside, chimpanzees were not provided with trained conspecific demonstrators or human demonstrations to offer social information about 'Always effective' techniques. Had the chimpanzees in this study entirely failed to discover 'Always effective' techniques, this lack of experimentally-provided social information would be a plausible explanation for the relatively diminished behavioural flexibility observed. However, the majority of individuals tested used 'Always effective' techniques in the 'Narrow Tube' phase, and indeed had access to social information in the form of others using 'Always effective' techniques, indicating that they were not limited by a lack of knowledge of the existence of such techniques, but rather failed to employ them as frequently as they used 'Partially effective' techniques.

As in the current study, apes in Manrique et al. (2013) and Lehner et al. (2011) had to discover more efficient solutions to the provided tasks without additional information from experimenters (though in both Lehner et al., 2011, and the current study, apes were tested in a group context and thus had access to any social information conspecifics provided). Though three individuals did use an 'Always effective' technique that was novel to them in the 'Narrow Tube' phase (Table 3), indicating a capacity for acquisition of novel behaviours via either social or individual learning in response to the change in task, only three of the seven observed solutions (*leafy stick dip, leaf squash*, and *stick drop*) were 'Always effective' in the 'Narrow Tube' phase. This limited range of available solutions may have restricted chimpanzees' ability to respond flexibly to the change in task. In comparison, orangutans in the Lehner et al. (2011) study exhibited six effective solutions in 'Restricted Condition 1' (analogous to our 'Narrow Tube' phase) and so had knowledge of a wider range of potential solutions that could be usefully applied to the narrow tube. Comparison of the range of solutions discovered by chimpanzees in the current study with the range of solutions

observed by Tonooka, Tomonaga and Matsuzawa (1997) in response to a task similar to the 'Wide Tube' phase of our study may indicate that chimpanzees in our study were somewhat limited in their exploration of the task, with Tonooka et al. (1997) observing 16 different solutions in comparison to only seven solutions seen in the current study. Although chimpanzees in Tonooka et al. (1997) had access to a wider range of tool materials, which, rather than a lack of exploration, may account for the discrepancy in the number of solutions observed in their study and the current study, there were tool materials available to chimpanzees in our study (namely *cloth* and *wood wool*) that were never used in the 'Wide Tube' phase, when there were few limitations to the efficacy of solutions.

The fact that chimpanzees in our study did not explore the potential of absorbent materials as tool solutions to the task could suggest a role for 'functional fixedness' (Hanus et al. 2011) in limiting their exploration of the task. While the chimpanzees are familiar with these absorbent materials, they are primarily used as nesting material. The chimpanzees may therefore have struggled to perceive them as having an alternative use. This does not appear to have constrained the chimpanzees' use of leafy sticks as tools (despite such browse often also being used as nesting material), though their reluctance to use the leaves of these sticks to dip with may also reflect a level of 'functional fixedness', as only the stick portion of such leafy sticks appeared to be considered functional by the chimpanzees.

In contrast to the current study, the tasks provided by Manrique et al. (2013) and Davis et al. (2016) did not require the use of tools, and were solvable by hand. Tasks requiring tool use are typically more challenging than those requiring purely manual actions, with the inclusion of tool use more challenging for causal cognition (Seed et al. 2009; Völter & Call 2014). The necessity of tool use in the latter conditions of this study ('Narrow Tube' phases) may therefore have impeded behavioural flexibility, perhaps by confounding the chimpanzees' comprehension of the efficacy of their solutions, or impeding the acquisition of further 'Always effective' solutions via social or asocial means.

3.5.2 The Impact of Scaffolding

The limited exposure to scaffolding provided to four chimpanzees in the third and final phase of this study did not lead to the acquisition of novel techniques by any individual. This scaffolding (providing the task with a leafy stick already inserted) aimed to approximate a form of information chimpanzees have access to in the wild – the products and debris of other

chimpanzees' tool use, hypothesised to be a facilitator of learning local techniques by Tennie et al. (2009) (e.g. "...nut crackers and termite fishers leave their tools and detritus behind, and in the right place, which makes the learning of their offspring and others much easier", pp.2406). This information in the form of residual, enduring artefacts has been argued to facilitate technical activities in New Caledonian crows (Holzaider, Hunt & Gray 2009), Japanese macaques (Lecca, Gunst & Hoffman 2010) and bearded capuchins and chimpanzees (Fragaszy et al. 2013), although we are not aware of any direct experimental evidence for such hypothesised effects.

Although we are cautious in our interpretation of our results regarding scaffolding, given that only four individuals had very limited interaction with the scaffolding, more extensive efforts to provide this kind of information in experimental settings have often proven unsuccessful in encouraging the invention of novel behaviours. Wild bearded capuchin monkeys from a population that does not habitually use probing tools, when presented with a dipping task with stick probes already inserted, never acquired probing behaviour (Cardoso & Ottoni 2016). Using a similar task to the current study, Gruber et al. (2009) found that two communities of wild chimpanzees had distinct tool use preferences when extracting honey from a cavity, with one community solving the task using a stick tool while the other solved it using their hands or leaf sponges. Subsequently providing this task to the hand/leaf-sponge community with a stick tool already inserted failed to elicit stick tool use (Gruber et al. 2011). The authors interpret this finding as evidence of "cultural bias" towards existing traditions of tool use, which constrains how individuals perceive and evaluate the affordances of their environment (Gruber et al. 2011), but it may also be that presenting chimpanzees with scaffolded solutions in this manner (at least when numbers of such presentations are limited, with the majority of chimpanzees in Gruber et al.'s study receiving only one or two exposures) simply provides insufficient information to elicit acquisition of novel tool use behaviours. Gruber et al. (2011) argue that such limited exposure may be ecologically valid, and tests the hypothesis that novel tool behaviours will emerge in direct response to favourable affordances (a situation that highlights the physical properties of potential tool materials and indicates the potential relationship between tool and goal), but the possibility remains that such limited exposure to scaffolding is insufficient to impact behaviour.

Similarly, experiments incorporating 'ghost conditions', in which the operational affordances of a task are demonstrated without the presence of a demonstrator individual (e.g. task

components are moved by fine fishing line or similar), perhaps also corroborates the insufficiency of such scaffolding. Hopper et al. (2007, 2015) found that demonstration of the workings of a 'Panpipes' apparatus in such a ghost condition did not lead chimpanzees to discover the solution to the task. The efficacy of such ghost demonstrations may be affected by the complexity of the task (Hopper et al. 2008), with complex tool use perhaps proving more challenging to learn via such demonstrations. The information provided by these scaffolded conditions (as the current study, and Gruber et al., 2011) can also be argued to be even more impoverished than that provided by ghost conditions as it does not incorporate movement, and so may not demonstrate the affordances of a task to the same extent as moving displays.

Providing further groups of chimpanzees with scaffolding approximating the artefacts of other's tool use they might encounter in the wild, perhaps in the context of novel tool use tasks for which no pre-existing cultural biases are likely to exist, could shed further light on the ability of chimpanzees to learn novel behaviours from this sort of information, and indicate whether chimpanzees are limited by cultural biases, by the relative poverty of the information provided by scaffolding, or simply require more extensive exposure to scaffolding in order to acquire novel behaviours.

3.5.3 Subgroup differences

Subgroup membership was found to have no significant effect on the likelihood of individuals using 'Always effective' techniques in either the 'Wide' or 'Narrow' tube phase, with both groups increasing their use of 'Always effective' techniques in the 'Narrow' tube phases. Previous research has found that chimpanzees reared in captivity perform more poorly than wild-born chimpanzees in tool-use tasks. Morimura and Mori (2010) found that captive-reared chimpanzees were less likely to succeed than wild-born chimpanzees on a tool use task involving retrieving juice from a bottle using a provided stick tool. Similarly, Brent et al. (1995) found that both captive mother-reared and captive nursery-reared chimpanzees were less likely to succeed than wild-born chimpanzees (in captivity) on a reaching tool task. Rearing history has also been found to have an impact on nest-building, with wild-born chimpanzees, and using more time constructing and using nests than captive-born chimpanzees, and using more complex techniques in their nest building, while within the captive-born chimpanzee sample, mother-reared individuals spent more time than nursery-born individuals making and using nests (Videan 2006). Some research indicates that housing

can influence performance on cognitive tests, with Vlamings, Hare and Call (2010) finding that sanctuary-housed chimpanzees and bonobos outperform zoo-housed apes in a detourreaching task testing inhibitory control. However, Wobber and Hare (2011), using a subset of the Primate Cognition Test Battery (Herrmann et al. 2007), found no impact of housing (zoo vs sanctuary) on the performance of mother-reared chimpanzees on tests of social or physical cognition, but did find that mother-reared individuals (regardless of housing) outperformed orphaned individuals on physical cognition tests – this effect was due to improved performance on a tool properties task in which individuals chose between a functional and non-functional tool. Similarly, Herrmann, Wobber and Call (2008) found no difference in performance between zoo- and sanctuary-housed chimpanzees and orangutans on a tool functionality choice task.

We did not find evidence of subgroup differences in the current study, though the subgroups compared here were based upon the chimpanzees' housing history rather than their rearing. Although only the Beekse Bergen group includes individuals hand-reared by humans, and this is the most common rearing history for this subgroup (five of nine individuals), both groups include both wild- and captive-born mother-reared individuals. Sample size precluded any analysis based upon rearing history (with only three individuals categorised as wild-born, only two of which participated in both the 'Wide' and 'Narrow Tube' phases of the task), and given the difference in origin of the two groups (laboratory vs. zoo) it was thought a subgroup analysis might capture any differences in performance related to early life experiences. It may be that, between captive environments housing chimpanzees with mixed rearing histories, there is little difference in performance to be found using artificial foraging tasks such as the current task. However, further groups of chimpanzees in different captive facilities would have to be provided with the task in order to test this. Examination of the impact of both housing and rearing histories upon chimpanzee performance in experimental tasks is essential for a full understanding of chimpanzee cognition (Boesch 2007).

3.5.4 Limitations to the current study

Although some previous studies of chimpanzee and great ape behavioural flexibility have tested individuals in isolation (Marshall-Pescini & Whiten 2008; Manrique & Call 2013, 2015), and this approach allows for control over chimpanzees' access to social information about the task and the avoidance of issues around task monopolization by dominant individuals, we note that many previous studies have presented tasks in a group context

(Gruber et al. 2009, 2011; Lehner et al. 2011; Davis et al. 2016). This may be due to the constraints of conducting research at captive facilities (or, in the case of Gruber et al., 2009, 2011, in the wild), or be a methodological choice in order to explore the social learning abilities of subjects (Davis et al. 2016). The open presentation of the task in the current study to the group of chimpanzees prevents us from making claims regarding the process by which novel behaviours emerged and spread in individuals during the trials (whether this occurred via social learning or innovation). However, following Lehner et al.'s (2011) definition of behavioural flexibility, as the continued acquisition of novel techniques via either social or asocial learning, group testing in this manner allows flexibility to be demonstrated through either form of learning.

This study focused upon a community of chimpanzees with particular life histories (primarily captive born) and was also limited to adult chimpanzees, with no infants or juveniles in the population. Previous research has shown that behavioural flexibility (referred to as 'cognitive flexibility' by Manrique and Call, 2015, and measured by a simple reversal task) follows a Ushaped curve in great apes, with optimum performance in terms of error avoidance appearing to occur between seven and 27 years of age (Manrique & Call 2015), and so the age of some individuals in the current study may have impaired their performance (with five of the ten individuals that provided data in both the 'Wide' and 'Narrow Tube' phases being over 27 years old). Position in the dominance hierarchy could also impact performance on an artificial foraging task such as that of the current study. Low ranking individuals may be more likely to innovate novel behaviours (Reader & Laland 2001), and in a group context, dominance may impact the likelihood of others acquiring a behaviour from an individual via social learning (Horner et al. 2010; Kendal et al. 2015, though see also Watson et al. 2017). With a sample of only ten individuals providing data across the 'Wide' and 'Narrow Tube' phases, analyses of age, rearing history, and rank effects were not possible in the current study, but these previous findings demonstrate the importance of considering the impact of such factors upon task performance when possible. Future work would benefit from expanding the sample to include a more diverse range of ages and rearing histories, in sufficient numbers to enable analysis of the potential effects of these and other factors upon participation and performance in artificial foraging tasks.

3.6 Conclusions

Chimpanzees in this study did respond flexibly to a changing task, increasing their use of 'Always effective' techniques when task alterations rendered previously used solutions unrewarding. However, no individual altered their behaviour to the extent of using 'Always effective' solutions for a majority of attempts, indicating relatively limited behavioural flexibility in comparison with some previous research (Lehner et al. 2011; Manrique et al. 2013; Davis et al. 2016) and a tendency to continue to use previously rewarded behaviours. The relatively limited flexibility observed here may be due to the complexity of the task, which required tool use. A subset of chimpanzees did not acquire a more effective, novel, tool technique when provided with a single instance of scaffolding towards the solution.

Research on behavioural flexibility in chimpanzees, both in the wild and in captivity, using a variety of artificial foraging tasks, continues to provide divergent results, with some studies indicating strong conservatism, while others find an ability to relinquish known solutions in favour of more rewarding or efficient techniques. Further work must been done to investigate what factors limit or encourage flexibility in great apes, with promising avenues for further study being the relative complexity of the task (for example, the requirement for tool use versus tasks which can be solved by hand), the disparity in efficacy between known and alternative techniques (whether the established solutions become entirely unrewarded or simply less efficient or rewarding than an alternative) and investigation of individual characteristics such as age or rank which may promote or constrain behavioural flexibility.

Chapter 4: Sanctuary housed chimpanzees (*Pan troglodytes*) exhibit group differences in behavioural flexibility in response to a changing foraging task requiring tool use

This chapter is currently being prepared for submission, with authorship as follows: Harrison, R. A., van Leeuwen, E. J., and Whiten, A.

Chapter 4: Chimpanzees (*Pan troglodytes*) housed in an African sanctuary exhibit group differences in behavioural flexibility in response to a changing foraging task requiring tool use

<u>Abstract</u>

The artificial foraging task provided to chimpanzees in the previous chapter was given to two groups of sanctuary-housed chimpanzees (22 individuals). As in the previous chapter, following an initial phase in which juice could be retrieved by hand or using tool materials, effective solutions were then restricted by narrowing the diameter of the tube, necessitating the abandonment of previously successful solutions. Chimpanzees in both groups responded flexibly to this change, but group differences were apparent in the responses, with one group more likely than the other to use effective techniques when the task required them. Toolcomposite techniques were observed in both groups, but primarily in the more behaviourally flexible group. The less behaviourally flexible group was then provided with scaffolding towards tool-composite techniques, while the more flexible group had effective solutions restricted further by removing a selection of tool materials. As in the previous chapter, scaffolding proved ineffective, but restricting tool materials in the group already using toolcomposite techniques led to some modification of these techniques. This finding of group differences in apparent behavioural flexibility may explain some of the apparent inconsistency in previous studies of chimpanzee behavioural flexibility, which have at times indicated strong conservatism in chimpanzees. The possible causes of group differences in performance on this task are discussed.

4.1 Introduction

The capacity for behavioural flexibility includes the ability to alter behaviour based upon environmental feedback and to inhibit previously successful behaviours (Griffin & Guez, 2014). This capacity is necessary (although not sufficient) for supporting cumulative culture (Dean et al., 2013), as it allows individuals to modify known behaviours, and to abandon previously successful behaviours in favour, in the case of cumulative culture, of socially learned improvements to such behaviours.

Chimpanzees have previously been found to be conservative in their approach to artificial foraging tasks, continuing to use the same solution despite the prospect of greater reward (Marshall-Pescini & Whiten, 2008; van Leeuwen & Call, 2017) or their solution becoming impossible to implement (Hrubesch, Preuschoft & van Schaik, 2009). However, recent studies have shown that under certain conditions, great apes may be capable of flexibly altering their behaviour in response to a changing task (Lehner, Burkart & van Schaik, 2011; Manrique, Völter & Call, 2013; Davis et al., 2016). Davis et al. (2016) found that chimpanzees were capable of socially acquiring a more efficient solution to a task, as long as their known, habitual solution was rendered comparatively highly inefficient. Acquisition of the novel, efficient, solution appeared to depend upon the presence of a large disparity in efficiency between the two solutions. Lehner et al. (2011) and Manrique et al. (2013) both used experimental designs in which solutions, once acquired, were rendered entirely impossible by alterations to the task, prompting further exploration and innovation by subjects. Lehner et al. (2011) found that orangutans presented with a task in which tool materials could be used to retrieve juice from within a tube were able to switch to more efficient techniques and to abandon established techniques in response to task changes (narrowing of the tube and later, removal of preferred tool materials). In doing so, the orangutans also invented novel techniques that appeared to build upon previous techniques in a manner the authors argue was cumulative - for example, using a stick to push absorbent material into the tube and then retrieve it. However, it must be noted that this cumulation did not involve any apparent social learning (although social information was available to the orangutans due to group testing conditions) and therefore remained within the scope of techniques inventable by an individual. Manrique et al. (2013) provided chimpanzees, orangutans, bonobos, and gorillas with an extractive foraging task in which a grape could be

retrieved from within a Plexiglas box. In the first condition, this could be achieved by reaching through a hole in the front of the box. When this had been mastered by the subjects, the box was altered such that the floor of the box had to be pushed upward in order to reach the grape through the hole. Finally, the hole at the front was removed entirely, and the piston at the floor of the box had to be pushed upwards forcefully to 'shoot' the grape through the top opening of the box. At each stage, the number of potential solutions reduced. Chimpanzees, bonobos and gorillas were able to flexibly switch solutions in response to the task alterations and solve all three task settings. In the studies of both Lehner et al. (2011) and Manrique et al. (2013) great apes were able not only to flexibly alter their behaviour in response to changing tasks, but also to innovate novel methods of solving the foraging tasks they were presented with.

In both Lehner et al. (2011) and Manrique et al. (2013), the use of artificial foraging tasks allowed the authors to assert that the techniques observed were truly 'novel'; because the apes tested had never attempted such tasks before, any solution that emerged during testing could be classed as a novel behaviour, and by Kummer & Goodall's (1985) definition, could be classed as an innovation (being "a solution to a novel problem or a novel solution to an old one", Kummer & Goodall, 1985, p.205). However, when considering these studies in the broader context of culture and cumulative culture, it must be noted that one would not expect novel behaviours to emerge only in response to novel problems (indeed, for cumulation to occur, individuals must modify existing behaviours that presumably solve existing problems). These experimental studies seek to induce innovation and behavioural flexibility by changing the parameters of provided tasks, which gives an insight into species' capacity for behavioural flexibility, but species' propensity for spontaneous innovation and behavioural flexibility (or spontaneous exploration), in a situation where a problem does not change over time, are surely relevant when considering whether a species is likely to exhibit cumulative culture in the wild. Studying these abilities in the wild is challenging, although the establishment of long-term field sites increasingly allows researchers to assert that neverbefore-seen behaviours do in fact constitute true innovations (eg. Hobaiter et al., 2014, in which novel 'leaf-sponge re-use' and 'moss-sponging' behaviours were observed in a community which has been studied for 20 years). It should also be noted that innovation and behavioural flexibility are separate capacities, and that while Lehner et al. (2011) and Manrique et al. (2013) discuss the emergence of innovations during their studies, behavioural

flexibility can be achieved via individual or social learning; an individual does not have to innovate in order to behave flexibly, but can acquire behaviours socially, or apply known behaviours when the environment requires it.

Given the mixed findings in the current experimental literature regarding chimpanzees' ability to behave flexibly in response to changing tasks, the current study offers an investigation of chimpanzees' capacity for behavioural flexibility when experimental conditions require it of them. The use of a changing, artificial foraging task to test for flexibility allows discussion of results in the context of the existing literature, much of which has used this approach (Hrubesch et al., 2009; Lehner et al., 2011; Manrique et al., 2013; Davis et al., 2016; Harrison & Whiten, 2018). However, there is also relevant research on the subject which uses token exchange paradigms, in which reward contingencies can be manipulated in order to examine behavioural flexibility, rather than tasks in which the physical parameters of the task change. The results of these token exchange studies should also be considered when building a picture of chimpanzee behavioural flexibility.

Token exchange studies have found that chimpanzees can behave flexibly in response to changing reward contingencies (Hopper, Kurtycz, Ross & Bonnie, 2015; van Leeuwen et al. 2013; though see also van Leeuwen & Call, 2017; Hopper, Schapiro, Lambeth & Brosnan, 2011 for evidence of conservatism in token exchange studies). Chimpanzees have been shown to flexibly alter their token exchange strategy, abandoning their first-learned exchange location when it was rendered comparatively inefficient by the introduction of increased rewards at an alternative location (van Leeuwen et al, 2013), and to continue to explore novel alternative exchange locations despite receiving rewards at a known location (Hopper, Kurtycz, Ross & Bonnie, 2015). However, while chimpanzees in these studies successfully and flexibly altered the location at which they exchanged tokens, the form of the behaviour remained the same (the same token exchange behaviour was required at each location). Therefore, whilst these studies provide evidence for behavioural flexibility in chimpanzees, they may present less of a challenge than tasks in which novel behaviours must be acquired. Chimpanzees have also shown some limited capacity to socially learn demonstrated tokenexchange behaviour that contradicts individually trained behaviour, with chimpanzees studied by van Leeuwen and Call (2017) switching on around 40% of trials to exchange a token-type they had observed another chimpanzee exchanging rather than the token-type they

themselves had been trained to use. Chimpanzees were more likely to do this when the observed token-type had elicited a higher reward than their trained token-type, demonstrating some capacity to follow a "copy-if-better" strategy. However, for the majority of trials, chimpanzees in this study remained conservative to their trained token-type, indicating that even in apparently simple token exchange paradigms, conservatism can still be the dominant response.

As well as task type, age can also have an apparent effect upon behavioural flexibility in chimpanzees. For example, Gruber (2016) reports that chimpanzees able to successfully apply a known 'leaf-sponging' technique to a novel task tended to be juveniles or subadults (up to 12 years old), while the majority of adults did not apply this technique, which the author suggests may be due to a period of plasticity prior to the onset of functional fixedness (which then renders the generalisation of such tool behaviours to novel tasks more difficult). This finding implies that juvenile and subadult chimpanzees may be better able to flexibly apply known behaviours to novel tasks. A study of reversal learning (a measure of cognitive flexibility) indicates a U-shaped curve relating age to performance, with apes at the youngest and oldest ends of the age-range tested (five to 48 years) most likely to perseverate with incorrect responses following the reversal (ie. to continue to perform the previously rewarded behaviour despite the lack of reward), again suggesting that juvenile and subadult apes may be better able to respond flexibly to task changes (Manrique & Call, 2015). Regarding the acquisition of novel tool behaviours, it has been found that capuchin monkeys aged 10 years or older at first exposure to a tool site are less likely to acquire tool probing behaviour in comparison to those aged nine years or younger at first exposure (Westergaard et al., 1998). This finding appears to correspond to Matsuzawa's suggestion of a 'critical period' for the acquisition of nut-cracking in wild chimpanzees, which is based upon the observation at Bossou that three individuals (two immigrant females, and a juvenile female with a snare injury) did not crack nuts, which Matsuzawa argues is due to a lack of observation of others cracking nuts, or of practice of stone and nut manipulation, during the proposed critical period (Matsuzawa, 1994; 2007). Furthermore, Biro, Sousa and Matsuzawa (2006) and Biro, Carvalho and Matsuzawa (2010) note that individuals observed at Bossou who had not succeeded in nut cracking by the age of seven (four of 26 individuals) were never observed to acquire the behaviour at an older age. Together with Manrique and Call's (2015) finding of an age effect in cognitive flexibility, these findings relating to nut-cracking at Bossou, and

Gruber's (2016) finding regarding leaf-sponging, suggest that younger chimpanzees might be more capable of acquiring novel tool behaviours in order to respond to task changes than older individuals. However, when considering the potential for a 'critical period' in acquisition of tool-use behaviours, it is also important to consider the role of social context in this acquisition. Biro, Sousa and Matsuzawa (2006) note that juveniles are not tolerated to the same extent as infants when scrounging tools or interacting with tool-using adults, and that this reduced opportunity to access social information about tool-use might contribute to the end of the 'critical period'. This would suggest that the proposed critical period is, at the very least, due to multiple factors including social context, and not purely the result of increasing behavioural conservatism with age. The potential effect of age (and of a proposed 'critical period') upon the acquisition of novel behaviours in the context of a novel, artificial, foraging task is therefore uncertain.

4.2 Chapter aims and hypotheses

In the present study, I aimed to expand upon the findings of the previous chapter (Harrison & Whiten, 2018) by providing the same liquid-retrieval task, inspired by that used by Lehner et al. (2011) with orangutans, to two groups of chimpanzees housed in the Chimfunshi Wildlife Orphanage (CWO), a sanctuary in Zambia. Hypotheses are outlined below.

4.2.1 Behavioural flexibility

Chimpanzees were presented with the task in the social environment of their group, and therefore had access to both individual and social information about the task and potential solutions. This means that individuals were not limited to what they themselves could invent in terms of task solutions, which I believe provides an ecologically valid measure of behavioural flexibility, as this has been defined in the past as the continued acquisition of new solutions through either innovation or social learning (Lehner et al. 2011). If chimpanzees are capable of responding flexibly to changes in task conditions (as shown by Manrique et al. 2013), I predicted individuals in this study would increase their use of techniques that remained effective, and to decrease their use of techniques that had been rendered ineffective, in the face of task restrictions. Alternatively, if chimpanzees are behaviourally inflexible, I predicted the continued use of ineffective techniques and no
increase in the use of effective techniques by the chimpanzees in this study. As chimpanzees provided with the same task under similar conditions at Edinburgh Zoo responded with limited flexibility (increasing their use of effective techniques, but persisting in the use of ineffective techniques, Harrison & Whiten, 2018), it was predicted that chimpanzees at CWO might thus respond similarly. However, there are key differences between the two populations that had the potential to lead to different results with the CWO population.

Firstly, conducting the study at CWO offered the opportunity to include infants, juveniles and subadults in the sample, an addition I anticipated would increase the probability of greater levels of flexibility and innovation. As discussed previously, age has been reported as a factor affecting the acquisition of tool-based foraging behaviour (Matsuzawa, 1994; 2007; Biro et al., 2006; Biro et al., 2010), and affecting cognitive flexibility in chimpanzees (Manrique & Call, 2015). Only adults could be tested at Edinburgh Zoo (Harrison & Whiten, 2018), and so this difference between the two populations was expected to produce different results.

Other factors, in addition to age, could also lead to different results with the CWO population than were found with the Edinburgh Zoo population. While no effect of rearing history (operationalised for the purposes of analysis as captive care facility of origin) was found in the Edinburgh Zoo population (Harrison & Whiten, 2018), a greater proportion of chimpanzees at CWO are wild-born than at Edinburgh Zoo, and these individuals have a history of human-rearing, while captive-born chimpanzees at CWO are, with very few exceptions, mother-reared in their captive social group. This is a different distribution of rearing histories than at Edinburgh Zoo (where only three of 18 individuals were wild-born, and a third of captive-born individuals were human-reared), and this difference could have resulted in a different response to the task between sites. However, in these groups at CWO, rearing history is almost perfectly correlated with age (all but one adult chimpanzee are wildborn and human-reared, and all non-adult chimpanzees are captive-born, with only one nonadult chimpanzee in the sample being captive-born and hand-reared by humans). While the differences in rearing history between Edinburgh Zoo and CWO could have led to different results between the two sites (and so a different outcome in the current study than that of Harrison and Whiten, 2018), given the existing evidence of age-related differences in tool-use acquisition and cognitive flexibility in chimpanzees, and lack of evidence of rearing effects in Harrison and Whiten (2018), analysis in the current study focused on age differences rather

than rearing history, while acknowledging that in this population, teasing apart the potential effects of these two variables within the current sample of chimpanzees is not possible.

