ON THE FACTORS INFLUENCING GREAT APE CULTURAL BEHAVIOURS

by

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Abstract

This thesis has described six studies to investigate the factors influencing great ape cultural behaviours. The data presented were collected from all extant species of non-human great apes (apes). Chapters 2, 3 and 4 test the assumption of the Zone of Latent Solutions (ZLS) hypothesis that ape cultures are the product of socially-mediated reinnovations rather than culture dependent traits. Chapters 2 and 3 generally find support for the ZLS hypothesis, concluding that social learning, whilst important, is not necessary to explain patterns of ape cultural behaviours. Chapter 4 presents a potential caveat to the ZLS hypothesis, where a wild-type behaviour was not expressed in a captive population. However, Chapter 5 supports another assumption of the ZLS hypothesis: imitation is beyond the capacity of other extant members of our clade. Finally, Chapter 6 considers the ecological factors that might influence the expression of material culture in bonobos, a species not known for their prowess in this. Overall, this thesis acts to test the claims of the ZLS hypothesis, in doing so the individual, social and ecological factors that might influence the expression of ape cultural behaviours are highlighted and discussed.

For my children, I do not know you yet, but this is for you.

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I cannot even begin to hope to thank all of the right people for their help in this thesis, but here is my best attempt! This thesis stands as evidence of what being totally belligerent can amount to. Throughout the process of doing the research that forms the basis of this piece and finally writing it, I have gotten married to the love of my life, moved house twice, been on more adventures than I can count, met friends who will last a lifetime, laughed, cried and generally lived.

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[1] Haha, you love a good footnote, I knew you'd read this! Did you like the little "Claudioisms" I threw in there?

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CHAPTER 1: GENERAL INTRODUCTION

1.1 Overview

From the strange pieces of material covering our feet to the shape of the hair on our head, culture pervades every aspect of the modern human condition. Our culture has changed more in the brief time in which our species, as we recognise it today, has existed than perhaps any of the flora or fauna that co-inhabit this planet of ours. However, the cultures of non-human animals (hereafter: animals) are, arguably, mostly stationary, the mechanisms underlying them and influencing the expression of them are highly debated in the comparative psychology, anthropology, biology and cultural evolutionary literature. This thesis sits at the intersection of these literatures and asks and attempts to answer some questions about the cultures of our closest extant relatives, the non-human great apes (henceforth: apes). For example, can ape cultures emerge without the inclusion of special variants of social learning? What are the social learning capacities of apes (do apes "ape")? Overall, what are the factors influencing ape cultures, and how do these compare to what we know of our own culture. In this thesis, I will build on already existing methodologies, e.g., the Latent Solutions methodology (Tennie & Hedwig, 2009), and apply them in novel ways. In doing so I will target some of the more controversial issues in the aforementioned fields and attempt, using controlled and consistent testing procedures, to add new understanding of culture and social learning in apes to the literature surrounding it.

Before embarking on the empirical chapters, I will review the current state of the relevant literature. Within this introduction, I will discuss social learning and break this down into its constituent mechanisms. I will then go on to discuss culture, in its various guises and specifically outline the key debates around ape culture, which have arisen in the last decade. Finally, I will discuss tool use in apes and how this relates to the debates of culture in the literature today.

1.2 Theoretical background

1.2.1 Social Learning

In its simplest form, social learning is the act of one individual acting on information derived, in some way, from or via another, the result may then alter the observable behaviour of the first individual. Social learning pervades virtually every aspect of human life and it has been assumed (perhaps rightly so) that it similarly pervades the lives of other animals, especially apes. Here I qualify exactly what we refer to as social learning in the literature and in splitting it into its variants I attempt to provide a framework from which it is possible to separate resultant cultures (Galef, 1976). Notwithstanding the recent debates around even making such a choice (Stout, Rogers, Jaeggi, & Semaw, 2019) as it is necessary to divide social learning to empirically devise which of its variants are necessary for the emergence of ape culture.

1.2.1.1 ***Definitions of Social Learning Mechanisms***

Michael Tomasello and colleagues (1993, p. 496) conceptualised social learning, in its broadest sense, as “individual learning that is influenced in some way by the social environment” citing Bandura (1986). Within this seminal piece, Tomasello *et al*. conceptualised a key difference between the more basic variants of social learning, e.g., local and stimulus enhancement, and the variants of social learning that they term "cultural learning". The distinction between these being that cultural learning is where the learner acquires information "through another", as opposed to "from another", suggesting a more understanding and considered learning process. The distinction between these pathways of acquisition is that, in “cultural learning”, through another, the learner attempts to take the perspective of the demonstrator/model. These “cultural learning” variants are common in humans, by contrast, Tomasello *et al* suggest that even these more basic variants of social learning are “instrumental” in the development of some aspects of chimpanzee (*Pan troglodytes sp.*) tool use, a suggestion that has been heavily debated (see Section 1.2.4.2).

Since then several attempts to introduce a finer-grained classification of social learning variants have been made. This thesis will use that of Whiten *et al* (2004), who collected and provided comprehensive definitions of the main social learning variants (see Table 1), which are widely cited (a Google Scholar search on 24/06/2019, for articles citing Whiten et al. 2004, resulted in 354 articles). Each mechanism will be discussed below in reference to ape social learning but here we will refer to physical cognition only (sensu Tomasello & Call, 1997). This is because the primary focus of this thesis will be on material cultures, particularly tool use. The debate surrounding social cognition (including vocal learning; e.g., Janik, 2014; Janik & Slater, 2000) is beyond the scope of this thesis.

Table 1.1. Social learning mechanisms as described by Whiten et al (2004, p. 39). Descriptions listed here are those used throughout this thesis unless otherwise stated.

Group	Mechanism	Description	Resultant 'cultural' variant
Copying	Imitation	"Copying the form of an action"	Cumulative culture/CDT
	Object Movement Re-enactment	"Copying the form of a caused object movement" – can be imitative or emulative according to Whiten et al.	
	End-State Emulation	Copying only the end or outcome of an action sequence	
Affordance Learning	Properties Relationships Functions	Learning about operating characteristics of objects or environment	Minimal culture/tradition
Observational Conditioning*		Learning the positive or negative value of an object or event	
Enhancement	Local** Stimulus	Focusing attention on part of the environment	

Notes:
*Observational conditioning is considered by Whiten et al. (2004, p. 39) as its own group, thus no group entry.
** Whiten et al. (2004, p. 39) use "locale", however throughout this thesis this mechanism will be referred to as "local" enhancement as this is the more accepted spelling in the literature (e.g., Heyes & Galef, 1996).

The social learning variants described by Whiten *et al* (2004) can be divided into copying and non-copying variants; non-copying variants include affordance learning, observational conditioning and enhancement. Enhancement was described by Thorpe (1963) as the learning that occurs when the attention of the learner is drawn to an aspect resulting from the behaviour by the demonstrator. Tomasello *et al* (1993) use the example of a chimpanzee mother and offspring interacting around a nut-cracking station (Boesch & Boesch, 1983). Both enhancement mechanisms could be at play here, the presence of the mother around a fixed anvil and holding a hammer stone/log would cause enhancement, to both the location (local enhancement) and the tools (stimulus enhancement), in the offspring. This, perhaps most basic, variant of social learning is common to many species (Whiten & Ham, 1992) and has previously been misinterpreted as other so-called "high-fidelity" (otherwise termed copying) variants of social learning, through the use of confounded methodologies (i.e., the two-target task; Tennie, Call, & Tomasello, 2012). This said, it is possible to control for this by ensuring the target is in the same location but can be moved one way or another (i.e., a bi-directional lever or door); even then, the two-target methodology cannot distinguish between the variants of copying (Table 1.1). Observational conditioning is best exemplified in terms of fear response (though positive observational conditioning is possible too); this is where the learner acquires the fear response of others through observing the interactions of others with a given stimuli, e.g., macaques socially learn a snake based fear response in this way (Mineka & Cook, 1988).

When only non-copying social learning variants merely mediate/catalyse the process of the *individual* learning the behavioural form, this is termed a socially mediated reinnovation (Bandini & Tennie, 2017). A reinnovation, in this context, is a behaviour that is being innovated for the first time within a population, but has already been identified in the species as a whole (i.e., in at least one other population); hence *re*innovation (previously termed re-invention by Tennie et al. 2009; the distinction between these terms – and the reason for using the term innovation rather than invention - is a debate that can be found in

Bandini & Tennie, 2017 and will not be repeated here). The process of socially mediating an individual reinnovation can be considered similar to a chemical reaction using a catalyst. By being socially mediated towards specifics of an individual's environment (e.g., towards certain locations or stimuli) this merely increases the likelihood that the individual will reinnovate a behaviour themselves, but without the need for copying (compare Bandini & Tennie, 2017).

Non-copying variants of social learning are present in many species from insects to humans and the existence of these outside the human genus is beyond debate (Tomasello, 1996; Whiten et al., 2004). However, the presence or absence of copying variants of social learning, in other apes, is often debated (e.g., Tennie, Call, & Tomasello, 2009). Broadly, copying variants can be divided into emulative processes and imitative processes. The difference is that the actions of the demonstrator are not copied in purely emulative processes, but the results of those actions are. Within emulative learning it is possible to further subdivide social learning mechanisms into those involving "sensitivity to observed outcomes" and those involving "sensitivity to object movements" (Huang & Charman, 2005, p. 278 citing Whiten & Custance, 1996). The former consists of end-state emulation and goal emulation, whilst the latter consists of object movement re-enactment and affordance learning (Custance, Whiten, & Fredman, 1999). The emulative variants most pertinent to this thesis, owing to the specific methodologies and research questions, are end-state and goal emulation; only these will be discussed further.

End-state emulation can be achieved by attending to and copying the *outcome* of actions; in this sense, the actions themselves are not socially learned, the outcome is. An easy to envisage example of this social learning mechanism is the spaghetti tower experiment, often applied by developmental and comparative psychologists to assess the ability of children to copy the designs of previous “generations” (Caldwell & Millen, 2009; Reindl, Apperly, Beck, & Tennie, 2017). This task requires participants to build the tallest tower possible from dry spaghetti and modelling clay within a set time, each participant’s final design is shown to the next generation of participant to inform their tower. In such experiments, a generation is considered as the individual that came before the current participant. The importance of this task is, by showing a child the product of another’s actions it is possible to impart socially produced information that allows subsequent replications of those actions; even improving on them. Thereby the ‘learner’ takes on information about the ‘demonstrators’ results and reverse-engineers them to inform their actions. Crucially, the learner should not consider the action in relation to the demonstrator’s goal (Huang & Charman, 2005), i.e., in its purest form end-state emulation should be goal independent.

Should the demonstrator’s goal be copied instead, the mechanism would be considered goal emulation (Huang & Charman, 2005). It may be that the spaghetti tower task uses a combination of both variants of emulation, however, for this example, the reader should set this aside and assume it is possible to parse these variants using this task. Goal emulation is not simply a graduation from end-state emulation; in goal emulation, whilst the goal (or even *intention* see Tomasello, Carpenter, Call, Behne, & Moll, 2005 for further discussion on the distinctions) of the model is copied, the method by which the goal is achieved must be individually derived. Continuing the spaghetti tower analogy, imagine a human child, engaging in private speech during solitary play (Krafft & Berk, 1998), i.e., audibly labelling their goal to build a tower from spaghetti pieces. An observer would be engaging in goal emulation if they then copied this goal to build the tower but came up with their own design for the tower, regardless of whether or not the result was successfully copied. However, it should be noted that Tomasello (1998a) argued that the notion of goal emulation "twisted" the concept of emulative learning as he described it (because the original description was intended to cover environmental results) and therefore should be considered with caution.

The identification of imitation has been considered of paramount importance as it has been argued to be the social learning mechanism at the heart of human culture (Tomasello, 1999a). It is considered important that imitation is only attributed when "insightful imitation" occurs (Carpenter & Call, 2002) as this is the mechanism underlies the majority of human culture. Insightful imitation is where the goal, action and result of the demonstrator's behaviours are copied by the learner (Call & Carpenter, 2002; Carpenter & Call, 2002). If the goal is not copied the mechanism should be classified as 'blind' imitation or mimicry (Tomasello, Kruger, et al., 1993). Imitation is distinct from other copying variants of social learning as it involves the learner acquiring and expressing social information about the "bodily actions of the tool user" (Buttelmann, Carpenter, Call, & Tomasello, 2013, p. 755) in this sense imitation is perhaps less ambiguously termed "action-copying" (term used *sensu* Tennie, Call, & Tomasello, 2006). The importance of action copying in classifying imitation is a factor shared across other definitions also (e.g., Whiten et al., 2004). In this thesis when referring to 'imitation' or 'action copying', I follow Carpenter and Call (2002) in reserving the label to those cases that combine goal, action and result copying unless otherwise specified.

A common issue when identifying imitation is that it is often unclear whether a behaviour is replicated due to chance, simplicity, bias in the task/social group or the learner is attending to the bodily actions of the demonstrator. For this reason, one of the best ways to identify true imitation is through identifying so-called "over-imitation" (Hoehl et al., 2019) where *all* aspects of a behaviour, even those causally irrelevant ones, are copied by the learner. Through over-imitation it is possible to build causally irrelevant actions into behavioural demonstrations, which are highly unlikely to occur by chance, or because of a causal understanding of the situation by the observer. They would only occur if imitation was responsible.

1.2.1.2 ***Evidence of imitation in non-humans***

There is no doubt that humans imitate one another (Tomasello, 1999a). Despite the somewhat ubiquitous nature of imitation in our species, evidence for imitation in other apes is far from conclusive. Despite claims of imitation in various species (Akins & Zentall, 1996; Kis, Huber, & Wilkinson, 2015), this thesis will focus on primates in the interest of brevity.

Whiten and Ham (1992) discuss a "century of research" into social learning, with a particular focus on imitation. The findings of this review were that cases of monkey imitation can be largely dismissed, owing to a lack of experimental controls meaning imitation cannot be distinguished from other social learning mechanisms. However, apes, particularly chimpanzees, provide several examples of apparent imitation. Based on a review of the available evidence (e.g., Gardner & Gardner, 1969; Hayes, 1951; Kearton, 1925), Whiten and

Ham conclude that ape imitation is likely. However, it should be noted that the cases provided as evidence of imitation were from "enculturated" subjects and should, therefore, be treated with extreme caution or even disregarded when the goal is to determine natural capabilities (Henrich & Tennie, 2017). This thesis is not concerned with the capacity of enculturated individuals, their relation to our cultural evolution is questionable, therefore henceforth, I will follow Henrich and Tennie in dismissing these data from the imitation debate.

Data from unenculturated individuals is much less clear. Dean, Vale and Whiten (2018) capture the difficulty of successfully identifying imitation, in general, by presenting a three-fold "enigma". As expressed in Section 1.2.1.2, one needs to assess the intentionality of behaviour to distinguish imitation from mimicry. Next, it is important to consider the novelty of the response; if a response is not novel then one cannot be sure that its form was learned from the demonstrator (Tennie et al., 2012). Finally, Dean et al. (2018) express the importance of utility; just because a species has been 'shown' to be capable of imitation, this would not imply that imitation is at the heart of their culture or that they would naturally utilise it.