There is no systematic behavioural enrichment programme at CWO, and so the chimpanzees tested in this study may well have had different historic tool use experiences than those at Edinburgh Zoo, where both tool-based enrichment and tool-based experimental studies (eg. V West, 2013, unpublished master's thesis; R Harrison, 2013, unpublished master's thesis) are common. Chimpanzees at Edinburgh Zoo did not make use of absorbent materials provided for use with the dipping task, potentially due to functional fixedness regarding the established function of these materials as nesting material (Harrison & Whiten, 2018). Chimpanzees at CWO may not have had the same experience regarding the function of provided tool materials, and so it was possible that they would show greater exploration of techniques involving a wider variety of tool materials. It was also possible that they would have different biases regarding tool materials than observed at Edinburgh Zoo, in a similar vein to those examined by Gruber et al. (2011) in wild communities of chimpanzees.

4.2.2 Scaffolding towards an effective solution

The previous chapter (Harrison & Whiten, 2018) added to a limited experimental literature on the acquisition of tool-use behaviours through exposure to 'scaffolding'. No experimental study has yet demonstrated that scaffolding leads to acquisition of novel behaviours (Gruber et al., 2011; Cardoso & Ottoni, 2016), and so I did not predict that scaffolding would prove effective in this case. However, providing scaffolding to one group of chimpanzees at CWO as part of the current study further increased the number of experimental investigations into this issue. Furthermore, chimpanzees at CWO were provided with scaffolding which aimed to encourage a behaviour that had previously been observed in their group, performed infrequently by a very limited number of individuals. The potential presence of social information was expected to increase the possibility of scaffolding proving effective, as it could be bolstered by social observation of an individual performing the behaviour, and therefore function in a manner more similar to the artefacts of tool use chimpanzees encounter in the wild, where such artefacts are only part of the social information an individual has access to when acquiring a new behaviour (Fragaszy et al., 2013).

4.3 Methods

4.3.1 Subjects and study site

Subjects were 22 chimpanzees housed in two separate groups (Groups 3 and 4, see **Chapter 2, Table 2** for details) at the Chimfunshi Wildlife Orphanage (CWO) in northern Zambia. Chimpanzees in Groups 3 and 4 are able to hear the other group, and there is a stretch of fence line (approx. 3m) where it is possible for chimpanzees from the two groups to see one another.

4.3.2 Apparatus

Echoing the earlier study of Lehner et al. (2011) and the previous chapter (Harrison & Whiten, 2018) two polycarbonate tubes provided the two stages of the task (see Chapter 2, Figure 5). These tubes were bolted to a mesh door attached to the chimpanzees' indoor facility (Figure 2b), facing out into their enclosure (Figure 2c), and could be filled with diluted juice reward and emptied by the experimenter through the mesh. The task was presented in part of the enclosure where it was not possible for chimpanzees from either group to observe individuals from the other group. Alongside the tubes, chimpanzees were provided with a selection of tool materials (Figure 2d) comprising plain sticks, straw, leafy sticks (most frequently bamboo which grows throughout the sanctuary), strips of cloth, and strips of paper. These tool materials were dropped into the enclosure beside the apparatus at the start of each session. Sufficient amounts of each material were provided at the beginning of each session for all group members to use them if they chose; however, it was not possible to prevent chimpanzees from removing materials from the immediate testing area, though these remained within the chimpanzees' enclosure. As fresh materials were provided at the start of each session, materials could also accumulate in the testing area across sessions. Chimpanzees could also use any materials found within their enclosure to attempt the task, and could also use food provided as part of their diet to attempt the task. The use of sugar cane as an absorbent material (specifically, the internal fibrous part of the cane, which could be chewed and was absorbent) occurred in both groups. This sugar cane was provided to chimpanzees as part of their regular diet.



Figure 2: *a*) The 'wide' tube attached to the mesh door in Group 4's enclosure and filled to around 7cm with diluted juice, *b*) The wider context in which the tube was attached, with the tube circled in yellow, attached to a mesh door forming part of the chimpanzees' indoor facility, *c*) The experimenter's view of the task when fitted, facing out into the chimpanzees' enclosure, *d*) The selection of tool materials provided to the chimpanzees (from left; plain sticks, straw, leafy sticks, strips of cloth, strips of paper).

4.3.3 Procedure

In the first stage of the study ('Wide Tube' phase), chimpanzees were provided with the wide tube, filled with diluted juice to a depth of around 7cm. This was presented alongside the aforementioned selection of tool materials. The apparatus remained fitted within the chimpanzees' enclosure 24hrs a day during the testing period, but was filled with juice reward for only 10hrs of testing in total. Testing sessions lasted between one and three hours, and up to two sessions were held per day: in the morning prior to the chimpanzees' indoor

feeding at 11:30 and in the afternoon post-feeding after 13:30, when the chimpanzees were released back into their outdoor enclosure. Chimpanzees had access to the task within their enclosure as a group. The tube was refilled with reward by the experimenter during testing when the chimpanzees had emptied it, and was emptied of reward by the experimenter at the end of each testing session.

In the second stage ('Narrow Tube' phase), only the narrow tube was presented, alongside the same selection of tool materials. The tube was filled with reward for approximately 20hrs of testing, again in sessions lasting between one and three hours. The narrow tube prevented chimpanzees from inserting their hands into the tube in order to solve the task.

The third stage of testing differed for Groups 3 and 4, in response to the chimpanzees' behaviour in the previous two stages. Group 4 had responded to the 'Narrow Tube' phase with the use of innovative, tool-composite techniques, and so, as in Lehner et al. (2011), we removed tool materials which were being used successfully in order to provoke further flexibility and technique modification. Group 4 was therefore provided with the narrow tube for a further 10hrs, but was no longer provided with cloth or sugar cane (part of the chimpanzees' diet provided occasionally by their keepers), two absorbent materials used successfully by the group as components of tool-composite techniques in the previous phase (this intervention formed the 'Narrow Restricted' phase).

Group 3 had limited success in the 'Narrow tube' phase, and did not show extensive use of tool-composite techniques, so we provided scaffolding towards such a technique that had emerged in Group 4 in a manner similar to the previous chapter (Harrison & Whiten, 2018). Group 3 was therefore provided with the narrow tube with a plain stick with a piece of cloth tied to the end inserted into the tube prior to the start of each session (this intervention formed the 'Narrow Scaffolded' phase).

4.3.4 Data collection and coding

Chimpanzees' responses to the task were video recorded (see **Chapter 2**) while the experimenter narrated chimpanzees' actions as well as the identity and presence of other individuals in the task area. The video and narration were later coded together. The identity,

tool material choice, action and success of individuals attempting the task were coded for each attempt. The presence of other individuals at the task or in the task area, and their distance from the task, was also coded for each attempt.

Techniques were then classified as 'Effective' or 'Ineffective' based upon their efficacy in the 'Narrow Tube' phases. Techniques which involved inserting a hand into the tube were classified as 'Ineffective', as the width of the tube in the 'Narrow Tube' phases prevented their use.

4.3.5 Data analysis

Data were analysed using a generalised linear mixed model with a Laplace approximation (GLMM). The effect of predictor variables upon the number of 'Effective' vs 'Ineffective' technique attempts in the 'Wide Tube' and 'Narrow Tube' phases was assessed. The full model contained fixed effects for all variables of interest: the effect of Phase ('Wide Tube' vs. 'Narrow Tube') and Group (Group 3 vs Group 4), along with a random intercept and slope by Phase for each Individual nested within Group (N=21), and was compared with a null model (containing only the random intercept and slope by Phase for each Individual nested within Group a binomial error structure due to the binary nature of the response variable (Effectiveness) and a logit link function.

4.4 Results

All chimpanzees in both groups (except for the infant Brent in Group 3) interacted with the task during testing. In Group 3, nine chimpanzees (all group members with the exception of the infant Brent) attempted the task in both the 'Wide Tube' and 'Narrow Tube' phases, with eight chimpanzees then attempting the task in the 'Narrow Scaffolded' phases (Barbie did not attempt the task in this phase). A total of 3,317 attempts were made across the three phases and 40 hours of testing. Chimpanzees in Group 3 successfully used 15 techniques to solve the task (Table 2). Ten of these techniques emerged in the 'Wide Tube' phase, with the remaining five occurring in the 'Narrow Tube' and 'Narrow Scaffolded' phases. Two tool-composite techniques (Shumaker, Walkup & Beck, 2011) emerged in the 'Narrow Tube' phase, involving the use of sticks to retrieve materials from within the tube. Five of the 15

techniques successfully used by Group 3 were classified as 'Effective' for the 'Narrow Tube' phases (Table 2).

In Group 4, all 12 chimpanzees participated in the 'Wide Tube' and 'Narrow Tube' phases, making at least one attempt to extract juice from the tube in each phase. Three of the 12 individuals (Commander, Kambo, and Jewel) did not participate in the 'Narrow Restricted' phase. A total of 6,379 attempts were made across the three phases and 40 hours of testing. Chimpanzees successfully used a total of 24 techniques to retrieve juice from the tube (Table 3). Twelve of these techniques were observed in the 'Wide Tube' phase, with the remaining 12 emerging in the 'Narrow Tube' and 'Narrow Restricted' phases. Nine tool-composite techniques (Shumaker, Walkup & Beck, 2011) emerged in the 'Narrow Tube' and 'Narrow Restricted' phases, involving the use of sticks to retrieve materials from the tube, or to both push materials into the tube and then retrieve them. Of the 24 techniques successfully used by Group 4, 12 were classified as 'Effective' for the 'Narrow Tube' phases (Table 3). Two 'Ineffective' techniques were used successfully by these chimpanzees in the 'Narrow Tube' phase (see Table 3, sugar cane dip and sugar cane retrieve). These techniques relied upon insertion of a hand directly into the tube, and so are categorised as 'Ineffective'; while they were used successfully in this phase, and so are included in Table 3, they could only be used with very limited success due to the task restrictions, and are therefore classed as 'Ineffective'.

Table 2.

Techniques used successfully by Group 3 to solve the task.

Technique	Description	Time to first occurrence from start of testing (hh:mm:ss)	Efficacy in Narrow Tube phases
Wide Tibe phase			
Cloth dip	Dip cloth into juice with hand	00:01:28	Ineffective
Cloth drop	Drop cloth from hand into tube and retrieve	00:01:38	Ineffective
Hand dip	Dip hand directly into juice	00:02:10	Ineffective
Cloth mouth drop	Drop cloth from mouth into tube then retrieve by hand	00:03:26	Ineffective
Cloth retrieve	Cloth that has accrued in tube removed with hand	00:29:32	Ineffective
Fruit stone mouth drop	Drop fruit stone from mouth into juice then retrieve by hand	03:21:25	Ineffective
Sugar cane drop	Drop sugar cane from hand into tube and retrieve	05:54:53	Ineffective
Sugar cane dip	Dip sugar cane into juice with hand	05:55:06	Ineffective
Sugar cane retrieve	Sugar cane that has accrued in tube removed with hand	05:56:02	Ineffective
Sugar cane mouth drop	Drop sugar cane from mouth into tube then retrieve by hand	08:46:26	Ineffective
Narrow Tube phase			
Stick dip	Dip stick into juice with hand	13:19:21	Effective
+ Stick retrieval paper	Stick used to retrieve paper that has accrued in tube	13:20:53	Effective
Stick retrieve	Stick already in tube removed with hand	13:21:13	Effective
+ Stick retrieval cloth	Stick used to retrieve cloth that has accrued in tube	13:27:39	Effective
Narrow Scaffolded ph	ase		
Stick drop	Drop stick into tube then retrieve by hand	32:09:22	Effective

Note. Horizontal lines and shading indicate transitions between the three phases.

† Tool Composite technique

Technique	Description	Time to first occurrence from start of testing (hh:mm:ss)	Efficacy in Narrow Tube phases
Wide Tube phase			
Paper dip	Dip paper into juice with hand	00:00:31	Ineffective
Paper drop	Drop paper from hand into tube and retrieve	00:03:12	Ineffective
Paper retrieve	Paper that has accrued in tube removed with hand	00:04:16	Ineffective
Cloth dip	Dip cloth into juice with hand	00:11:04	Ineffective
Cloth retrieve	Cloth that has accrued in tube removed with hand	00:12:59	Ineffective
Cloth drop	Drop cloth from hand into tube and retrieve	00:13:09	Ineffective
Hand dip	Hand dipped directly into juice	00:14:40	Ineffective
Cloth mouth drop	Cloth dropped from mouth into tube then retrieved with hand	00:44:08	Ineffective
Paper mouth drop	Paper dropped from mouth into tube then retrieved with hand	01:34:03	Ineffective
Stick drop	Drop stick from hand into tube and retrieve	05:23:54	Effective
Stick dip	Dip stick into juice with hand	05:24:05	Effective
Fruit shell drop	Drop fruit shell from hand into tube and retrieve	08:10:03	Ineffective
Narrow Tube phas	e		
Stick retrieve	Stick already in tube removed with hand	10:16:56	Effective
+ Stick retrieval paper	Stick used to retrieve paper that has accrued in tube	10:26:23	Effective
+ Stick retrieval stick	Stick used to retrieve stick already in tube	10:28:57	Effective
+ Stick push cloth and retrieve	Stick used to push cloth down into juice and then retrieve by pushing cloth against wall of tube and pulling upwards	14:17:49	Effective
+ Stick retrieval cloth	Stick used to retrieve cloth that has accrued in tube	15:03:10	Effective
Sugar cane dip	Sugar cane is dipped directly into juice with hand	19:09:29	Ineffective
Sugar cane retrieve	Sugar cane that has accrued in tube removed with hand	19:25:26	Ineffective
+ Stick retrieval sugar cane	Stick used to retrieve sugar cane that has accrued in tube	19:27:52	Effective

Table 3.Techniques used successfully by Group 4 to solve the task.

+ Stick push sugar cane and retrieve	Stick used to push sugar cane down into juice and then retrieve by pushing sugar cane against wall of tube and pulling upwards	19:35:51	Effective
+ Cloth drop stick retrieve	Cloth dropped from hand into tube then retrieved with stick	22:48:25	Effective
Narrow Restricted	Tube phase		
† Stick push straw and retrieve	Stick used to push straw down into juice and then retrieve by pushing straw against wall of tube and pulling upwards	30:13:18	Effective
+ Stick retrieve plastic wrapper	Stick used to retrieve plastic wrapper already in tube	30:56:56	Effective

Note. Horizontal lines and shading indicate transitions between the three phases.

† Tool Composite technique

4.4.1 Behavioural flexibility

In order to examine the behavioural flexibility demonstrated in the chimpanzees' response to the task restrictions imposed by the transition from the 'Wide Tube' to 'Narrow Tube' phases, it was useful to categorise the techniques described above as 'Effective' and 'Ineffective' according to their potential effectiveness in the 'Narrow Tube' phase. Techniques involving the insertion of a hand into the tube were classified as 'Ineffective', as insertion of the hand into the tube was made impossible by the width of the tube in the 'Narrow Tube' phase, whilst techniques that did not involve insertion of a hand into the tube were classified as 'Effective', as they had the potential to be used successfully in the 'Narrow Tube' phase (see Tables 2 and 3). This designation does not assume such techniques necessarily to be efficient or to have particularly high success rates, as techniques classified as 'Effective' could be challenging to perform in terms of manual skill (eg. stick push and retrieve techniques) and thus have a relatively low success rate (though success would still be higher than the 'Ineffective' techniques that were generally rendered impossible by task constraints) or such techniques could be time consuming to perform and therefore be relatively inefficient. Similarly, 'Ineffective' techniques could on rare occasion be used successfully in the 'Narrow Tube' phases (for example, if a large amount of material built up in the tube during a session, it could be possible to successfully use techniques such as *sugar* cane retrieve). However, use of these 'Ineffective' techniques, which relied upon inserting a

hand into the tube, indicated continuing use of an approach that was not well-suited to the task constraints.

Comparison of the use of 'Ineffective' and 'Effective' techniques in the 'Wide Tube' and 'Narrow Tube' phases answers the key question regarding the extent to which chimpanzees altered their behaviour in response to the change in task, and the extent to which they were able to set aside techniques that had been rendered ineffective by the change in tube width. Grouping behaviours in this manner allows analysis of behavioural flexibility, as it indicates whether individuals stopped using 'Ineffective' techniques (those involving inserting a hand into the tube) when task constraints made such techniques uproductive. In comparison with an analysis based upon rate of use of specific techniques (eg. an analysis of rates of use of the *stick dip* technique) this approach avoids potential confounds such as individual differences in skill or preference, and also allows for potential changes in the availability of tool materials over the course of a session (as 'Effective' techniques were always achievable for individuals even if specific tool materials were depleted).

Only one individual (Bobby, Group 4) used primarily 'Effective' techniques in the 'Wide Tube' phase (5 of 6 attempts), with all other individuals in both groups using 'Effective' techniques for fewer than 4% of their attempts in the 'Wide Tube' phase (see Figure 4). Therefore, the imposition of the narrow tube and the resulting necessity of the use of 'Effective' techniques represented a genuine restriction upon the behaviour of almost all individuals. Fourteen individuals (eight in Group 3, six in Group 4) had never used an 'Effective' technique at the introduction of the narrow tube. Individuals in Group 4 used 'Effective' techniques for a mean of just 7.5% (SD = 23.9) of their attempts in the 'Wide Tube' phase, but this increased to a mean of 72.9% (SD=27.7) of their attempts made in the 'Narrow Tube' phase (note that these group means are based upon the percentage of 'Effective' attempts each individual made in a given phase). Group 3 used 'Effective' techniques for a mean of 0.4% (SD=1.2) of their attempts in the 'Wide Tube' phase (see Figure 4).



Figure 4: Percentage of attempts made using 'effective' (for narrow tube) techniques in the 'Wide' vs 'Narrow' tube phases by individual chimpanzees in Groups 3 and 4. Points show the percentage of attempts made using Effective techniques by individuals. Solid horizontal bars show the group means.

Table 4.

	Estimate	[Wald 95% CI]	Std. Error	z value	P value
(Intercept)	-9.28	[-11.75, -6.80]	1.26		
Phase	8.08	[5.92, 10.24]	1.11	7.31	2.59 ^{e-13} ***
Group	2.60	[0.76, 4.44]	0.94	2.78	0.006 **
	0.01				

Results of full model GLMM on the effects of Phase and Group upon 'Effective' technique use.

*** = p<0.001, **=p<0.01.

The full model (see Table 4) indicates that use of 'Effective' tool techniques increased significantly in both groups in the 'Narrow Tube' phase (b = 8.08, p < .001), but that individuals in Group 4 were significantly more likely to use 'Effective' tool techniques than individuals in Group 3 (b = 2.60, p = .006). See Figure 4 for predicted values based upon the full model. A likelihood ratio test comparing the full and null models indicated that the full model was a significantly better fit ($\chi^2 = 41.44, df = 2, p < .0001$; dAIC = 37.5).

An additional analysis was conducted to explore the potential effect of Sex upon behavioural flexibility. This model had the same specifications as the main analysis described above, with the additional predictor variable of Sex (Male vs. Female). This model indicated no main effect of Sex upon use of Effective techniques (see Table 5). A further analysis considered the effect of Age (operationalised as a binary categorical variable, Adult vs. Subadult, with all individuals younger than Adult grouped into the Subadult category, in order to give a practicable group size for analysis). Included in the model alongside Group and Phase, Age had no significant effect upon use of Effective techniques (see Table 6).

Models incorporating either Sex or Age in interaction with Phase, along with a main effect of Group, failed to converge, and so to check for a potential interaction between these variables and Phase, reduced models were fitted including Sex or Age in interaction with Phase as predictors of Effective technique use. The results of these models are provided in full in Appendix A (Tables A1 and A2), but did not find a significant effect of either Sex or Age in interaction with Phase.

Table 5.

Results of full model GLMM on the effects of Phase, Group, and **Sex** *upon 'Effective' technique use.*

	Estimate	[Wald 95% CI]	Std. Error	z value	P value
(Intercept)	-9.08	[-11.59, -6.57]	1.28	-7.10	
Phase	8.06	[5.96, 10.16]	1.07	7.53	5.00 ^{e-14} ***
Group	2.82	[0.80, 4.84]	1.03	2.74	0.006 **
Sex	-0.55	[-2.41, 1.32]	0.95	-0.57	0.57

*** = p<0.001, **=p<0.01.

Table 6.

Results of full model GLMM on the effects of Phase, Group, and Age upon 'Effective' technique use.

	Estimate	[Wald 95% CI]	Std. Error	z value	P value
(Intercept)	-9.39	[-12.08, -6.70]	1.37	-6.84	
Phase	8.09	[5.79, 10.39]	1.17	6.90	5.25 ^{e-12} ***
Group	2.58	[0.73, 4.42]	0.94	2.74	0.006 **
Age	-0.32	[-1.44, 2.09]	0.90	0.36	0.72

*** = p<0.001, **=p<0.01.



Figure 4: Predicted percentages of 'Effective' (for narrow tube) technique use in the 'Wide' and 'Narrow' tube phases, based upon the full model for Groups 3 and 4. Predicted values for each group in each phase are shown by bold crosses, while the observed means are shown by solid horizontal bars. Points show the observed percentage of attempts made using Effective techniques by individual chimpanzees.

4.4.2 "Narrow Restricted" condition – Group 4

Five individuals in Group 4 had used tool-composite techniques involving the combined use of a stick and absorbent material (paper, cloth or sugar cane) during the 'Narrow Tube' phase. By removing these absorbent materials in the 'Narrow Restricted' phase, I aimed to investigate whether these individuals would modify their techniques by substituting alternative absorbent materials (such as straw or leaves, which were still provided).

Straw (a provided tool material), fruit shells (part of the chimpanzees' provided diet) and a plastic wrapper (found material from within the enclosure) were all used in this condition as the absorbent component of the chimpanzees' tool-composite techniques (see Table 7). Straw

and fruit shells had been used previously, by Nicky in the 'Wide Tube' phase (three attempted *fruit shell drop and retrieve* of unknown success), and Kathy in the 'Narrow Tube' phase (one attempted *straw dip* of unknown success); however, in comparison to other tool materials, use of fruit shells and straw was very limited (comprising only 0.12% of Kathy's attempts in the 'Narrow Tube' phase and 0.80% of Nicky's attempts in the 'Wide Tube' phase).

The first individual to use an alternative absorbent material as part of a tool-composite technique in the 'Narrow Restricted' phase was Jack, making an attempted straw 'push and retrieve' in the first session of the 'Narrow Restricted' phase. This was Jack's first use of straw, though he had had the opportunity to observe Kathy's unsuccessful straw dip in the previous testing session as he was within 5 metres of the task during her attempt. Jack also made two attempts at both 'retrieve' and 'push and retrieve' techniques using a plastic wrapper in place of the absorbent material component. This was his first use of a plastic wrapper, and other individuals had never used plastic wrappers during testing. Jack arrived at the task with the plastic wrapper, which he had found in the enclosure – this type of material is not something the chimpanzees would generally come into contact with, and it had presumably entered their enclosure by accident (therefore it is unsurprising that this material had not been used at the task before, as the chimpanzees would have had no access to this type of material). While not an absorbent material, the surface area of the plastic wrapper did appear to pick up juice. Miracle then attempted a 'push and retrieve' using straw, after making two attempts to dip straw into the juice by hand. She had never observed another chimpanzee using straw. Finally, Kathy twice attempted to 'retrieve' a fruit shell, having dropped it into the tube by hand immediately previously. She had never observed another chimpanzee using fruit shells at the task.

In all of these cases, individuals made use of tool materials that were novel to them in the context of the dipping task in order to modify tool-composite techniques when known materials were removed. However, it must be noted that such attempts were rare in the 'Narrow Restricted' phase, comprising just 0.89% of all attempts, while '*stick dip*' made up the majority (96.99%) of attempts made at the task in this phase. Thus, while chimpanzees appeared capable of modifying their known Tool Composite techniques, they did not then use these new solutions frequently, and indeed, these modified solutions most often proved

unsuccessful (see Table 7). As known techniques (most notably, *stick dip*) remained possible during the 'Narrow Restricted' phase, there was not the same necessity to behave flexibly as there was in the transition from 'Wide' to 'Narrow Tube' phases. Individuals could continue to solve the task using an 'Effective' technique that had also worked in the previous phase, and this is primarily what they did.

Table 7.

Tool Composite attempts in the 'Narrow Restricted' phase made using novel tool materials.

Individual	Attempted technique (number	Latency (from	Success
	of attempts)	beginning of	
		'Narrow Restricted'	
		phase)	
		hh:mm:ss	
Jack	Straw push and retrieve (x1)	00:03:45	Yes
Jack	Plastic wrapper push and	00:37:22	No
	retrieve (x2)		
Jack	Plastic wrapper retrieve (x3)	00:43:07	Yes (once)
Miracle	Straw push and retrieve (x1)	04:43:22	No
Kathy	Fruit shell retrieve (x2)	04:59:49	No

4.4.3 "Narrow Scaffolded" condition – Group 3

Chimpanzees in Group 3 were exposed to the task with a stick and attached piece of cloth already inserted, in an attempt to explore the potential use of tool-composite techniques when scaffolded in this way, given the minimal prior innovations in this group. Some limited use of tool-composite techniques had been observed in Group 3 prior to this, with Roxy and ET both having successfully used sticks to retrieve cloth from the tube in the 'Narrow Tube' phase (Roxy on one occasion, ET on two occasions) and ET having used a stick to retrieve paper successfully on one occasion. The scaffolded solution was presented at the beginning of 'Narrow Scaffolded' sessions a total of six times. Three individuals (Brian, Bruce and ET) interacted with the example solution, and these interactions are described in Table 8.

Only ET attempted a tool-composite technique following exposure to the scaffolded solution, making four unsuccessful attempts to retrieve cloth that had accrued in the tube earlier in the day 28 mins and 23 secs following exposure to the example solution, though ET had in previous sessions successfully retrieved cloth from the tube using a stick. Thus it would appear that the provision of a scaffolded solution in this manner did not elicit the use of tool-composite techniques by individuals that had not already performed them.

Table 8.

Individual	Individual's exposure to scaffolding	Interaction with scaffolding
Brian	First exposure	Pulls at end of cloth, which is protruding from top of tube. Does not interact with stick.
	Second exposure	Removes stick from tube (without cloth) and gets juice from it (<i>stick retrieve</i> technique).
	Third exposure	Removes stick from tube (without cloth). Unclear if he gets juice from it (<i>stick retrieve</i> technique).
	Fourth exposure	Pulls on stick to retrieve stick and cloth from tube, gets juice from both and then discards.
Bruce	First exposure	Pulls at end of cloth, which is protruding from top of tube. Then pulls at stick but does not remove from tube. Finally pulls cloth off stick and discards it (without getting any juice).
ET	First exposure	Manipulates stick inside tube but does not retrieve stick or cloth. Eventually removes stick from tube (without cloth) and gets juice from it (<i>stick retrieve</i> technique).
	Second exposure	Pulls on end of cloth to retrieve stick and cloth from tube, gets juice from both, then spends time detaching cloth from stick.

Chimpanzees' interactions with the scaffolded solution of a stick and piece of cloth pre-inserted into the tube.

4.5 Discussion

Chimpanzees in both groups responded flexibly to the changing artificial foraging task. Group differences were apparent in the responses, with Group 4 more likely than Group 3 to use 'Effective' techniques when the task required them. Tool-composite techniques were observed in both groups, but primarily in Group 4. Restricting the available tool materials in the 'Narrow Restricted' phase presented to Group 4 resulted in some modification of these tool-composite techniques, but performance of these modified tool-composite techniques was limited. Providing Group 3 with scaffolding towards tool-composite techniques in the 'Narrow Scaffolded' phase proved ineffective.

4.5.1 Behavioural flexibility

Both groups of chimpanzees responded with some degree of flexibility to the change in task parameters, and the change in parameters represented a genuine restriction to both groups, as individuals in both groups (with only one exception, Bobby in Group 4) had little experience of 'Effective' techniques in the 'Wide Tube' phase. Use of 'Effective' techniques increased significantly in the 'Narrow Tube' phase. The majority of chimpanzees in Group 3 continued to primarily use 'Ineffective' techniques in the 'Narrow Tube' phase, indicating a failure to relinquish these solutions, and therefore somewhat more limited behavioural flexibility than chimpanzees in Group 4. Most chimpanzees in Group 4 primarily used 'Effective' techniques in the 'Narrow Tube' phase, indicating more pronounced behavioural flexibility in that they not only used novel solutions in response to the change in task, but were also able to relinquish 'Ineffective' techniques to a greater extent than individuals in Group 3.