This said debate continues as to whether imitation is present in apes. Researchers on one side of this 'fence' suggest that spontaneous ape imitation *is* present and claim that this has been shown experimentally (Whiten, McGuigan, Marshall-Pescini, & Hopper, 2009). However, Section 1.2.1.2 dismisses the results of two-target tasks as unable to distinguish imitation from emulation as only the results need to be copied to 'pass' the task. Accordingly, others maintain that spontaneous imitation is *not* present in apes. In one of the most recent attempts to discerning apes' capacity for 'true' imitation, a chimpanzee (Mawa) was trained in performing a novel gesture (Tennie et al., 2012). Tennie et al. suggest that apes cannot copy actions, as they failed to meet the aforementioned criteria for imitation. Therefore suggesting that spontaneous imitation is outside chimpanzees’ capacity; this conclusion is further supported by two similar studies with negative results (in bonobos; *Pan paniscus*; Clay & Tennie, 2018 and chimpanzees; Tomasello et al., 1997). The data presented by Tennie et al. do not totally exclude chimpanzees, and by extension all ape species, from being capable of imitation. However, when combined with the data presented by Clay and Tennie, these data present a picture of ape copying that is clearly distinct from human copying.

Despite proponents of both sides of this debate demonstrating, what they consider to be, clear evidence of the presence/absence of imitation in apes the debate continues. Throughout this section I have outlined social learning mechanisms, these mechanisms are at the heart of culture, regardless of the species expressing that culture. However, what exactly constitutes this, highly provocative, word "culture" is a subject of a potentially even more fervent debate, going so far as being described as a "war" (Kendal, 2008; McGrew, 2002). The debate continues to this day.

1.2.2 Culture

In this section, I will define and describe some of the types of culture and explain the contention between them, before concluding why the study of material culture is important. As before, my discussion will revolve around material culture unless otherwise stated; that is, behaviours that may be deemed cultural (in some sense) that result in a change in the physical environment (e.g., some tool use).

1.2.3 Types of culture

Culture and social learning are inseparable, regardless of which definition (or "type" of culture) one subscribes to or considers, social learning is implicated. However, the ‘slider’ of culture ebbs and flows based on the degree to which social learning is required for that type of culture to emerge; equally, which of the social learning variants, described in Section 1.2.1.1, are necessary for that culture to emerge.

1.2.3.1 ***Culture or tradition?***

Galef (1976) introduced the concept of a “tradition”, these were behaviours *influenced* by social learning. In a later publication, Galef (1992) made clear the distinction between culture and tradition and classified researchers into ‘splitters’ and ‘lumpers’. Simply, splitters are those who divide culture into various ‘levels’ and attribute these levels to species as they find evidence for them (as will I). Contrastingly, for lumpers if a species fulfils *any* of the cultural criteria they can be considered a “cultural species”, the idea being that these must *rely* on similar social learning mechanisms (sensu Wilson, 1975).

Galef (1992, p. 159) is a splitter himself and so he describes culture as a sub-component of traditions that differ on the "behavioural processes that support" them; in Galef’s terms, "behavioural processes" refer to social learning variants. To be considered as cultural, the acquisition of behaviours should be supported by imitation or teaching. Here I will retain my focus on imitation, but a few words on teaching first. Teaching is simply an active variant of social learning (Hoppitt et al., 2008), which, for some authors, may also require the intentional passing of knowledge from one individual to another (Strauss & Ziv, 2012). The presence or absence of teaching in apes has been debated (see Boesch, Bombjaková, Meier, & Mundry, 2019 but also see Moore & Tennie, 2015); however, the concept of teaching is tangential to the topic of this thesis as here I consider only less active demonstrations of social learning. These variants, as described by Whiten et al. (2004) relate directly to the empirical work making up the bulk of this piece; therefore, teaching will not be addressed in any detail.

Galef claimed that many, if not all, supposed cases of animal culture could be explained through enhancement (see Section 1.2.1.1) and he, therefore, calls for a splitting approach, instead he classifies these 'cultures' as traditions (culture, to Galef, would require imitation or teaching). This topic will be revisited in Chapter 2 within my empirical work. However, Galef's insights allow us to draw a very clear line between modern human culture, which relies on imitation/teaching, and that of apes.

1.2.3.2 ***Culture dependent traits***

In 2016, Reindl, Beck, Apperly and Tennie introduced the term Culture Dependent Trait (CDT). A CDT is a behaviour or an artefact that *requires* copying variants of social learning for its emergence. A behaviour that can instead be individually reinnovated from scratch cannot be considered a CDT. Galef would consider the latter a tradition, and the former true culture (Galef, 1992). In the next section, we turn to the general process that produces CDTs and keeps them in place, cumulative culture.

1.2.3.3 ***Cumulative culture***

1.2.3.3.1 Standing on the shoulders of ever-smaller hobbits

The exact definition of cumulative culture can be debated, however, common to many, if not all, of the definitions, is the ratchet mechanism described by Tomasello et al. (1993). The ratchet mechanism describes how across several generations the cultural knowledge of a species or population builds up in a stepwise manner where one generation improves upon the knowledge of the last one. The crux of the ratchet metaphor is the prevention (or reduction) of slippage; this requires variants of social learning that can make faithful copies (copying variants of social learning; Tennie, Hopper, & van Schaik, in press). A widely spread (though not ubiquitous, see Mesoudi & Thornton, 2018 for debate) definition of cumulative culture (in this case human culture) is that put forward in a seminal paper by Boyd and Richerson (1996, p. 80):

> *"Human cultures do accumulate changes over many generations, resulting in culturally transmitted behaviours that no single human individual could invent on their own".*

What can be seen here is that cumulative culture refers to both the process (copying variants social learning) and the product ("behaviours that no single human individual could invent on their own", i.e., CDTs). Note that, in the literature, authors use two terms in relation to this process, cumulative culture and cumulative cultural evolution (Boyd & Richerson, 1996); often these terms are used interchangeably (Tennie, Caldwell, & Dean, 2018) to describe the process of cumulative culture (the ratchet; Tomasello et al., 1993). Henceforth, I will use the umbrella term of cumulative culture to describe both process and product.

The possible mechanisms underpinning cumulative culture include emulation *and* imitation; both are copying social learning mechanisms (see above), and both have been empirically shown to be able to transmit cumulative culture (Caldwell & Millen, 2009; Reindl et al., 2017). However, the variants of cumulative culture that have been identified in the lab have been a source of recent contention. Some argue that 'laboratory cumulative culture' is a diluted form and should not be considered equal to modern human culture (Miton & Charbonneau, 2018). Despite these objections, I shall err on the side of caution by assuming that the cumulative culture expressed in the lab *is* representative of cumulative culture 'in the wild'. Thus, accepting the evidence of Caldwell and Millen (2009) and Reindl et al. (2017) as evidence of cumulative culture resulting from emulation alone. This is important as it re-opens the possibility of cumulative culture in apes, because, even though they appear incapable of spontaneous imitation (Section 1.2.1.2; Tennie et al., 2012; Tomasello et al., 1997), they do have capability of spontaneous emulation (e.g., Hopper, Lambeth, Schapiro, & Whiten, 2008), though a seemingly limited one (Tennie et al., in press).

1.2.3.3.2 Uniquely human?

This section will focus on the claims of animal cumulative *material* culture. Some of the most convincing cases of animal cumulative culture reside outside of the material, for example, in bird (e.g., Fehér, Wang, Saar, Mitra, & Tchernichovski, 2009) and whale (Allen, Garland, Dunlop, & Noad, 2018) communication. Despite their seeming veracity, these are cases of *vocal* cultures and are thus not relevant to the question of tool use. Three of the best-proposed examples of animal cumulative culture to date will follow, however, each of these is not without doubt and the reasons for this trepidation will also be outlined. Claims of cumulative *material* culture are principally in birds and primates. In the interest of space, within this thesis, a single example will be selected each from birds, monkeys and hominids, each case is included because there is a claim or possible inference that the behavioural form may be a CDT. However, as we will see, actually all of these cases are unlikely to be outside an individual's capacity within their lifetime, i.e., individuals may still be able to "reinvent the wheel" (Schofield et al., 2017 citing Tomasello, 1999b). If so, these cases would be better classified as latent solutions (Tennie et al. 2009).

The first, avian, example is the New Caledonian crow (*Corvus moneduloides*), which has been widely noted to use tools in extractive foraging, even manufacturing and modifying these tools (Weir, Chappell, & Kacelnik, 2002). The use of pandanus tools (made from the leaves of the *Pandanus spp.* plant) has been claimed to be evidence of cultural evolution, based on the seemingly progressive shapes of tools (Hunt & Gray, 2003). The so-called "multi-step tool" design is supposedly an evolution of the standard "wide" design; in a three-stage process where the tools went from "wide" to "narrow" or "one-step", cumulating in the "multi-step" design. This tool is a piece of pandanus leaf, wide at the base, 'stepping' up into narrower sections; it is used by the crows to extract invertebrates from holes in trees and fallen branches. To date there is no evidence of a naïve individual reinnovating this tool, however, a long-term test of naïve birds (especially from within the genetic sub-population of occurrence in the wild) is still outstanding.

A recent claim for cumulative culture in non-human primates is in monkeys, specifically in Japanese macaques (*Macaca fuscata*; Schofield et al., 2017). These monkeys take human provisioned, sweet potatoes and wash them in a body of water, supposedly to remove contaminants (Hirata, Watanabe, & Kawai, 2001). This has been closely documented, from its first innovation, by "Imo" (Kawai, 1965), to the behaviour today. The cumulative culture claim is that the behaviour has altered, over nearly 60 years, from 'dunking' in freshwater to in saltwater, advancing to contact washing (where the subject rubs the contaminants from the tuber as it is submerged) and finally to water wash-hole digging (where a personal hole is dug by the washer, with the express purpose of washing tubers; Schofield et al., 2017). This may be a form of cumulative culture, however, given the speed of ratcheting and relative simplicity of the final behavioural form (which is likely not outside the capacity of a single individual, a claim which should be tested), this should not be considered the equal of human cumulative culture.

A third example of potential cumulative culture comes from one of our closest extant relatives, chimpanzees. Whiten, Horner and Marshall-Pescini (2003) discuss two potential cases of cumulative traits in chimpanzees: firstly, the use of a longer ant-dipping wand to transfer ants from hand to mouth at Gombe and Bossou, which is claimed to be 'ratcheted up' from the shorter sticks where ants are consumed directly from the stick. The former behaviour is claimed to be as much as four times more efficient (Whiten et al., 2003). Given the only variation in the behavioural form is the shift in consumption medium from stick to hand and an increase in stick length it seems unlikely that this represents a true case of cumulative culture, similar to our own.

Whiten et al's (2003) second example is perhaps more convincing but still fails to meet the standards of cumulative culture as defined by Boyd and Richerson (1996). Whiten et al. (2003) claim that the use of smaller stones to stabilise anvils whilst using stone hammers to crack nuts (Matsuzawa, 1994) represents a cumulative build-up from nut-cracking without these stabilising stones. It is plausible that this is true, and that this technique represents one of the few cases of *true* cumulative material culture outside our lineage, however, there is no evidence (for or against) that speaks to the question of whether this lies outside the individual capacity of a single chimpanzee. As would be predicted if this were true, Whiten et al. (2003) acknowledge that this behaviour has failed to take hold in any communities. It is, therefore, more likely that this behaviour *does* represent a cumulative technique learned by an individual through trial and error which then fails to be passed on to the next generation; clearly distinguishing it from a case of socially transmitted cumulative culture.

From the limited examples described here, it can be seen that animals may well display traits that increase in complexity across their lifetime (ontogenetically). Indeed, such cases may blur the lines between common or garden culture and the special case of cumulative culture (Dean, Vale, Laland, Flynn, & Kendal, 2014) creating a 'grey-zone' (Tennie et al., in press), such cases require more investigation before definitive claims are made. However, such uncertainty should not be considered as evidence of cumulative culture by default, given the mounting evidence that many cases of ape culture are explicable through non-copying social learning mechanisms (see Section 1.2.4.2.3; Tennie et al., in press) a CDT explanation seems to lack support.

1.2.4 Non-human material culture

Chimpanzees have the largest material cultural repertoire in the animal kingdom (except our species). It is probably owing to this fact that the animal culture literature has a disproportionate focus on apes, particularly chimpanzees, a so-called "chimpocentrism" (Beck, 1982). Fortunately, this thesis is concerning ape cultural behaviours, therefore the remainder of this section will be dedicated to discussing ape culture.

1.2.4.1 ***Geographical patterns in ape cultural traits***

Commonly used to support the claim of culture in apes is the "method of exclusion", also termed the ethnographic method (Krützen, van Schaik, & Whiten, 2007). The method of exclusion consists of a systematic survey about the behavioural phenotypes of the individuals within their respective field sites. This survey was provided to several field sites and is based on a literature review and the experiences of the researchers. This methodology was chosen as the authors highlight the impact that publication biases would have on a simple meta-analysis or literature review (Whiten et al., 2001). The first and potentially largest of these endeavours is Whiten et al.'s (2001, 1999) with data from nine chimpanzee field sites. Responses are classified on a continuum see Table 1.2. Responses are collated and behaviours are broadly grouped into putative cultural traits and those failing to meet the criteria (i.e., species "universals" or very rare behaviours). Putative cultural traits are those identified as customary or habitual (see Table 1.2) in at least one site, whilst being absent in at least one other. The results of these efforts revealed 39 putative cultural traits in chimpanzees (Whiten et al., 2001, 1999). These efforts have since been replicated in the other three species of resulting in even more putative cultural traits (bonobos: Hohmann & Fruth, 2003; gorillas (*Gorilla gorilla sp.*): Robbins et al., 2016; orangutans (*Pongo sp.*): van Schaik et al., 2003).

Table 1.2. Classifications from the method of exclusion, note that these definitions are all direct quotes from Whiten et al. (2001, p. 1488) to avoid author ambiguity.

Classification	Description
Customary	Pattern occurs in all or most able-bodied members of at least one age-sex class (e.g. adult males).
Habitual	Pattern is not customary but has been seen repeatedly in several individuals, consistent with some degree of social transmission.
Present	Pattern is clearly identified but neither customary nor habitual.
Absent	Pattern is not recorded and no ecological explanation for absence is apparent.
Ecological explanation	Absence of pattern is explicable because of a local environmental or ecological constraint.
Unknown	Pattern is not recorded, but we cannot be sure of absence because of inadequacy of relevant observational opportunities.

The method of exclusion provides a useful ‘broad brush’ approach to identifying putative cases for culture. However, Laland and Janik (2006) highlighted some of the key limitations to the method of exclusion. They argue that this method, in attempting to control for the influence of genetics, fails to account for the fact that genes and culture are likely interdependent and therefore may miss cases of true culture. This is because genetics and culture are likely to coevolve (Feldman & Laland, 1996), given that they are both adaptive processes, therefore any attempt to exclude genetic influences would mask many cases of genuine culture. Laland and Janik also argue that the importance of the interaction between genes, culture and ecology is missed by this method, because of the inherent lack of cause and effect data in such a survey. They also present several critiques of the way that data collected using the method of exclusion have been interpreted. Despite these critiques, this method can be considered a useful starting point for further research (Krützen et al., 2007; Neadle, Allritz, & Tennie, 2017). A more detailed discussion of the method of exclusion is outlined in Chapter 2, the study on which this is based was a response to a method of exclusion paper in gorillas (Robbins et al., 2016).