The limited flexibility shown by Group 3 appears to concur with the results of some previous studies of chimpanzee behavioural flexibility in response to artificial foraging tasks (Marshall-Pescini & Whiten, 2008; Hrubesch et al., 2009; Harrison & Whiten, 2018), in which chimpanzees continued to use ineffective or inefficient techniques in response to task changes. In Hrubesch et al. (2009), chimpanzees continued to attempt a task solution that had been rendered completely ineffective by task manipulations, whilst in Marshall-Pescini & Whiten (2008) chimpanzees failed to socially acquire a more effective solution to a task. The results of the current study are perhaps closer in character to those of Hrubesch et al (2008),

as techniques the chimpanzees had mastered in the 'Wide Tube' phase were rendered ineffective in the 'Narrow Tube' phase. The results from this group therefore appear to add to a literature in which chimpanzees show only limited evidence of the capacity to respond flexibly, at least in the medium term, to task changes in artificial foraging tasks.

In the 'Wide Tube' phase, chimpanzees in Group 3 did not use a solution to the task that would remain effective in the 'Narrow Tube' phase. The resulting necessity for innovation in the 'Narrow Tube' phase may have contributed to their apparently limited flexibility, and indeed, they did not successfully use an 'Effective' technique until three hours of the 'Narrow Tube' phase had passed. The necessity to invent novel solutions to a problem may be an additional challenge in artificial foraging tasks aiming to assess behavioural flexibility, and one that may not be shared by measures such as reversal learning, or indeed studies in which novel techniques can be socially learned (eg. Marshall-Pescini & Whiten, 2008; Davis et al., 2016). However, the chimpanzees in Group 3 invented 15 task solutions, all of which were successfully used in either the 'Wide' or 'Narrow Tube' phases – while not all of these techniques were 'Effective' in the 'Narrow Tube' phase, this would appear to demonstrate a level of task exploration and potentially innovative tool use within both the 'Wide' and 'Narrow Tube' phases. Considering that the 'Wide Tube' phase could be solved simply by dipping a hand directly into the juice, the use of cloth, fruit stones and sugar cane as tool materials in the 'Wide Tube' phase, when such tool use was possible, represents spontaneous exploration, not driven by necessity.

The response of Group 4, in contrast with Group 3, bears closer resemblance to studies such as Davis et al. (2016), Manrique et al. (2013), and Lehner et al. (2011), in which some great apes successfully relinquished previously successful techniques in favour of novel solutions to artificial foraging tasks. In contrast to Davis et al. (2016), effective solutions had to be invented by group members and were not experimentally seeded, and so although the presentation of the task in a group context may have provided the opportunity to socially learn solutions, like the orangutans studied by Lehner et al. (2011) and the great apes studied by Manrique et al. (2013), chimpanzees in the current study were challenged with inventing novel task solutions. Unlike the tasks used by Davis et al. (2016) and Manrique et al. (2013), the current task required the use of tools, which is believed to present a greater challenge in terms of causal cognition (Seed, Call, Emery & Clayton, 2009; Völter & Call, 2014). Despite

this, like the orangutans given a very similar task by Lehner et al. (2011), chimpanzees in Group 4 not only responded flexibly to the change in task parameters, but also invented novel tool-composite techniques in order to solve the task during the Narrow Tube phases. Such techniques (described by Lehner et al. as "Drop-and-Fish" and "Squash-and-Fish", 2011, pp.450) are argued by Lehner and colleagues to constitute 'cumulative technology', due to the fact that these techniques were only observed in individuals which had previously performed the component techniques (ie. individuals which had already used paper as an absorbent material and had used a stick to retrieve debris from within the tube – these two techniques form the basis of the more complex 'Drop-and-Fish' and 'Squash-and-Fish' techniques). The authors therefore argue that these behaviours fulfil the criteria to be considered 'ratcheted' techniques, as they build upon previous solutions, resulting in more complex techniques which are more widely applicable (as they can be used successfully in both the 'Wide' and 'Narrow Tube' task type). However, because these techniques were elicited by restricting the other solutions available to the orangutans, the extent to which they represent evidence of a capacity for cumulative technology under stable conditions is questionable. The orangutans did not have to overcome satisfaction with their current technique or forgo small rewards in order to invent techniques that would gain even greater rewards, which seems necessary for cumulative culture to emerge in a stable context. In the current study, the potential difference between forced and spontaneous behavioural flexibility can be seen in Group 4's response to the 'Narrow Tube' and 'Narrow Restricted' phases. When individuals had to invent novel techniques and behave flexibly in order to solve the task at all (ie. in the transition from the 'Wide' to the 'Narrow Tube' phase), they were capable of doing so. However, when the 'Effective' technique stick dip remained possible in the transition from the 'Narrow' to 'Narrow Restricted' phase, chimpanzees continued to use this technique rather than engaging in exploration of alternative tool-composite techniques for the vast majority of their attempts. This may indicate that chimpanzees are not able to overcome satisfaction with known behaviours to a sufficient extent to be able to modify and improve upon them, though Dean et al. (2012) found that chimpanzees in their study did not engage in satisficing and continued to explore further task components after finding one lowreward solution. The likelihood of chimpanzees satisficing might be contingent upon the relative difference in reward values and the cost of further exploration. Further exploration of the task in Dean et al. (2012) might have been less costly than in the current study as it did not involve tool use, which is more cognitively taxing than tasks not requiring the use of tools (Seed, Call, Emery & Clayton, 2009). It is also possible that the reward gained by

chimpanzees in the current study when using *stick dip* was more rewarding than the lowvalue reward gained by chimpanzees in the first stage of Dean et al.'s (2012) study and so was more satisfactory.

Whilst the tool-composite techniques observed in the current study could be considered, like the tool-composite behaviours observed by Lehner et al. (2011), to be combinations of previous solutions (the combination of dipping an absorbent material by hand as in *cloth dip* or *paper dip*, using a stick to dip into the juice as in *stick dip*, and retrieving an absorbent material using a stick as in *stick retrieval cloth*), we did not find that performance of the most complex stick push and retrieve techniques was limited to individuals that had first mastered the component behaviours. Jack, the first individual to use such a technique, successfully performed stick push cloth and retrieve without firstly using a stick to simply retrieve material from the tube. This indicates that it was within individuals' capability to invent the technique without first knowing the component behaviours. However, Jack had been within 5 metres of the task during the performance of successful stick retrieval paper, stick retrieval stick, and attempted stick retrieval cloth techniques by Kathy, and an attempt by Nicky to push paper into the tube using a stick (as this technique was never used successfully, it does not appear in Table 3), prior to his own performance of stick push cloth and retrieve. It is possible, therefore, that Jack had gained important information about these simpler toolcomposite techniques through observation, which allowed him to then perform the more complex technique without firstly mastering its component techniques.

Tool-composite techniques were a subject of interest in the current study – these techniques were observed in both groups, though to a greater extent in Group 4 than in Group 3 (both in terms of frequency of use and variety of materials employed). Scaffolding provided to Group 3 was intended to encourage this behaviour, while in Group 4 I removed tool materials in an effort to encourage modification of the behaviour. A tool-composite is the simultaneous use of two tools, usually each in a different mode (with 'mode' here meaning the action being undertaken with the tool, for example, Drop or Probe), to achieve a single outcome (Shumaker, Walkup & Beck, 2011). Perhaps the most well-known form of tool-composite use in wild chimpanzees is the use of a hammer and anvil to crack open nuts (Sakura & Matsuzawa, 1991) – note this only constitutes tool-composite use when both the hammer and anvil are portable and manipulated, as they are in Bossou. The tool-composite example most

relevant to the current study is that documented by Matsuzawa (1991 in Sugiyama, 1997), in which a juvenile female chimpanzee at Bossou was observed using a stick to push a leaf sponge into a tree hollow of water, and then to retrieve the leaf sponge again using the stick. This is a very similar instance of tool use to the tool-composites observed in the current study at CWO, where individuals used stick tools to retrieve absorbent materials from the tube, or to push and then retrieve absorbent materials from the tube. According to Whiten et al. (2001), this "sponge push-pull" behaviour has also been observed at Tai, Mahale M, and Gombe. The use of tool-composites has only been documented (in wild ape populations) in orangutans (using a tree branch to hook and pull closer a destination tree during travel, Fox & bin'Muhammad, 2002) and chimpanzees (nut-cracking with portable anvils, Sakura & Matsuzawa, 1991; sponge push-pull behaviour, Matsuzawa, 1991 in Sugiyama 1997). Use of tool-composites has not been documented in wild New or Old World monkeys, prosimians, or birds (Schumaker et al., 2011). The rarity of tool-composite behaviour in wild non-human animals may be due to its complexity, as it requires an animal to take account of the relationships between multiple objects and the target (Sanz & Morgan, 2010), but it may also be due to a limited range of ecological problems that could be solved using tool-composites.

Neither group in the current study used leaf sponges to solve the task. The chimpanzees had been provided with leafy sticks as part of the selection of tool materials provided alongside the task, and chimpanzees also had access to a variety of plant material growing within their enclosure (see Ron and McGrew, 1988, for detailed list of plant species prevalent in the woodland at CWO). The use of leaves as tools for drinking water has been observed at most long-term wild chimpanzee field sites and has been suggested to be a universal chimpanzee behaviour for this reason (Whiten et al., 1999; Whiten et al., 2001). Wild chimpanzees use leaf techniques such as leaf sponging and leaf folding (Tonooka, 2001) to solve a problem very similar to the task I presented to the chimpanzees at CWO; to access water which has accumulated in tree hollows (Goodall, 1964; Sanz & Morgan, 2007), though they have also been observed using leaf sponges to drink from streams and rivers (eg. at Semliki, Hunt and McGrew, 2002; at Mahale, Matsusaka et al., 2006). Similarly, wild chimpanzees at Tongo have been observed using moss, rather than leaves, to sponge water from tree hollows (Lanjouw, 2002). Given the prevalence of leaf sponging in wild chimpanzees, it is somewhat surprising that I did not observe this technique in either group tested. However, chimpanzees in the current study had access to a range of absorbent tool materials (ie. cloth, paper, and

sugar cane fibre), and often used these materials in a similar manner to how wild chimpanzees use leaf sponges, dipping them into the liquid by hand before sucking the liquid from them. While leaf sponges are processed prior to use, by tearing leaves from a plant, removing portions with the teeth and hands, and finally folding or chewing leaves in the mouth to produce a sponge (Tonooka, 2001; Sousa, Biro & Matsuzawa, 2009), cloth and paper strips provided in the current study could be used without modification. It may be the case that the alternative absorbent materials provided were more attractive as tools as they did not require any modification, or they may have been more salient to the chimpanzees because they were unusual materials provided alongside the task. Sugar cane fibres were used by chimpanzees at CWO in a manner similar to wadge-dipping (Boesch, 1991), in that the fibrous inner part of the sugar cane was first chewed to produce a clump of fibres that could then be dipped into the liquid. These sugar cane wadges were then reused, and were also used by chimpanzees in both groups to soak up water at the water taps in their enclosures. Chimpanzees presumably got the sweet flavour of the sugar cane when they used it in this manner (along with the sweet juice) and so it is understandable that this would be an attractive tool material. Wild chimpanzees have also been observed to use probe tools to retrieve water; using either leaves or twigs to dip into water, and a similar probing behaviour is used to dip honey from nest cavities (Kummer & Goodall, 1985; Sanz & Morgan, 2007). This is a similar technique to the *stick dip* observed in both groups in the current study, and is referred to as 'fluid-dip' by Whiten et al. (1999). The chimpanzees in both groups at CWO responded to all phases of the task with tool-use behaviours that broadly correspond to behaviours observed in wild chimpanzees, with the obvious addition of non-natural tool materials such as cloth.

4.5.2 Group differences

Group differences were apparent in the extent to which chimpanzees were able to respond flexibly to the change in task parameters. Members of Group 4 were better able to alter their behaviour and abandon ineffective techniques than were those in Group 3. As this comparison was made across the 'Wide' and 'Narrow' tube phases only, in which task presentation was the same for both groups, an examination of the possible factors promoting these group differences is necessary. The two groups live in near-identical enclosures, and do not differ systematically in either individual backgrounds (human vs chimpanzee reared, wild vs captive born) or subspecies (all individuals are believed to be *Pan troglodytes schweinfurthii*). The two groups also do not differ greatly in terms of age distribution, with both groups including infants, juveniles, and adults (and my analysis indicates that age differences do not contribute to explaining the levels of behavioural flexibility observed). One documented difference between the groups is in their level of social tolerance (Cronin, van Leeuwen, Vreeman & Haun, 2014). In a study of the social dynamics of both groups, using both experimental and observational measures, Cronin et al. (2014) found that Group 3 consistently appeared less socially tolerant than Group 4, a difference the authors suggest may be at least partially due to the characteristics or dominance 'style' of the dominant male in each group.

Social tolerance could conceivably influence performance on the current task in a variety of ways. One possibility is that socially tolerant individuals possess cognitive characteristics which promote behavioural flexibility. Another possibility is that social tolerance promotes social learning as tolerance allows closer proximity to other individuals foraging, providing opportunities for observational learning (van Schaik, 2003), which in this task could aid individuals in acquiring new task solutions for use in the Narrow Tube phases. Lastly, social tolerance may lead to individuals gaining uninterrupted access to the task more easily by making displacement by others less likely, perhaps facilitating innovation (van Schaik, 2003) by allowing individuals to discover effective solutions in the Narrow Tube phases. To further explore this possibility, it must first be established whether the documented difference in social tolerance between the two groups in fact affected their social behaviour in terms of proximity during testing. This would be necessary for social tolerance levels to affect performance assuming the second two scenarios outlined previously, in which social tolerance impacted this task through its effect on social learning opportunities and opportunities for uninterrupted exploration of the task. Analysing social proximity during testing sessions for the current study would also allow examination of whether the two groups' levels of social tolerance have changed since the Cronin et al. (2014) study, as the dominant male of Group 3 at the time of that study has since died, potentially altering the social dynamic of the group.

4.5.3 Failure of scaffolding

Scaffolding provided to Group 3 in the 'Narrow Scaffolded' phase was intended to approximate the physical artefacts of others' tool use chimpanzees would encounter in the wild, which are believed to promote the acquisition of new behaviours (Tennie, Call & Tomasello, 2009; Fragaszy et al., 2013). None of the chimpanzees that encountered the scaffolded solution acquired a novel tool-composite solution as a result. As discussed in the previous chapter (Harrison & Whiten, 2018), it seems this physical information alone may not be sufficient to seed novel tool use behaviours in chimpanzees. Along with Gruber et al. (2011), Cardoso and Ottoni (2016), and Harrison and Whiten (2018), the current chapter forms a limited experimental literature on whether primates are able to acquire novel behaviours through the debris of others' tool use (in all of these studies, these artefacts are the result of experimental manipulation). None of these studies found that this information was sufficient for a novel behaviour to emerge. While Gruber et al. (2011) argue that this is due to existing behavioural traditions limiting chimpanzees' assessment of tool affordances, the possibility remains that this form of information, perhaps particularly when animals receive only a limited number of presentations, is insufficient to establish novel behaviours. Further research is therefore required, in order to examine whether additional exposure to scaffolding (more presentations over a longer period of time) might give animals time to acquire novel behaviours through interaction with it. Whilst enduring physical artefacts aid in chimpanzees' and bearded capuchin monkey's acquisition of skills in the wild (Fragaszy et al., 2013), and are also part of the development of tool use behaviours such as leaf sponging (Sousa et al., 2009), they encounter these artefacts in a broader social context, which may provide further information (for example, allowing the observation of actions) or greater motivation, facilitating the acquisition of behaviours in a way the scaffolding manipulation in this study could not. Although some individuals in Group 3 had performed tool-composite techniques prior to the scaffolding, so there was the potential for social observation of this behaviour along with interaction with the scaffolding, there were only 12 attempts at this behaviour (and only 4 successful attempts), and so the potential social information available was very limited. Future research could examine the extent to which a combination of physical scaffolding and social observation may facilitate the acquisition of novel behaviours in controlled conditions, and consider the relative exposure to each type of information that might be necessary.

4.6 Conclusions

This study found group differences in chimpanzees' behavioural flexibility in response to a changing artificial foraging task. While chimpanzees in one group were unable to relinquish previously successful techniques when task parameters altered, and demonstrated only limited behavioural flexibility, another group were able to abandon previously successful techniques in favour of more effective solutions. This group also invented novel, complex, tool behaviours to solve the task when task constraints demanded it, and even made limited attempts to modify these complex techniques when materials were restricted. My finding of group differences in apparent behavioural flexibility may explain some of the apparent inconsistency in previous studies of chimpanzees. Further work will attempt to examine what the cause of these apparent group differences may be, with established differences in social tolerance levels between the groups appearing to be a promising candidate for further investigation.

Chapter 5: The relationship between social tolerance and performance on a changing foraging task measuring behavioural flexibility in two groups of captive chimpanzees (*Pan troglodytes*).

<u>Chapter 5: The relationship between social tolerance and performance on a changing</u> <u>foraging task measuring behavioural flexibility in two groups of captive chimpanzees</u> <u>(Pan troglodytes).</u>

<u>Abstract</u>

The previous chapter examined behavioural flexibility in two groups of chimpanzees (Group 3 and Group 4) at the Chimfunshi Wildlife Orphanage, Zambia. Group differences were found in the extent to which these chimpanzees responded flexibly to a changing foraging task. The present study examined the role of social tolerance as a factor contributing to this group difference in performance. Social tolerance was measured using social network analysis of co-presence at the artificial foraging task, as well as observations of relevant social behaviours during the presentation of the artificial foraging task. Group 4 had significantly more frequent positive social interactions while at the task than did Group 3, and positive interactions made up a greater proportion of Group 4's interactions at the task than in Group 3. However, the two groups did not differ in the majority of social network measures calculated. The group which performed more flexibly during a changing artificial foraging task showed a greater frequency of social behaviours indicating social tolerance at the task.

5.1 Introduction

The previous chapter presented data related to the behavioural flexibility of two communities of chimpanzees (Chimfunshi Wildlife Orphanage Groups 3 and 4) in response to an artificial foraging task in which potential solutions were restricted over time. Group differences were apparent in the responses of the two groups, with Group 4 responding more flexibly to the change in task demands than Group 3 (**Chapter 4**). In this chapter, I will explore the groups' social tolerance, one potential difference between the groups which could have contributed to the group-level difference in performance seen between the two groups.

5.1.1 Social tolerance

One previously measured difference between Chimfunshi Groups 3 and 4 is in their level of social tolerance (Cronin, van Leeuwen, Vreeman & Haun, 2014a). Social tolerance is defined as the probability of group members being in proximity to one another around valuable resources, with little or no aggression (Cronin & Sanchez, 2012). Social tolerance has been shown to influence cooperative behaviour in bonobos and chimpanzees, with bonobos being found to be more socially tolerant when cofeeding and also more frequent and effective cooperators when presented with a monopolizable food resource (Hare et al., 2007). This between-species difference also appears to apply to within-species variation in tolerance, with pairs of chimpanzees that co-fed with higher levels of tolerance also being more likely to cooperate in a food retrieval task (Melis, Hare & Tomasello, 2006). Chimpanzees also display differences in inequity aversion that may relate to social tolerance, with individuals from well-established social groups (sometimes used as a proxy for tolerance) accepting rather than refusing unequal rewards (Brosnan, Schiff & de Waal, 2005). Levels of social tolerance also affect the prevalence and distribution of social behaviours such as play between species, with more socially tolerant, egalitarian Macaca tonkeana playing more frequently than less socially tolerant, despotic Macaca fuscata (Ciani, Dall'Olio, Stanyon & Palagi, 2012).

Using both social network-based and experimental measures, Cronin et al. (2014a) found that despite their similar group size, demography, and background, Groups 3 and 4 differed in terms of social tolerance. However, since that study, both deaths and births have occurred within the two groups, and these changes in group composition may have affected the social tolerance of the groups, particularly as the dominant male in Group 3 died after data collection for Cronin et al.'s study (2014a) and prior to data collection for the 'dipping' study

reported in this thesis. Cronin et al. (2014a) argue that group-level differences in social tolerance emerge from individual-level differences in key group members regarding resource monopolization, and point out that dominant males in particular may have had a large influence upon the behaviour of the entire group in the two experimental measures of tolerance. The loss of this dominant individual may therefore have altered the tolerance level of the entire group. Sapolsky and Share (2004) documented the effect of the death of a large proportion of males upon the social tolerance of a group of wild savanna baboons (Papio anubis), finding that the social behaviour of the group changed as a result of the death of the more aggressive males (46% of adult males died in a disease outbreak). The group showed greater rates of grooming between males and females in comparison with a control group, as well as lower rates of aggression from males towards females. This 'pacific' social behaviour was later maintained despite subsequent male migration, leading the authors to suggest that adolescent males migrating into the group socially acquired this social style. Sapolsky and Share's study (2004) demonstrates the influence key group members can have upon the social style of a group, and the effect that a change in group composition can have upon social tolerance. It also shows that social style can be a culturally acquired and maintained behaviour, which may be why the two Chimfunshi groups have such different documented levels of social tolerance despite the demographic and environmental similarities between the groups.

Social tolerance may be an important factor in facilitating the social learning of foraging behaviours, as it allows for proximity during foraging (permitting observation of behaviours), reduces the likelihood of antagonistic interactions (again, permitting uninterrupted observation of behaviours), and allows subordinate animals to retain any food acquired (Coussi-Korbel & Fragaszy, 1995; van Schaik, 2003). van Schaik argues that, as well as facilitating social learning, social tolerance may also promote innovation, by providing increased opportunities for uninterrupted object manipulation. This argument is supported by the correlation between a composite social tolerance score (including interbirth interval, the percentage of parties consisting of lone individuals, the rate of meat sharing, the percentage of collaborative hunts, the ratio of female-female grooming and medicinal plant use) and tool kit size in wild chimpanzee communities (van Schaik, Deaner & Merrill, 1999), and the correlation between the percentage of time independent individuals spend in parties and the number of food-related cultural behaviours as reported by Whiten et al. (1999) (van Schaik, 2003). Both of these correlations indicate greater numbers of behavioural variants within

chimpanzee communities that appear to be more socially tolerant. However, I note that some of the behaviours included in van Schaik et al.'s (1999) composite social tolerance score are indirect measures that require assumptions to be made about the drivers of social tolerance – for example, interbirth interval is used as an 'index of habitat productivity', and habitat productivity is then assumed to positively impact social tolerance. Similarly, medicinal plant use (the number of medicinal plant species used) is assumed to reflect the frequency of opportunities for close observation of other individuals (with medicinal plant use being assumed to be socially learnt). The inclusion of medicinal plant use as a cultural behaviour indicative of greater opportunities for social learning seems somewhat circular when attempting to explain the prevalence of other cultural behaviours (ie. groups with larger cultural repertoires in one behavioural category).

More recent experimental work lends support to van Schaik's (2003) argument, and adds a potential mechanism by which increased social tolerance (and more specifically, an increased number of contacts with social partners) might affect the likelihood of innovation of novel behaviours. Damerius, Graber, Willems and van Schaik (2017b) found that, along with a previously established positive effect of human contact during development (Damerius et al., 2017a), the number of enclosure-mates captive orangutans lived with positively affected their curiosity. Both Bornean (Pongo pygmaeus) and Sumatran (Pongo abelii) orangutans in captivity at rehabilitation stations were individually presented with a battery of response-andexploration-style tests, and those with a greater number of enclosure-mates showed both a positive response to novelty (engaging quickly with novel food, a novel object, and a novel human) and a high exploration tendency (exploring a novel object gently and with a wide variety of actions). These 'curious' individuals scored more highly on a variety of cognitive tests (including reversal learning and a flexibility test in which boxes containing a reward could first be opened by flipping the lid, and this solution was then blocked, and boxes could be opened only by sliding a door). As the orangutans were tested individually, the authors point out that direct social facilitation was not possible, but suggest that increased social contacts during a sensitive period of development may increase an individual's curiosity, and that this curiosity is applied in non-social contexts (Damerius et al., 2017b).

In the context of the 'dipping' task of the present study, van Schaik's (2003) argument would predict that more socially tolerant groups would invent more solutions to the task, and be

more likely to acquire solutions socially, by observing others. Both increased innovation and increased social learning could conceivably influence the apparent behavioural flexibility of a group.

5.1.2 Measuring social tolerance

Social tolerance in primates can be assessed in a variety of ways, including both observational and experimental approaches. Experimental paradigms designed to measure group level social tolerance provide limited food resources to create competitive situations, and the equity of resource sharing (Burkart & van Schaik, 2013), or tolerance of others in a feeding situation (Cronin et al., 2014; Fichtel, Schnoell & Kappeler, 2017), can then be measured quantitatively. Observational studies have assessed social tolerance by recording how individuals organize themselves spatially; by creating proximity networks (Cronin et al., 2014), by recording and creating networks of affiliative relationships between individuals (Sueur et al., 2011b), and by recording the frequency of social behaviours such as aggressive interactions, displacements, and affiliative behaviours (eg. grooming) (Duboscq et al., 2009). I constructed proximity-based social networks and measured a variety of social behaviours in the current study.

Social behaviours at the 'dipping' task were measured in order to attain an insight into the social tolerance of both groups, and the behaviours measured also had the potential to impact directly upon task performance. Displacements, (also termed 'approach-retreat' or supplant interactions), are often used as a means of assessing dominance hierarchies in non-human animals (Silk et al., 2010; Sicotte, 2002; Alados & Escos, 1992; Boyd & Silk, 1983; Seyfarth, 1976; Rowell, 1974), with higher-ranking individuals more likely to succeed in displacing lower-ranking individuals. While it is the direction, symmetry, and response to displacements, rather than their frequency, that is often referred to in studies of social tolerance (eg. Sapolsky & Share, 2004), van Schaik (2003) predicts that individuals in socially intolerant groups will be more likely to be displaced from a foraging bout, suppressing their opportunity to innovate. Similarly, Horner (2010) suggests that social tolerance facilitated chimpanzees' close observation of demonstrators and subsequent acquisition of a novel tool-use behaviour (reported in Whiten, Horner & de Waal, 2005), as tolerance allowed observers to approach and observe without displacing the demonstrator.

Aggression between individuals is also likely to impede innovation (if the individual acting on the task is aggressively displaced by another chimpanzee), and may also impede the possibility of social learning (if the individual acting upon the task threatens or aggresses potential observers in order to maintain control of the task) (van Schaik, Deaner & Merrill, 1999). As an artificial foraging task often presents a monopolizable resource, it is possible that its presence increases the chance of aggressive conflict between individuals, as food conflict in wild female chimpanzees is more likely to occur over monopolizable items (Wittig & Boesch, 2003). Willingness to co-feed from a monopolizable food resource has been used as a measure of social tolerance, with bonobos (considered a more socially tolerant species) being more likely to co-feed than chimpanzees, and showing no aggression during cofeeding, while aggressive interactions were observed (though rarely) in chimpanzees (Hare et al., 2007). The ability to access an artificial foraging task with infrequent or limited aggression may not only lead to greater success (as individuals can perform the task uninterrupted), but may also indicate a level of social tolerance through the ability to co-feed at a monpolizable resource.

Social behaviours which are positive indicators of social tolerance, and also likely to promote the social learning of behaviours, as per van Schaik's (2003) hypothesis, were also measured. Peering (attentive, close-range observation) has been argued to be an important means of acquiring information socially, with wild infant orangutans peering more at their mother when she fed on less-familiar foods which required a greater complexity of processing, and then exploring more having peered (Schuppli et al., 2016). Schuppli et al. (2016) also found that peering decreased as young orangutans became more competent (and so required less social information), and that as juveniles aged, they began to peer more at individuals other than their mother, allowing them to acquire information beyond that which observing their mother could provide. Yamanashi et al. (2016) found that providing an artificial foraging task to captive chimpanzees elicited peering behaviour, particularly in an infant, who, like the wild orangutans studied by Schuppli et al. (2016), showed selectivity in his peering, tending to peer more at adults following his failed attempts than following successful attempts. Peering therefore appears to be a means of acquiring social information, and so may have allowed individuals to acquire new solutions to the task, improving performance, and may also be an indicator of social tolerance, as in order to peer closely at another's actions, individuals must be in close proximity while at the task.

While food transfer is not uncommon in wild chimpanzees, with sharing (unresisted or voluntary transfer of defensible food from a food-motivated possessor to a recipient; Feistner & McGrew, 1989) occurring both between adults and their offspring and between adults and

other adults (Jaeggi & van Schaik, 2011), tool transfer appears less frequently than meat or other food sharing in the wild literature (Pruetz & Lindshield, 2011). Tool transfer is defined by Pruetz and Lindshield (2011) as "the exchange of a resource between one dyad within an uninterrupted feeding or foraging bout", and unlike Feistner and McGrew's (1989) definition of sharing, this definition does not require the transfer to be voluntary. Theft, passive and active transfers were all considered examples of tool transfer by Pruetz and Lindshield (2011), and transfers were further categorised by the extent to which they were actively initiated by the possessor of a tool (following Boesch and Boesch, 1989).

Pruetz and Lindshield (2011) document ten cases of tool transfers amongst chimpanzees at Fongoli, Senegal. The tools transferred between individuals in these cases were stick tools used for Galago hunting (eg. Pruetz & Bertolani, 2007) for termite fishing, or for ant-dipping. The authors suggest that the high incidence of transfers at Fongoli (in comparison with Mahale and Bossou) fit with expectations for a cohesive community, in which the average party size is more than 40% of the community (Pruetz & Bertolani, 2009), and argue that the higher incidence of male-male transfers at Fongoli in comparison to Mahale and Bossou indicates greater tolerance between Fongoli males in feeding situations. Pruetz and Lindshield (2011) note that the level of transfer behaviour they document may be environmentally driven, and related to the costs and benefits of food sharing in a savannah environment, but in making this argument they suggest the environment promotes a "high degree of tolerance" and "high social cohesion" which is then demonstrated by the prevalence of food and tool transfer. Tool transfers have also been documented in the Goualougo Triangle, Republic of Congo (Musgrave et al., 2016), primarily occurring between adult females and their immature offspring. The authors argue that these transfers constitute teaching, as the tool donors experienced a reduction in feeding events following the transfer, while recipients experienced an increase in feeding events following the transfer. Tool transfers may therefore be considered, along with peering, as a potential source of social information during a tool-based foraging bout. As Pruetz and Lindshield (2011) argue, tool transfers also indicate social tolerance between the donor and the recipient, and this may be why the majority of transfers observed by Musgrave et al. (2016) were between mother and offspring.

McGrew and Feistner (1992) suggest that tolerated scrounging (the theft of food with little or no resistance from the owner) is the most common form of food sharing in chimpanzees, and primarily occurs between mother and offspring. In wild chimpanzees, infants scrounge nut

kernels, primarily from their mothers (Inoue-Nakamura & Matsuzawa, 1997). Similarly, in wild tufted capuchin monkeys (Sapajus spp.), observers scrounge food from individuals who are nut-cracking (Coelho et al., 2015), with infants scrounging more frequently than juveniles or adults. In captive chimpanzees attempting an artificial foraging task, tolerated theft was significantly more likely to occur between mother-offspring pairs with the juvenile taking food from its mother than vice-versa (Dean et al., 2012). Horner (2010) suggests 'excessive' scrounging might discourage proficient individuals from performing a behaviour, and argues that social tolerance would be shown by limited scrounging, and Giraldeau and Lefebvre (1987) found that pigeons (Columba livia) were less likely to learn a foraging behaviour if they scrounged from knowledgeable individuals. However, Dean et al. (2012) found a significant correlation between the amount of scrounging events an individual perpetrated and their performance on the artificial foraging task. Scrounging has also be argued to facilitate social learning (Caldwell & Whiten, 2003), with common marmosets (Callithrix *jacchus*) that had the opportunity to scrounge from a demonstrator during an artificial foraging task more likely to acquire the demonstrated behaviour than those that were only able to observe and not scrounge. Following these findings, I interpret tolerated scrounging as a positive indicator of social tolerance, as it indicates individuals were in close proximity during a foraging bout, and indicates tolerance on the part of the individual that has produced the resource being scrounged (at least when this individual is the more dominant of the two, as in mother-offspring scrounging).

If individuals are sufficiently socially tolerant to share close proximity at a foraging site, the opportunity arises for both concurrent action and co-action. In the current study, I define concurrent action as two or more individuals acting upon the task at once (ie. making simultaneous but separate attempts, or rapidly alternating attempts). This was possible due to the group testing situation, and due to the nature of the 'dipping' task, which was potentially monopolizable but also amenable to concurrent action if individuals positioned themselves on either side of the tube. In a study conducted with Groups 3 and 4 at the Chimfunshi Wildlife Orphanage, Cronin et al. (2014b) presented dyads of group-members with a task in which a tray containing food rewards hung within a mesh tower. By sitting on top of the tower and pulling on two chains, chimpanzees could lift the tray towards themselves and retrieve the reward. While the study aimed to examine collaborative problem solving, in order to have the opportunity to solve the task collaboratively, individuals would have to both occupy the 1m² panel on top of the tower, and their willingness to do this provides some idea of their ability
to concurrently attempt to gain a food reward while in close spatial proximity to one another. Cronin et al. (2014b) found that individuals simultaneously occupied the tower for an average of 11.2% of sessions (or, 1.2 minutes of each 10 minute session), though those that succeeded in solving the problem collaboratively spent more time together on the tower (these dyads included two composed of individuals still present in the current study; Val and Kathy, and Kit and Kathy), and time spent together on the tower was positively correlated with a dyad's proximity-based social network association index. Cronin et al. (2014b) also found that monopolization of the task was common, with 80% of sessions being entirely monopolized by one partner in a dyad. These results indicate that concurrent action at an artificial foraging task may be relatively rare, but the correlation between a dyad's time spent together on the tower and association index implies that a certain level of inter-individual tolerance is required in order for this to occur, which may make concurrent action a useful indicator of social tolerance.

Coaction has been observed in experimental studies of chimpanzee social learning (Horner, Whiten, Flynn & de Waal, 2006; Horner, 2010), in wild chimpanzees (McGrew, 1977; Sanz & Morgan, 2013) and captive capuchins (Westergaard & Fragaszy, 1987). It describes the situation in which an observer touches the tool or hand of an individual performing a behaviour (Visalberghi & Fragaszy, 1990). Fragaszy and Visalberghi (1990) suggest that coaction requires a high level of inter-individual social tolerance, and it is thought to facilitate social learning.

5.1.3 Social networks

Observations of social behaviour within a group can be used to construct social networks. The networks allow complex social systems to be described and analysed, and can be built using data on affiliative or agonistic interactions between individuals, or simply proximity measures (Sueur et al., 2011a). Metrics derived from these social networks can be used to make inferences about the relative social tolerance of a group or species (Sueur et al., 2011b; Cronin et al., 2014a). In a study of the same chimpanzees studied in this chapter, Cronin et al. (2014a) found that Group 4 had a higher median association index and a higher clustering coefficient than Group 3, while Group 3 had higher modularity (were more likely to split into defined subgroups) than Group 4, indicating that Group 4 was more tolerant and less avoidant of conspecifics than Group 3. Sueur et al. (2011b) examined a range of social network measures in four species of macaque (*Macaca mulatta, Macaca fuscata, Macaca nigra*,

Macaca tonkeana). The differing social styles of these species are already well-documented (Thierry, Iwaniuk & Pellis, 2000; Thierry, 2007), and Sueur et al. (2011) found that more socially tolerant species had higher network density (more connections between individuals), lower modularity (were less likely to split into defined subgroups), and a lower centrality index (dominant individuals were less central to the social network) than more socially intolerant species.

5.2 Chapter aims and hypotheses

In the current study, I assess and compare the social tolerance of the two Chimfunshi groups within the specific context of the artificial 'dipping' task provided to them in the previous chapter, with particular interest in how any differences in tolerance at the task might have affected the groups' task performance and apparent behavioural flexibility. Social tolerance at the task is assessed in two ways; firstly, by examining the social interactions between individuals at the task, and secondly, by constructing social networks of co-presence at the task.

5.2.1 Hypotheses

The group which performed more flexibly on the artificial foraging task (Group 4) is predicted to show higher levels of social tolerance. This would be reflected by higher frequencies of 'tolerant' behaviours (ie. peering, tool transfer, tolerated scrounging, concurrent action, and co-action) and lower frequencies of 'intolerant' behaviours (ie. displacement and aggression), whilst in contrast, Group 3 is predicted to show lower levels of 'tolerant' behaviours, and higher frequencies of displacement and aggression.

However, it is also possible that 'intolerant' behaviours (displacement and aggression) might occur more frequently in a socially tolerant group if they are simply reflective of a greater tendency to interact socially at the task. In that situation, one would expect higher frequencies of all social behaviours at the task to occur in Group 4 than in Group 3.

In terms of social networks, a group with a high mean association index and low social differentiation would be considered socially tolerant, as this would indicate that most group members had been observed in proximity to most others at a relatively high rate (Cronin et al., 2014a). Therefore, Group 4 is predicted to have a higher mean association index and lower social differentiation than Group 3. Group 4 is also predicted to have lower modularity than Group 3, indicating an absence of meaningful subgroups. These findings would correlate

with those of Cronin et al. (2014a). In addition, Group 4 is predicted to have a lower centrality index (the dominant male is predicted to be less central to the network than in Group 3), and to have higher network density than Group 3, indicating more connections between individuals, as found by Sueur et al. (2011b) in more tolerant macaque species.

5.3 Methods

5.3.1 'Dipping' task social networks

Undirected social networks were calculated for both groups, based upon co-presence at the 'dipping' task (detailed in Chapter 3). During the dipping task, I recorded the presence of observer individuals via narration, thus creating a record of individuals within five metres of the task during another individual's attempt. Social networks have been calculated based upon these records. The social networks are undirected and based upon group membership, thus if individual A is attempting the task, with individuals B and C both within five metres, all three individuals become connected in the network. Whilst this undirected form of network may not be highly relevant in the context of social learning, as it does not provide information on which individuals observed others active on the task, it is relevant to the question of social tolerance as it indicates the extent to which individuals were willing to be within a close range of others around the task.

To construct the social networks, 1/0 sampling was used, with experimental sessions split into 15min blocks. If two individuals were observed simultaneously within five metres of the task during a 15min block, they were considered associated and received a "1"; if they were not associated within that 15min block, they received a "0". Fifteen-minute blocks were chosen as this length of time provided sufficient data points to construct a network, and also represented a sufficient period of time in which the group composition at the task tended to have changed. Twice-weight association indices (Whitehead, 2008) were then extracted, using the formula shown below, as these are least biased when there is a sampling bias towards identifying individuals together (Cairns & Schwager, 1987; Whitehead, 2008).

$$AI = x / x + 2yAB + yA + yB$$

Note: AI = association index; x = number of sampling periods with individuals A and B observed associated; y_A = number of sampling periods with only A observed; y_B = number of sampling periods with only B observed; y_{AB} = number of sampling periods with both A and B observed but not associated.

The infant, Brent, in Chimfunshi Group 3, was not included in the social network analyses, as she did not leave her mother at any point during testing (thus creating a highly inflated association index between the two, who were never seen apart). The infant Jewel, in Chimfunshi Group 4, spent a large amount of time with his adopted mother Kathy, but was old enough during testing to frequently appear within 5 metres of the task without her, and was therefore considered sufficiently physically independent to be included in the social networks.

Network measures were calculated in order to further compare social tolerance between the two groups. The mean AI (association index), social differentiation, modularity, mean eigenvector centrality, centrality index, and density for each group are reported (see Table 1 for descriptions of these terms).

Table 1.

Social network statistics with their descriptions

Social network measure	Description
Mean association index	The mean strength of association within each group (see p.128 for equation demonstrating the calculation of individual association indices). A high mean association index relative to another group would indicate stronger relationships between a greater number of individuals in the group.
Social differentiation	A measure of how even association strengths are across the group, with high differentiation indicating more variation in the strength of associations, while low differentiation indicates the majority of associations are close to the group mean (Whitehead, 2008).
Modularity	Modularity indicates whether a group can be split into subgroups, with a modularity greater than 0.3 indicating an important division, and a modularity of 1 indicating that individuals never associate with individuals outwith their cluster (Newman, 2004; Whitehead, 2008). Such subgroups could be based upon matrilines or age classes (Kasper & Voelkl, 2009).
Mean eigenvector centrality	Eigenvector centrality measures the importance of an individual within a network, and takes into account the number and strength of connections, and the centrality of those connected partners (Kasper & Voelkl, 2009; Whitehead, 2008). Here the group mean is calculated.
Centrality index	The difference between the eigenvector centrality of the dominant male and the mean eigenvector centrality of other group members. Ranges from -1 to +1, and is close to 0 for egalitarian networks in which all individuals have equal relationships (Sueur et al., 2011b).
Density	The number of observed connections (edges) between individuals, divided by the maximum number of possible edges if all individuals were connected (Sueur et al., 2011b; Kasper & Voelkl, 2009).

5.3.2 Indicators of social tolerance during the dipping experiment

All video records from the dipping task (Chapter 3) were recoded with a specific focus upon social interactions relevant to social tolerance. Behaviours assumed to be 'positive' and 'negative' indicators of social tolerance were coded for. The behaviours coded for, along with their definitions, are provided in Table 2. All individuals visible on these video records were included in the coding (ie. interactions between individuals were coded whenever they were visible, not only when one individual was active at the task).

For each of these social behaviours, the time of occurrence, identity of the individual active at the task (or occupying the space directly in front of the task), the identity of the second individual involved, the type of behaviour, the direction of the behaviour (eg. individual A displaces individual B; individual A scrounges from individual B), and the identity of the individual active at the task following the behaviour was recorded. In addition, notes described pertinent details of the behaviour (eg. for episodes of peering, the technique being observed by the peering individual was noted; for tool transfers the transfer was described in detail).

In addition, I recoded the video records to measure the amount of time each group spent at the task (previous coding had recorded the timing and frequency of attempts at the task, but did not reflect time individuals spent present at the task without making an attempt). This was a binary measure, recorded whenever at least one individual was present at the task (with 'at the task' meaning an individual was either sat at the mesh to which the task was attached, or visible sitting on the ground directly below the task). The measure of how long each group spent physically present at the task provides some context for the frequency of social behaviours observed, as such behaviours could only be recorded from this video record during times at which individuals were present at the task.

Table 2.

Social behaviours recorded at the task, with the definition followed during video coding

Behaviour	Coding definition
Aggression	Agonistic behaviour directed at another individual. Included physical contact aggression (eg. biting or hitting) and displays or threats if clearly directed toward another individual.
Displacement	An individual retreats spatially within 5 seconds of another individual approaching.
Co-action	An individual touches the acting individual's hand or part of a tool during use.
Concurrent action	Two or more individuals act upon the task at once (ie. making simultaneous but separate attempts, or rapidly alternating attempts)
Peering	An individual observes another for at least 5 seconds from a distance of less than 1 metre. The head movements of the peering individual follow the demonstrator's actions.
Scrounging	 An individual gains juice reward as a result of another's action at the task (ie. the scrounger licks juice from the actor's tool item or hand after the actor has attempted the task) In cases where juice was retrieved from a tool, this is distinct from tool transfer in that during scrounging, the tool remains in the possession of the original owner. Instances in which absorbent materials were discarded by their owner and taken by an observer are categorised as scrounging.
Tool transfer	The exchange of a tool between two individuals. This included transfers in which one individual took a tool item out of the hands of another chimpanzee, and in which transfer occurred mid-attempt (individual A inserts item into tube, individual B immediately takes over attempt with A's inserted material). Instances in which an individual took an absorbent material that the owner had discarded are classed as scrounging.

5.4 Results

5.4.1 Co-presence at dipping task: Social networks

Social networks were constructed for both groups based upon individuals' co-presence at the 'dipping' task. As discussed previously, social networks were constructed with data split into 15min samples. The network measures calculated are given in Table 3. Association indices, social differentiation and modularity were calculated using SOCPROG 2.6 (Whitehead, 2009). Eignevector centralities were calculated using Gephi 0.9.2 (Bastian, Heymann & Jacomy, 2009). In order to calculate each group's centrality index, the dominant male in each group (Brian in Group 3 and Commander in Group 4) was identified using keeper reports and in the case of Group 4, a previously published hierarchy (van Leeuwen et al., 2013).

Table 3.

Network statistics with standard deviation

	Group 3	Group 4
Mean association index	0.15 [sd = 0.05]	0.16 [sd = 0.06]
Social differentiation*	0.49 [se = 0.08]	0.61 [se = 0.05]
Modularity	0.15	0.16
Mean eigenvector centrality	0.69 [sd=0.21]	0.80 [sd=0.18]
Centrality index	0.18	- 0.16
Density	1.00	0.97

*Social differentiation was calculated using the maximum likelihood method with bootstrap standard errors as outlined by Whitehead (2008).

Neither group had modularity measuring above 0.3, suggesting no meaningful divisions in either group (Newman, 2004; Whitehead, 2008). Mann-Whitney tests indicated that there was no significant difference in the mean association index between the groups (Median Group 3 = 0.14, Median Group 4 = 0.14, U = 1144.5, p = 0.76) and no significant difference between the groups in terms of mean eigenvector centrality (Median_{Group 3} = 0.68, Median_{Group 4} = 0.81, U = 43.5, p = 0.48). However, it is worth noting that Group 4 had a larger range of association strengths than Group 3 (Range_{Group 4} = 0.76, Range_{Group 3} = 0.32).

Both groups had very high network density, indicating that most or all individuals were observed together at least once. In Group 3 all individuals had been observed together on at least one occasion, and in Group 4, only Bobby and Kambo and Bobby and Miracle were not observed together during the study. The density of these networks is perhaps unsurprising given the small group sizes and the presence of the artificial food resource during testing. Although in Figure 1, Group 4's network diagram may appear to be more densely connected, it should be noted that only associations stronger than 0.1 are shown in the diagram, whilst all associations are included when calculating network density. This means that individuals in Group 3 were connected, but many of these associations were below 0.1 and so are not depicted in the diagram.

Social differentiation was slightly higher in Group 4 than in Group 3 (Table 3), indicating more variability in the strength of associations between individuals, which makes intuitive sense given the greater range of association indices recorded in Group 4. The centrality index (the difference between the eigenvector centrality of the dominant male and the mean eigenvector centrality of the other group members) was higher in Group 3 than in Group 4 (Table 3) indicating that the dominant male (Brian in Group 3, and Commander in Group 4) was more central in relation to other group members in Group 3 than in Group 4. This can be seen in the network diagrams (Figure 1), in which the nodes are sized according to eigenvector centrality, and it can be observed that relative to their group members, Brian has a greater eigenvector centrality than Commander. It can also be seen that Brian is strongly associated (shown by the weight of the edges connecting the nodes) with individuals who are themselves central to the network, while Commander has relatively weak connections to individuals who are not particularly central.



Figure 1: Undirected social networks of co-presence at the task for a) Group 3 and b) Group 4. Each circle (node) represents an individual, and each is labelled by name. The width of the lines (edges) between nodes is proportional to the association index between the individuals. Only association indices > 0.1 are shown for clarity. Nodes are sized based upon their eigenvector centrality. Nodes representing males are green, and nodes respresenting females are gold. Networks were made using Gephi 0.9.2 (Bastian, Heymann & Jacomy, 2009), and nodes are spatially arranged using a Fruchterman-Reingold layout.

5.4.2 Time present at task

Group 3 was presented with the baited apparatus for a total of 39hrs 30mins. At least one individual was present at the task for 31% (12hrs 15mins) of this time. Group 4 was presented with the baited apparatus for a total of 40hrs 09mins. At least one individual was present at the task for 52% (21hrs) of this time (Figure 2).

In the first stage of the task (the 'Wide Tube' phase), at least one individual was present at the task for 73% (7hrs 22mins) of the 10hr 04mins presentation in Group 4, in comparison with 62% (6hrs 3mins) of the 9hrs 50mins presentation in Group 3. In the following 'Narrow Tube' phases, at least one individual from Group 4 was present for 45% (13hrs 38mins) of the 30hrs 05mins presentation, in comparison with 21% (6hrs 13mins) of the 29hrs 40mins of 'Narrow Tube' presentation in Group 3. Throughout all phases of the task, Group 4 spent more time at the task than Group 3. This difference in attendance was more pronounced in the 'Narrow Tube' phases, in which the task was more challenging.

100-



Figure 2: The percentage of the presentation time for which at least one group member was present at the task for each group, in the 'Wide Tube' phase (approximately 10 hours), 'Narrow Tube' phases (approximately 30 hours) and across all phases (Total, approximately 40 hours).

5.4.3 Social behaviour at the task

A total of 135 social interactions of the types listed in Table 2 were recorded in Group 4, and 54 social interactions of these types were recorded in Group 3. The number of observed social interactions for each behaviour type are listed in Table 4.

However, as Group 4 spent a greater amount of time at the task than Group 3, in order to compare the frequency of these social interactions between the groups, it is necessary to control for the amount of time for which the groups could be observed at the task. In Table 5, I present the frequency of each event type in terms of events per hour of observation for each group (the time for which at least one individual in a group was present at the task). Frequencies of all behaviours were too low to allow statistical comparison between the groups, and so arithmetic differences are presented.

Individuals in Group 4 engaged in co-action 3.8 times more frequently than those in Group 3, and in concurrent action 2.5 times more frequently than those in Group 3. Scrounging was observed 14.25 times more frequently in Group 4 than in Group 3, and tool transfers occurred 3.3 times more frequently in Group 4 than in Group 3. Conversely, displacements occurred 1.8 times more often in Group 3 than in Group 4. Occurrences of both aggression and peering were slightly more frequent in Group 3 than in Group 4.

In considering these behaviours as indicators of social tolerance, they can be grouped into likely 'positive' indicators and likely 'negative' indicators (with co-action, concurrent action, peering, scrounging and tool transfer as 'positive' indicators, and aggression and displacement as 'negative' indicators). Grouping the behaviours in this manner allows comparison of the difference in frequency of positive and negative indicators between the two groups. A chi-square test indicated that the two groups differed in terms of the proportion of positive and negative social interactions observed (χ^2 (1) = 13.9, *p* <0.001), with a greater proportion of positive indicators observed in Group 4.

Table 4.

The number of social interactions observed in each group

Interaction	Events in Group 3	Events in Group 4
Aggression	4	5
Co-action	2	13
Concurrent action	5	22
Displacement	21	20
Peering	17	28
Scrounging	1	24
Tool transfer	4	23

Table 5.

Social interactions in each group per observation hour

Interaction type	Events per hour	Events per hour
	Group 3	Group 4
Aggression	0.33	0.24
Co-action	0.16	0.62
Concurrent action	0.41	1.05
Displacement	1.71	0.95
Peering	1.39	1.33
Scrounging	0.08	1.14
Tool transfer	0.33	1.10



Figure 3: The rate per hour of social interaction behaviours considered positive indicators of social tolerance for each group.



Figure 4: The rate per hour of social interaction behaviours considered negative indicators of social tolerance for each group.

5.4.3.1 Aggression at the task

In both groups, aggression was a relatively unusual form of social interaction at the task in comparison to the other social behaviours recorded, and only nine instances of aggression were recorded across both groups (see Table 5 and Figures 3 and 4). In all cases of aggression, juveniles and infants were the recipients of aggression (Group 3: Lods on 3 occasions, Bruce on one occasion; Group 4: Kenny on two occasions, Jack on three occasions). Males were the aggressors in eight of the nine instances, with the only female aggressor being Kathy in Group 4, who threatened Jack with an open-mouthed biting movement towards his hand, eliciting a scream and retreat from the task from Jack. In five cases, the aggressor was not the individual active at the task prior to the aggression, and in four cases, the aggressor was the individual already active at the task, suggesting that aggression was used both in attempting to retain control of the task, and in attempting to take control of the task.

5.4.3.2 Displacement

Displacement was more frequent in Group 3 than Group 4, with displacements occurring more than once an hour (1.71 occurrences per hour) in Group 3, and nearly once an hour (0.95 occurrences per hour) in Group 4. There was no significant difference between the groups in terms of the age-categories most frequently displaced, with adults displaced less frequently than no-adults in both groups (χ^2 (1) = 0.92, *p* = 0.34). Combining data from both Group 3 and Group 4, juveniles (22/41 occurrences), adult females (8/41 occurrences), and infants (6/41 occurrences), were the groups most frequently displaced from the task. Both adult males and adult females were observed displacing others, and adults were the most frequent initiators of displacement (16/41 adult male occurrences, 16/41 adult female occurrences).

5.4.3.3 Concurrent action

Concurrent action was observed in both groups, but was observed more frequently in Group 4 than Group 3 (occurring 1.05 times per hour in Group 4, and 0.41 times per hour in Group 3). Four of five instances of concurrent action in Group 3 were between Bruce (juvenile male) and Buffy (unrelated adult female), with the fifth instance being between Bruce and his mother, Barbie. These instances occurred during the 'Wide Tube' phase, and in all cases the individuals alternated hand or cloth dipping attempts. In Group 4, Kathy was the most

frequent participant in concurrent action (14/22 instances included Kathy). Her most frequent partner in concurrent action was Jack (8/14 instances). The majority of instances of concurrent action in Group 4 included a juvenile or infant as one of the partners (19/22 occurrences), but only six of 22 instances were a mother-offspring partnership.

5.4.3.4 Coaction

Coaction was observed more frequently in Group 4 than in Group 3. Only two instances were observed in Group 3, both between Barbie and her offspring (Bruce and Brent). In both cases, Barbie's infant and juvenile sons held either her hand or the cloth while she engaged in cloth dipping at the task. In Group 4, the majority of instances of coaction were between family members (10/13 instances, 7 were between Kathy and her adopted infant Jewel, and 3 were between sibling pairs Jack and Jewel or Kenny and Kit). In the majority of cases (11/13), the co-actor (the individual observing an attempt at the task) was an infant (in 10 of 13 cases, Kathy's adopted infant Jewel), and this meant that in the majority of cases the individual observing was younger than the individual acting on the task. In the majority of instances of coaction in Group 4, the observing individual touched or held a stick tool as the active individual attempted the task, with only one instance of coaction involving any other tool material (infant male Kenny mouthing and touching the end of a piece of cloth while adult male Nicky inserted it into the tube).

5.4.3.5 Peering

Instances of peering were observed at a similar rate in both Group 3 and Group 4. In Group 3, only juveniles and infants were observed peering (Bruce, Lods, and Brent). These individuals most frequently peered at adult females (12/17 instances), but in only four of 17 instances was this peering between family members. In Group 4, 20 of 28 instances of peering were by juveniles or infants, but as in Group 3, peering occurred between both family and non-family members (7/28 instances of offspring towards mother, 3/28 instances between siblings, 18/28 instances between unrelated individuals). There was no difference between the groups in terms of the proportion of peering events that occurred between kin and non-kin pairs (χ^2 (1) = 0.73, *p* = 0.39).

5.4.3.6 Tolerated scrounging

Scrounging occurred more frequently in Group 4 than in Group 3 (1.14 times per hour of observation vs 0.08 times per hour of observation). Scrounging was observed only once in

Group 3, in an incident in which Bruce licked juice from his mother Barbie's hand. In Group 4, 24 instances of scrounging were observed. The majority of these (14/24 cases) were instances in which Jewel scrounged from his adoptive mother, Kathy. Twenty-two of the 24 instances of scrounging observed in Group 4 were either juveniles or infants scrounging from older individuals, and in 18 of 24 cases the older individual was kin (16 mother-offspring, 2 siblings). In only two instances an older individual scrounged from a younger individual (Nicky, an unrelated adult male, scrounged from infant male Kenny; Kit, a subadult male, scrounged from his infant brother Kenny).

5.4.3.7 Tool transfers

Tool transfers were observed more frequently in Group 4 than Group 3 (0.33 incidents per hour of observation in Group 3 vs. 1.10 incidents per hour of observation in Group 4). Four tool transfers were observed in Group 3, and in three of these, juvenile male Bruce was the recipient. Bruce took tools from adult females Buffy and Barbie (his mother), taking cloth from Buffy's hands, retrieving Barbie's piece of cloth from within the tube during her attempt, and taking a stick from Barbie's hands following her attempt at the task. The fourth instance of tool transfer in Group 3 was adult female ET taking a stick from juvenile female Lods prior to beginning an attempt at the task.