1.2.4.2 ***Hypotheses surrounding animal culture***

There are two primary hypotheses to explain the emergence, presence and maintenance of animal cultures, in particular, they attempt to explain the patterns identified through the method of exclusion. In this section, I will discuss each of these hypotheses in turn.

1.2.4.2.1 Culture Dependent Trait hypothesis

This is often the default hypothesis within the animal culture literature. This hypothesis is championed by many researchers (e.g., Boesch et al., 2019; Dean et al., 2014; Whiten et al., 1999) and is often portrayed more generally through documentaries (e.g., the recent BBC Planet Earth documentary). The culture dependent trait (CDT) hypothesis assumes that social learning is required to explain some or all ape cultural trait forms, that is, without social learning, these behavioural forms and artefacts could not exist (i.e., be transmitted and maintained).

The term "CDT hypothesis" is not yet commonplace within the literature, however, it assumes that copying variants of social learning are necessary to establish and maintain ape cultures (consistent with Reindl et al.'s (2017) definition of a CDT). Throughout this thesis, I will term what others have called the "social learning hypothesis" (van Schaik et al., 2003), the CDT hypothesis. This is primarily in the interest of clarity, as is explained in Section 1.2.4.2.2, the principal competing hypothesis (Zone of Latent Solutions; Tennie et al., 2009) also recognises the importance of social learning in animal cultures without assuming a ‘dependence’. Thus, to attempt to divide the two based on the presence of social learning alone would be a ‘straw-man’ arguement and should be avoided.

Early proponents of the CDT hypothesis even suggested that “[i]t is difficult to see how such behaviour patterns could be perpetuated by social learning processes simpler than imitation” (Whiten et al., 1999, p. 685). This demonstrates that, at least some, advocates of the CDT hypothesis consider apes capable copiers and assume that copying variants of social learning underly ape culture. The veracity of this claim will be tested empirically in Chapters 4 and 5, the latter of which (along with Section 1.2.1.2) contains more detailed discussion about imitation outside our lineage.

1.2.4.2.2 Zone of Latent Solutions hypothesis

The Zone of Latent Solutions (ZLS) hypothesis was initially outlined by Tennie, Call and Tomasello (2009). The underlying assumption of the ZLS is that non-copying social learning mediates frequencies of cultural variants; i.e., increases the frequencies of behavioural or artefact forms. Contrary to the CDT hypothesis, the ZLS hypothesis does not assume that copying variants of social learning must transmit behaviour or artefact forms for a trait to be classified as cultural (see also Chapter 2). Instead, the ZLS assumes that behaviour and artefact forms are explained biologically, i.e., by an interplay between environment and ontogeny (including genetic predispositions), but also mediated via evolved cognition (Tennie et al., in press). The role of social learning according to the ZLS, in species that are restricted to their ZLS (e.g., apes; Reindl, Bandini, & Tennie, 2018) is in influencing the frequencies of these forms.

The ZLS hypothesis predicts that behaviours within a species' ZLS can be reinnovated (Tennie et al., 2009). Therefore, an infant chimpanzee placed on an island (assuming that they had some way of acquiring the necessary nutrition) could theoretically, within the course of their lifetime, reinnovate all of the behaviours expressed by any wild conspecifics without the need to copy. I introduce the qualifier "theoretically" here because Tennie et al. (2009), suggested that *some* behaviours may require specific ecological/individual circumstances/experiences to be reinnovated. For example, nut-cracking may require that a chimpanzee first learns, individually, that pieces of stone or wood can be used as natural hammers. This could occur by chance and therefore would not require copying; e.g., a piece of wood could fall from a tree and break a seed pod below or it may occur through trial and error. If more individuals were introduced to the metaphorical island the relative probability of those individual reinnovating the behaviours expressed by the first chimpanzee would be increased, i.e., they would become socially mediated reinnovations (Bandini & Tennie, 2017).

The ZLS hypothesis accepts that processes such as local enhancement (or even emulation) increase the frequencies of behavioural and artefact forms in affected populations and help maintain the patterns identified by the method of exclusion (Whiten et al., 1999). The ZLS hypothesis, therefore, shares the prediction of the CDT hypothesis regarding the variability of forms across populations. However, the ZLS assumes that these differences depend to varying degrees on environmental and genetic differences, but also on chance events such as the order of innovations and subsequent social effects on the frequency of these forms being reinnovated (Tennie et al., in press).

However, the ZLS hypothesis is incompatible with action copying/imitation; this is because this form of copying, by way of copying error alone, can lead to CDTs beyond the species' ZLS (Kempe, Lycett, & Mesoudi, 2014). The ZLS hypothesis, therefore, claims that unenculturated apes cannot and do not spontaneously imitate (Tennie et al., 2012; but see Call, 2001 for evidence of imitation in enculturated apes). This is in stark contrast to the proponents of the CDT hypothesis (see Section 1.2.4.2.1 and Whiten et al., 1999, 2009). Furthermore, in the newest iteration of the ZLS hypothesis, Tennie et al. (in press) suggest that even results copying/emulation might not be as prevalent in ape cultures as previously assumed. From this, they assume that spontaneous emulation in apes should be of such poor fidelity or so rare that is likely to produce CDTs, by copying error alone, and may yet be excluded by a ZLS account.

Moreover, the ZLS hypothesis is one of capacity, a key assumption of the ZLS is that no individual member of a species is 'special'. Instead, the ZLS assumes that if one individual can reinnovate a given behaviour so too (theoretically) will all typically developing members of the species, given the same/similar ecological conditions and ontogenetic histories (Tennie et al., 2009). Therefore, every individual within a species (or sub-species) has the potential to individually reinnovate their entire species repertoire, though ecological conditions may not favour this. In this way, it is possible, within the remit of the

ZLS to explain how certain populations only express select parts of the entire species repertoire, e.g., the patterns described by the method of exclusion.

As with the CDT hypothesis, the ZLS hypothesis has come under substantial scrutiny, however, unlike the CDT hypothesis, it is the *assumptions* underlying the ZLS theory that constitute the main source of contention. The primary nature of these contentions is around the assumption for the ZLS hypothesis that modern human and animal cultures differ markedly, in that human culture is reliant on imitation (Tomasello, 1999a) and perhaps other copying variants (Caldwell & Millen, 2009; Reindl et al., 2017). Whereas, animal culture is simply the product of the aforementioned socially mediated serial reinnovations utilising non-copying social learning variants (Tennie et al., 2009). Though, some contest this notion (Stout et al., 2019) more data are needed before a conclusion is drawn.

1.2.4.2.3 Diverging evidence

The methodology used for testing the ZLS hypothesis is known as the Latent Solutions (LS) methodology (Bandini & Tennie, 2018; Tennie & Hedwig, 2009). Evidence for the ZLS hypothesis is primarily from captive studies (e.g., Tennie et al., 2008), though some ‘natural’ ZLS type studies exist (e.g., Sherry & Galef, 1984). In these ‘natural’ experiments, behavioural/artefact forms are observed in culturally unconnected (Neadle et al., 2017) wild populations; therefore (if the assumptions of the ZLS hypothesis are correct), these behaviours/artefacts must have been reinnovated within the population. Whichever method used to collect it, the resulting data (if affirmative) is difficult to explain from a CDT hypothesis framework. The LS methodology effectively excludes all social learning variants as an explanation for the behaviour’s emergence. To explain the results of a positive LS test, within a CDT framework, one would need to assume that a "rare innovator" (Hopper et al., 2007) had been identified, or accept that the behaviour cannot constitute a CDT. Given the mounting evidence of ‘positive’ LS tests, even with multiple independent innovators (e.g., Bandini & Tennie, 2017), the parsimony of the "rare innovator" argument is waning. LS tests are applied, and methodological considerations outlined in Chapters 3 and 4.

In its first iteration, the LS methodology was considered appropriate to provide evidence for a whole species, based on the findings in just one subject (Tennie & Hedwig, 2009) – this follows the logical thought exercise that it takes one black swan to prove not all swans are white. Whilst logically acceptable, this application of the LS method does not allow researchers to reduce the likelihood of a ‘rare innovator’ being tested, this means that by chance alone the researcher might have happened upon an individual that would be included under a CDT explanation. Based on such critiques and to further reduce the likelihood of a ‘rare innovator’ being identified, Bandini and Tennie (2017) introduced the "double-case standard". Behaviours with a high relative probability of occurrence, i.e., simpler behaviours, require evidence of the behaviour in *two* unconnected populations (meaning, at a minimum in two culturally unconnected individuals) before behaviours can be confirmed to be within the species’ ZLS. Those behaviours with a lower relative probability of occurrence, continue to require only one reinnovation.

Behaviours expressed during LS tests are most parsimoniously explained as products of individual learning; therefore, are within a species ZLS. LS testing requires that subjects are first and foremost naïve to the target behaviour. Without this, it is difficult to be sure exactly *when* the behaviour was reinnovated. In this context, a naïve subject must have never expressed, or seen others expressing a target behaviour; ergo, subjects can be naïve to one behaviour and not naïve to another. Subjects must also be placed exposed to an ecological situation wherein the target behaviour can be reinnovated, e.g., if leaf sponging, subjects would require an environment containing leaves suitable for sponging. Finally, subjects should be unenculturated and 'undeprived' (Henrich & Tennie, 2017), to increase the likelihood that the resultant data are generalisable to conspecifics. Unenculturated individuals are those that are not reared by humans, trained to perform the target behaviour by humans or otherwise habituated to the extent that their behavioural phenotype is no longer species-typical. This presents a challenge in many captive studies as, in the past, zoo rearing/husbandry has left many captive apes enculturated. For an individual to be considered undeprived it should have never been subjected to substantive or prolonged mistreatment, e.g., a chimpanzee kept on a leash outside. The results of LS tests with enculturated or deprived individuals should be treated with caution as they lack ecological validity.

In this sense the 'perfect' subject has been reared in wild or at least wild-type conditions, by their mother, with as little contact with humans as possible. This subject should be at a stage appropriate to express the behaviour being investigated (see Chapter 4) and be sufficiently motivated to engage with the task. However, the 'perfect' subject does not necessarily exist without the required conditions, this is what they LS methodology aims to provide.

1.2.5 Open questions and issues

One issue that plagues the literature relevant to this thesis is that of terminology. Often, researchers appear to dedicate larger proportions of their academic works to debating semantics than discussing large scale conclusions that their results lead to. Of particular relevance to this thesis is the term ‘culture’, discussion of whether a behaviour is ‘cultural’ and what this means often leads to heated debate (Kendal, 2008; McGrew, 2002). Thus, the field requires a term, similar to ‘tradition’ (Galef, 1976), that does not remove the status of a ‘cultural species’ from those restricted to it.

An open question is that of the CDT vs. ZLS hypotheses. Which of these most effectively describes the patterns observed in ape behaviour? The LS testing methodology provides an ‘acid test’ between the two hypotheses, therefore more research is required to lend support to one or the other hypothesis. Moreover, the basic assumptions of the two hypotheses need further clarification. It becomes necessary, as the ZLS approaches 10 years from first publication, to determine whether spontaneous action copying in apes is indeed impossible or whether it remains a possible explanation for ape cultural behaviours. Also, the influence of social and ecological influences on individuals, the so-called "right" conditions (Tennie et al., 2009), must be quantified.

1.3 This thesis

The remainder of this thesis will attempt to contribute some evidence towards these open questions. In the first three Chapters, I will use the variants of the LS methodology to assess the validity of the ZLS claim; in so doing I will address the concept of culture in apes and set a new proposed standard for its terminology; also considering to what extent cognitive cladistics can be included within the ZLS. Chapter 2 will address the question of a recently documented “putative” case for culture (Robbins et al., 2016), and determine its place within the ZLS of gorillas through an adaptation of an LS test. Chapter 3 will examine the influence of cognitive cladistics within the ZLS hypothesis, that is, to what degree species' ZLS overlap. Completing the traditional ZLS methodology studies; the first condition of Chapter 4 will consider whether nut-cracking, potentially the most complex of ape tool use behaviours, belongs within the ZLS of chimpanzees or whether this behaviour is the exception to the ZLS rule to date.

Next, Chapter 4 will also assess the capacity for apes to acquire nut-cracking through social facilitation through the 'improved' ZLS methodology proposed by Bandini and Tennie (2018). This chapter will directly test the claims of both the CDT hypothesis and the ZLS hypothesis, whilst also touching on other more specific hypotheses (captivity effect and sensitive learning periods). Chapter 5 will test the capacity of apes to imitate in a social learning task. By removing the possibility of success via emulation, I attempt to coax apes into demonstrating "true" imitation, facilitated by social learning biases (Laland, 2004), thus creating a social environment that removes potential barriers to ape imitation.

Finally, in Chapter 6, the question of ecological influences on the expression of material culture in apes will be addressed. This chapter utilises data from semi-wild, sanctuary reared, bonobos in a naturalistic setting, stripped of many survival pressures and compares these data to that of wild conspecifics. This is in the hope of demonstrating that the ecology of apes is as important, if not more so than their genetic predispositions in explaining many putative cases of culture. These data are also analysed to assess the influences of developmental stage and rearing history in this sample.

I have undertaken this research to seek answers to the question: what are the factors that influence the expression of material culture in apes? This thesis will explore the genetic predispositions, social learning capacities and ecological sensitivities of apes with a focus on material culture and tool use. Chapter 7 will summarise these findings, relate them to the relevant literature and finally provide some recommendations for future research, some of which I intend to embark on myself.

CHAPTER 2: FOOD CLEANING IN GORILLAS: SOCIAL LEARNING IS A POSSIBILITY BUT NOT A NECESSITY

This chapter, largely in its current form, is published as:

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The changes that I have made to the 2017 paper are largely reflective of changes in terminologies since the publication of the manuscript; e.g., the term "low-fidelity" has been removed. This is because, since this paper was accepted in its final form, other research from our group, questioned the utility of this terminology (Bandini & Tennie, 2017; Reindl et al., 2017; Tennie et al., in press). Furthermore, phrasing has been changed throughout the chapter as my writing style has developed since this initial publication. There have been no substantive changes to the aims, method of analysis, data, figures, or the conclusions drawn.

The author contribution statement as presented to PLoS One at the time of publication was:

Conceptualization: DN
Data curation: MA
Investigation: DN, MA
Methodology: DN, MA, CT
Formal analysis: DN
Project administration: DN
Resources: MA
Supervision: CT
Writing – original draft: DN
Writing – review & editing: DN, MA, CT

I was first author, responsible for the conceptualisation of the study, i.e., the idea for reanalysing the data using the final code scheme. I coded the data, obtained second coder reliability, conducted all analyses, wrote the original draft, and was responsible for organising the day-to-day running of the project, i.e., passing the manuscript between co-authors, and also completed later drafts and edits, including actioning reviewer comments. MA was responsible for collecting the data for the first study, which was then recoded for this study. MA was also a liaison with the MPI EVA, Leipzig, Germany and provided comments and edited drafts. Finally, CT acted as a supervisor throughout the project, he was involved in the initial study design and edited drafts for publication.