Twenty-three tool transfers were observed in Group 4. All of these events involved a nonadult individual (infant, juvenile or subadult) as either owner or recipient of the tool being transferred. Six instances were transfers between mother-offspring pairs, and in all six such cases the infant was the recipient of the tool (in 5 instances the infant was Jewel, in 1 instance the infant was Kenny). In addition, there were four sibling transfers, but in these cases the transfer was not always in the direction of the younger sibling, with subadult male Kit taking a tool from his infant brother Kenny on one occasion (the remaining three instances were Kenny taking a tool from Kit twice, and Jewel taking a tool from his juvenile brother Jack once).

Of the 23 tool transfers observed in Group 4, the majority (13/23) were between non-kin. These included one instance in which infant male Kenny used a tool possessed by unrelated adult male Nicky (manipulating a piece of cloth which Nicky had inserted into the tube while Nicky's attempt was ongoing and Nicky remained present at the task). Kenny also took a tool from unrelated adult female Miracle, removing a stick from the tube while her attempt was still ongoing and she remained at the task. Jewel took tools from unrelated adult female

Miracle on two occasions, once removing a stick from the tube during Miracle's attempt at the task, and once taking a piece of cloth from the top of the tube during Miracle's attempt at the task. On three occasions, Miracle took tools from the two infants, twice taking hold of Kenny's stick tool during his attempt at the task and continuing to dip with it, and once taking a stick from Jewel's hands.

The participation of non-adult individuals in the tool transfers in Group 4, as either owner or recipient of the tool, perhaps suggests two types of transfer in this group. The first (8/23 instances) are those in which an older, more dominant individual takes a tool from a younger individual, and the second (15/23 instances) are those in which an older, more dominant individual tolerates the actions of a younger, subordinate individual. In Feistner and McGrew's (1989) definitions of sharing and theft, the first category (older recipient and younger original owner) cannot be distinguished from theft, as the younger individual may not resist the actions of the older individual. The second category, in which tools are transferred from older owners to younger recipients, fits Feistner & McGrew's (1989) definition of sharing, as the older individual's passive tolerance implies their assent. All would be classed as tool transfers under Pruetz and Lindshield's (2011) coding scheme.

5.5 Discussion

Whilst social network analysis indicated few differences between the groups in terms of their patterns of association at the 'dipping' task, behavioural observations indicated that Group 4 were more socially tolerant, as a greater proportion of their interactions at the task were positive than in Group 3, and a lower frequency of negative interactions was observed in Group 4 than in Group 3.

5.5.1 Social interactions

Across the social behaviours examined, Group 4 had a higher rate of positive interactions than Group 3. Group 4 were less likely to displace one another at the task, and had a higher rate of tolerant interactions, including those likely to aid in social learning, such as coaction and tool transfer.

In line with van Schaik's (2003) hypothesis, displacements occurred less frequently in Group 4 than in Group 3. This may have allowed individuals in Group 4 to attempt the task without interruption, facilitating innovation (and indeed, as a group, more solutions were observed in

Group 4 than in Group 3). It may also have facilitated the spread of techniques via social learning, as individuals could observe one another without displacing each other. The higher rate of concurrent action in Group 4 than in Group 3 also indicates that individuals in Group 4 were able to attempt the task while in close proximity to one another, and even to attempt the task simultaneously, without one individual monopolizing it. The capacity for some individuals at Chimfunshi to attempt a task concurrently was previously documented by Cronin et al. (2014b). Interestingly, during their study, Kathy was a member of two of the dyads that shared space on the tower apparatus most frequently, and in the current study, Kathy was the most frequent participant in concurrent action. This demonstrates that individual differences in social tolerance may have important implications in experimental studies, across a range of paradigms.

The finding that adults were the age group that most frequently displaced others fits with evidence from wild primates. Lee & Cowlishaw (2017) found that in wild chacma baboons (*Papio ursinus*), displacements occurred most frequently when an adult moved to within arm's reach of another individual. Juveniles who moved into this proximity were more likely to be tolerated, rather than displacing the occupant. I did not code for approaches in the current study, and so it is not clear whether juveniles and infants approached others at the task but did not displace them, or whether juveniles and infants simply did not attempt to approach the task if another individual was already present.

Unlike Pruetz and Lindshield (2012), no clear sex difference was observed in tool transfers in the current study, with both male and female tool owners having tools taken from them. All tool transfers observed by Pruetz and Lindshield (2012) were between a male owner and a female recipient, and all were either passive transfers in which the receiver took an item and this was tolerated by the owner, or active-passive transfers, where the owner moved to facilitate the transfer, but did not present or offer the item to the receiver. The authors also note, however, that at Fongoli, females are not focal subjects, and so female owners may have been underrepresented within their study (Pruetz & Lindshield, 2012). This may be an important limitation, given that more recent research indicates that females more frequently engage in tool-assisted *Galago* hunting than males at Fongoli (Pruetz et al., 2015). While non-adult individuals were always involved in tool transfers in the current study, whether their involvement in the transfer was as owner or recipient has different implications for social tolerance. When younger individuals were the initial owners, the transfer might be

better thought of as theft, and an expression of dominance on the part of the older recipient. However, in the majority of transfers in Group 4, younger individuals were the recipients of tool transfers, and these interactions would seem to be more indicative of inter-individual social tolerance, as older individuals had the necessary dominance to potentially resist the transfer.

The majority of incidents of tolerated scrounging also featured juveniles or infants as the recipients, and in the majority of cases, scrounging occurred between mother-offspring pairs, with the infant scrounging from its mother. This suggests a high level of inter-individual tolerance may be required for this kind of scrounging to occur, perhaps largely limiting its occurrence to tolerant kin. Similarly, coaction tended to occur between kin, particularly mother-offspring pairs, again suggesting that a high level of tolerance between a pair may be required for this behaviour to occur. However, in a study of a small sample of captive chimpanzees, Hirata and Celli (2003) found that in an artificial honey-dipping task, adult females were equally tolerant of their own and unrelated infants licking honey from their stick tools, though infants were more likely to reach for their own mother's tool than an unrelated female's. Future work could examine the extent to which it is infant choice that limits such interactions to kin, or whether infants attempt such interactions with non-kin but are rebuffed.

Peering was the only positive behaviour that occurred at a similar rate in both groups. Juveniles and infants in both groups peered at both kin and non-kin adults. This may reflect the age of the juveniles and infants involved, as Schuppli et al. (2016) found that model preference in infant orangutans when peering changed with age, suggesting that infants initially learn from their mother, and then begin to peer at alternative social models as they get older. A greater number of observations of peering, conducted as infants aged, would be required in order to establish whether such an age effect exists in chimpanzees. Peering required an observer to be within 1m of a demonstrator for at least five seconds. It may be that peering was observed at a similar rate in both groups because this requires less tolerance on the part of the demonstrator than coaction or tolerated scrounging, both of which require physical contact between observer and demonstrator, and both of which may interfere with the demonstrator's success at the task (by physically impeding their actions during coaction, or by taking some or all of their earned reward in tolerated scrounging).

A limitation of the current study is that low frequencies of all relevant social interactions were recorded at the task, especially in Group 3. This prevented more thorough statistical comparison between the two groups, though the difference in proportion of positive and negative indicators, and the arithmetic differences in the rate of behaviours between the groups appear to indicate that Group 4 is more socially tolerant. However, more extensive long-term observation of the groups would be necessary to confirm these initial findings, as data collection for the current study was by necessity limited to the 40hrs of experimental task presentation.

5.5.2 Social network measures

According to the network metrics calculated, the groups' networks of inter-individual proximity at the artificial foraging task did not differ to a large extent. One measure in which they did appear to differ was in their centrality index, a measure of the relative centrality of the dominant male. In macaques, groups from intolerant species (rhesus macaques and Japanese macaques) have been found to have more central dominant males than groups from tolerant species (Tonkean macaques and crested macaques) (Sueur et al., 2011b). Group 3's dominant male, Brian, was more central to his social network than Group 4's dominant male, Commander, was to his, and this would concur with Cronin et al.'s (2014a) finding that Group 4 was more socially tolerant than Group 3. This may reflect a difference in dominance style between the two individuals, suggested to be a cause of the differences in social tolerance found by Cronin et al. (2014a), although in Group 3, the dominant individual has changed in the period between the two studies.

The groups had similar and very high network densities. This may have been due to the small size of the groups, as the fewer group members there are, the more likely it is that an individual will be observed with most of them at least once (though Sueur et al., 2011b, find no relationship between group size and network density in four species of macaque). The network densities observed in the current study were high in comparison to primate networks studied by Kasper and Voelkl (2009), who compared affiliative networks of 70 primate groups (including prosimians, New World and Old World monkeys, and both wild and captive groups ranging from four to 35 individuals). The maximum network density measured by Kasper and Voelkl (2009) was 0.93. However, Kasper and Voelkl's networks were based upon affiliative social interactions such as grooming, while in the current study, individuals had only to be within proximity of one another in order to be connected in the

network. Individuals may have to have a closer affiliation to one another in order to engage in grooming or play behaviour than they do to simply share spatial proximity, and so the fact that the social networks in the current study are proximity-based may contribute to the higher network density observed.

This also raises the issue of selecting the appropriate basis for a social network. Castles et al. (2014) found that proximity-based and interaction-based social networks were not comparable in chacma baboons, and argue that social networks should be viewed as "snapshot[s] of a particular group at a particular time" (p.66). While the networks in the current study provide information on groups' tendency to share spatial proximity at the 'dipping' task, and so provide an insight into their social tolerance in this particular situation, they may not provide generalisable information regarding the groups' social tolerance in other situations. Along with the fact that group composition has changed, and consequently group social tolerance may have changed, over time following Cronin et al.'s (2014a) study, the difference in context between the social networks presented here and Cronin et al.'s (2014a) social networks may contribute to the difference in social network metrics observed. In the current study, the mean association index of both groups was higher than that observed by Cronin et al. (2014a); while this may reflect a change in the association patterns of individuals over time, it seems highly likely that the presence of an artificial foraging task increased the groups' tendency to congregate, thereby increasing their association strength.

5.5.3 Social tolerance and behavioural flexibility

While previous studies of behavioural flexibility have not examined the potential impact of social tolerance upon performance, previous work has found that relevant behaviours are affected by levels of social tolerance. Acquisition of novel tool use is facilitated by social tolerance, with chimpanzees acquiring a behaviour more rapidly than gorillas and attending the task in larger groups and in closer proximity than gorillas (Lonsdorf, Ross, Linick, Milsteain & Melber, 2009). Likewise, affiliation promotes social learning of hand-clasp grooming in chimpanzees (Bonnie & de Waal, 2006). In common ravens (*Corvus corax*), affiliation improved performance on a social learning task, with affiliative sibling pairs matching one another's' behaviour more frequently than non-siblings (Schwab, Bugnyar, Schloegl & Kotrschal, 2008). Centrality in the social network predicted the speed with which captive squirrel monkeys (*Saimiri sciureus*) solved an artificial fruit foraging task (Claidiere,

Messer, Hoppitt & Whiten, 2013). These findings demonstrate that intra and interspecific differences in social tolerance can influence behaviour in experimental settings.

Many studies of behavioural flexibility in chimpanzees examine only one group of chimpanzees (Bonnie et al., 2012; Manrique, Völter & Call, 2013; Hopper, Kurtycz, Ross & Bonnie, 2015). The findings of this chapter indicate that this approach risks failing to provide generalizable results, as the two groups in my study, despite sharing identical environments and similar rearing histories, performed very differently. The findings presented in this chapter highlight the fact that group-level, intraspecific differences in social tolerance may affect social behaviour at artificial tasks, particularly if these tasks are presented in group contexts (eg. Lehner, Burkart & van Schaik, 2011). Damerius et al.'s (2017b) finding that captive orangutans living in larger social groups were more curious and performed better on a cognitive test battery implies that differences in captive primates' social environments may also affect their performance when tested individually. Further research is required in order to tease apart the mechanisms by which differences in social style might impact upon either performance on artificial foraging tasks (for example, by examining whether differences in rates of behaviours such as coaction and tool transfer lead to enhanced social learning of task solutions) or upon cognition directly (by examining whether individuals in more tolerant groups continue to show enhanced task performance when tested individually, as Damerius et al.'s, 2017b, finding might lead one to suspect).

Individual-level tolerance should also be considered. Following Damerius et al.'s (2017b) finding, one might predict that individuals that regularly have social contact with a variety of individuals might exhibit more curiosity and so respond more favourably to artificial foraging tasks. While Damerius et al. (2017b) simply considered the number of group-mates an individual had, it is possible that more peripheral group members do not interact with the same number of potential social partners as more central group members, and so the same positive effect upon curiosity may not be observed in all group members. Rawlings, Flynn and Kendal (2016) suggest that in children, social network position is likely to be linked to individual personality, with more extraverted, cooperative individuals likely to occupy more central positions, while individuals who interact with multiple subgroups may be more likely to innovate (Baer et al., 2015). Watson et al. (2018) conducted a meta-analysis of 16 social learning studies conducted with the same group of captive chimpanzees, and found that over

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half the variance in whether an individual made use of social information was accounted for by individual identity, and the authors suggest that personality is likely to be a key source of this inter-individual variance. In a group-testing context, individual differences such as these may affect the social information an individual has access to, their likelihood of using this information, and their propensity to innovate.

5.6 Conclusions

This study revealed differences between two captive groups of chimpanzees in the frequency of positive and negative social interactions at the artificial 'dipping' task presented in the previous chapter. Group 4, which performed most flexibly at the 'dipping' task, also appeared more socially tolerant in their interactions at the task, with lower rates of displacement and higher rates of coaction, tool transfer and tolerated scrounging. This meets some of the expectations one might have of a socially tolerant group following van Schaik's (2003) hypotheses; that social tolerance facilitates social learning, and facilitates innovation by reducing the risk of displacement. Differences between the groups' social networks, based upon proximity at the 'dipping' task were not apparent, though the centrality of dominant males to the networks differed in a manner consistent with differences in social tolerance. While group-level differences in social tolerance shown in this chapter broadly follow the group-level difference in behavioural flexibility, more research is needed to explore the potential relationship between the two, ideally incorporating multiple measures for tolerance and flexibility at both an individual and group level.

Chapter 6: The transmission of symbolic and non-symbolic images in transmission chains of four- to eight-year-old children

<u>Chapter 6: The transmission of symbolic and non-symbolic images in transmission</u> <u>chains of four- to eight-year-old children</u>

Abstract

This exploratory study examines a thought experiment first posed by Sperber (2000), aiming to illustrate the relative importance of replication and reconstruction in cultural transmission. The question of whether replicative or reconstructive processes explain the of stability of cultural items over time and space is integral to a debate between two schools of thought; 'standard' cultural evolution, and the cultural attraction or epidemiology of representations approach. In the current study, Sperber's thought experiment was conducted by diffusing both a symbolic and non-symbolic image along transmission chains of four- to eight-year-old children. The resulting groups of drawings were then presented to independent adult judges tasked with placing the drawings into the order they were produced (in other words, recognising which drawings were 'copies' of each other). Neither the symbolic nor the nonsymbolic model images survived the transmission process, with both being radically transformed. Drawings in both types of chain were subject to a loss of complexity (as measured by file size), though this occurred more rapidly in chains starting with the nonsymbolic model image. Independent judges were more successful at placing images from symbolically-seeded chains into the correct order. These results are contrasted with the predictions made by Sperber (2000), and the results of similar studies conducted with adult transmission chain participants. The possible cognitive constraints limiting children's ability to successfully transmit the model images are discussed.

6.1 Introduction

Two major frameworks for understanding and studying the transmission and transformation of cultural information can be distinguished; one, termed the 'standard' cultural evolution approach by Acerbi and Mesoudi (2015), suggests that this process can be understood in much the same way as biological evolution, as a Darwinian process in which cultural variants such as different behaviours or artefacts are subject to selection and so evolve as a result (Boyd & Richerson, 1985; Acerbi & Mesoudi, 2015; Mesoudi, 2016). The alternative approach, known as cultural attractor theory or epidemiology of representations, argues instead that cultural items (including, according to Scott-Phillips, 2017, both mental representations, such as beliefs, and their expression, such as behaviour or physical artefacts) are transformed by individual learners due to cognitive and environmental factors, and that cultural items are reconstructed by individuals rather than replicated (Sperber, 1996; Claidiere, Scott-Phillips & Sperber, 2014; Claidiere & Sperber, 2007; Scott-Phillips, 2017). Sperber argues that rather than being copies of an earlier model, most cultural items are instead 're-produced', and that while there are causal links between these reproductions, this process cannot be analysed in the same way genetic transmission is (in which units are replicated, with mutation driving variation) (Sperber, 2000). Whichever framework is favoured, both cultural variation and stability must be addressed by it, explaining both the consistency of cultural behaviours across time and space, and the extreme variation and rapid change in cultural behaviours that is also observed in human culture (Sperber & Hirschfeld, 2004).

The stability of culture has often been explained as the result of high-fidelity social transmission of cultural units. Indeed, such a capacity for high-fidelity social transmission has been argued to be a key factor facilitating the evolution of cumulative culture in humans, and may not occur even in our closest living relative, the chimpanzee (Tennie, Call & Tomasello, 2009). However, it has also been argued that high-fidelity social transmission of cultural units is not necessary to explain the stability and consistency of human culture, and that individuals instead recognise and reconstruct examples of cultural items (Scott-Phillips, 2017). This reconstruction is shaped by factors including the individual's cognition, and both ecological and social constraints, resulting in a tendency for cultural units to transform non-randomly toward a range of types called cultural attractors (Driscoll, 2011; Claidiere, Scott-Phillips & Sperber, 2014). Sperber describes a cultural attractor as "an abstract, statistical concept" (Sperber, 1996, pp.111), in that during the process of transformation, transformations occur

with greater probability in the direction of a specific point and then cluster around that point. However, Buskell (2017) points out an ambiguity in this conception of cultural attractors, in that this description could describe the transformation pattern ("the aggregation of all the transformation probabilities in a population", Buskell, 2017) or the point at which transformations cluster. The most common meaning of the term 'cultural attractor' appears to be the second concept Buskell suggests – the point or area at which transformations cluster. Sperber (2012) provides examples of cultural attractors, including a Happy Ending in stories, and rounded numbers, but also 'efficiency' in the manufacture of hunting tools. These examples are points, or areas, around which behaviours could cluster. If the cognitive, environmental, or social factors promoting transformation of a cultural unit toward an attractor are shared across disparate human populations, similar cultural practices may emerge independently (Miton, Claidiere & Mercier, 2015). This tendency for reconstructions to be shaped towards attractors is argued to lead to apparent stability of a trait without requiring high-fidelity transmission (Claidiere et al., 2014). The importance of individuals' transformation of cultural traits has not only been put forward by proponents of the cultural attractor approach, but is also included in models by Boyd and Richerson (1985) and described as 'guided variation' - a process whereby cultural traits are transformed in nonrandom directions by individuals (as opposed to random mutation, which an approach directly analogous to biological evolution would rely upon).

To address the question of whether replication (high-fidelity transmission) or reconstruction best describes the process by which cultural traits are passed on with minimal change, Sperber (2000) put forward the thought experiment which has been adopted as the focus of this study. Taking issue with Dawkins' promotion of a concept of cultural transmission based on replicated 'memes' (memetic units analogous to genes (Dawkins, 1976; 1982)) Sperber (2000) suggested that if participants are shown a non-symbolic figure (he offered the 'squiggle' in Figure 1) and asked to reproduce it, it is "most likely that each drawing will differ from its model and that the more distant two drawings are in the chain, the more they are likely to differ. A judge given the ten drawings in a random order and asked to put them back in the order in which they were produced should perform, if not perfectly, at least much better than random" (Sperber, 2000, p.166). Conversely, if participants are given a symbolic figure (Sperber suggested a five-pointed star, see Figure 1) to reproduce, two drawings in the chain are predicted to differ independently of their distance from one another, and a judge asked to put the drawings in order should be unable to do better than random – individual

variations are very unlikely to compromise this pattern. With the non-symbolic image, participants have the challenge of forming a mental image of an unfamiliar drawing, storing this information, recalling it and reproducing it, whereas participants shown the symbolic figure recognise the symbol and can produce another of the same type. In other words, participants in the non-symbolic condition are relying upon their ability to copy, while participants in the symbolic condition have no need to, but instead use their existing knowledge to produce a drawing of the same type. Sperber argues through this thought experiment that high-fidelity transmission is not the only potential source of stability in cultural traits (Sperber, 2000). Sperber contrasts his view directly with that of Dawkins' (1976) concept of 'memes' as replicating units of culture analogous to genes. Sperber's own prediction is that the symbolic star would show superior transmission compared to the nonsymbolic squiggle, and that a chain of drawings starting with the latter could be ordered by judges better than a chain that began with the symbolic star, whereas he suggests Dawkins' memetic conception would instead predict the non-symbolic squiggle could be transmitted faithfully and the 'chain test' would deliver a similar result. This debate effectively pits one thought experiment against another thought experiment, each author proposing how it would turn out. In the present study I set out to turn this debate directly into an empirical study.

Other experiments relating to the theoretical issues at stake here have been conducted using transmission chain designs to examine how images change as a result of repeated transmission events. Tamariz and Kirby (2015) compared the transmission of two nonsymbolic images along chains of adult participants, with two transmission-type conditions; in the 'Memory' condition, the model image was removed before participants were asked to reproduce it (therefore requiring participants to remember the image), while in the 'Copy' condition, the model image remained in view, allowing the participant to reproduce it without needing to commit it to memory. The authors found that images in the 'Memory' condition became less complex (they became smaller and were made up of fewer and shorter lines) and were more likely to turn into conventional symbols (for example, letters or numbers), while images in the 'Copy' condition retained more complexity (remained larger and were made up of more, longer, lines) and did not become symbolic. Tamariz and Kirby (2015) suggest that this effect is due to participants in the 'Memory' condition having to remember the images, with simpler images being less taxing to remember, and symbolic images like letters and numbers also making images more easily memorable. This study is relevant but does not directly test the contrast invoked by Sperber (2000), as the model images were both nonsymbolic; and although independent ratings were sought in measuring the 'abstractness' of the resulting images, the ability of independent judges to sort the images by their position in the transmission chain was not explored. Tamariz and Kirby (2015) demonstrate that both learning (the challenge of committing an image to memory) and reproduction (the process of producing the image) can transform transmitted images. Learning (assessed in their 'Memory' condition) led to increased compressibility, meaning images that could be compressed and stored using a smaller number of bytes. Images in the 'Memory' condition were also transformed into conventional symbols such as letters, which the authors argue likely increased their memorability. Reproduction (assessed in their 'Copy' condition) introduced random innovations via copying error. Relating this study to the Sperber (2000) thought experiment, the balance of 'learning' vs 'reproduction' in the symbolic vs. nonsymbolic model image conditions is expected to differ, with the symbolic image requiring less 'learning' (as it is recognisable), while the non-symbolic image requires more 'learning' as it cannot be classified as a known type. The symbolic image might therefore be relatively immune to the impact of modifications to increase compressibility and memorization, though random copying error might occur, while the non-symbolic image would be subject to the same alterations seen in Tamariz and Kirby's study – increasing simplification and perhaps facilitating increasingly symbolic images.

Scott-Phillips (2017) demonstrates how symbolic and non-symbolic images may be subject to different amounts of transformation during the transmission process using a paradigm that combines Tamariz & Kirby's (2015) with the Sperber (2000) thought experiment, providing participants with one of two model images, one showing the letters 'ABC' and the other a meaningless rearrangement of the component lines of these letters. In half of the transmission chains participants were required to memorise and then reproduce the model images, whilst participants in the other condition were required to trace the model images. Requiring participants to trace over the model images rather than copying them freehand as in Tamariz and Kirby (2015) might be expected to reduce the amount of copying error even further than that seen by Tamariz and Kirby (2015), and indeed, the resulting chains of images for both the symbolic and non-symbolic model images remained visually very similar to their starting models, with some limited effect of copying error. In the 'reconstruction' condition (in which participants were tasked with memorising and then reproducing the model images), the non-symbolic chains appeared to change more rapidly and did not result in images resembling the starting model image, whilst the symbolic chains resulted in images recognisable as the

letters 'ABC', though they did not closely match the model image in terms of style. This seems to demonstrate the effect Sperber (2000) predicted; that recognisable symbolic images would remain recognisable through repeated transmission events, and, Scott-Phillips argues, that this transmission is reconstructive rather than replicative. However, no statistical analysis was applied, and again, this study does not investigate the second part of Sperber's (2000) thought experiment; that independent judges should be able to ascertain the order in which images were drawn in the non-symbolic chain more easily than in the symbolic chain.

Sperber's thought experiment rests on the assumption that the symbolic image will be recognised by participants (thus allowing them to largely bypass the process of committing the image to memory, instead simply recalling that it was a five-pointed star and then producing an image of the same type when required). If the symbolic image is not recognised by participants (if, for example, it is a symbolic image derived from a different culture than that of the participants), one would expect the image to be passed along a chain in much the same way as a non-symbolic image might be – each participant attempting to commit it to memory before reconstructing it. However, a cultural attractors approach might suggest that such an image (symbolic in a different culture than that of the participants) already contains characteristics that might render it more memorable, and so might be transmitted more successfully along a chain.

A comparison of adult and child transmission chains transmitting patterns of dots on a grid found that algorithmic complexity was lost more rapidly when children reproduced patterns, but that the accuracy of transmission did not differ between adults and children (Kempe, Gauvrit & Forsyth, 2015). The authors suggest this is due to radical changes to the model patterns made by children in the early generations of transmission chains, which made patterns less complex and therefore more easily transmissible, allowing children to match adult levels of copying accuracy. Processing limitations in children may encourage reconstruction of the image being remembered and allow bias towards prototypes to affect this reconstruction (Kempe et al., 2015).

6.2 Chapter aims and hypotheses

Against the background of a very limited corpus of studies relevant to the thought experiment that Sperber (2000) set out, in the present study I sought to turn Sperber's thought experiment into an empirical experiment, with children participating in the transmission chains and adult participants then acting as independent judges, as Sperber suggested, to attempt to place the

resulting images in their correct order. Due to the limited amount of previous research in this area, the current study is exploratory in nature.

6.2.1 Replication vs. reconstruction

Sperber (2000) sets out clear predictions for how the symbolic vs non-symbolic images will be transformed by reconstruction as they are transmitted along chains. The chains seeded with the non-symbolic image will result in drawings that differ from the seeded image, and the further along the chain an image is, the more it will differ from the seeded image. The chains seeded with the symbolic image will result in reconstructions of the seeded image (drawings which resemble the seeded image), and while drawings within the chain may differ, this will not be related to how far along the chain they are (ie. drawings will not be exact facsimiles, but drawings at the end of the chain will be as similar to the seeded image as those at the start). In the current study, from Sperber's predictions, I would expect chains seeded with the non-symbolic image to result in ten drawings of stars, while chains seeded with the non-symbolic image will result in images that change along the chain, and may stabilise if a participant in the chain draws a symbolic image. Conversely, a 'memetic' approach would suggest that both symbolic and non-symbolic images will be transmitted along the chain equally well, each relying upon high-fidelity copying.

6.2.2 Independent judges

Integral to Sperber's (2000) thought experiment is the assessment of independent judges, asked to put the drawings resulting from the transmission chains into the order in which they were drawn. Sperber predicts that this will be impossible in symbolic-seeded chains (as all the drawings will be similar depictions of a star), but that in non-symbolic-seeded chains, a judge would be able to observe gradual, increasing transformations in the images, and therefore be able to place them into an order closely approximating the order in which they were drawn. As well as testing this assertion made by Sperber (2000), independent human judges will also provide subjective impressionistic assessment of the differences between drawings that would not be easily achievable via computerised methods.

6.2.3 Differences between adult and child performances

A wide age range of 4- to 8-years-old was used. Previous research has shown that children at 4-years-old are able to both understand and draw graphic symbols (Callaghan, 1999), and that children begin to draw human figures at an average age of 3 years and 7 months (Kellogg,

1969), which gave me reason to believe 4-year-olds might be able to recognise a symbolic image and also draw sufficiently well to engage in the task meaningfully. However, in this exploratory study it was unclear how children this young might respond to drawing on a tablet, and so a wide age range was recruited, to allow for the event that younger age categories might need to be excluded, and the age range narrowed, after testing began. A warm-up task was included to exclude any children who struggled with the physical task of drawing a recognisable image, and children up to 8-years-old were recruited in case large numbers of children in the younger age categories proved unable to pass this warm-up task.