2.1 Introduction

There is evidence of the general behaviour of removing contaminants from food in many animal species, including: wild boars (*Sus scrofa*; Sommer, Lowe, & Dietrich, 2016), Japanese macaques (Hirata et al., 2001; Nakamichi, Kato, Kojima, & Itoigawa, 1998; Sarabian & Macintosh, 2015), vervet monkeys (*Chlorocebus aethiops*; van de Waal, Krützen, Hula, Goudet, & Bshary, 2012) and capuchin monkeys (*Cebus apella*; Visalberghi, Savage-Rumbaugh, & Fragaszy, 1995), along with all species of great ape (Allritz, Tennie, & Call, 2013). The removal of unpleasant contaminants from food is likely adaptive; the repeated consumption of dirt, sand or grit can wear down and/or damage the teeth (Fraser & Theodor, 2011), whilst also reducing the risk of parasite infection (Sarabian & Macintosh, 2015). This said, it is possible that the consumption of some of these ‘contaminants’ might actually improve digestion, as has been identified in some species of birds (Gionfriddo & Best, 1995, 1996).

In the most recent incarnation of the method of exclusion (see Section 1.2.4.1, exploring the wild behavioural repertoire of mountain (*Gorilla gorilla beringei*) and Western (*Gorilla gorilla gorilla*) gorillas, Robbins et al. (2016) identify food cleaning as “customary” in Western lowland gorillas. Robbins et al. apply the method of exclusion across five gorilla field sites: three Western lowland sites (Moukabala-Doudou National Park, Gabon; Bai Hokou, Central African Republic & Mondika, Republic of Congo) and two mountain sites (Karisoke Research Center, Rwanda & Bwindi Impenetrable National Park, Uganda). Data include combined observations of the gorillas at these sites between 1998 and 2015 (19 groups of western lowland gorillas and 12 groups of mountain gorillas). These observations of gorilla behaviours were used to generate a list of 41 behaviours.

From these 41 behaviours, Robbins et al. (2016) identified 23 “potentially cultural traits”: 12 within species variants (variation between sites of one sub-species of gorilla) and 11 between species variants (variation *only* observed between mountain and western lowland gorillas). Also highlighted were: three “universal” traits, 10 “rare behaviours” and five traits with ecological explanations (see Section 1.2.4.1, Table 1.2).

Amongst the putative cultural traits only one food processing behaviour was noted, namely fruit cleaning. This behaviour will be the focus of this chapter. Robbins et al. (2016, p. 8) describe fruit cleaning as: "Rubbing fruit against [the] arm or body, presumably to remove dirt; for some fruit, it may be to remove spines". Based on this definition it can be assumed that the form of the behaviour (*sensu* Reindl, Beck, Apperly, & Tennie, 2016) is the rubbing of food (fruit) on the body to remove an unwanted substance/part. In this context, behavioural form refers to the actions required to attribute behavioural patterns to an individual. The action required to remove parts or substances is the same regardless of food being cleaned or contaminant; namely, to rub the food against a body part or substrate. Thus, the form of the behaviour is independent of the food type and the substrate to be removed. Hereafter, I will refer to the behavioural form of rubbing any food against the body (including extremities) as ‘food cleaning’.

Food cleaning was observed at all western lowland gorilla research sites; however, it was never observed at mountain gorilla research sites. This pattern led the authors to conclude that this behaviour is potentially cultural based on "variation between mountain and western gorillas" (Robbins et al., 2016, p. 8). For this chapter a more general definition of culture will be used, where a behaviour's facilitation through social learning is sufficient to attribute cultural status (*sensu* Kendal, Kendal, Hoppitt, & Laland, 2009); closer to Galef's (1976) concept of tradition. This definition will be revisited in the discussion of this chapter.

As discussed in Section 1.2.4.1, the method of exclusion attempts to identify cultural traits through geographical variations in behaviour, assuming that innovations and copying variants of social learning are responsible for these patterns (Whiten et al., 1999). Practitioners of the method of exclusion have attempted to control for ecological confounds by identifying when behaviours are ecologically not possible, i.e., when a required artefact or situation necessary for a given behaviour is not present (for example, fruit availability being permanently limited in a particular ecology would be an ecological explanation for fruit cleaning being absent; Robbins et al., 2016). Applications of the method of exclusion typically use ecological explanations as a simple dichotomous category, i.e., the behaviour is ecologically possible or not possible (e.g., Hohmann & Fruth, 2003; van Schaik et al., 2003; Whiten et al., 1999).

Besides ecology, genetic differences may also play a confounding role when applying the method of exclusion. Generally, the most convincing reports, to date, that suggest cultural (rather than environmentally and/or genetically induced or mediated) differences between great ape field sites are when populations of the same subspecies live close to each other. That is, in very similar environments, with a high likelihood of genetic mixing, i.e., without physical barriers (Langergraber et al., 2010). The fact that differences can and do still exist in these cases (e.g., Langergraber et al., 2010; Luncz, Mundry, & Boesch, 2012) makes the conclusion that these behaviours are ‘cultural’ plausible. These are among the best-supported cases for culture in (wild) apes.

However, even in these most convincing cases, there is always the possibility that subtle differences at the genetic and/or environmental level are ultimately responsible for the observed differences. Thus, even the best applications of the method of exclusion (e.g., Langergraber et al., 2010) are a broad-brush approach, yielding conclusions which should be verified through captive studies. Despite its utility, the method of exclusion cannot detect the social learning variants underlying the trait and its frequency nor whether social learning is necessary to explain the form of the behaviour. Determining the underlying mechanisms, and their necessity, requires controlled experimentation in captive environments (see Bandini & Tennie, 2018 and Chapter 4)

This study aims to test the veracity of the assumption that food cleaning is culture dependent by testing a group of captive western lowland gorillas for reinnovation of the form of this behaviour. This chapter uses an adaptation of the LS methodology (see 1.2.4.2.3) that does not assume that subjects are naïve to food cleaning. Given the likely high prevalence of somewhat dirty food in both captive and wild populations it is implausible to think to discover dirty-food naïve subjects. Instead, here we test for evidence of a *culturally unconnected population-level* instance of food cleaning to add to the cases reported by Robbins et al. (2016). ‘Culturally unconnected’, refers to the status of individuals that have not had contact with a member of a population previously shown to perform the target behaviour. Accordingly, our sample of western lowland gorillas has not been in contact with any of Robbins et al.’s (2016) samples.

As the populations are unconnected, the behaviour cannot have been socially learned from conspecifics, therefore passing from the aforementioned wild populations and the captive population tested here. It is possible, though unconfirmed, that at least two of the three wild populations (Moukalaba-Doudou national park and Mondika, Dzanga-Sangha national park) reported by Robbins et al. (2016) were culturally unconnected (given the substantial geographic distance; approx. 890km between them). If this assumption is correct, our captive sample would constitute a third, independent, population observed for food cleaning.

In this study, we provided captive Western lowland gorillas with affordances that may encourage food cleaning (i.e., by provisioning them with peeled apples that were covered in sand); therefore, we fulfilled the ecological requirement of the LS test methodology. We recorded instances of food cleaning behaviours and categorised the specific methods of cleaning. The results are discussed in light of the data presented by Robbins et al. (2016).

2.2 Method

The recordings used in this study are taken from a larger set containing data for all genera of great apes; here we only re-coded the western lowland gorilla recordings (data collected by Allritz et al., 2013). Forty-eight recordings of gorillas being exposed to dirty (sand-covered) peeled apples (1 hour 50 minutes = 24 recordings) and clean peeled apples (1 hour 1 minute = 24 recordings; total across both apple types = 2 hours 51 minutes) were re-coded and reanalysed for this study; this was done with the goal to code for food cleaning, which was not recorded in the previous study (Allritz et al., 2013). The data contained no evidence of food washing (i.e., cleaning by using water; Allritz et al., 2013) in any trial despite there always being an open basin of freshwater available.

2.2.1 Subjects

The subjects in the selection of videos were five Western lowland gorillas (1M/4F; mean age at time of testing: M age=16.60, SD=12.58; both years) located and housed together at the time at the Wolfgang Köhler Primate Research Centre in Leipzig Zoo, Germany (see Table 2.1 for details of apes along with familial relations; these gorillas comprised the entire group of gorillas at WKPRC at the time data was collected). One subject, Zola, a three-year-old female juvenile was also tested, however, her data were excluded from further analyse because Zola was always tested with her mother, who monopolised virtually all food.

All individuals in the sample were captive-born, apart from one female, "Bebe", who was wild-born. "Bebe" was captured in Cameroon (rather than from the Republic of Congo or Gabon, as the populations in Robbins et al.’s study; 2016). Given that there is no reported claim, to our knowledge, for wild gorillas in Cameroon displaying food cleaning it is unlikely that the subject "Bebe" socially learned this behaviour from wild conspecifics. However, it must be noted that we know of no studies directly observing food cleaning in this population. Even so, with the information available to date, we assume that even if we did not capture the very first reinnovation of this behaviour, any noted reinnovation would be the result of individual learning as it could not have been transmitted, via social learning, from a wild population.

Table 2.1. Subject rearing information, italicised mother/father indicates that parents were not involved in this study.

Subject	Sex	Year of birth	Place of birth
Bebe	Female	~1979	Wild, Cameroon
Gorgo	Male	1981	Krefeld, Germany
Viringika	Female	1995	Zurich, Switzerland
Kibara	Female	2004	Leipzig, Germany
Louna	Female	2006	Leipzig, Germany
Zola	Female	2008	Leipzig, Germany

Per the recommendations of the Weatherall report "The use of non-human primates in research" all the gorillas were housed in semi-natural indoor and outdoor enclosures containing climbing structures, such as ropes and platforms; and natural features, such as vegetation, trees and streams. They received regular feedings, primarily consisting of vegetables, had access to enrichment devices including shaking boxes and poking bins, and water ad-lib. Subjects voluntarily participated in the study and were never food or water-deprived. The research was conducted in the observation rooms.

No medical, toxicological or neurobiological research of any kind is conducted at the Wolfgang Koehler Primate Research Center. The research was non-invasive and strictly adhered to the legal requirements of Germany. The study was ethically approved by an internal committee at the Max Planck Institute for Evolutionary Anthropology (members of the committee are Dr J. Call, Dr D. Hanus, veterinarian Herr Nötzold, head keeper F. Schellhardt and assistant head keeper M. Lohse). Animal husbandry and research comply with the "European Associations of Zoos and Aquaria Minimum Standards for the Accommodation and Care of Animals in Zoos and Aquaria", the “World Association of Zoos and Aquariums Ethical Guidelines for the Conduct of Research on Animals by Zoos and Aquariums” and the “Guidelines for the Treatment of Animals in Behavioral Research and

Teaching" of the Association for the Study of Animal Behavior. IRB approval was not necessary because no special permission for the use of animals in purely behavioural or observational studies is required in Germany.

2.2.2 Experimental conditions

All trials were conducted between 08:00 and 12:30 (by MA), and subjects completed one trial per testing day. Subjects were tested in a separate testing room (2.52 x 2.61m). They were video recorded from the time that they entered the room; recording ceased once all three apples had been consumed or after 10 minutes. Each individual was tested four times in each condition. In both conditions, three peeled apples were placed in the centre of the testing room. In the dirty condition, the peeled apples were rolled in play-sand (Redsun branded; fine-grained quartz sand) designed for children and deemed free of harmful substances by TUV Nord, Germany, in testing. The sand was dried in an oven for approx. 20 minutes at 200°C before rolling the apples in it. The trials were counterbalanced with three gorillas being exposed to clean apples first and two being exposed to dirty apples first.

2.2.3 Data Coding

DN coded all recordings using the categories in Table 2.2. To assess the interrater reliability of the coding, a randomly selected 25% of these sequences were further analysed by another independent coder (HH). This random sample was stratified to ensure that reliability was attained for at least one video for each gorilla in each condition. The chosen videos were randomly selected by assigning numbers 1- 4 for each trial in each condition and then randomly generating numbers between one and four to coincide with a video for reliability analysis. Cohen’s Kappa Coefficient (Cohen, 1960) was computed based on the agreement between both coders. The results are reported below. Reliability was assessed based on whether the coders agreed on the method of cleaning employed (as described in Table 2.2). Instances of food cleaning were coded into bouts for ease of reliability analysis. A new cleaning bout was coded if the individual:

A. set the apple on the floor for more than 5 seconds
B. swapped method of cleaning
C. swapped hand used for cleaning
D. moved from one apple to another (because of eating the apple or abandoning it)
E. Ceased cleaning for more than 30 seconds
F. Took a bite from the apple

Table 2.2. Methods of cleaning fruit coded, along with a description, as provided to independent coders.

Method	Description
Palm	Rubbing the apple with, on or between the palm(s) of the hands
Back of hand	Rubbing the apple with the back of the hand (this does not include rubbing ON the back of the hand)
Forearm	Rubbing the apple on the hair of the forearm or the back of the hand, this is distinct from ‘back of hand’ in that the apple is being moved in this case whereas, in the former, the hand is moving.
Finger	Rubbing the apple with one finger.
Substrate	Rubbing the apple on any substrate (e.g., the floor)

2.3 Results

2.3.1 Frequency of food cleaning

The results of a Cohen's Kappa Coefficient test show that both coders achieved a satisfactory level of agreement ($\kappa = 0.71$, SE = 0.07, $p<.001$) in the *method* (i.e., which technique) of cleaning used (see Table 2); an example of a typical food cleaning sequence is shown in Figure 2.1. Both coders agreed fully in their classifications of forearm (our equivalent of the behaviour described by Robbins et al., 2016) and also that no cleaning behaviour occurred in any of the clean apple trials.

Figure 2.1. Food cleaning sequence in an adult female Western lowland gorilla ("Kibara") cleaning and eating a peeled sand-covered apple using the method described by Robbins et al. (2016).

The results showed food cleaning behaviour occurred in 95% of dirty apple trials and in 0% of clean apple trials. Only in a single trial were all the apples eaten whilst still dirty, this trial was the first exposure of Louna (3-year-old female) to the dirty apple condition. All gorillas expressed food cleaning at least once in at least 75% dirty apple trials. Not all subjects attempted to clean all dirty apples; from a total of 60 dirty apples, 8 were eaten uncleaned (Bebe: 1 apple in 1 trial; 8.3% of total dirty apples and Louna: 7 apples in 4 trials; 58.3% of total dirty apples), see Figure 2.2.

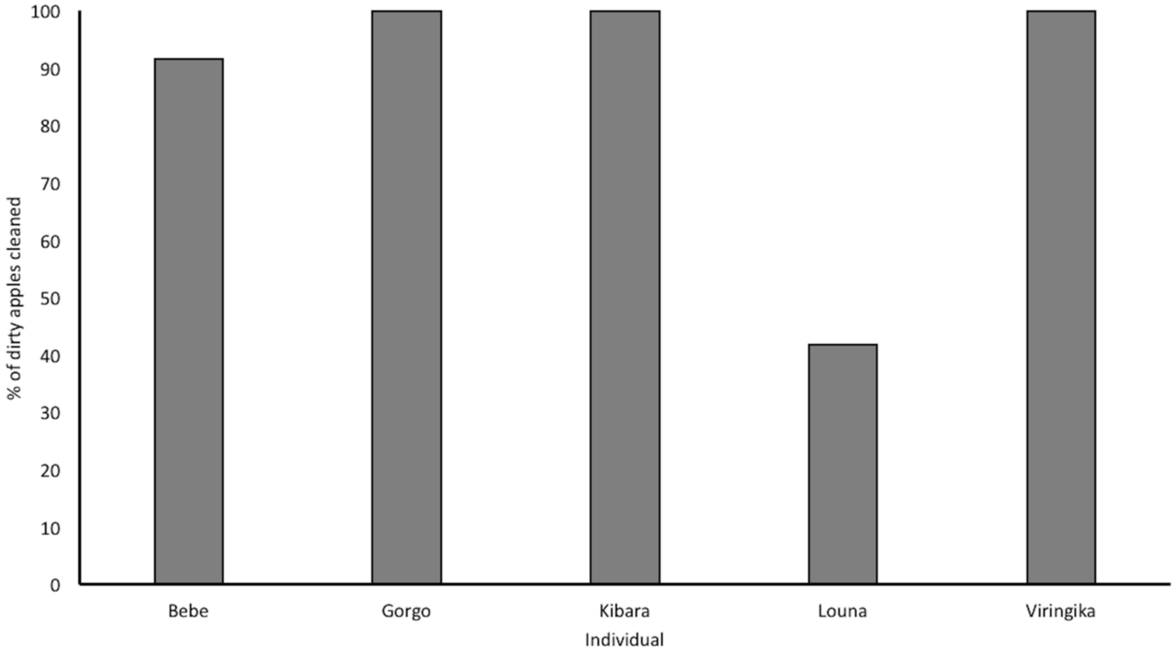

Figure 2.2. Percentage of dirty apples cleaned before first bite was taken, separated by individual.

The mean latency (time passed since entering the test room) to first clean an apple was 19 seconds (SD=27 seconds). Average individual latency to clean apples differed substantially between subjects, ranging from one second to 91 seconds (across trials; see Figure 2.3).

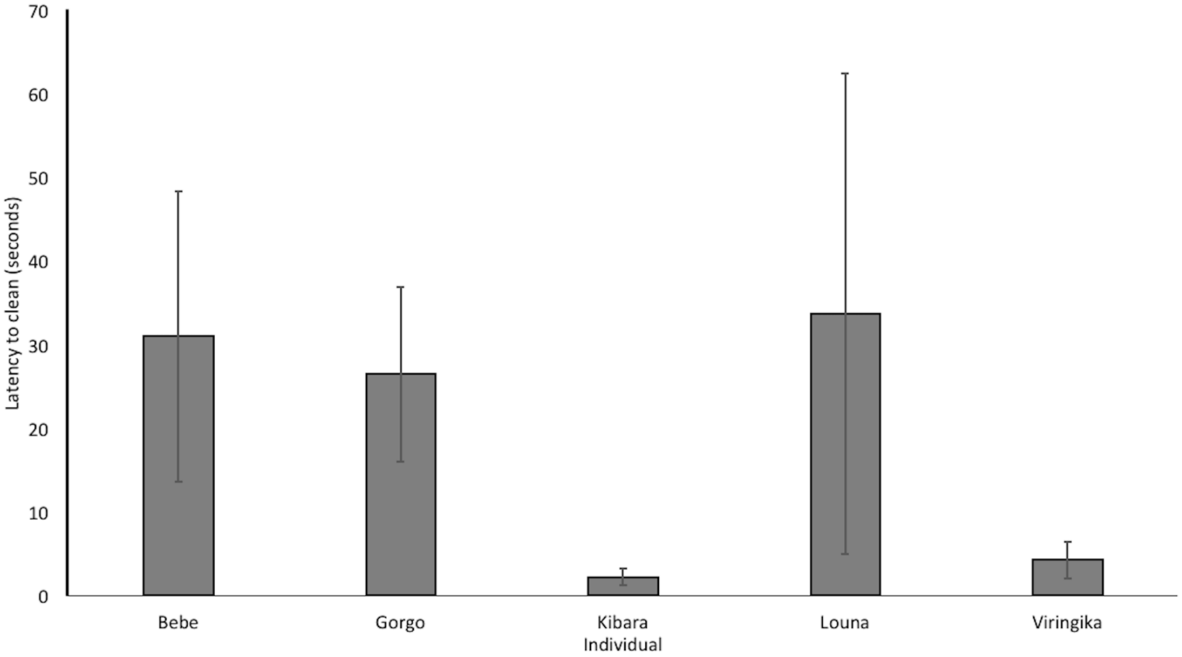

Figure 2.3. Mean individual latency to begin cleaning. Showing variation between subjects, error bars indicate ± 1 standard error of the mean.

2.3.2 Methods of food cleaning.

The methods of cleaning the fruits used in these data, listed in order of frequency of bouts, were *finger* (41%), *back of hand* (20%) *palm* (20%), *forearm* (18%) and finally *substrate* (1%); see Figure 2.4. For examples of the cleaning methods used, see Figure 2.5. The more frequent expression of the *finger* technique is owing to the way that bouts were coded, meaning that if an individual swapped hand, a new bout began. This meant that the *finger* cleaning method (which frequently swapped from using the left index finger to the right) often resulted in a high number of bouts. The *palm* and *back of hand* methods were coded more frequently for a similar reason; Viringika often used these techniques in quick succession, e.g. slapping the sand off the apple with the palm followed by the back of the hand and vice versa. As a result, this inflated the values. The frequency data serves to highlight individual differences, see Table 2.3.

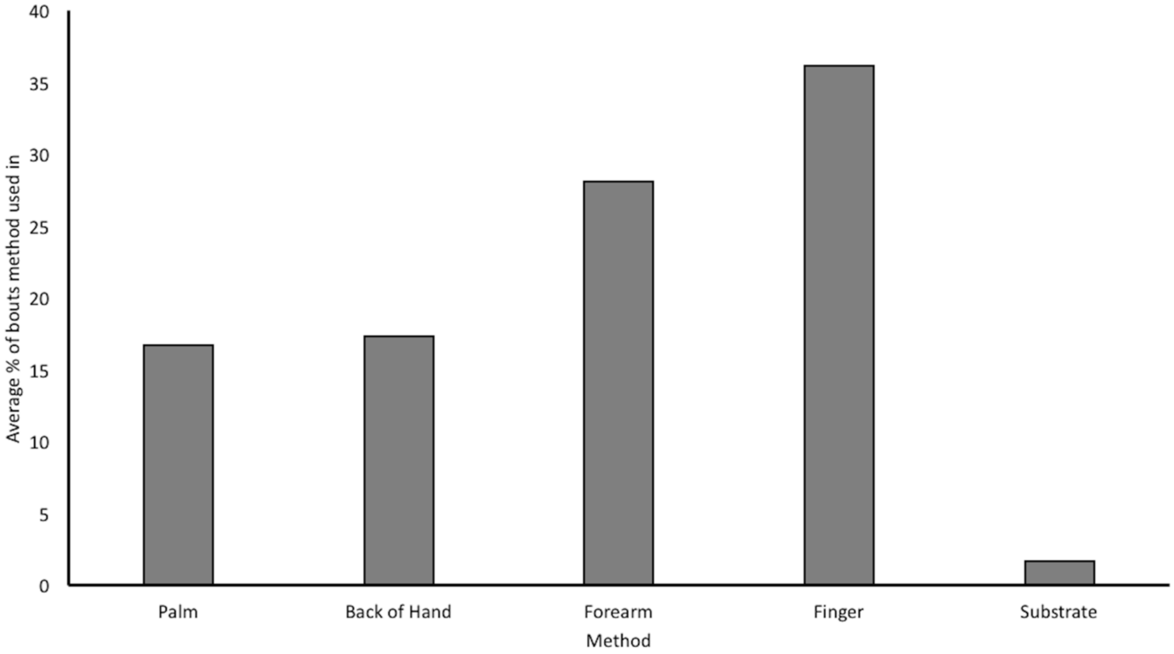

Figure 2.4. Methods of cleaning used in this study. Bars indicate average % of times that a method was used to clean the apples, data implicates all individuals across all trials.

Figure 2.5. Five methods of food cleaning used by Western lowland gorillas in this study: A) Finger B) Palm C) Back of Hand D) Forearm E) Substrate.

Table 2.3. Number of bouts using each method, divided by individual.

	Bebe	Gorgo	Kibara	Louna	Viringika	Total
Palm	2	0	3	1	**38**	44
Back of Hand	5	0	3	0	37	45
Forearm	**8**	0	**22**	2	8	40
Finger	1	**82**	4	**4**	1	92
Substrate	0	0	3	0	0	3
Total	16	82	35	7	84	224

Note. Figures in bold show the most commonly used method by each individual.

2.4 Discussion

We report here a behaviour markedly similar to that reported by Robbins et al. (2016). Our results show that food cleaning was present in a culturally unconnected sample of captive western lowland gorillas. We also show a degree of individual variation in methods used to clean contaminants from dirty food, with a further four methods being expressed. Taken together, this would imply that some degree of individual learning is present in the reinnovation of the behavioural goal and form.

These data show another populational instance of food cleaning occurring in western lowland gorillas, specifically in a culturally unconnected, captive, population. Access to some dirty food can be assumed to be a common feature of most wild and captive populations; therefore, it is implausible to expect to test a truly dirty-food naïve subject. Instead, we argue that being culturally unconnected to any populations in which the behaviour is reported is sufficient to assume that the studied group would have had to reinnovate target behaviour. As such, we conclude that food cleaning cannot be considered a CDT. If it had been a CDT, the behaviour should not reappear in culturally unconnected populations.

This said, it possible that this study did not capture the original first reinnovation(s) of food cleaning (this could have happened before the study, given ubiquitous access to dirty food). However, this population is culturally unconnected, meaning at least one naïve individual must have reinnovated food cleaning. Therefore, the timing is inconsequential to the present argument, i.e., of whether a reinnovation of the behaviour can occur in the absence of social learning. Our findings show that food cleaning can be individually reinnovated by naïve western lowland gorillas. Therefore, the form of the behaviour cannot be reliant on social learning. Instead, these findings are consistent with food cleaning being an example of a socially mediated reinnovation (Bandini & Tennie, 2017), where individual learning is sufficient to explain its emergence. That is, food cleaning can be considered a “latent solution” in Western lowland gorillas. This conclusion is drawn based both on the data presented here and data presented by Robbins et al. (2016). To date, all Western lowland gorilla groups, observed for it, show food cleaning.

Robbins et al. (2016) applied the method of exclusion to identify putative cultural traits, the interpretation of their results is complicated by differences between the groups of gorillas for whom they collected data, with regard to genetic variation (Garner & Ryder, 1996) and with regard to ecology (Nkurunungi, Ganas, Robbins, & Stanford, 2004). The failure of mountain gorillas to express food cleaning may result from a combination of genetic variation and ecological differences. It is possible that the genetic differences between these two subspecies of gorillas (Garner & Ryder, 1996; Ruvolo et al., 1994) have led to distinct behavioural phenotypes. This would not imply a "direct genetic code" for food cleaning, rather, the cognitive abilities that lead to an individual cleaning food might have become advantageous at some point and thus were selected for. This may have happened in conjunction with the frequency increasing effects of non-copying social learning variants.

Given the abundance of food cleaning in primates (Allritz et al., 2013; Hirata et al., 2001; Nakamichi et al., 1998; Sarabian & Macintosh, 2015; van de Waal et al., 2012; Visalberghi et al., 1995), a more plausible argument is that differences between mountain and Western lowland gorilla *ecology* are the primary cause of this difference. It is possible that wild mountain gorillas do not show food cleaning because their relevant ecology differs from that of Western lowland gorillas (Nkurunungi et al., 2004). Therefore, if wild mountain gorillas were to share the ecology of Western lowland gorillas, and thus were forced to consume foods that would benefit from cleaning; then they may also independently innovate food cleaning.

The feeding ecology of mountain gorillas and Western lowland gorillas differs quantitatively, i.e., the relative presence of dirty fruit (an item that is associated with food cleaning; Robbins et al., 2016). The mountain gorilla data presented by Robbins et al. (2016), is taken from Karisoke Research Centre, Virunga Volcanoes Rwanda and Bwindi Impenetrable National Park, Uganda. At Karisoke, there are no large fruiting trees within the mountain gorillas range (Robbins et al., 2016). Fruit foraging accounts for a small proportion of the total time spent foraging in some groups of mountain gorillas: <1% at Karisoke (Watts, 1984) and 11% at Bwindi (Robbins & McNeilage, 2003). Contrastingly, Western lowland gorillas have been reported to spend as much as 70% of foraging time in search of fruit (Doran-Sheehy, Mongo, Lodwick, & Conklin-Brittain, 2009); accordingly, 98% of faecal samples contained evidence of fruit consumption (Doran et al., 2002). Therefore, lowland gorillas have more opportunity to encounter dirty fruit; especially as mountain gorillas, being primarily folivores (Watts, 1984), are more likely to consume growing plants (Byrne & Byrne, 1993). If food cleaning had been identified in either of these samples we would have expected it to be in the Bwindi group, which consume more fruit. In spite of this, mountain gorillas *may* be able to reinnovate food cleaning; however, their ecology neither provides sufficient opportunities (van Schaik, Deaner, & Merrill, 1999) nor necessity (Koops, McGrew, & Matsuzawa, 2013) for them to do so. Mountain gorillas are substantially less common in captivitiy, and so an experimental study like ours, to address this question, is less practical; though, such an endeavour would be decisive in this debate.

To date, there is no evidence that food cleaning in Western lowland gorillas constitutes a CDT. Yet, whilst it does not require social learning, behaviours that are CDTs may exist. All candidate cases (identified through the method of exclusion) require testing in populations that are, at least, culturally unconnected; to determine whether they do require social learning. Therefore, testing captive, unconnected individuals under controlled conditions and exposing them to the material used in/for the target behaviour, without demonstrations of behavioural form, makes an important contribution to our understanding of how and why these behaviours emerge and are maintained.

It is established that some primates have culture, i.e., they employ several of the social learning variants (outlined in Section 1.2.1.1). Culture, defined in this way is not unique to our lineage, or even primates; it is common in the animal kingdom. Such minimal cultural forms range from insects (Alem et al., 2016) to birds (Lefebvre, 1995) and from reptiles (Kis et al., 2015) to cetaceans (Sargent & Mann, 2009); along with other mammals, e.g., rodents (Terkel, 1996) including primates (Whiten, 2000).

The question of whether non-human apes have culture, which resembles human, i.e., cumulative, culture (Tomasello, Kruger, et al., 1993) remains open. Some believe this is "uniquely human" (Tomasello, 1998b); meanwhile others suggest that there *is* evidence for *limited* forms of cumulative material culture in other species (Schofield et al., 2018). This seeming uniqueness may be related to the need for copying variants of social learning, which allow exact behavioural and artefact forms to be transmitted successfully (Boyd & Richerson, 1996; Lewis & Laland, 2012; Tennie et al., 2009, in press; Tomasello, 1999a).

While food cleaning is not a case of cumulative culture, we may turn next to the question of whether it fulfils the less demanding criterion of culture, more generally. Rather than assuming that social learning is *necessary*, we suggest a new definition, based on the results presented here. The, often implicit, assumption that social learning is essential in all forms of culture comes from the working assumption that individual learning is not at the heart of many of the behaviours observed in wild primate populations. There exists mounting evidence that this alternative is a very real possibility (Bandini & Tennie, 2017; Motes-Rodrigo et al., 2019; Reindl et al., 2016; Tennie et al., 2009, 2008). A more general, i.e., conservative, definition, therefore, becomes more suitable, we term this 'minimal culture': a behaviour can be considered cultural, if social learning (of any variant, including learning from artefacts) plays any role at all in the form *and/or* the frequency of the behaviour (and/or any produced artefacts, compare also "tradition"; see Galef, 1976).