Following Kempe et al.'s (2015) argument that processing limitations in children may encourage the reconstruction of images and the addition of structure, children might be expected to more rapidly add structure and symbolism to the non-symbolic model image being transmitted in Sperber's (2000) thought experiment than adults. Therefore, child participants may lead to more extreme changes in images than those observed by Scott-Phillips (2017) with adult participants. These changes may be more easily observable to independent judges, and may lead to more extreme change over the limited number of generations it is feasible to simulate in a transmission chain experiment. Kempe et al.'s (2015) results also suggest that the complexity of images produced can be expected to decrease rapidly with child participants, and following the prediction that the symbolicseeded chains will maintain the seeded image, I would predict this loss of complexity to occur to a greater extent in non-symbolic-seeded chains (in which greater transformation is expected).

6.3 Methods

6.3.1 Drawing

6.3.1.1 Participants

One hundred and five four- to eight-year-old children (mean age 79 months / 6.6 years) were recruited at three locations; Edinburgh Zoo, a university open day event, and the Dundee Science Centre (see **Chapter 2** for details). Five children were excluded from the study during testing due to parental interference. Due to the transmission chain design, these exclusions were made immediately, in order to preserve the integrity of each chain. Children were randomly assigned to chains, and this resulted in chains with mixed participant ages.

6.3.1.2 Materials

Each chain was started with one of the images suggested by Sperber (2000) and shown in Figure 1, displayed on an iPad. Children drew their responses on the iPad using the Paper app by FiftyThree, Inc. and a basic stylus.



Figure 1: The two starter images. 'Non-symbolic' on the left and 'Symbolic' on the right.

6.3.1.3 Procedure

Children were taken to a quiet area and sat opposite the experimenter. They were shown the iPad and stylus, and invited to draw a smiley face. This gave children an opportunity to practice drawing on the iPad, and also allowed the experimenter to assess their drawing skill. Children who failed to draw anything, or to draw anything recognisable as a smiley face, at this stage were to have been excluded from the study (this situation never arose). Each child was then shown an image on the iPad and asked to "look at it very carefully, because you are going to try and copy this drawing". They were shown either one of the model images (Figure 1) if they were the first child in a chain, or the drawing done by the previous participant if they were further along in the chain. The child was then given the iPad and stylus and asked to "do your best to draw as much as you can remember of the picture you just saw". Children who hesitated were encouraged to draw "anything you remember of that drawing". All children were then rewarded with a sticker for participation in the study.

6.3.1.4 Analysis

The mean age of participants within each chain was compared using an ANOVA. To analyse the drawings produced, they were exported from the Paper app and converted into JPEG file format. The exported and converted images all measured 2048x1536 pixels and 96 dpi resolution. As all images were the same size (ie. while the drawing might be larger or smaller, the overall image including blank space around the drawing always measured 2048-1536 pixels) and all drawings were made using the same set line thickness, they did not require further manipulation for JPEG file sizes to be standardized to allow for image comparison. JPEG file sizes were compared as detailed below, as a proxy measure of image complexity (these file sizes indicate the *compressibility* of the images – the extent to which the image can be stored in as short a sequence of numbers as possible, shortened when images contain few elements, Forsythe et al., 2011). Such file sizes have been found to be predictive of subjective complexity ratings (Donderi, 2006; Forsythe et al., 2008). As previous studies have shown strong correlations between file size measures and subjective human ratings of image complexity, file sizes were used in the current exploratory study to allow rapid analysis of the large number of images produced. The file sizes were analysed using a linear mixed-effects model (LMM), using the function lmer in the R statistics package lme4 (Bates, Maechler & Bolker, 2012). This model fitted Position in Chain and
Starter Image (Symbolic vs Non-symbolic) as predictor variables, with JPEG file size as the outcome variable, and a random effect of Chain.

6.3.2 Rating

6.3.2.1 Participants

Thirty-three adults were recruited as image raters via online advertisement (Appendix B) at the University of St Andrews.

6.3.2.2 Procedure

Participants were presented with the ten chains of drawings completed by children in the 'Drawing' portion of the study. The drawings were presented on the Qualtrics online survey platform in a random order. Each question posed to raters was accompanied by all of the drawings from a single chain, in a random order. Participants were told that the drawings had been done by participants in a previous study, and the transmission chain process was briefly explained using the following text:

"In a previous study, we asked participants to copy simple drawings. Each participant was shown a drawing done by a previous participant and asked to do their best to memorize and copy it. Their drawing was then shown to the next participant, to form a 'chain' of 10 participants, with each person copying the drawing of the previous participant.

We are now interested in whether people are able to put these 'chains' of drawings into the order in which they were drawn - in other words, can we recognise which drawings are copies of others?

In this study, you will be shown 10 chains of 10 drawings each, and asked to place them in the order in which you think they were drawn. In each case, you will be shown the first drawing, and can then place the following drawings in whichever order you think is correct. Participants in the original study sometimes struggled to remember and copy the drawings accurately, and so the correct order may not always be obvious."

Participants were asked to attempt to place the ten drawings of each chain into the order that they had been drawn, by dragging and dropping the images into a grid (Appendix C). Multiple images could be placed in the same category of the grid if participants were unsure as to their order (for example, if a participant struggled to differentiate their drawing six from drawing seven, both could be placed in category six). All participants rated all ten chains.

6.3.2.3 Analysis

Each participant's responses were downloaded and coded to produce numerical sequences. The order in which participants placed the 10 images of each chain produced a sequence of numbers (the "given position"). A participant who correctly ordered the images would produce the sequence [1, 2, 3, 4, 5, 6, 7, 8, 9, 10]. Two values were calculated to measure the dissimilarity between the participants' submitted sequences and the true order of the images, using the R package 'stringdist' (van der Loo, 2014). The Levenshtein distance (Levenshtein, 1966) is the minimum number of insertions, deletions or swaps needed to transform a target sequence into a source sequence (in this case, to transform the raters' sequences into the correct order of the images). The longest common substring (LCS) is the longest subsequence which can be made by pairing integers from the target and source sequence – the value generated by the stringdist package indicates the number of unpaired integers after the longest common substring has been formed. Both Levenshtein distance and LCS were analysed using GLMMs with poisson distributions, a main effect of Starter Image, and random effects of both Chain and Participant.



Figure 2: Example image chains drawn by participants (six of ten chains are shown in their entirety). On the left are three example chains starting with the Symbolic image and on the right, three example chains starting with the Non-symbolic image. All participants' drawings are numbered in the order drawn.

6.4 Results

6.4.1 Age of participants

An ANOVA shows that age did not differ significantly by chain (F(1, 97) = 0.69, p = 0.41), indicating that while chains were composed of a mixture of ages, no chains were composed of significantly older or younger children than others.

6.4.2 Children's drawings

Visual inspection of the children's drawings shows that no chain, in either the star or squiggle condition, successfully maintained the form of the original starting images across all ten participants (representative example chains are shown in Figure 2), and in the majority of chains this starting form was lost rapidly. In only two of the five Symbolic chains did a child successfully reproduce a five-pointed star, and in both cases this was only achieved by the first participant. In one of these chains, the second child drew a six-pointed star, but the third participant did not draw a star of either kind. No child successfully reproduced the Non-symbolic image in the five chains for which this was the model. In some chains other symbolic figures appear to emerge (Figure 2), for example, in separate Non-symbolic chains shown in Figure 2, a heart shape appears in some images, and in another chain figures resembling the number 7 and letter L appear; however, these symbolic figures do not remain throughout the chain. In all chains, both continuity between images and substantial change can be observed.

6.4.2.1 Drawing complexity

A linear-mixed effects model (Table 1) shows that position in the chain had a significant impact upon image complexity as measured by file size, with file size decreasing as position in the chain increased. There was a significant interaction between position in chain and starter image (Symbolic vs Non-symbolic) such that chains with the Symbolic starter image began from the first participants' drawing with lower complexity, but saw a smaller decrease in file size with each increasing position in the chain after that than did chains which began with the Non-symbolic image (note that the model images themselves were not included in the chains, and so the image in the first position in the chain was the image drawn by the first participant – first position participants in the Non-symbolic condition tended to draw images that had greater complexity than those in the Symbolic condition).

For each additional position along the chain, drawings in Non-symbolic chains decreased in file size by a factor of 0.008, while drawings in Symbolic chains decreased in file size by a factor of 8.05^{e-10} for each additional position along the chain, or in other words decreased 14 times less per position than those in Non-symbolic chains. A likelihood ratio test indicated that a model containing this interaction was a significantly better fit than a model with no interaction between position in chain and starter image ($\chi^2 = 10.37$, df = 1, p = 0.001; dAIC = 8.37), and better than a null model containing only the random effect of chain ($\chi^2 = 60.10$, df = 3, p < .0001; dAIC = 54.1). It should be noted that the Non-symbolic starter image (255kb and 125kb, respectively). However, this image was photocopied from the literature, resulting in heavier line weight than the Symbolic starter image, which was drawn in the same application, and converted to a jpeg at the same size and resolution as the Symbolic image filesize. It seems likely therefore that the two images were well-matched in terms of compressibility.



Figure 3: The JPEG file size of each image plotted by its position in the transmission chain (position 1 being the first participant, rather than the starter image). Points are coloured by the starting image of the chains. Lines show the fitted linear mixed effects model (Table 1) for each starting image, with JPEG file size predicted by position in chain and starter image. Shaded areas indicate the 95% confidence interval. Plotted using R package sjPlot (Lüdecke, 2017).

Table 1.

	Estimate	[Wald 95% CI]	Std. error	t value	P value
Intercept	114.31	[103.60, 125.02]	5.46		
Position in chain	-4.77	[-5.89, -3.65]	0.57	-8.35	9.09 ^{e-13} ***
Starter image (Symbolic)	-18.82	[-33.96, -3.67]	7.73	-2.44	0.022*
Position * Starter (Symbolic)	2.65	[1.07, 4.24]	0.81	3.28	0.001**
*n<0.05 $**n<0.01$	***n<0.00	1			

Results of a linear mixed-effects model on the impact of 'Position in chain', 'Starter image', and an interaction between the two on JPEG file size, with random effect of 'Chain'

°p<0.05, **p<0.01, ***p<0.001

6.4.3 Independent ratings

The ratings given by the independent raters were analysed as sequences. These rater sequences were compared with the correct sequence. Dissimilarity between the two indicates how accurately raters were able to order the images from the chains. The median rating for each image (Figure 4) shows that images in Symbolic chains were more frequently given their correct position in the chain by independent raters than were images in Non-symbolic chains, with the median rating for Symbolic chain images matching the images' true position in the chain. Two metrics were calculated to measure this dissimilarity; the Levenshtein distance (see Figure 5 and Table 2) and the longest common substring (see Figure 6 and Table 3). In both cases, the higher the value, the more dissimilar the two sequences.



Figure 4: Median and interquartile range of ratings given to images by the independent raters, grouped by starter image (Non-symbolic vs Symbolic). Boxes indicate the 25th to 75th percentile, and horizontal lines indicate the median rating given to each image by raters. Vertical lines indicate data points within 1.5 times the interquartile range. Points indicate outliers (values outwith 1.5 times the interquartile range).



Figure 5: The median and interquartile ranges of the Levenshtein distances produced by comparing each participant's sequencing of the images with the true sequence, displayed by Starter image (Non-symbolic vs Symbolic). Boxes indicate the 25th to 75th percentile, and horizontal lines indicate the median rating given to each image by raters. Vertical lines indicate data points within 1.5 times the interquartile range. Points indicate outliers (values outwith 1.5 times the interquartile range). For explanation of the significance of the contrast, see text.

A GLMM (Table 2) found that participants' sequences generated from chains starting with the Symbolic starter image had a significantly lower Levenshtein distances than those generated from chains starting with the Non-symbolic starter image (Figure 5), such that sequences generated from Symbolic chains had a lower Levenshtein distance by a factor of 0.61 in comparison with Non-symbolic chains. A likelihood ratio test comparing this model with a null model containing only the random effect structure of Chain and Participant showed that the full model was a significantly better fit ($\chi^2 = 7.54$, df = 1, p < .006; dAIC = 5.5).

Table 2.

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Results of a GLMM using Starter image to predict Levenshtein distance, with a random effect of Chain and Participant

	Estimate	95% Confidence	Std. Error	z value	p value
		Interval			
Intercept	1.79	[1.59, 2.00]	0.10		
Starter (Symbolic)	-0.49	[-0.77, -0.20]	0.15	-3.34	< 0.001***
*** . 0.001					

*** = *p* < 0.001.

Table 3.

Results of a GLMM using Starter image to predict Longest Common Substring values, with a random effect of Chain and Participant

	Estimate	95% Confidence	Std. Error	z value	p value
		Interval			
Intercept	2.09	[1.85, 2.33]	0.12		
Starter (Symbolic)	-0.56	[-0.89, -0.23]	0.17	-3.36	< 0.001***
*** < 0.001					

*** = p < 0.001

A GLMM (Table 3) found that participants' sequences generated from chains starting with the Symbolic starter image had significantly fewer integers remaining outside the longest common substring than those generated from chains starting with the Non-symbolic starter image (Figure 6), such that sequences generated from Symbolic chains had fewer remaining integers by a factor of 0.57 in comparison with Non-symbolic chains. A likelihood ratio test comparing this model with a null model containing only the random effect structure of Chain and Participant showed that the full model was a significantly better fit ($\chi^2 = 7.56$, df = 1, p < .006; dAIC = 5.6).

Both of these measures of sequence similarity (Levenshtein distance and LCS), indicate that participants were better able to approximate the true order of the images for chains which began with the Symbolic image than the Non-symbolic image, with both measures being significantly lower for chains with a Symbolic starter image.



Figure 6: The median and interquartile ranges of the number of integers remaining outside the longest common substring formed when comparing each participant's sequencing of the images with the true sequence, displayed by Starter image (Non-symbolic vs Symbolic). Boxes indicate the 25th to 75th percentile, and horizontal lines indicate the median rating given to each image by raters. Vertical lines indicate data points within 1.5 times the interquartile range. Points indicate outliers (values outwith 1.5 times the interquartile range). For explanation of the significance of the contrast, see text.

6.5 Discussion

This study found that when four- to eight-year-old children transmitted images across transmission chains, image complexity (as measured using file size) decreased more rapidly in chains beginning with a non-symbolic image than in those beginning with a symbolic image. Independent adult judges also had less success placing images from non-symbolic chains into the order in which they were drawn than images from symbolic chains. No chain, symbolic or non-symbolic, resulted in an image resembling the model images. Under both a cultural attractors and a standard cultural evolution framework, one would predict successful transmission of the symbolic image along transmission chains. In a cultural attractors framework, this would be achieved through each participant recognising the symbol and reconstructing it, while a standard cultural evolution approach would suggest a greater role for high-fidelity copying. However, only a standard cultural evolution approach would predict successful transmission of the non-symbolic image (through high-fidelity copying), while a cultural attractors approach would predict transformation of this image by each successive participant, perhaps towards a more symbolic attractor. In this study, neither image type was successfully transmitted. Both lost complexity, and no chains resulted in images recognisable as the seeded image (Figure 2). Moreover, independent judges were able to place images from both chains back into the order in which they were produced (Figure 4), doing so more successfully with images from chains seeded with the symbolic image.

The results from the independent judges differ from the predictions put forward by Sperber (2000) in his description of the thought experiment. Sperber (2000) predicted that independent judges would be able to place images from a transmission chain seeded with the non-symbolic image into an order well approximating their true order of production, but would perform at chance when attempting to place images from a transmission chain seeded with the symbolic image into their correct order. Here, we instead find that independent judges were in fact better able to place images from the symbolic-seeded chains into their correct order. This difference between the predicted results from independent judges and our findings points to a larger discrepancy between Sperber's (2000) predictions and our findings, in that the symbolic-seeded chains did not result in a "stable pattern" of close approximations of the model image, and instead the model image was lost fairly rapidly. This result is also different from that of Scott-Phillips (2017), who found that transmission chains of adult participants, asked to remember and reproduce symbolic and non-symbolic model images, were able to retain the symbolic model image in a recognisable form, but that the

form of the non-symbolic model image was lost within a few generations. There are several reasons why children might perform differently from adults on this type of task.

It is possible that children, especially those at the younger end of the sample, were limited in their capacity to draw this specific symbolic model image (a five-pointed star), due to motor control issues. If children early in the symbolic-seeded chains were unable to produce a fivepointed star for this reason, the transmission chain design meant that the model image was then lost for the remainder of the chain. The age of the children founding each chain was not controlled as children were randomly assigned to a chain, and could therefore range from 4years-old to 8-years-old, and this variability in the age of the first participants could have contributed to the loss of model images in some chains (although the mean age of participants did not differ between chains, these ages were distributed differently throughout each chain). Future work would benefit from a larger sample size, to allow analysis of such age effects which is not feasible given the limited sample size of the current study (for example, comparing chains which began with younger children with those beginning with older children), and would also benefit from constructing chains with more limited age ranges, which would allow comparison of age groups. Selecting model images with motor requirements easily achievable for children in this age range might also have improved fidelity of transmission in both symbolic and non-symbolic chains.

Within a 'cultural attractors' framework however, one might expect that even if unable to produce a five-pointed star, children would attempt to produce the concept of a star, perhaps resulting in six-pointed or asterisk style star images. Indeed, in a previous, unpublished study (Whiten, Mesoudi & Brown, unpublished data) in which adults passed Sperber's symbolic and non-symbolic images along transmission chains of 10 or 20 participants, this was a frequent outcome, with five of nine chains seeded with a five-pointed star culminating in a six-pointed star (the remaining four chains did not result in either type of star image; Appendix C). In the current study this occurred only in one symbolic-seeded chain (chain 1, Figure 2), and the six-pointed star produced was not then itself copied accurately. Other than this case, it appears that children in the early generations of symbolic-seeded chains made unsuccessful attempts to faithfully copy the five-pointed model image, though a larger sample would be required to examine this issue, as only five chains were seeded with the symbolic image. It may be that the instruction given to children, to "try and copy the drawing", promoted a focus on high-fidelity copying, discouraging children from producing images matching the general token (a star) rather than the specific form (a five-pointed star

drawn without lifting pen from paper) of the model image. Had children been asked for example, to "draw the same thing this person tried to draw", we may have seen the emergence of star drawings of different forms, rather than the loss of the star-type model image. Sperber (2000) suggests that what will be reproduced in symbolic-seeded chains in this experiment is "the implicit instruction ("draw a five-branched star without lifting the pen")" (2000: p.168), however, it is not clear that this is how children in the early generations of the transmission chains in fact interpreted the task they were faced with. Comparing transmission chains in which children are given the instruction to either "copy the drawing" or an explicit instruction based upon what Sperber argues is implicit in the task, to "draw a five-branched star without lifting the pen" would indicate whether children in fact placed greater emphasis on high-fidelity copying than they did the reproduction of the token-type (a star) in this study.

Although no alternative star-type images emerged in the symbolic-seeded chains, there are chains in which 'conventional' images do appear to emerge (for example, Figure 2: '7C' in images 7-8, chain 4; a heart shape in images 2-5, chain 5; a smiling face in image 10, chain 3). Some of the images produced by children also resemble the drawings documented by Kellogg (1969); for example, chain 1 (Figure 2) is primarily composed of images depicting overlapping shapes, a type of drawing Kellogg terms "Combines". Kellogg suggests this type of drawing is a developmental step that can be observed in many children, with this developmental process resulting in the depiction of human figures, which first begin to be drawn when children are an average of 3 years and 7 months old. 'Combines' and 'Diagrams' (Kellogg's terms for overlapping shapes, and "deliberate line formations that enclose an...area" 1969, pp. 45) are seen in drawings produced by children aged 2 years upwards (Kellogg's study only includes children aged 2 years and older, so it is possible these types of drawing emerge even earlier). While these images are not easily interpretable as meaningful from an adult perspective, it is possible that they hold some meaning or are recognisable to the children producing them. However, emerging symbolic images in the chains are also not retained. Given that these emergent symbolic images would seem to be simpler to produce in motor terms than a five-pointed star, this may hint that it is not purely motor complexity that prevents symbolic model images from being retained along transmission chains in children. The fact that in Whiten et al.'s unpublished data set, no transmission chain of adult participants resulted in a five-pointed star despite being seeded with this recognisable model

image also lends some weight to the argument that limited motor ability alone did not result in this outcome in child participants.

It is also possible that both model images were too complex to be retained in children's working memory. However, the 'conventional' nature of the symbolic model image would be expected to render it more easily memorable (Bartlett, 1932; Tamariz & Kirby, 2015). The reduction in complexity (as measured by file size) in both symbolic and non-symbolic-seeded chains suggests that children's working memory did constrain the images that were produced, as repeated transmission promoted compression of the images, an effect also seen in adult participants in Tamariz and Kirby's (2015) transmission chain study, and in children and, to a lesser extent, adults, in Kempe et al. (2015). The symbolic-seeded chains in the current study did see a more gradual reduction in image complexity than the non-symbolic-seeded chains, but given the general rapid loss of the model image in these chains (Figure 2), it seems unlikely that this is due to enhanced memorability of the symbolic image as the majority of children in these chains for more generations may have resulted in a level of image complexity at which reduction in complexity ceased, perhaps indicating an optimum level of complexity at which children were able to remember and reproduce an image.

The model images used in the study (the images shown to the first participant in each transmission chain) were those proposed by Sperber (2000); a five-pointed star, and a non-symbolic 'squiggle'. While the focus of Sperber's thought experiment and the current study is upon the effect of the symbolic vs. non-symbolic nature of the stimuli, there are additional differences between these two model images; both can be drawn without lifting pen from paper, but the non-symbolic 'squiggle' includes curved lines while the five-pointed star is composed of straight lines. The five-pointed star is self-contained in that all the lines join up, whereas the 'squiggle' is open in that the lines forming it do not join. For the purposes of this exploratory study, I chose to use these images proposed by Sperber (2000); an alternative approach that future work could benefit from would be to follow Scott-Phillips (2017) and use the lines that make up the symbolic image to form a non-symbolic image. This would ensure that the only difference between the two starter images is their symbolic meaning.

It is possible that the less rapid loss of complexity in symbolic-seeded chains contributed to the independent judges being better able to place these images into their correct order. More rapid change in the non-symbolic-seeded chains, particularly in the early generations (Figure 2, Figure 3) may have made it more challenging to identify images from early and late generations in the chain. Impressionistic visual inspection of the images produced by early participants in the symbolic-seeded chains indicates that these early images may have held greater visual similarity to the seeded image (Figure 2), which may have allowed independent judges to more easily identify early vs late images in symbolic-seeded chains.

Differences between adult and child performance on image transmission tasks, shown by Kempe et al. (2015), and implied when considering the current study in comparison with that of Scott-Phillips (2017), should be examined further. Differences in cognitive capacity might lead to different biases in terms of cultural item transformation. Studying cultural transmission in children, for example, might shed light on the effect of reduced working memory in the transformation of cultural items, and this understanding would be useful whether working within a cultural attractors framework or from the perspective of 'guided variation'. Kempe et al. (2015) argue that as children are learners of cultural behaviours and social conventions, and may play an important role in processes such as creolisation of language (Senghas & Coppola, 2001), it is crucial to understand how cultural units might be transformed as a result of being learnt and transmitted by children.

Comparison of child and adult performance might also provide information on what qualities promote stability in the transmission of cultural traits. In the current study, stability in the transmission of the model images did not occur, although visual inspection of the resulting drawings (Figure 2) does perhaps indicate some stability in the transmission of images at the end of some chains (eg. Figure 2: images 5-10, chain 3; images 8-10, chain 6). Notably, neither of these instances of stability appear to involve symbolic images, and so by Sperber's predictions, one might expect chains seeded with such images to be subject to transformation rather than faithful reconstruction. Neither high-fidelity copying of the model images or the reconstruction of known cultural tokens (eg. stars) appears to have occurred in a manner allowing the reproduction and stability of the model images. A key question within a cultural attractors framework must be why certain cultural items are particularly reproducible (Scott-Phillips, 2017), and beyond this, what cognitive, ecological, or social factors render certain cultural items easily reproducible. Equally, when considered from the perspective of 'guided variation' (Boyd & Richerson, 1985) within the 'standard' cultural evolution approach (Acerbi & Mesoudi, 2015), the question of what factors guide this variation is worthy of exploration. Comparison of adult and child performance on transmission chain tasks like that in the current study could highlight cognitive abilities that develop with age, such as working memory, that may influence the transformation of cultural items in predictable ways.

While this study focused upon the transmission of drawings, and particularly examined the effect of a recognisable symbolic model image upon the transmission of drawings by children, far more research using this methodology has focused upon the transmission of cultural items in the form of solutions to physical tasks (Horner, Whiten, Flynn & de Waal, 2006; Flynn & Whiten, 2008; Flynn, 2008; Hopper, Flynn, Wood & Whiten, 2010; McGuigan & Graham, 2010; Tennie, Walter, Gampe, Carpenter & Tomasello, 2014). In all these cases, children appear to be capable of sustaining a stable pattern of behaviour across generations, and to some extent even when the behaviour is composed of several actions. For example, McGuigan & Graham (2010) found that when three-year-old children passed on behaviour in which a puzzle box was opened using a three-step process, two of these steps were maintained across all generations of the chain. Comparison of the stability in transmission chains of cultural units from different domains of behaviour might also give some insight into the cognitive abilities required either for high-fidelity transmission or for successful reconstruction of behaviours (whether examined from a cultural attractors or 'standard' cultural evolution framework). If children are indeed more successful at passing on and acquiring physical solutions to problems than they are at successfully transmitting drawings, as in the current study, what are the qualities and components of these behaviours which result in this difference? Learning a physical solution to a task in a transmission chain paradigm is likely to require working memory, and some level of physical dexterity to then produce the behaviour when needed. Despite the possibility that they make similar cognitive demands, children appear to perform better when faced with this type of cultural product than with the drawings in the current study. However, there are likely to be far greater degrees of freedom in the drawing task than in a physical problem solving task, as children were entirely unconstrained in what they chose to draw, whereas in many artificial problem solving tasks there may be only a limited number of potential actions a child could use to interact with the task. The role that these degrees of freedom play in making a cultural item more or less sustainable over a transmission chain could be examined by manipulating the degrees of freedom in the current task – for example, providing children with pre-drawn lines that can be assembled into relevant shapes rather than requiring them to draw freehand. Conversely, one could also increase the degrees of freedom in physical problem solving tasks, for example, by

adding 'distractor' tool items to tasks involving the use of tools, or by adding additional ways of interacting with the task (eg. additional moving parts).

6.6 Conclusions

Sperber (2000) put forward the thought experiment that is the focus of the current study in order to argue that cultural transmission, and the stability over time and space of cultural items, can be (and often is) achieved via reconstruction rather than by replication. Our study finds that children neither replicate nor reconstruct the model images put forward by Sperber to illustrate his thought experiment. As predicted by Sperber, the non-symbolic model image is lost rapidly in the transmission chain, but against Sperber's prediction, children faced with a symbolic model image fail to either copy the specific form, or to reconstruct a similar token (as cultural attraction theory might suggest). Stability does appear to occur in some chains (Figure 2), perhaps indicating that this is only possible when images have reached a reduced level of complexity, perhaps due to decreased demands on children's working memory or motor skills. The fact that this stability emerged for images which held no obvious symbolic meaning may lend support to the 'standard' cultural evolution approach; though potentially constrained by working memory capacity (and therefore by the complexity of the image), children were able to successfully reproduce these images, against Sperber's prediction that non-symbolic images would be repeatedly transformed to the point of being unrecognisable. While the findings of the current study do not lend clear support to either side of this debate, as they do not neatly fit with the predictions made in favour of either cultural attractors or standard cultural evolution, some aspects of the study do make more sense when viewed in a standard cultural evolution framework. The emergence of stability in some chains (Figure 2), when images reached a lower level of complexity, and crucially without the clear emergence of symbolic images, indicates a role for high-fidelity copying in achieving this stability.