This definition similar to others, e.g. Kendal et al. (2009, p. 1), define culture (in its broadest form) as "any instance of social transmission of behaviour regardless of the underlying social learning processes". However, this definition refers to the *transmission* of behavioural forms. We hesitate to restrict cultural status to those behaviours that require social learning, thereby restricting culture those species that are capable of displaying CDTs. Behaviours that do necessitate social learning should be explicitly named as CDTs (Reindl et al., 2017), once this is confirmed experimentally. Minimal culture allows for increases in the frequency of the behavioural form to qualify as culture, without the need to have the form copied. Given the plethora of claims for culture in various species (with no evidence of behavioural form copying; e.g., Alem et al., 2016; Kis et al., 2015; Lefebvre, 1995; Sargent & Mann, 2009) we believe this, soft, definition better reflects the current state of knowledge of non-human animal culture.

Though our minimal definition may appear to widen, rather than simply move, the proverbial goalposts it is important to attribute accurate terms to behaviours as they are identified. The term "tradition" (Galef, 1976) seemingly did not take root in the literature, with many authors tending towards culture; therefore, defining culture minimally may bridge the gap between the two camps and provide some common ground between the two opposing sides of the “culture war”. This said, given that this definition requires only that a species can act on social information, this definition present a very low bar for attributing culture. Therefore, researchers should consider how low this bar is when making claims from it, here I propose that a more useful definition is that of a CDT (see Section 1.2.3.2). However the minimal culture definition does provide some recognition that species restricted to it are capable of social learning and that this might reflect something approaching culture; hence the use of the word minimal.

Whiten et al. (2001, p. 1494) defined “behaviours recorded as absent at no sites studied” as “species universals”. Given that food cleaning has been shown to occur in each sample of western lowland gorillas that have been tested/observed for it to date (Robbins et al., 2016 and this study), it fulfils the definition of a species universal at present, though, further data are required before this should be considered as concrete. Even species universals *can* be affected by social learning (Laland & Galef, 2009, p. 84). The currently available data on food cleaning in gorillas (as described here and in; Robbins et al., 2016) do not show a clear signature of any social learning. Therefore, food cleaning remains theoretically explicable purely via individual learning (except in mountain gorillas). In principle, food cleaning may simply be expressed without social learning even playing a role in increasing frequency of expression. In this case, the behaviour would not count as cultural even in the minimal sense; however, in the wild, non-copying social learning variants are likely to have acted as a catalyst in the past, increasing the behavioural frequency within populations. If so, when we apply our minimal definition of culture, food cleaning would still represent a cultural trait.

In sum, we have demonstrated that individual learning, in reacting to ecological settings, likely plays a key role in the emergence of food cleaning behaviours in gorillas. We acknowledge that non-copying social learning variants may play a role in facilitating the spread of food cleaning behaviours within populations. Accordingly, it seems unlikely that food cleaning can be considered in any way analogous to human cultures, due to a lack of reliance on *any* copying social learning variant, hence our use of a new definition of culture. This status is consistent with food cleaning being considered as a socially mediated individual reinnovation within populations, therefore a latent solution (Tennie et al., 2009).

CHAPTER 3: A PARTIALLY SHARED ZONE OF LATENT SOLUTIONS

3.1 Introduction

Tool use is far from unique in the animal kingdom, it is shared between some species of birds, cetaceans and primates (Shumaker, Walkup, & Beck, 2011). A definition of tool use that has become common in the academic literature is:

> *"[T]he external employment of an unattached or manipulatable attached environmental object to alter more efficiently the form, position, or condition of another object, another organism, or the user itself, when the user holds and directly manipulates the tool during or prior to use and is responsible for the proper and effective orientation of the tool" (Shumaker et al., 2011, p. 5).*

A clade that stands out for their tool-using abilities are the great apes (Shumaker et al., 2011). Tool use behaviours have been argued to be among those behaviours within a species Zone of Latent Solutions (ZLS; Tennie, Call, & Tomasello, 2009). A species' ZLS is a repertoire of behaviours, which can be observed in that species provided the "right" environment, without the need for social learning; though, social learning may mediate the expression/harmonisation of these behaviours within communities (Tennie et al., 2009). "Right" is a term used in the initial formulation of the hypothesis (Tennie et al., 2009) to describe the required external ecology and internal motivation for behaviours to emerge. For example, a hungry chimpanzee in an environment with nuts and material to use as a hammer and anvil might be in the "right" environment to reinnovate nut-cracking.

The ZLS can be related to the classical Vygotskian notions of a Zone of Actual Development and Zone of Proximal Development, which alter ontogenetically (Reindl, 2017; Vygotsky, 1978). The ZLS is thought to be simply a baseline for humans where copying social learning variants (including teaching) leading to cumulative culture acts as a springboard allowing our species to go beyond our ZLS. Meanwhile, a species' ZLS remains an upper limit for non-humans, which have hitherto failed to show evidence for the social learning mechanisms (copying) or resulting behavioural traits of human type cumulative culture (Tennie et al., 2018). The size/reach of this supposed upper limit has been proposed to vary by species (see below).

Closely related to the ZLS, the cultural intelligence (CI) hypothesis offers an explanation for how human culture came to differ from that of our ape cousins. There are two forms of CI (Tennie & Over, 2012); ontogenetic (Herrmann, Call, Hernàndez-Lloreda, Hare, & Tomasello, 2007) and phylogenetic (van Schaik & Pradhan, 2003). The former can partially explain how human culture came to differ from apes; the ontogenetic CI hypothesis assumes that 'culture makes us smarter'. That is, an individual growing up in a society saturated in culture, e.g., human society, would be able to go beyond the capacity which they otherwise might be restricted to through individual learning alone (Tennie & Over, 2012); this is a notion echoed recently by Heyes (2018), who suggests that humans 'self-enculturated' through the use of "cognitive gadgets", which in turn allow culture.

Over many years and generations, the ontogenetic CI of a species may feed into that species overall (phylogenetic) CI, meaning that the species is then able to go beyond their baseline (i.e., ZLS). However, this is only a possibility in those species which are able to copy (van Schaik & Pradhan, 2003)(van Schaik & Pradhan, 2003)(van Schaik & Pradhan, 2003)(van Schaik & Pradhan, 2003)(van Schaik & Pradhan, 2003)(van Schaik & Pradhan, 2003)(van Schaik & Pradhan, 2003)with sufficient 'fidelity' to maintain the cultural ratchet effect, i.e., able to imitate. Tennie et al. (2009, 2012, in press) propose that humans are the only ape species capable of this. Therefore, the ability to effectively utilise copying allows a species to begin to canalise their cultural niche. This is a process known as niche construction (Olding-Smee, 2003; also termed the "behavioural drive hypothesis").

The ZLS of some species may be 'wider' than others, i.e., they contain more behaviours. Tennie et al., (2009) supposed that chimpanzees would have the widest ZLS of all, extant, ape species, though, this could the product of a disproportionate focus on chimpanzees in the culture literature, a so-called 'chimpocentrism' (Beck, 1982). Regardless, it is certain that chimpanzees have the largest repertoire of known *wild* ape tool use behaviours (compare Gruber & Clay, 2016; Robbins et al., 2016; van Schaik et al., 2003; Whiten et al., 1999).

Given the genetic proximity between all species of apes and the similarity of their habitats, it is plausible to assume that the ZLS' of these species would overlap somewhat. Chimpanzees shared their last common ancestor with bonobos as little as 1.45_{MYA} (Langergraber et al., 2012); it is, therefore, reasonable to assume that the selection pressures that the species leading up to the last common ancestor faced left shared skills in each. Thus both species' potential for tool use/object manipulation may remain somewhat similar after the split partly due to phylogenetic similarity (Gruber, Clay, & Zuberbühler, 2010). As the great ape clade only began to diversity from the lesser apes approximately 17_{MYA} (Byrne, 1995) it is highly likely that some degree of behavioural overlap exists between all modern species of great ape. By examining this behavioural overlap, and therefore the extent of the (phylogenetically) "shared ZLS", it is possible to determine/estimate the latent innovative capacity of that species (or the breadth of their ZLS).

Reindl et al. (2016) undertook a similar project with human children, where human children were exposed to the, most likely for them, novel feat of spontaneously expressing chimpanzee and orangutan tool use behaviours, through problem-solving tasks based on wild type behaviours. This was done to identify behaviours that were common between humans and the two ape species that display the most prolific *wild* tool use, i.e. chimpanzees and orangutans (van Schaik et al., 2003; Whiten et al., 1999). It was found that in all but the most complex task (nut-cracking) human children, aged 2.5-3 years, spontaneously matched the behavioural form of their ape cousins. This finding led the authors to conclude that the last common ancestor of humans and great apes *was* likely capable of using similar tools in similar ways without an absolute need for social learning; i.e., that the ZLS of humans and apes (including the last common ancestor) overlaps.

This chapter aims to test, using two LS tests, the existence of a partially shared ZLS across all extant species of apes. In particular picking and scooping, modelled on wild behaviours of marrow picking and algae scooping (Whiten et al., 2001, 1999). These tasks differ in their complexity, with picking likely being simpler as it does not rely on specific behavioural actions, unlike scooping (Humle, Yamakoshi, & Matsuzawa, 2011). Accordingly, we would expect picking to be expressed more readily across species, whereas scooping may only be shared between *some* species. These studies, when combined with others from the "Tools and Culture Among Early Hominins" research group (e.g., Bandini, 2018; Bandini & Tennie, 2017; Reindl et al., 2016), represent the first complete clade LS testing of potential ZLS behaviours, therefore they present the first opportunity to empirically test the notion of a shared ZLS in all extant species of great ape.

3.1.1 Behaviours

3.1.1.1 ***Picking***

Chimpanzees hunt other primates (relevant here are Western red Colobus monkeys, *Colobus badius,* but other species of mammals are also hunted; Boesch & Boesch, 1989). At Taï National Park, Ivory Coast, after the prey has been captured and the meat consumed, the long bones (e.g., femurs) are bitten in half exposing soft marrow. Small sticks are then used to extract the marrow, which is subsequently licked from the stick (Boesch & Boesch, 1989). At the time of the initial publication, this behaviour had only been reported at Taï Forest, Côte d'Ivoire (Whiten et al., 1999). However, this behaviour has since been reported at another field site, approximately 2600km away; Goualougo Triangle, Republic of Congo (Sanz & Morgan, 2007). Here, the technique was used to access marrow from the bones of a duiker (*Cephalophinae*; exact genus and species unknown).

The behavioural form of picking involves inserting a stick into a substance contained within a vessel that fingers cannot fit inside, the substance is subsequently extracted and consumed from the stick directly. It is inconsequential whether bone marrow or another similar substance is consumed, the behavioural forms are the same. As in the case of food cleaning (Chapter 2); accordingly, we refer to this behaviour as "picking" rather than "marrow picking" (Sanz & Morgan, 2007; Whiten et al., 1999). The behaviour is seemingly unique to wild chimpanzees, at least amongst apes (Gruber & Clay, 2016; Robbins et al., 2016; van Schaik et al., 2003; Whiten et al., 1999).

3.1.1.2 ***Scooping***

Similar to picking, scooping is referred to, more generally as “algae scooping” (Humle et al., 2011; Whiten et al., 1999). Here we follow Bandini & Tennie (2017) in removing the substrate “algae” from the term, as the target object again is unimportant to the form of the behaviour.

Scooping is identified as "customary" at Bossou, Guinea (Whiten et al., 1999), however, the ecological conditions at other field sites did not allow for the behaviour, meaning it was not possible to truly ascertain the cultural status. The behaviour involves using a long stick (or “wand”), held in the hand, to “scoop” algae floating on the surface of standing water (using a swivelling motion of the wrist; Humle et al., 2011). Again, the substrate has little consequence, the behavioural form, in this case, is the swivelling motion of the wrist, whilst using a long stick to extract an out of reach substrate floating on water. This behaviour has not been noted in any *wild* ape species other than chimpanzees (Gruber & Clay, 2016; Robbins et al., 2016; van Schaik et al., 2003); indeed, ecological restrictions dictate that this behaviour is limited to only one community of chimpanzees (Whiten et al., 1999).

Picking has been demonstrated in two groups of captive chimpanzees (Bandini, 2018) and one group of human children aged 24-36 months old (Reindl et al., 2016). Scooping has also been demonstrated in two groups of captive chimpanzees (Bandini & Tennie, 2017) and the same group of children (Reindl et al., 2016).

3.2 General ethics statement

Subjects were never deprived of water or food and continued to receive their regular diet throughout the duration of either of these studies. All participation was voluntary. This research project was granted ethical approval by The University of Birmingham AWERB committee (reference UOB 31213), STEM committee (ERN_17-1729) and by the host zoo following SSSMZP, EAZA, BIAZA and WAZA protocols on animal research and welfare.

3.3 Study 1 – Picking

3.3.1 Method

3.3.1.1 *Subjects*

Data was collected, between February and May 2017, from five bonobos (female *n* = 4, male *n* = 1) aged between 5 and 39 years (M=18.20, SD=13.95), 5 western lowland gorillas (female *n* = 3, male *n* = 2) aged between 4 and 43 years (M=24.80, SD, 14.24) and 4 Bornean orangutans (*Pongo pygmaeus*; female *n* = 3, male *n* = 1) aged between 6 and 40 years (M=23.75, SD=14.06); see Table 3.1 for rearing histories. All ages correct as of the first day of testing.

A larger sample of bonobos *was* present at the host zoo at the time when this study took place. However, during the first trial, a keeper handed the subjects the sticks and tubes through the mesh simultaneously, thus contravening the methodology used in this and related studies. In doing so, this keeper drew particular attention to the sticks and their relation to the tubes. Following this, the group showed evidence of picking, however, owing to the potential for non-copying variants of social learning (e.g., stimulus enhancement) these results are confounded and are not considered in the present study.

All species have similar enclosures with private management areas and enrichment devices, with both indoor and outdoor facilities containing climbing structures. Other enrichment devices were provided throughout the study period, the only enrichment item present at the same time as the apparatus was "browse"; a selection of tree branches with leaves still attached, which the animals strip and consume.

Table 3.1. Demographic information about all subjects in both studies from chapter 3, S1 age refers to picking, S2 age refers to scooping.

ID	Species	S1 Age	S2 Age	Sex	Rearing	Born
DU	Bonobo	39	38	Female	Hand	Captive
BY	Bonobo	27	25	Female	Parent	Captive
KK	Bonobo	23	21	Male	Parent	Captive
MG	Bonobo	18	17	Female	Parent	Captive
ML	Bonobo	6	5	Female	Parent	Captive
LP	Bonobo	5	3	Female	Hand	Captive
MZ	Bonobo	3	2	Male	Parent	Captive
MK	Orangutan	22	21	Female	Parent	Captive
KB	Orangutan	40	38	Female	Hand	Captive
MY	Orangutan	6	4	Female	Parent	Captive
BT	Orangutan	27	26	Male	Parent	Captive
BD	Gorilla	43	41	Female	-	Wild
LZ	Gorilla	31	30	Female	Hand	Captive
UM	Gorilla	24	23	Male	Parent	Captive
OZ	Gorilla	22	21	Female	Parent	Captive
LO	Gorilla	4	2	Male	Parent	Captive

3.3.1.2 ***Pre-test questionnaires and interviews***

A larger, multi-faceted questionnaire was given by another researcher (EB) from the University of Birmingham in September 2015 (Bandini, 2018). The data from this questionnaire indicated that none of the subjects had ever engaged in a behaviour similar to picking.

As the questionnaire data was approaching two years old, interviews were conducted, with keepers before the first trial with each species. DN described the picking behaviour (as per Humle et al.'s (2011) description) and asked keepers whether they had witnessed the behaviour in the animals concerned. During informal conversations with keepers, after testing had been completed with bonobos, it transpired that all species had been given similar apparatus in the past for enrichment. These objects were much larger tubes (length~60cm, diameter ~5cm) not sealed at either end, containing oats & dried fruit mixed with peanut butter. Keepers did not provide the apes with sticks in these cases, however, keepers reported that the subjects had used sticks, already present in the enclosure, to perform behaviours analogous with picking. Although these had been given to the subjects for an extended period this was not reported in the questionnaire (given in 2015; Bandini, 2018). However, keepers reported that the apes were not shown how to access the food (using tools or otherwise). Therefore picking, if it occurred previously, would have still been individually reinnovated in the first ape to show it, as a product of individual learning, and did not require social learning; social learning cannot be excluded as a catalysing mechanism after the initial reinnovation. This follows the logic of the 'natural' LS tests described in Section 1.2.4.2.3 and Chapter 2 (see also Neadle et al., 2017).

In the case of the tested species, it is implausible that the target behaviour could have been transmitted from the wild (picking has never been reported in any wild conspecifics; Gruber, Clay, & Zuberbühler, 2010; Robbins et al., 2016; van Schaik et al., 2003). Thus, we would consider these individuals to be "culturally unconnected" (*sensu* Neadle, Allritz, & Tennie, 2017). This implies, should the group express the behaviour during testing, individual learning is still likely at the heart of the reinnovation.

3.3.1.3 ***Experimental procedure***

In optimal conditions, an LS test would take place with the subject in isolation (Tennie & Hedwig, 2009) to maximise the effective, i.e., naïve, sample size and exclude enhancement. This was not possible at the host zoo, and therefore group tests were used.

3.3.1.3.1 Stimuli

Constraints at the host zoo meant actual bones could not be used, due to resultant animal health risks. Therefore, “simulated” bones were used. These were a white non-toxic PEX barrier pipe, cut to length (Diameter=15mm, Length=15cm). The resulting tube was sealed at one end using a white non-toxic push-fit stop-end (Diameter= 30mm, Length=32mm), which fitted 27mm over the end of the tube and was secured with an epoxy adhesive (see Figure 3.1; adhesive became non-toxic when cured for 24hrs). The tube was then filled with 10g of smooth peanut butter (warmed for 60 seconds; 800w microwave), using a long syringe to ensure peanut butter was placed directly at the bottom of the tube; reducing the chances that subjects could lick or extract it with their tongue or fingers.

The tube’s diameter was designed that none of the adult apes could fit their fingers inside; infants that could fit their fingers inside were not able to reach the peanut butter due to their fingers not being long enough to reach the base of the tube. As with bones, it was possible that the apes could sufficiently damage the tubes with their teeth to avoid having to use a tool. However, due to the malleable characteristic of the tubes, this would have taken considerable time. Thus, a tool was required to complete the task most efficiently; sticks were provided. Sticks were taken from a garden willow trellis and cut to 20cm in length, the diameter was ~5mm, with a maximum of 7.5mm (see Figure 3.1), sizes were modelled from reports of wild chimpanzee marrow picking tools (Boesch & Boesch, 1990). Filled tubes were refrigerated for at least 24 hours before testing to set the peanut butter at the base of the tube.

Figure 3.1. Photograph of tubes ("simulated bones"; left) and sticks (right) as provided to all species

3.3.1.3.1 Procedure

Before subjects entered the testing areas, three tubes and three sticks were placed throughout the indoor enclosure by keepers. Sticks were never placed within 1m of the tubes to avoid the potential for enhancement influencing the speed of reinnovation. The use of 1m was simply to standardise proximity across tests and to provide keepers with a guide of where to place the sticks.This occurred between 8 am and 10 am (species dependent) when a 'scatter feed' was usually provided to the subjects. As per the Weatherall report, subjects were not denied their usual food routine, other foods were present at the time of testing. This was unavoidable, as it was required that the stimuli were placed inside the enclosure *without* the subjects present, a policy at the host zoo is to reduce human interference as much as possible.

All trials were video recorded using a Sony HandyCam HDR-CX240E from the time when the subjects were allowed into the testing area to the point at which the trial ended. Every attempt was made to document all interactions with the tubes; however, in some cases, simultaneous interactions took place. These interactions were not added to the data set as no video evidence existed and could not be accurately assessed through inter-rater reliability checks. Trials lasted an initial 10 minutes if after 5 minutes a subject was still in contact with the tube another 5 minutes were added; this continued once more for a total of 20 minutes. Each species took part in three trials.

3.3.1.3.2 Coding

The data were coded in ‘bouts’; where a bout is defined when an individual attempts to access the peanut butter inside the tubes. A bout lasted from the time that initial contact with the tube was made, to the point at which the subject relinquished contact for more than one minute; if another individual took possession of the tube a new bout began. A new bout was also started if a new behaviour (see Table 3.2) began, e.g., the subject switched from picking to the finger technique.

Table 3.2. Ethogram used during coding, this ethogram was informed by a prior study by Bandini (2018), DN's study notes of which behaviours occurred and finally, new behaviours were added as required during coding. This, completed, version of the ethogram was provided to the second coder.

Method	Description
Picking	A stick is inserted into the tube using the hand(s), it then contacts the peanut butter and the individual removes the now peanut butter coated stick and consumes the peanut butter.
Picking (Mouth)	Same as "Picking" but the mouth is used to assist or take the place of the hand(s) when manipulating the stick, the stick can then be turned in the mouth or taken out of the mouth by hand, the individual must consume the peanut butter.
Picking (other)	The subject used an object other than the sticks provided to dip into the tube and consume the peanut butter.
Push-Through	The subject will have removed the end stop from the tube; the subject then inserts an object into one end of the tube and pushes the object through to the other side of the tube, thus removing peanut butter in the process. The subject must consume the peanut butter.
Finger	The subject will have torn the tube along its length to leave a long wide opening. The subject will then use its finger to consume the peanut butter from the now destroyed tube.
Hand	The subject uses their fingers to try to access the peanut butter from inside the tube (without having destroyed it first), by inserting the tip of a finger into the tube and consuming peanut butter from the finger.
Mouth	The subject places the tube directly in the mouth and tried to consume the peanut butter by either sucking the tube, chewing the end or using the tongue to consume any residue of peanut butter near the tip of the tube.
Hand/Mouth	The subject uses first their finger and then their mouth to suck and consume the peanut butter from the top of the tube.
Mouth/Hand	The subject individual first attempted to use their mouth or tongue to extract the peanut butter, and then their fingers.
No relevant behaviour is seen	This code was used when the coder did not witness any attempt to consume the peanut butter from the tube. This was used for reliability coding "dummy clips" only.

To assess the reliability and accuracy of the coding, a second, hypothesis naïve, coder second coded a randomly selected 33% of the behaviours. The video recordings of these behaviours were isolated from the full videos and sent to the second coder with a randomly assigned (arbitrary) file name. Also, an equal number of "dummy" clips, that contained a subject in the frame, when this subject was not performing a behaviour from the ethogram, were included.

Cohen’s Kappa was then used to assess the level of agreement between the coders, a level of $\kappa = 0.6$, was required before analyses were completed (Cohen, 1960; McHugh, 2012). An acceptable level of agreement ($\kappa = 0.75$, $p<.001$; Cohen, 1960; McHugh, 2012) was attained between the second (JC) and primary (DN) coders.

3.4 Results

One individual from each species reinnovated the picking behaviour (see Figures 3.2 & 3.3). The first reinnovation in the: bonobo sample was 2 minutes 20 seconds into the second trial (MG; female; 19), gorilla sample was 18 minutes 47 seconds into the third trial (OB; male; 25) and orangutan sample was 10 minutes 3 seconds into the first trial (BT; male; 28). Overall, two bonobos, one gorilla and all four orangutans successfully reinnovated the picking behaviour. The orangutan sample spent the largest proportion of time (43%) picking, as opposed to other methods, followed by bonobos (16%) and gorillas (10%). Whilst interesting, it must be noted that these values are confounded by the fact that only one gorilla and two bonobos reinnovated the picking behaviour. The inflated value in the orangutan sample is likely due to the larger number of individuals that expressed picking.

Figure 3.2. Sequence of picking behaviour in an immature female orangutan (ML).

Figure 3.3. Stills of a member of each species expressing the picking behaviour, note that in these images only the bonobo (panel B) is using a stick that was provided.

All species also expressed other behaviours from the ethogram: bonobo and gorilla samples expressed four other techniques (mouth, hand, hand/mouth & mouth/hand) prior to expressing the picking behaviour; whereas, the orangutan sample only expressed two (mouth & hand). See Figure 3.4 for details of methods expressed by each species.

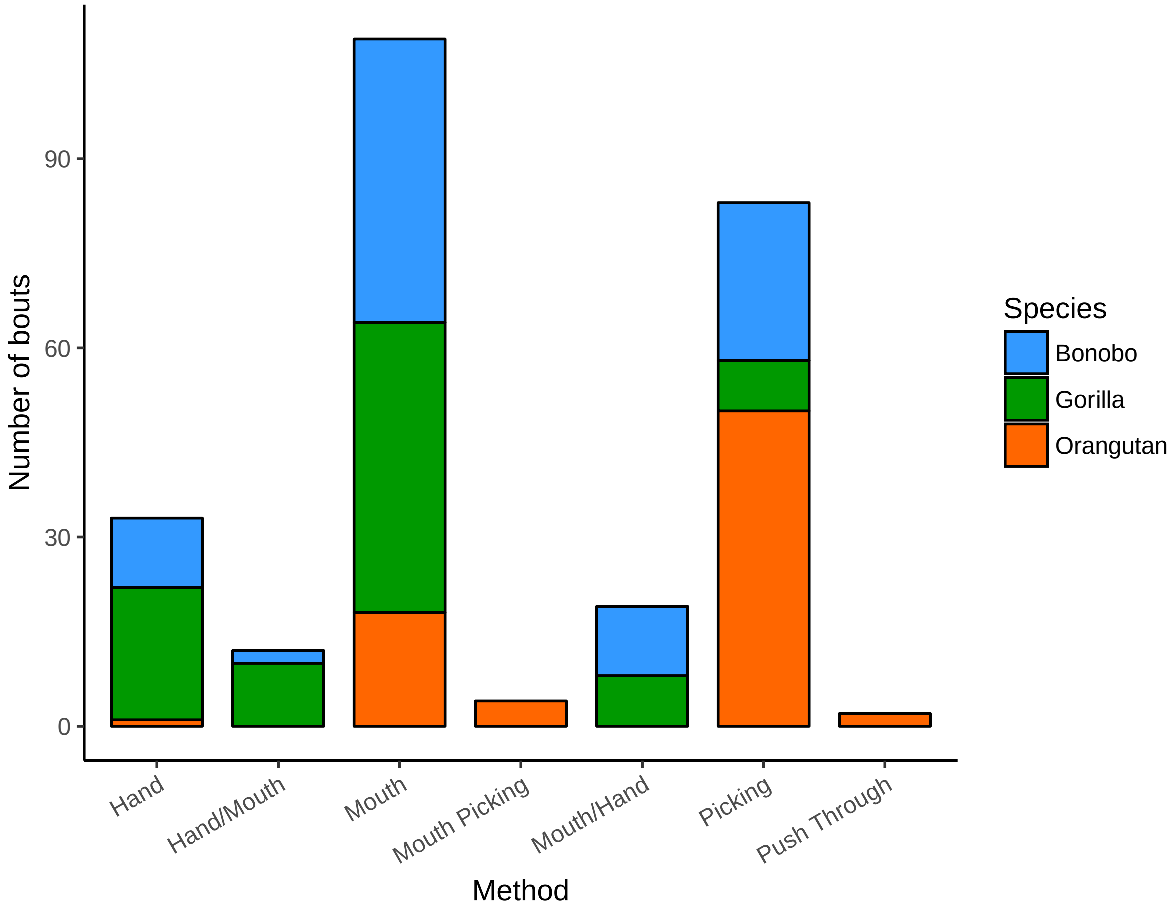

Figure 3.4. Number of bouts each species engaged with each behaviour, note that not all species expressed all methods of manipulation.

3.5 Study 2 – Scooping

3.5.1 Method

3.5.1.1 ***Subjects***

Data was collected, between December 2015 and June 2017, from seven bonobos (female = 5, male = 2) aged between 2 and 38 years (M=15.86, SD=13.40), 4 western lowland gorillas (female = 3, male = 1) aged between 21 and 41 years (M=28.75, SD=9.03) and 4 Bornean orangutans (female = 3, male = 1) aged between 4 and 38 years (M=22.25, SD=14.10); see Table 3.1 for rearing histories, all ages correct as of first day of testing. All species remained in the same enclosure as in Study 1, however, this experiment took place in the management areas. Browse was again present in the gorilla management area; bedding materials were present in all species.

This group is the same group that took part in Study 1, however, two individuals BY & MZ were transferred from one group to another between the picking and scooping tests. These transfers were related to the breeding programme at the host zoo and thus beyond the control of this study. See Section 3.5.1.3.1 for an explanation of why the second group did not participate in Study 2. The gorilla sample was tested in 2015, at which point LP was 2 years old. Gorillas were tested individually and at this point, he was not eligible to take part in this study as only adults and subadults were considered.

3.5.1.2 ***Pre-test questionnaires and interviews***

As in Study 1, pre-test questionnaires were distributed to keepers prior to the task taking place (see Bandini & Tennie, 2017); similarly to Study 1, there were no reports of the use of sticks to access out of reach, floating, objects, certainly not whilst displaying the key behavioural wrist swivelling form integral to scooping. The questionnaires were, again, followed up by interviews, which revealed no behaviours analogous to scooping and therefore the subjects could be considered fully naïve to scooping.

3.5.1.3 ***Experimental procedure***

As this study took place solely within the management areas it was possible, in the gorilla sample, to test subjects in isolation; visual contact was limited between subjects; subjects were tested at a rate of one subject per test day. It was possible for a gorilla in the neighbouring sleeping areas to see the individual immediately to their left/right. However, subjects could not see past an obstruction, therefore, we can consider this sample as two smaller groups (Group 1: AS & BD; Group 2: UM & OZ). See Appendix A. Isolated testing was not possible in the bonobo or orangutan samples; therefore, as in Bandini and Tennie (2017) and Study 1, only the first reinnovation of a behaviour would qualify as a spontaneous reinnovation as a product of individual learning.