Chapter 7: General Discussion

Chapter 7: General Discussion

7.1 Summary of findings

In **Chapters 3** and **4** I investigated the capacity of multiple groups of chimpanzees to behave flexibly in response to a changing artificial foraging task, based upon the tool-use task used by Lehner et al. (2011). In order to succeed, chimpanzees had to abandon previously successful behaviours in order to overcome task constraints. I found that all groups responded with some flexibility, with individuals increasing their use of effective solutions and decreasing their use of techniques which had been rendered ineffective. However, no individual in the group tested in **Chapter 3** used effective solutions for more than 50% of their attempts, suggesting that they did not fully abandon techniques which had been made ineffective by the change in task parameters. In **Chapter 4**, a comparison of two groups both resident at an African sanctuary (the majority of whom were wild born, though often hand raised by humans) showed that one group altered their behaviour in response to the change in task to a greater extent than the other. This group also showed more extensive use of novel Tool Composite techniques, and modified these techniques when required tool materials were removed. Despite the introduction of scaffolding, the second group did not use Tool Composite techniques extensively.

In **Chapter 5**, I explored social tolerance as one potential explanation for the difference in performance between the two groups of chimpanzees studied in **Chapter 4**, prompted by a previously documented difference in the level of social tolerance between these two groups (Cronin et al., 2014). Social tolerance was measured via observation of inter-individual social interactions at the task and additionally via social networks based upon co-presence at the task. While the two groups did not differ in the majority of social network measures taken, the more flexible group had more positive social interactions at the task, indicating a higher level of tolerance.

In **Chapter 6**, I extended the scope of my studies and research training by conducting a transmission chain study based upon a thought experiment proposed by Sperber (2000) to examine the roles of replication and reconstruction in cultural transmission, comparing the transmission of symbolic and non-symbolic model images along transmission chains of four-

to eight-year-old children. Neither model image survived the transmission process, with both being transformed as they were passed along participants in the chains. Drawings in both types of chain were subject to a loss of complexity (as measured by file size), though this occurred more rapidly in chains starting with the non-symbolic model image. The drawings produced by children in the transmission chains were then given to independent adult judges to place in the order in which they had been drawn, and these judges were more successful at placing images from symbolically-seeded chains into the correct order.

7.2 Behavioural flexibility in chimpanzees

Previous experimental studies of behavioural flexibility in chimpanzees have provided mixed results. In some studies, chimpanzees have appeared highly conservative (Hrubesch et al., 2009; Marshall-Pescini & Whiten, 2008; Hopper et al., 2011; Gruber et al., 2011; van Leeuwen & Call, 2016), while in others, they have behaved flexibly (Yamamoto et al., 2013; Manrique et al., 2013; van Leeuwen et al., 2013; Hopper et al., 2015; Davis et al., 2016; Vale et al., 2017). In **Chapters 3** and **4**, while all groups of chimpanzees were able to significantly increase their use of effective techniques (indicating flexible behaviour), individuals in one group did so to a far greater extent than those in the other groups.

These studies presented in this thesis add to the existing literature on the ability of chimpanzees to behave flexibly when faced with a changing foraging task. Like Hrubesch et al. (2009), Marshall-Pescini and Whiten (2008), Gruber et al. (2011), Yamamoto et al. (2013), and Vale et al. (2017), the task required chimpanzees to use tools to successfully retrieve a reward, and like the results of these previous studies, the results from **Chapters 3** and **4** are mixed regarding behavioural flexibility. The overall finding, that all groups altered their behaviour to some extent and were significantly more likely to use efficient techniques when task changes required them, supports findings from Yamamoto et al. (2013), Manrique et al. (2013), Davis et al. (2016), and Vale et al. (2017) suggesting that chimpanzees can behave flexibly in response to artificial foraging tasks. However, previous experimental studies have not explicitly compared performance from multiple groups on this type of task, while I found in **Chapter 4** that one group performed significantly more flexibly than another at the same facility, with a third group in **Chapter 3** failing to adopt efficient techniques for more than 50% of their attempts. While methodological differences in terms of task

presentation and the availability of different techniques preclude direct statistical comparison between the Edinburgh Zoo results and Chimfunshi Wildlife Orphanage (CWO) results, it appears that, like Group 3 at CWO, the Edinburgh Zoo group responded to the task with more limited flexibility than did Group 4 at CWO, using fewer techniques and continuing to use inefficient techniques for more than 50% of their attempts. This may indicate that some of the divergence in findings in the existing literature could be due to differences between the groups of chimpanzees included in different studies. In **Chapter 5**, I examined the potential influence of two groups' social tolerance upon performance in the behavioural flexibility task, but the age of individuals tested, and the rearing history and enculturation of chimpanzees in different groups and facilities could also influence the results of these studies.

Davis et al. (2016) found that chimpanzees relinquished a known foraging technique only when it was rendered highly inefficient, and it may be that in foraging tasks, techniques must be either highly inefficient or entirely impossible in order for chimpanzees to be prepared to flexibly alter their behaviour (in comparison to studies such as Marshall-Pescini and Whiten, 2008, in which chimpanzees' known technique remained effective, though less rewarding than an alternative). This was the case in the task used in Chapters 3 and 4, and may have facilitated the flexible behaviour observed. The complexity or difficulty of the task may also affect the likelihood of chimpanzees exploring alternative methods, as the potentially timeconsuming effort required to find alternative solutions may outweigh the cost of continuing to use relatively inefficient known solutions. Further research is required to investigate the possibility that a large discrepancy in reward, or a relative cost of acquiring an alternative behaviour lower than that of continuing a known behaviour, is required to prompt flexible behaviour in chimpanzees. If this proves to be the case, it has implications for the evolution of cumulative culture. If chimpanzees are substantially constrained in their exploration of alternative solutions (through either individual learning, as in Hrubesch et al., 2009, or social learning, as in Marshall-Pescini and Whiten, 2008) until their known solution is rendered highly inefficient or entirely unrewarding then we can expect it will be unlikely they would engage in the gradual modification and improvement of behaviours which is crucial for cumulative culture.

However, many wild chimpanzee habitats are currently undergoing rapid, human-induced, environmental change (Hockings et al., 2015; McLennan, Spagnoletti & Hockings, 2017),

and this may prompt behavioural change as previously exploited resources disappear, or when novel opportunities arise as a result of human activities such as agriculture. This anthropogenic environmental change could lead to situations in which current behaviours become impossible or unrewarding, and prompt exploration of alternative behaviours. Indeed, several studies have shown behavioural changes in chimpanzee populations impacted by human activity. McCarthy, Lester and Stanford (2016) found that chimpanzees (P. t. schweinfurthii) living in forest fragments between the Budongo and Bugoma Forests in Uganda often nested in introduced tree species such as eucalyptus and also reused nests substantially; both behaviours, the authors suggest, are flexible responses to deforestation and agricultural development. Crop-feeding is a common response to human agricultural activity in chimpanzee habitats (Hockings & McLennan, 2012), and as crops are often energy-rich, digestible, and grown in concentrated areas, they likely offer an advantage over naturallyoccurring foods (Hockings, Anderson & Matsuzawa, 2012), though crop-feeding carries the risk of potentially fatal conflict with humans (McLennan, 2008). Chimpanzees have been shown to adjust their activity budget to incorporate crop-feeding, with chimpanzees (P. t. *verus*) at Bossou spending more time travelling, feeding, and socialising, and less time resting, on days they crop-fed (Hockings et al., 2012), and males in particular reducing their resting time substantially during periods of wild fruit scarcity. The Sebitoli chimpanzees (P. t. schweinfurthii) in the Kibale National Park in Uganda crop-feed at night, an unusual and likely novel behaviour as lengthy, repeated nocturnal activity, outside of moonlit nights, has not been reported in chimpanzees before (Krief et al., 2014). While Krief et al. (2014) do not speculate on the emergence of this nocturnal crop-feeding, it is possible that this behaviour is a modification of day-time crop-feeding, which is observed in other chimpanzee communities. Chimpanzees may gradually acquire knowledge of crop resources over time, with long-term crop-feeders at Bossou feeding on a greater variety of available non-fruit crops (such as cassava and maize) than chimpanzees at Bulindi (P. t. schweinfurthii), where the same crops are available but crop-feeding is believed to be a more recent behaviour (McLennan & Hockings, 2014), suggesting that chimpanzees may expand their crop-feeding repertoire to include more novel foods over time. Snares placed within chimpanzee habitats have also elicited novel behaviours; chimpanzees at Bossou have been observed dismantling snares (Ohashi & Matsuzawa, 2011), while at Budongo, there is a report of chimpanzees (P. t. schweinfurthii) capturing a blue duiker (Cephalophus monticola) from human-laid snares (Brand, Eguma, Zuberbühler & Hobaiter, 2014). While these observations of wild chimpanzees altering their behaviour in response to anthropogenic change provide evidence

of innovation and behavioural flexibility, it remains to be seen whether any resulting behavioural changes will undergo the repeated process of modification and social transmission required for cumulative culture. As it stands, the majority of these examples are cases of accumulation (addition of behaviours to the repertoire) rather than cumulative change (with the possible exception of nocturnal crop-feeding, if this proves to be a modification and improvement of previous crop-feeding behaviour).

There may also be an important distinction between instances in which behavioural flexibility occurs in response to environmental change, and in which flexible exploration of alternative solutions occurs spontaneously, without environmental necessity. Experimental studies of behavioural flexibility in chimpanzees have largely focussed upon the former, but the spontaneous exploration of alternative behaviours, and modification of known behaviours, may be critical for the emergence of cumulative culture. Dean et al. (2012) found that chimpanzees continued to explore and manipulate pieces of a puzzlebox having already discovered one, low-value reward, solution, indicating a capacity for spontaneous exploration of problems following the discovery of a solution. The emergence of multiple solutions within groups during the course of the 'Wide Tube' phases of the dipping task in Chapters 3 and 4 also indicates that chimpanzees were motivated to continue exploring potential solutions to the task, despite having a functional solution. However, when the 'Narrow Restricted' phase was imposed upon CWO Group 4 (Chapter 4), chimpanzees primarily continued to use the *stick dip* technique they had used in the previous phase, rather than modifying tool-composite techniques that were within their previous repertoire. It may be that within the 'Wide Tube' phase, when the task could be solved by hand, or by dipping tool materials directly by hand into the tube, the cost of exploring novel potential solutions was lower than in the 'Narrow Restricted' phase, when tool materials could be manipulated in the tube only by use of a stick. Further research could explore the effect that an increasing cost of acquiring behaviours has upon the likelihood of chimpanzees behaving flexibly in problemsolving tasks. Along with Davis et al.'s (2016) suggestion that decreasing benefits (in the form of withheld or low-value rewards) may prompt exploration and flexibility, it is possible that increasing costs of exploration, caused by the complexity of the behaviour required, might suppress exploration. If chimpanzees engage in spontaneous flexible exploration of novel solutions only when these solutions are simple, this could constrain the complexity of

any emergent behaviour in the wild, and potentially suppress the modification of known behaviours unless the benefit of such behaviours become severely devalued.

While studying chimpanzee cognition in captivity is beneficial, such studies should be informed and supported by research with wild chimpanzees – indeed, this is of importance for all studies of non-human cognition. Of the experimental studies relating to chimpanzee behavioural flexibility, only Gruber et al. (2011) examined this capacity in wild chimpanzees (and while this study is relevant to behavioural flexibility, it did not set out to test this capacity explicitly), and so it remains unknown whether the results of studies of this capacity in captive chimpanzees accurately reflect the species' ability in general. Observations of wild chimpanzees (Luncz et al., 2015; McCarthy et al., 2016; Luncz et al., 2018) suggest a greater capacity for behavioural flexibility than is often evidenced in experimental studies of captive chimpanzees (Marshall-Pescini & Whiten, 2008; Hrubesch et al., 2009). This may be due to the often limited interaction time chimpanzees have with artificial tasks in experimental settings in comparison with the amount of time they may have to explore and attempt to solve problems in the wild, the motivation of wild vs captive chimpanzees (as captive individuals are not reliant upon succeeding at these artificial foraging tasks in order to survive), and potential cognitive differences between wild and captive chimpanzees.

Some differences between wild and captive chimpanzees could be caused by differences in their developmental experiences. Meta-analyses have shown that nursery-reared captive chimpanzees are more likely to use social information than mother-reared captive chimpanzees, while wild-born chimpanzees are less likely to use social information than mother-reared captive chimpanzees (Watson et al., 2017). Enculturated individuals outperformed hand-reared and mother-reared individuals in tests of understanding of object permanence, functional properties of objects, and causal reasoning (Thornton & Lukas, 2012). Damerius et al. (2017) found that orientation towards humans (human orientation index, HOI), measured by examining captive orangutans' response to a human stranger, predicted the extent of orangutans' exploration of relevant parts of an artificial foraging task, and this exploration then predicted success in the foraging task. Damerius et al. (2017) did not find a clear relationship between any particular rearing history and HOI, though individuals who had spent their whole immature period in the wild tended to have low HOI compared with those who had spent time in captivity during development. The authors argue

that each individual's experience of human contact is more influential in the development of human orientation than simply the time spent in human contact, and suggest that this reflects humans taking the place of conspecific role models. Measuring human orientation may be more relevant as a tool for comparing individuals with different rearing histories at different facilities than simply categorising chimpanzees as mother-reared, hand-reared, or enculturated, as for example, the developmental experience of the individuals in the Beekse Bergen subgroup at Edinburgh Zoo who were hand-raised (**Chapter 3**) was likely very different from those hand-raised at CWO (**Chapter 4**). All of these findings (Thornton & Lukas, 2012; Watson et al., 2017; Damerius et al., 2017) would suggest that chimpanzees with more extensive experience of human contact during development would outperform those with little or no human contact during development in tests of problem solving, including multi-access puzzle box tests of behavioural flexibility.

However, all of these studies (Thornton & Lukas, 2012; Watson et al., 2017; Damerius et al., 2017) have compared performance amongst captive individuals, leaving it unclear whether increased human contact causes improved performance on these tests beyond that which a wild chimpanzee could achieve, or whether increased human contact simply compensates for a lack of sufficient natural conspecific social contact in captive animals. Forss et al. (2015) directly compared the novelty responses of wild and captive orangutans, finding that while captive orangutans were neophilic, wild orangutans avoided novel objects placed in the forest. Similarly, captive hyenas (Crocuta crocuta) were found to be less neophobic and more exploratory than their wild counterparts, and thus more successful at solving a novel artificial foraging problem (Benson-Amram, Weldele & Holekamp, 2013). These studies suggest a 'captivity effect', facilitating innovative problem solving in captive animals, by increasing neophilia and explorative tendencies. Without further direct experimental comparisons, it will remain unclear whether the behaviour of chimpanzees in captivity is representative of the abilities of their wild counterparts. Boogert, Monceau and Lefebvre (2010) demonstrate the possibility of conducting experimental research into behavioural flexibility with wild subjects (in this case, Zenaida doves, Zenaida aurita), and several studies have demonstrated that puzzlebox-style problem solving tasks can be provided to wild subjects (Benson-Amram & Holekamp, 2012; Thornton & Samson, 2012; Aplin et al., 2015; Botting, Whiten, Grampp & de Waal, 2018).

Chapters 3 and 4 demonstrate the potential importance of including multiple groups of captive chimpanzees in experimental studies. Some of the divergence in the current literature surrounding behavioural flexibility could also be the result of differences between groups of chimpanzees, particularly in captivity, where individuals can have very different rearing backgrounds and histories. It has been argued that development should be given more consideration when studying captive chimpanzee cognition (see Bard & Leavens, 2014, for review), particularly in the context of between-species comparisons, in which differences in rearing history (and therefore developmental experiences), for example, between captive chimpanzees and human children, are likely to be confounded with species. Chimpanzees studied in Chapter 4 were more likely to be wild-born than chimpanzees in Chapter 3, and so any direct comparison between the Edinburgh Zoo and CWO groups would be confounded by rearing history. In addition, those individuals born in captivity in the CWO groups are likely to have had very different developmental experiences than individuals born in captivity in the Edinburgh Zoo group – however, the differences between the two groups at CWO, described in Chapter 4, cannot be explained by rearing history or developmental experience, as no systematic differences exist in these factors between the groups. Many previous studies of behavioural flexibility in chimpanzees have included only one group of chimpanzees (Manrique et al., 2013; Hopper et al., 2015), or multiple groups in one facility (Hrubesch et al., 2009; Davis et al., 2016). In Chapter 5 I focused on one potential factor contributing to the group differences found in behavioural flexibility between the two groups at CWO; the level of social tolerance of the two groups.

7.3 Scaffolding

In both **Chapter 3** and **Chapter 4**, providing chimpanzees with scaffolding towards an effective solution did not result in individuals acquiring novel behaviour. In both chapters, the aim in providing scaffolding was to approximate a form of social information chimpanzees have access to in the wild, in the form of artefacts and debris of others' tool use. These artefacts have been argued to facilitate the acquisition of tool use and other foraging behaviours and to encourage object manipulation (Gunst, Boinski & Fragaszy, 2008; Tennie et al., 2009; Holzhaider et al., 2010; Leca et al., 2010; Fragaszy et al., 2013). Observations of wild populations provide support for this effect, with Gunst et al. (2008) finding that infant brown capuchins (*Cebus apella*) showed significantly more interest than subadults or adults

in the debris left by individuals foraging for larvae in bamboo segments, and that immature capuchins were more likely to show foraging behaviours after interacting with this debris than before. Holzhaider et al. (2010) found that 95% of Pandanus tools used by two- to threemonth-old New Caledonian crows (Corvus moneduloides) were recycled tools manufactured by others, decreasing to 5% by the time juveniles reached seven- to nine-months-old. Fragaszy et al. (2013) found that in wild chimpanzees at Bossou, unweaned young tended to re-use tools previously used by older individuals for nut-cracking, ant-dipping, and pestlepounding. This tendency decreased with age, and the authors suggest that these artefacts produced by others' tool use provide a crucial opportunity for immature individuals to practice tool behaviours and learn about the affordances of tool materials. The artefacts and debris of others' tool use and foraging behaviour are a form of niche construction: an alteration of the environment which forms an externally inherited resource, which then affects the learning opportunities of other organisms (Flynn, Laland, Kendal & Kendal, 2013). All organisms modify their environments and so construct niches (for example, animals modify their environments by building nests or burrows, plants alter the composition of the soil they grow in), and these modified environments are then inherited and exert selection pressures upon recipient organisms (Laland, Boogert & Evans, 2014). Flynn et al. (2013) suggest that human children are born into environments, structured by their parents, which facilitate cognitive development and cultural acquisition to an extent "unparalleled in any other species". This cultural niche incorporates natural pedagogy (behaviours from caregivers such as ostensive cues and 'motherese'), learning environments structured by contingent tutoring (providing assistance only when needed), and situated learning (learning behaviours in the same context in which they are applied) (Flynn et al., 2013). Physical artefacts of material culture are one form of niche construction which facilitates cultural learning in humans (Flynn et al., 2013) and in non-human primates (Fragaszy et al., 2013).

However, studies have found that experimentally-placed artefacts do not encourage novel tool use behaviour in wild chimpanzees (Gruber et al., 2011) or wild bearded capuchin monkeys (*Sapajus libidinosus*: Cardoso & Ottoni, 2016). The presentation of scaffolding in **Chapters 3 and 4** was limited both in terms of the number of individual chimpanzees who interacted with the scaffolding, and in terms of the frequency with which individuals encountered the scaffolding. It may be that within my studies, chimpanzees' exposure to the scaffolding was too limited for any learning to take place, but along with the studies of

Gruber et al. (2011) and Cardoso and Ottoni (2016), the results presented in this thesis suggest that providing only the physical artefacts or debris of tool use in this manner may be insufficient for individuals to acquire novel behaviour. Eshchar et al. (2016) found that immature wild bearded capuchin monkeys were 40 times more likely to strike a nut with a stone when they were in the presence of anvil stones, but that their likelihood of being near an anvil stone was strongly influenced by whether others were nut-cracking. The authors thus suggest that nut-cracking activity by others is important in the process of immature capuchins learning to nut-crack, as it draws them to areas where the physical materials are present for practice to take place. It may be that without some form of social facilitation, exposure to artefacts is insufficient to elicit novel behaviour. In wild non-human primates, physical artefacts are one source of information available to developing infants, along with observation of adults performing behaviours, and stimulus and local enhancement encouraging interaction with specific objects or locations. Flynn et al. (2013) outline multiple components of the human developmental niche, both physical and social, and it seems likely that isolated physical artefacts alone may be insufficient to support learning of novel behaviours in non-human primates.

7.4 Social tolerance

In **Chapter 5**, I described differences across multiple measures of social tolerance between the two groups of chimpanzees studied in **Chapter 4**. Although I suggest the effect of social tolerance upon performance in the 'dipping' task was likely mediated by opportunities for social learning and for innovation, rather than a direct link between increased tolerance and individual behavioural flexibility (though this remains an open empirical question), the finding that the apparently more socially tolerant group also performed the most flexibly demonstrates the need to consider the social context when conducting empirical research with great apes.

This finding is consistent with van Schaik's (2003) argument that social tolerance facilitates the innovation and transmission of foraging behaviours in great apes (see also Coussi-Korbel & Fragaszy, 1995), with the more socially tolerant group behaving more flexibly and discovering more solutions to the task than the less socially tolerant group. While the effect of social tolerance and affiliation have been discussed in the context of the social learning of

behaviours (Hirata & Celli, 2003; Huffman & Hirata, 2004; Bonnie & de Waal, 2006), and the use of social network analysis in primate studies is becoming increasingly common (see Sueur et al. (2011) for review), the results of this study suggest that the potential effect of group-level factors such as social tolerance should be considered whenever researchers provide tasks to chimpanzees in a group context (eg. Whiten et al., 2007; Davis et al., 2016).

Social tolerance is perhaps more often considered when making between-species comparisons (Lonsdorf et al., 2009; Hare et al., 2007; Ciani et al., 2012), but the results of this thesis suggest it should also be considered as a within-species variable of interest. While cross-species comparisons regarding social tolerance and tool use within the great apes have generally concurred with van Schaik's hypothesis that heightened tolerance promotes tool use, with less-tolerant gorillas (in comparison with chimpanzees, studied in captivity: Lonsdorf et al., 2009) and Bornean orangutans (in comparison with Sumatran orangutans: van Schaik et al., 1999) showing less tool use, bonobos stand out as a species deviating from the predicted pattern. Generally considered to be more socially tolerant than chimpanzees (Koops et al., 2015; Hare et al., 2007; Hare et al., 2012; though see Cronin et al., 2015 for evidence of more limited tolerance in a captive bonobo group), bonobos use few tools in the wild and have not been observed using tools for foraging (though captive bonobos use a diverse range of tools comparable to chimpanzees, Gruber et al., 2010). Koops et al. (2015) argue bonobos may possess a lower intrinsic motivation for object manipulation, which may explain the lack of tool use in the species' behavioural repertoire in the wild. Call (2017) makes more specific suggestions as to the psychological biases that might explain the lack of tool use in wild bonobos, citing evidence that bonobos are more socially-oriented in their problem solving than chimpanzees (Herrmann et al., 2010; Kano, Hirata & Call, 2015), that they are less bold than chimpanzees (Herrmann et al., 2011), and that they may be less tolerant of aversive stimuli (and thus, painful stimuli) than chimpanzees (Rosati & Hare, 2013). These psychological predispositions are posited to reduce bonobos' exploration of novel material resources, and make them less likely to explore food resources which have aversive physical or chemical defences and would therefore be accessible through tool use.

Within-species variation in social tolerance could be a productive avenue of investigation for researchers interested in cultural evolution. Sapolsky and Share (2004) document a culture of pacific behaviour in olive baboons (*Papio anubis*) which was socially transmitted and

maintained. Following the death of the more aggressive males in the group, a more tolerant social style emerged, and was maintained despite complete turnover of males due to migration between groups, indicating that incoming migrant males adopted the social style of the group. The adoption of existing social styles in this way by migrants could allow persistent inter-group differences in social tolerance to be maintained over the long term, and, following van Schaik's (2003) argument regarding social tolerance and the accumulation of traditions, this could result in inter-group differences in the size and complexity of the behavioural repertoire. As well as potentially affecting the size of a population's cultural repertoire, the social style itself, if it is indeed socially transmitted as Sapolsky and Share (2004) suggest, could also be studied as a cultural tradition. With the notable exceptions of the grooming hand-clasp (McGrew & Tutin, 1978; McGrew, Marchant, Scott & Tutin, 2001; Bonnie & de Waal, 2006; van Leeuwen et al., 2012) and the social scratch (Nakamura, McGrew, Marchant, & Nishida, 2000), the majority of research into chimpanzee cultural traditions has focused upon material culture and foraging behaviours. If they can be shown to be socially transmitted, differing social styles could be a further social tradition to be studied from the perspective of social learning and culture.

While Sapolsky and Share (2004) document a tolerant social style facilitated by an episode of disease transmission affecting only the most aggressive males, Cronin et al. (2014) documented differences in the level of social tolerance of CWO Groups 3 and 4 which they suggest are due to differences in the dominance style of the dominant males in each group. Foster et al. (2009) report differing dominance styles in three dominant male chimpanzees studied at Gombe, with the male with the smallest body mass engaging in more grooming and less contact aggression during his tenure as dominant male than did the larger males. Nishida et al. (1992) describe a dominant male at Mahale sharing meat with middle-ranking males only (rather than with beta males or young males ascending the hierarchy). By controlling resources in this manner, a dominant male can influence the apparent social tolerance of an entire group (as in Cronin et al.'s, 2014, resource equity measures of tolerance, in which the Group 3 dominant male monopolized 98% of rewards while the Group 4 dominant male took less than 50%). Future research could examine what attributes are shared by dominant males who follow similar strategies. While Foster et al. (2009) highlight low body mass as a potential cause of dominant males using a more 'coalitionary' strategy with high rates of grooming and low rates of aggression, while larger males can maintain dominance through

aggression, there may be other factors which influence the dominance style an individual adopts, such as individual differences in personality, or group-level factors such as the number of males in the group.

Though social tolerance can be considered as a group-level or species-level factor, it may also vary by individual. Damerius et al. (2017b) found that captive orangutans with more group-mates were more neophilic and more exploratory, indicating that the number of social interactions an individual has may affect their likelihood of innovative problem solving. Social tolerance may also affect the position an individual holds within a social network (with more tolerant individuals being more central; King, Clark & Cowlishaw, 2011), and social network position can then influence the social information an individual has access to, as well as the number of individuals who may be exposed to any novel behaviour the individual might perform. More central individuals may also have more influence over group decisions such as travelling (Sueur & Petit, 2008; Lusseau & Conradt, 2009). If more central, wellconnected individuals are more likely to innovate (as suggested by Damerius et al.'s, 2017b, finding), one would expect these innovations to be more likely to spread as a greater number of individuals would be exposed to them. However, research into chimpanzee innovation suggests innovators in this species are more often low-ranking (Reader & Laland, 2001), and combined with a bias towards copying high-ranking individuals (Kendal et al., 2015), this may suppress the spread of innovations in chimpanzees. The relationship between rank and social network position in chimpanzees, and the influence this may have upon how many group members have access to the social information produced by an individual, as well as any attentional biases, requires further investigation in order to tease apart the effect of social network position and rank upon social influence within a group.

7.5 Replication vs. reconstruction – the cultural attraction debate

The transmission chain study described in **Chapter 6** explored the role of replication versus reconstruction in the social transmission of cultural items by children. In both symbolic and non-symbolic seeded chains, the model image was lost entirely, though the more gradual loss of image complexity in the symbolic chains, and the improved ability of independent judges to place images into the order in which they were drawn, may indicate that the symbolic image was somewhat more faithfully transmitted. This finding of loss of image identity

during diffusion differs from that of Scott-Phillips (2017), employing a similar paradigm though with adult participants, but is similar to that of Tamariz and Kirby (2015) and Kempe et al. (2015), regarding the loss of complexity in transmitted images.

The results of the transmission chain do not provide support for Sperber's (2000) argument regarding cultural attraction. The symbolic image, assumed to represent a cultural attractor, was not reconstructed by children. Nor did children even produce images matching the model type (a star), which the cultural attraction approach might suggest as a likely outcome. Alternative symbolic images (including a heart shape, the letter C and number 7, all of which seem highly likely to be recognisable for this age-group) which did emerge within chains were also lost rapidly. Instead, children appear to have been limited in their capacity to faithfully copy (or, to use Sperber's term, 'replicate') either model image. However, this finding is limited to children, and, due to the study's exploratory nature and small sample size, further work is required to replicate these results, and to better control for important factors such as age. While there was no significant difference in the mean age of children in the 10 transmission chains presented in **Chapter 6**, children's ages were distributed differently throughout each chain, leaving the possibility that younger children may have been 'weak links' within chains, due to reduced working memory capacity and reduced motor skills in comparison to older children within the sample.

The finding that children did not successfully copy the images they had seen was somewhat surprising, given children's demonstrated ability to faithfully acquire and transmit other behaviours (eg. Flynn & Whiten, 2008; McGuigan & Graham, 2010). One possibility is that children were limited by being able to see only the outcome of the previous participants' actions, rather than observing the action itself. In this drawing task, it would be very challenging to reverse-engineer *how* the previous participant produced the image they did, beyond identifying potential start and end points for the lines composing the image. This could be investigated in future work by allowing children to observe the previous participant as they drew.

One difference between the drawing task provided in **Chapter 6** and the instrumental tasks used in previous studies of children's social learning (Horner, Whiten, Flynn & de Waal, 2006; Flynn & Whiten, 2008; Hopper, Flynn, Wood & Whiten, 2010; McGuigan & Graham,

2010) is in the degrees of freedom in potential responses. The effect of the complexity of the task in this regard could be investigated by manipulating the degrees of freedom in the task; for example, in a drawing task, providing children with pre-drawn lines that could be assembled into relevant shapes rather than requiring them to draw freehand. Physical problem solving tasks could also be altered by adding 'distractor' tool items to tasks involving the use of tools, or by adding additional ways of interacting with the task (eg. additional moving parts). Understanding the influence of the degrees of freedom in a task is important in terms of the way these tasks reflect the complex world children actually live in. While it is of course often necessary to simplify real-world scenarios in order to make empirical testing possible, it should be remembered that in their everyday lives, children are confronted with complex and varied physical and social environments, and if current social learning studies rely upon tasks with a limited problem solving 'space' for children to explore, they may not accurately reflect children's social learning tendencies.

Acerbi and Mesoudi (2015) suggest that the fidelity of social transmission is likely to vary in different behaviour domains; with causally opaque, sequence-dependent behaviours likely to be replicated faithfully, while other behaviours (such as story-telling) might be maintained by reconstructive processes. The instrumental tasks solved by children in previous social learning studies (Horner, Whiten, Flynn & de Waal, 2006; Flynn & Whiten, 2008; Hopper, Flynn, Wood & Whiten, 2010; McGuigan & Graham, 2010) appear to be the kind of behaviour described by Acerbi and Mesoudi (2015) as being particularly reliant upon high-fidelity social transmission, while the drawing task used in my study represents a different behavioural domain. Future work should take into consideration the fact that the balance between replication and reconstruction in transmission may be influenced by the behavioural domain of the task. The results of such studies may tell us about children's tendency to use high-fidelity social learning to acquire new skills in general, but they may also reflect the extent to which particular tasks elicit high-fidelity social learning.

As well as differences in task domain and degrees of freedom, studies also vary in the way tasks are framed. A limitation of the study presented in **Chapter 6** is that all children were instructed to 'copy' the image they were shown. Framing the task in this manner may have promoted a focus on high-fidelity copying of the specific image children saw, rather than encouraging children to emulate the *goal* of the previous participant by trying to draw an

image that represented the same thing. A different instruction might have resulted in more reconstruction rather than attempts at replication. The way in which tasks are framed may also impact the results of other social learning studies conducted with children. For example, VanderBorght and Jaswal (2008) found that when given a choice of an adult or child informant to ask for information about either unusual toys or food, three- to five-year-olds chose to ask the adult about food, but to ask the child about toys. If experimental tasks are described as 'games' or 'toys' (as in Wood, Harrison, Lucas, McGuigan, Burdett & Whiten, 2016) this may therefore affect the types of social models children attend to when learning about the task. In addition, children understand games as having a normative structure (that is, a way they should be played) from around three-years-old (Rakoczy, Warneken & Tomasello, 2008), and will spontaneously create and transmit arbitrary normative game rules when interacting with an instrumental task (eg. a marble run, in Göckeritz, Schmidt & Tomasello, 2014). Understanding a task as being normative may increase the fidelity with which children copy what they observe (Kenward, 2012). The way in which instrumental tasks are framed in studies of children's social learning may therefore influence not only the models from whom they choose to learn, but also the level of fidelity with which they copy what they observe. While further work is required to examine how children might interpret tasks in different behavioural domains differently in this respect (ie. to what extent children view tasks from various domains as 'games', with normative rules), it is possible that the drawing task used in Chapter 6 appeared less game-like than an instrumental task would have. Drawing, in particular, may also be a behavioural domain in which children are used to individual creativity being rewarded, which may influence the way in which children attend to and use social information in this context.

This study adds to a very limited literature on the transmission of non-problem-solving behaviours in children (Kempe et al., 2015; Raviv & Arnon, 2016), and the contrast between its results and those of Scott-Phillips' (2017) and Tamariz and Kirby's (2015) studies of image transmission in adults suggests further exploration of this subject is necessary. Recent meta-ethnographies of hunter-gatherer societies (Lew-Levy et al., 2017a, 2017b) indicate that child to child transmission may play an important role in the transmission of cultural norms and subsistence skills. An understanding of the ways in which cultural items and behaviours may be transformed when learnt and transmitted by children therefore seems an important area for future study. The apparent gulf between children's ability to faithfully copy the
images in **Chapter 6** and their capacity to learn solutions to physical problems in similar studies suggests that an exploration of how behaviours from different domains may vary in their propensity for high-fidelity copying by children is necessary.

7.6 Future directions

An important future goal following the studies presented in this thesis is replication and validation of the research presented here. The study with children presented in Chapter 6 was limited in its sample size and in the number of manipulations that were possible due to this limited sample size. Replicating these initial findings with a larger sample, and extending the study by including new conditions and comparisons, such as varying the instructions given to participants, exploring additional tasks from different domains and using a range of model images within this drawing domain, and examining the effect of age, are all necessary in order to validate the findings presented. The chimpanzee studies presented in Chapters 3, 4 and 5 also require replication. While the study in Chapter 4 to some extent replicates that of Chapter 3, there were unavoidable differences in task presentation which prevented direct comparison between the two sites. Given the group-level differences in response found at CWO in Chapter 4, further replication of this study at different facilities would allow exploration of the factors that may underlie such differences. While social tolerance was examined as a potential factor in Chapter 5, the addition of further groups of chimpanzees to this analysis would allow confirmation of the role social tolerance may have played in facilitating behavioural flexibility in this study.

In addition to replicating the studies presented here, future work should strive to include more diverse groups of participants. The chimpanzees included in the current study had experienced a range of rearing conditions, though sample size and correlation between age and rearing in the CWO population prevented thorough exploration of the potential effect of this. Leavens, Bard and Hopkins (2010) caution against generalising from BIZARRE chimpanzees (those raised in Barren, Institutional, Zoo, And other Rare Rearing Environments); only by including chimpanzees from across the spectrum of enculturation in cognitive studies, and using data from wild populations to inform these studies, will researchers be able to fully explore the cognitive capacities of chimpanzees. As Leavens et al. (2010) point out, no one environmental context will elicit the full range of chimpanzee

behaviour and cognition. In the target article which prompted Leavens et al. (2010) to put forward the idea of BIZARRE chimpanzees, Henrich, Heine and Norenzayan (2010) argue that the focus of research upon Western, Educated, Industrialised, Rich and Democratic (WEIRD) populations skews our view of human behaviour and cognition. Cross-cultural research will allow exploration of the processes which influence cultural evolution, and may reveal differences between cultures in terms of the use of social information. For example, Mesoudi, Chang, Murray and Lu (2014) found greater use of social information by participants in mainland China than by participants in the UK. Future work could explore whether there are cultural differences in the extent to which participants replicate or transform cultural behaviours.

The potential link between social tolerance and performance on an artificial foraging task explored in **Chapter 5** raises new avenues of investigation. While my study explored this relationship on a group level, thereby making the assumption that any differences in performance were due to increased opportunities for social learning or innovation, it is possible that tolerance and behavioural flexibility are in fact related on an individual level (Damerius et al., 2017b). Future work could investigate this through individual measures of behavioural flexibility, perhaps incorporating reversal learning or set shifting paradigms, and individual measures of social tolerance (such as dyadic co-feeding measures, Wobber et al., 2010, more long-term observation providing a larger data set per individual of social interactions than possible in **Chapter 5**, or social network measures, Claidiere et al., 2013). Previous studies (Lonsdorf et al., 2009; Cronin et al., 2015) have made species-level comparisons of social tolerance in great apes, and Manrique et al. (2013) demonstrated potential species differences in behavioural flexibility. Further cross-species comparisons would shed further light on any potential relationship between flexibility and social tolerance on an individual level.

A comparison of individual level performance on a reversal or set shifting paradigm with performance on a changing artificial foraging task would also allow validation of these tasks as a measure of behavioural flexibility in great apes. As discussed in **Chapter 1**, it has been suggested that reversal learning paradigms may measure a different ability than multi-access box or artificial foraging paradigms (Audet & Lefebvre, 2017), and Logan (2016a, 2016b) has demonstrated a dissociation between reversal learning and problem-solving in grackles

(though *changing* foraging tasks, as used in **Chapters 3** and **4**, and studies such as Manrique et al., 2013, are argued to call upon behavioural flexibility alongside problem solving abilities). Explicit comparison of individual performance on different measures of behavioural flexibility would provide some clarity on whether such measures are comparable, and whether they do in fact measure the same cognitive ability.

The studies presented in **Chapters 3 and 4** added to a very limited experimental literature on primates learning from the artefacts and debris of tool use left by others (Gruber et al., 2011; Cardoso & Ottoni, 2016). While there is more extensive evidence of this form of social learning in observations of wild populations (Gunst, Boinski & Fragaszy, 2008; Holzhaider et al., 2010; Leca et al., 2010; Fragaszy et al., 2013), the lack of evidence of primates acquiring novel behaviours from this form of information alone in experimental settings suggests that multiple sources of social information are required for artefact learning to elicit novel behaviour. Future experimental work could examine the role artefacts play within the context of exposure to other social information, and explore whether there are any instances in which exposure to artefacts alone is sufficient to elicit novel behaviour. Such studies could employ a more longitudinal approach, as a key limitation of this aspect of my studies was the limited contact individuals had with the provided scaffolding.

Children studied in **Chapter 6** did not succeed in transmitting drawings, even symbolic ones, along transmission chains. As multiple studies have shown that children are capable of relatively high-fidelity transmission of behaviours along transmission chains (Flynn & Whiten, 2008; McGuigan & Graham, 2010), an exploration of what aspect of the model images was troublesome for children to successfully remember or reproduce is needed. A first step would of course be to explore children's ability to faithfully copy and transmit simpler images, perhaps exploring whether the complexity of the image, or the complexity of the motor action required to produce it, limits children's ability to copy images. This might indicate whether children struggled to remember images (due to their graphical complexity) or to physically reproduce what they had seen (due to the complexity of the motor action of drawing).

However, it is also possible that children are simply more adept at learning and producing behaviours from alternative domains (eg. physical problem solving). Comparison of

children's ability to acquire and transmit behaviours from different domains might indicate whether children are biased towards socially acquiring certain types of behaviour (perhaps those which are more costly to acquire individually).

7.7 Conclusions

In this thesis, I set out to assess chimpanzees' capacity to respond flexibly to a changing artificial foraging task, finding a significant group difference in the level of behavioural flexibility shown by chimpanzees at CWO. This group difference may be related to different levels of social tolerance between the two groups, measured through observational methods, which could result in increased opportunities for social learning and innovation of task solutions in more socially tolerant groups. It is possible that the divergent results of previous studies of chimpanzee behavioural flexibility are at least partially due to intraspecific differences in this ability.

Further to this, I conducted a transmission chain experiment with children, in order to explore a thought experiment first proposed by Sperber (2000) and relevant to the ongoing cultural attraction debate within the field of cultural evolution. Contrary to Sperber's predictions, I found that both symbolic and non-symbolic model images were poorly transmitted by children, suggesting that 'attractor' images are not subject to more apparently faithful reconstruction. The lack of high-fidelity copying in the transmission chains is somewhat surprising given children's documented capacity for imitation of physical task solutions, but may suggest a need for investigation of the possibility of some level of domain-specificity in this capacity.

In light of these findings, I suggest that future work on cultural evolution in both humans and non-humans considers multiple demographic groups. This means the inclusion of multiple groups of apes, at different facilities and with different rearing histories, in studies of non-human primate cognition, and the consideration of how cultural behaviours might be transformed when acquired and transmitted by human children rather than adult populations, and whether this differs cross-culturally.

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Appendix A: Supplemental results from Chapter 4

Table A1.

Results of full model GLMM on the effects of Phase, *Age*, and an interaction between the two, upon 'Effective' technique use.

	Estimate	[Wald 95% CI]	Std. Error	z value	P value
(Intercept)	-8.17	[-11.65, -4.70]	1.77	-4.61	
Phase	8.40	[5.29, 11.50]	1.58	5.30	1.14 ^{e-07} ***
Age	0.18	[-4.27, 4.64]	2.27	0.08	0.935
Phase*Age Interaction	0.17	[-3.48, 3.81]	1.86	0.09	0.928
*** = p<0.001					

Table A2.

Results of full model GLMM on the effects of Phase, **Sex**, and an interaction between the two, upon 'Effective' technique use.

	Estimate	[Wald 95% CI]	Std. Error	z value	P value
(Intercept)	-8.52	[-12.08, -4.95]	1.82	-4.68	
Phase	8.58	[5.51, 11.65]	1.57	5.48	4.36 ^{e-08} ***
Sex	0.67	[-3.31, 4.66]	2.03	0.33	0.741
Phase*Sex Interaction	-0.17	[-3.42, 3.08]	1.66	-0.10	0.920
*** = p<0.001					

Participants wanted: Online study: Recognition of the Social Transmission of Drawings.

This project is being run by Rachel Harrison from the School of Psychology & Neuroscience. This study is part of Rachel's PhD research. It will take approximately 15 minutes to complete and you will be entered into a prize draw to win a £20 Amazon gift voucher.

In a previous study, we asked participants to copy simple drawings. Each participant was shown a drawing done by a previous participant and asked to do their best to memorize and copy it. Their drawing was then shown to the next participant, to form a 'chain' of 10 participants, similar to the game 'Telephone'.

We are now interested in whether people are able to put these 'chains' of drawings into the order in which they were drawn - in other words, can we recognise which drawings are copies of others?

You will be asked to look at groups of 10 drawings and place them in the order in which you believe they were drawn.

To complete this confidential questionnaire please click here:

You can contact the researcher directly with any questions: rh387@st-andrews.ac.uk

Appendix C : An example of the image ordering task as presented to independent raters



Appendix D : The final image produced in nine transmission chains of adult participants, seeded with the symbolic, five-pointed star model image.

Transmission chains were composed of either 10 or 20 participants.



Appendix E: Ethical permission letters from the University of St Andrews



University of StAndrews

School of Psychology & Neuroscience Ethics Committee

7 February 2014

Project Title:	Flexible tool use in chimpanzees
Researcher's Name:	Rachel Harrison
Supervisor:	Professor Andrew Whiten

Thank you for submitting your application which was considered at the Psychology & Neuroscience School Ethics Committee meeting on the 29th January 2014. The following documents were reviewed:

1. Animal Ethics Form 31/01/2014

The School of Psychology & Neuroscience Ethics Committee approves this study from an ethical point of view.

Approval is given for three years. Projects, which have not commenced within two years of original approval, must be re-submitted to the School Ethics Committee.

You must inform the School Ethics Committee when the research has been completed. If you are unable to complete your research within the 3 three year validation period, you will be required to write to the School Ethics Committee to request an extension or you will need to re-apply.

Any serious adverse events or significant change which occurs in connection with this study and/or which may alter its ethical consideration, must be reported immediately to the School Ethics Committee, and an application for ethical amendment Form submitted where appropriate.

Approval is given on the understanding that the ASAB Guidelines for the Treatment of Animals in Behavioural Research and Teaching (published in Animal Behaviour, 2003, 65, 249-255, <u>http://www.sciencedirect.com/</u>) are adhered to.

Yours sincerely

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Convenor of the School Ethics Committee

Ccs Prof Andrew Whiten (Supervisor) School Ethics Committee Dr Tamara Lawson (Home Office Liaison Officer)

> SEC Convenor, St Mary's Quad, St Andrews, Fife KY16 9JP, Scotland Email: <u>psyethics@st-andrews.ac.uk</u> Tel: 01334 462071 The University of St Andrews is a charity registered in Scotland: No SC013532



School of Psychology & Neuroscience Ethics Committee

2 February 2015

Project Title:	Flexible tool use in chimpanzees		
Researcher's Name:	Rachel Harrison		
Supervisor:	Professor Andrew Whiten		

Thank you for submitting your application for amendment which was considered at the Psychology & Neuroscience School Ethics Committee meeting on the 27th January 2015. The following documents were reviewed:

28/01/2015 1. Application for change(s) to a School Ethics Committee Form 28/01/2015

Amended Animal Ethics Form 2.

The School of Psychology & Neuroscience Ethics Committee approves the amendment to this study from an ethical point of view.

Approval is given for three years from the date of approval of the original application. Projects, which have not commenced within two years of original approval, must be re-submitted to the School Ethics Committee.

You must inform the School Ethics Committee when the research has been completed. If you are unable to complete your research within the 3 three year validation period, you will be required to write to the School Ethics Committee to request an extension or you will need to re-apply.

Any serious adverse events or significant change which occurs in connection with this study and/or which may alter its ethical consideration, must be reported immediately to the School Ethics Committee, and a further application for amendment submitted where appropriate.

Approval is given on the understanding that the ASAB Guidelines for the Treatment of Animals in Behavioural Research and Teaching (published in Animal Behaviour, 2003, 65, 249-255, http://www.sciencedirect.com/) are adhered to.

Yours sincerely

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Convenor of the School Ethics Committee

Prof A. Whiten (Supervisor) Ccs School Ethics Committee Dr Tamara Lawson (Home Office Liaison Officer)

> SEC Convenor, St Mary's Quad, St Andrews, Fife KY16 9JP, Scotland Email: psyethics@st-andrews.ac.uk Tel: 01334 462071 The University of St Andrews is a charity registered in Scotland: No SC013532



School of Psychology & Neuroscience Ethics Committee

30 March 2015

Project Title:	Innovation and flexibility in chimpanzees.
Researcher's Name:	Rachel Harrison
Supervisor:	Professor Andrew Whiten

Thank you for submitting your application which was considered at the Psychology & Neuroscience School Ethics Committee meeting on the 24th March 2015. The following documents were reviewed:

1.	Animal Ethics Form	24/03/2015
2.	External Permissions	24/03/2015

The School of Psychology & Neuroscience Ethics Committee approves this study from an ethical point of view.

Approval is given for three years. Projects, which have not commenced within two years of original approval, must be re-submitted to the School Ethics Committee.

You must inform the School Ethics Committee when the research has been completed. If you are unable to complete your research within the 3 three year validation period, you will be required to write to the School Ethics Committee to request an extension or you will need to re-apply.

Any serious adverse events or significant change which occurs in connection with this study and/or which may alter its ethical consideration, must be reported immediately to the School Ethics Committee, and an application for ethical amendment Form submitted where appropriate.

Approval is given on the understanding that the ASAB Guidelines for the Treatment of Animals in Behavioural Research and Teaching (published in Animal Behaviour, 2003, 65, 249-255, <u>http://www.sciencedirect.com/</u>) are adhered to.

Yours sincerely

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Convenor of the School Ethics Committee

Ccs Prof A. Whiten (Supervisor) School Ethics Committee Dr Tamara Lawson (Home Office Liaison Officer)



University of StAndrews

School of Psychology & Neuroscience Ethics Committee

26 July 2016

Dear Rachel

Thank you for submitting your application which was considered at the Psychology & Neuroscience School Ethics Committee meeting on the 8th July 2016. The following documents have been reviewed:

- 1. Animal Ethics Form
- 2. External Permissions (Budongo Trail scientific committee)

Project Title:	Social tolerance in chimpanzees			
Researchers Name:	Rachel Harrison			
Supervisor:	Professor Andrew	Whiten		
Approved on:	12/07/2016	Approval Expiry:	12/07/2021	

The School of Psychology & Neuroscience Ethics Committee approves this study from an ethical point of view.

Approval is given for five years. Projects, which have not commenced within two years of original approval, must be re-submitted to the School Ethics Committee.

You must inform the School Ethics Committee when the research has been completed. If you are unable to complete your research within the five-year validation period, you will be required to write to the School Ethics Committee to request an extension or you will need to re-apply.

Any serious adverse events or significant change which occurs in connection with this study and/or which may alter its ethical consideration, must be reported immediately to the School Ethics Committee, and an application for ethical amendment Form submitted where appropriate.

Approval is given on the understanding that the <u>ASAB Guidelines for the Treatment of Animals in Behavioural</u> <u>Research & Teaching (ANIMAL BEHAVIOUR, 2012, 83, 301-309)</u> are adhered to.

Yours sincerely

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Convenor of the School Ethics Committee

Ccs Professor Andrew Whiten (Supervisor) School Ethics Committee Dr Tamara Lawson (Home Office Liaison Officer)

> SEC Convenor, St Mary's Quad, St Andrews, Fife KY16 9JP, Scotland Email: <u>psyethics@st-andrews.ac.uk</u> Tel: 01334 462071 The University of St Andrews is a charity registered in Scotland: No SC013532



University Teaching and Research Ethics Committee

Dear Rachel

23 September 2016

Thank you for submitting your ethical application which was considered at the School of Psychology & Neuroscience Ethics Committee meeting on 22nd September 2016; the following documents have been reviewed:

- 1. Ethical Application Form
- 2. Participant Information Sheet
- 3. Consent Form
- 4. Debriefing Form
- 5. External permission documentation
- 6. PVG clearance/DBS
- 7. Data Management Plan
- 8. Copy of Fieldwork Risk Assessment

The School of Psychology & Neuroscience Ethics Committee has been delegated to act on behalf of the University Teaching and Research Ethics Committee (UTREC) and has granted this application ethical approval. The particulars relating to the approved project are as follows -

Approval Code:	PS12365	Approved on:	23/09/2016	Approval Expiry:	23/09/2021		
Project Title:	Social Transmiss	Social Transmission of Drawings by 4 – 8-year-old Children					
Researcher:	Rachel Harrison	Rachel Harrison					
Supervisor:	Professor Andrew	v Whiten					

Approval is awarded for five years. Projects which have not commenced within two years of approval must be resubmitted for review by your School Ethics Committee. If you are unable to complete your research within the five year approval period, you are required to write to your School Ethics Committee Convener to request a discretionary extension of no greater than 6 months or to re-apply if directed to do so, and you should inform your School Ethics Committee when your project reaches completion.

If you make any changes to the project outlined in your approved ethical application form, you should inform your supervisor and seek advice on the ethical implications of those changes from the School Ethics Convener who may advise you to complete and submit an ethical amendment form for review.

Any adverse incident which occurs during the course of conducting your research must be reported immediately to the School Ethics Committee who will advise you on the appropriate action to be taken.

Approval is given on the understanding that you conduct your research as outlined in your application and in compliance with UTREC Guidelines and Policies (<u>http://www.st-andrews.ac.uk/utrec/guidelinespolicies/</u>). You are also advised to ensure that you procure and handle your research data within the provisions of the Data Provision Act 1998 and in accordance with any conditions of funding incumbent upon you.

Yours sincerely

Madoll

Convener of the School Ethics Committee

cc Professor Andrew Whiten (Supervisor)

School of Psychology & Neuroscience, St Mary's Quad, South Street, St Andrews, Fife KY16 9JP Email: <u>psycthics@st-andrews.ac.uk</u> Tel: 01334 462071

The University of St Andrews is a charity registered in Scotland: No SC013532



University Teaching and Research Ethics Committee

27 October 2016

Dear Rachel

Thank you for submitting your amendment application which comprised the following documents:

- 1. Ethical Amendment Application Form
- 2. External Permission Documentation (Dundee Science Centre)

The School of Psychology & Neuroscience Ethics Committee is delegated to act on behalf of the University Teaching and Research Ethics Committee (UTREC) and has approved this ethical amendment application. The particulars of this approval are as follows –

Original Approval Code:	PS12365	Approved on:	23/09/2016	
Amendment Approval Date:	26/10/2016	Approval Expiry Date:	23/09/2021	
Project Title:	Social Transmission of Drawings by 4 – 8-year-old Children			
Researcher:	Rachel Harrison			
Supervisor:	Professor Andrew Whiten			

Ethical amendment approval does not extend the originally granted approval period of five years, rather it validates the changes you have made to the originally approved ethical application. If you are unable to complete your research within the original five year validation period, you are required to write to your School Ethics Committee Convener to request a discretionary extension of no greater than 6 months or to re-apply if directed to do so, and you should inform your School Ethics Committee when your project reaches completion.

Any serious adverse events or significant change which occurs in connection with this study and/or which may alter its ethical consideration, must be reported immediately to the School Ethics Committee, and an Ethical Amendment Form submitted where appropriate.

Approval is given on the understanding that you adhere to the 'Guidelines for Ethical Research Practice' (http://www.st-andrews.ac.uk/media/UTRECguidelines%20Feb%2008.pdf).

Yours sincerely

Jundedard

Convener of the School Ethics Committee

cc Professor Andrew Whiten (Supervisor)

School of Psychology & Neuroscience, St Mary's Quad, South Street, St Andrews, Fife KY16 9JP Email: <u>psycthics@st-andrews.ac.uk</u> Tel: 01334 462071

The University of St Andrews is a charity registered in Scotland: No SC013532



University Teaching and Research Ethics Committee

Dear Rachel

20 February 2017

Thank you for submitting your ethical application which was considered at the School of Psychology & Neuroscience Ethics Committee meeting on 9th February 2017; the following documents have been reviewed:

- . Ethical Application Form
- 2. Advertisement
- 3. Participant Information Sheet
- 4. Consent Form
- 5. Debriefing Form
- 6. Example of Task
- 7. Data Management Plan

The School of Psychology & Neuroscience Ethics Committee has been delegated to act on behalf of the University Teaching and Research Ethics Committee (UTREC) and has granted this application ethical approval. The particulars relating to the approved project are as follows -

Approval Code:	PS12592	Approved on:	17/02/2017	Approval Expiry:	17/02/2022		
Project Title:	Recognition o	Recognition of the Social Transmission of Drawings					
Researcher:	Rachel Harris	Rachel Harrison					
Supervisor:	Professor And	drew Whiten					

Approval is awarded for five years. Projects which have not commenced within two years of approval must be resubmitted for review by your School Ethics Committee. If you are unable to complete your research within the five year approval period, you are required to write to your School Ethics Committee Convener to request a discretionary extension of no greater than 6 months or to re-apply if directed to do so, and you should inform your School Ethics Committee when your project reaches completion.

If you make any changes to the project outlined in your approved ethical application form, you should inform your supervisor and seek advice on the ethical implications of those changes from the School Ethics Convener who may advise you to complete and submit an ethical amendment form for review.

Any adverse incident which occurs during the course of conducting your research must be reported immediately to the School Ethics Committee who will advise you on the appropriate action to be taken.

Approval is given on the understanding that you conduct your research as outlined in your application and in compliance with UTREC Guidelines and Policies (<u>http://www.st-andrews.ac.uk/utrec/guidelinespolicies/</u>). You are also advised to ensure that you procure and handle your research data within the provisions of the Data Provision Act 1998 and in accordance with any conditions of funding incumbent upon you.

Yours sincerely

Her Andered

Convener of the School Ethics Committee

cc Professor Andrew Whiten (Supervisor)

School of Psychology & Neuroscience, St Mary's Quad, South Street, St Andrews, Fife KY16 9JP Email: <u>psycthics@st-andrews.ac.uk</u> Tel: 01334 462071

The University of St Andrews is a charity registered in Scotland: No SC013532