3.5.1.3.1 Species-specific modifications

During the first trial (see below, for details) in the first bonobo group (*n*=5; M age=8.67, SD = 7.19), subjects proved able to reach with their arms through the standard mesh (5.08x5.08cm) and so retrieve the floating bread by hand. Thus, the experiment was modified for the remaining group of bonobos, this was achieved by reducing the size of the mesh openings (2.54x2.54cm; Figure 3.5). As the first group were able to reach the bread by hand their data were excluded and treated as pilot data, with only the second group's data being analysed further. Reaching through the standard mesh of the zoo we tested in was not possible in the other species tested, owing to the other species' anatomically greater size at their tested ages (Shea, 1984).

Figure 3.5. A & B show the size of the mesh in the bonobo enclosure prior to modification. C & D show the modifications made to the bonobo enclosure in order to prevent bonobos from being able to reach the bread by hand; note, the opening size is reduced by approximately half. Photograph curtesy of Twycross Zoo, UK.

3.5.1.3.2 Stimuli

In the wild, chimpanzees perform the scooping behaviour when they encounter *Spirogyra sp*. floating atop bodies of standing water. However, it was not logistically viable to import this plant to the UK; therefore, an alternative food reward was required. In a related study by Bandini and Tennie (2017), dried bread was deemed an appropriate substitute for algae. Slices of bread were cut in half, width-ways, had a 2cm^2 section removed from the white centre (see Figure 3.6). In this state the bread was able to emulate the key properties of algae; i.e., an elongated, floating object, which can be scooped onto a stick.

Figure 3.6. A model piece of dried bread to be used in the study; the section cut out of the middle was done prior to drying, thus the square dried distorted.

A rectangular, transparent, plastic container (16 cm × 66 cm × 20 cm) was positioned outside the mesh of each of the enclosures (the orientation of the container altered between species owing to local restrictions, see below). The container was ¾ filled, approximately 16 litres of water. Three bamboo sticks, 80cm long and 1-3cm diameter (see Figure 3.7) were placed inside the enclosure. Sticks were not placed directly next to the container. However, as the gorillas had to be tested within their sleeping areas, the gorilla sample were present whilst the sticks were placed inside the enclosure.

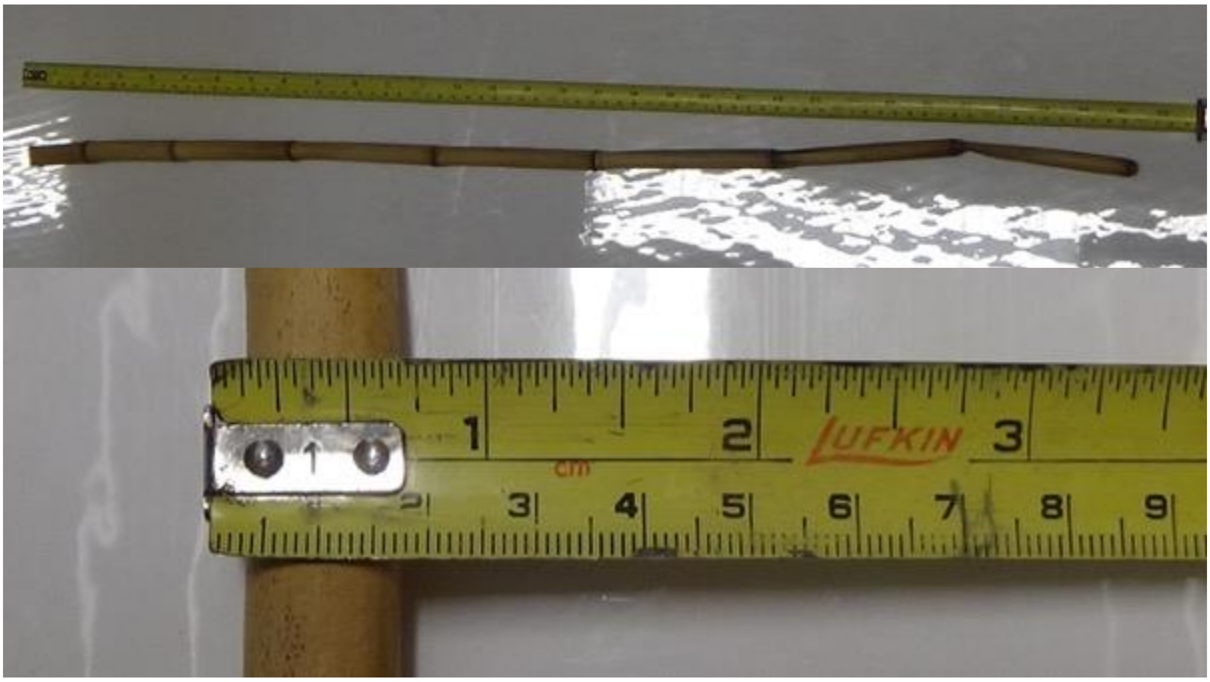

Figure 3.7. A model of the sticks used in this study, the actual sticks were selected based on this stick and so reflected a similar size and shape.

3.5.1.3.3 Procedure

Testing took place between 8am and 10am in the subjects' sleeping/management areas. Bamboo sticks were placed into the enclosure and the filled container was placed against the mesh. Once the subjects had access to all the required materials three pieces of cut, dried, bread were placed into the water. This study followed the same "result dependent" design outlined in Study 1 resulting in a maximum total testing time of 20 minutes per trial. A single camera (Sony HDR-CX330 Handycam) was focussed on the container with as much of the subject in the frame as possible. Each group (or subject, in the case of the gorilla sample) participated in three trials.

3.5.1.4 **Coding**

The data were coded in bouts, where a bout was defined as the time from which a subject began contact with a stick to the point at which they relinquished contact; a new bout began if the subject did not re-establish contact within one minute. Additionally, if a new individual contacted the stick a new bout began, similarly if a subject changed behaviour (see table 3.3) a new bout began.

Owing to the difficulty of this task, specifically keeping the bread on the stick, approximations at the behaviour were also considered, termed ‘attempts’. Attempts are defined as when the motor requirements of the behaviour were met, e.g., a swivelling wrist motion was used when scooping, however, the subject was unsuccessful in acquiring the bread. Therefore, each successful behavioural code had a corresponding ‘attempted’ code.

3.5.1.4.1 Interrater reliability

Reliability was assessed in the same way as in Study 1 behaviours were isolated from the main data and combined with “dummy clips” before a second, hypothesis naïve, coder (JC) coded 50% of the behaviours from the gorilla data set and 33% of the behaviours from the orangutan data set. No behaviours were identified through coding of the bonobo data set, as a result, no interrater reliability could be calculated. An acceptable level of agreement ($\kappa = 0.63$, $p<.001$; Cohen, 1960; McHugh, 2012) was attained between the second and primary coders.

Table 3.3. Ethogram used during coding in Study 2. This ethogram was previously informed by the behaviours noted in a prior study with chimpanzees into the same behaviour (Bandini & Tennie, 2017)*, behaviours were added to the ethogram during live coding by DN; the ethogram, as presented below, was provided to JC for reliability coding.*

Method	Description
Scooping	Inserting a stick (or other appropriate tool) **into the water** and, **with a swivelling of the wrist**, scooping the bread anywhere onto the stick. The subject must retrieve the bread.
Attempted Scooping	As above, however the subject was not successful in retrieving bread.
Lifting	Inserting a stick (or other appropriate tool) **into the water** and, **with no noticeable wrist movement**, lifts bread, from underneath, partly or fully out the water. The subject must retrieve the bread.
Attempted Lifting	As above, however the subject was not successful in retrieving bread.
Mouth Scooping	**Using the mouth,** the subject places the stick into the water and, still with the stick in the mouth, lifts the bread from the water. The subject must retrieve the bread.
Attempted Mouth Scooping	As above, however the subject was not successful in retrieving bread
Side Technique	The subject pushes the bread **against the side of the container** to force it onto the stick; here, the bread must touch the side of the container, between the edge of the container and the stick for this to apply. The subject must retrieve the bread
Attempted Side Technique	As above, however the subject was not successful in retrieving bread
No relevant behaviour seen	This code was used when the coders did not witness any interaction between the subject and the apparatus that was directed towards the goal, i.e., the bread. This was used for the purpose of reliability coding “dummy clips” only.

3.6 Results

3.6.1 Attempted scooping

In total there were 31 unsuccessful attempts at scooping, across the gorilla and orangutan samples; bonobos never attempted the scooping technique.

3.6.1.1 *Gorilla*

There were 20 attempts at scooping in the gorilla group. Eight of these attempts were by AS (female; 30) in her third trial. The remaining 12 attempts at scooping were by UM (male; 23), all these events were recorded in his first trial. UM could not have seen AS showing the swivelling behaviour required for scooping, prior to his reinnovation of the technique, which proved unsuccessful. Therefore, each attempt was independent, thus can be considered separate reinnovations.

3.6.1.2 *Orangutan*

There were 11 attempts at scooping in the orangutan group. Two of these events were by BT (male; 26). BT was the first in the orangutan group to successfully show the swivelling behaviour required for scooping; despite this attempt being unsuccessful. Given that BT was first to display the swivelling behaviour it is possible that MK (female; 21) had witnessed the technique prior to her own implementation of the scooping technique, which began later during trial one. The remaining events of failed attempted scooping were all involving; she unsuccessfully attempted the scooping technique on six occasions in trial one, two in trial two and one in trial three. There were eight failed attempted scooping attempts in total before a successful reinnovation.

3.6.1.3 ***Bonobo***

There were no recorded instances of bonobos ever *attempting* the scooping behaviour. However, worthy of note is that the relevant bonobo sample (i.e. the group that contributed data, see above) had to interact with a smaller sized mesh than the other species, which may have impeded the application of any scooping. This is evidenced by the fact that when the bonobos ML (female; 7) *did* interact with the apparatus, the stick became stuck between the mesh (she even seemingly had to put in much effort to remove the stick); this kind of technical problem was never noted in any of the other two species we tested here, nor did it occur in the chimpanzee sample tested by Bandini and Tennie (2017; personal communication). Two out of the nine bonobos (MG, female; 17 and ML, female; 5) attempted to use the stick as a tool; these individuals, combined, contributed three attempts, none of which involved any action from the ethogram, and only once did the stick touch the water.

3.6.2 Successful scooping

Only one individual fully reinnovated the scooping behaviour, i.e., with success, MK (orangutan; female; 21). The first successful application of scooping was after one minute and 11 seconds of the second trial and resulted in the successful extraction of one piece of bread; Figure 3.8). MK again displayed scooping during her second (after 4 minutes and 12 seconds) trial and twice more during her third trial (once after one minute and 46 seconds and again at three minutes and 47 seconds).

Figure 3.8. Sequence of events during first successful reinnovation of the scooping technique by MK, note the difference in wrist position between A and B showing the swivelling described in other studies.

In three out of the four successful scooping events, MK consumed the bread directly from the stick, after withdrawing the stick through the opening in the mesh. In the other attempt she used her hand to first remove the bread from the stick and then pull the bread against the mesh before consuming it directly from her hand through the mesh.

3.6.3 Other techniques

Scooping was not the only technique used to access the bread, subjects also attempted to use lifting, a side technique and mouth scooping (see Figure 3.9). Success in the lifting technique was limited to the orangutan sample, where MK (female; 21) was able to utilise the technique to obtain a part of a bread shape. Successful implementation of the side technique was restricted to the gorilla sample, where AS (female; 30) was able to obtain a small part of the bread. The mouth scooping technique was unique to the orangutan sample (BT; male; and MK), and was never successful in retrieving the bread.

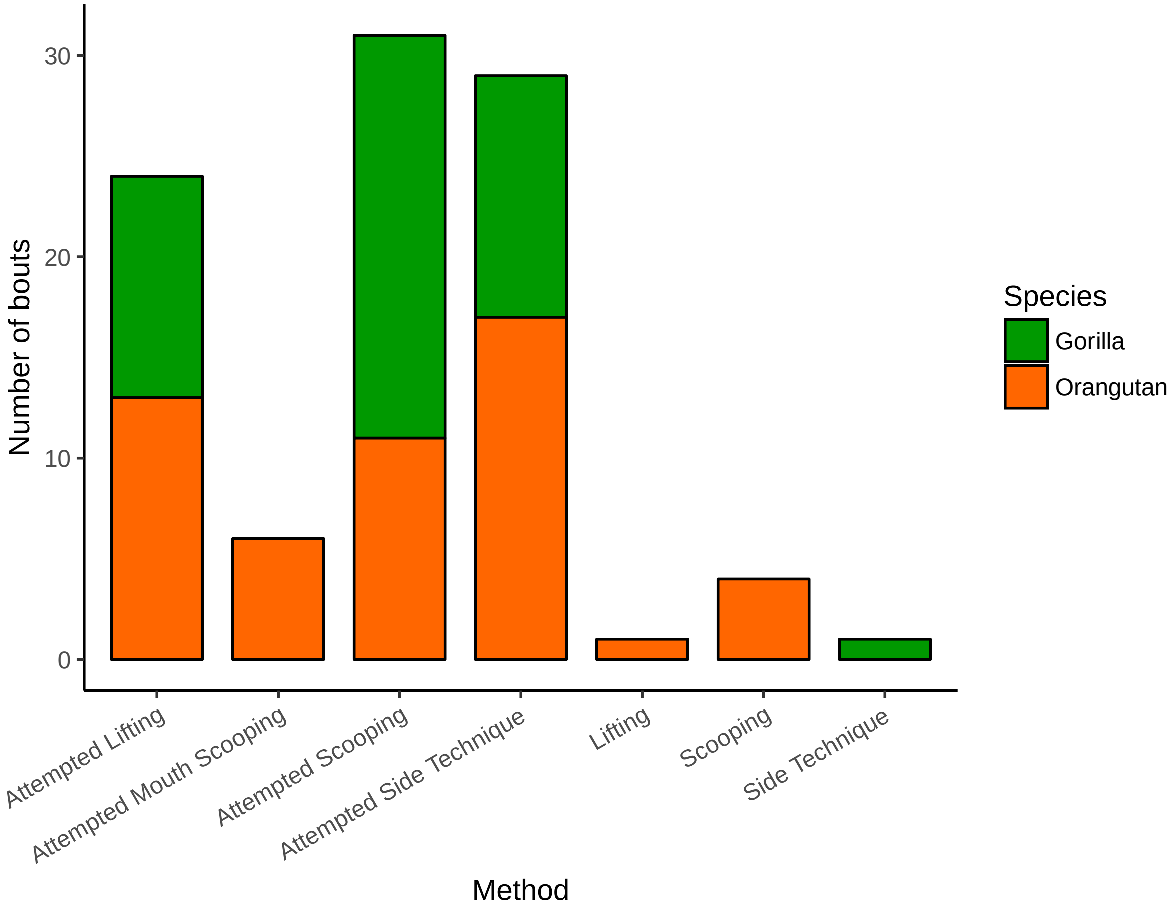

Figure 3.9. Number of bouts of each behaviour in the scooping ethogram expressed during the second study.

3.7 General discussion

The results of the above studies show that at least *some* aspects of the chimpanzee (Bandini, 2018; Bandini & Tennie, 2017; Motes-Rodrigo et al., 2019) and human (Reindl et al., 2016) stick tool use ZLS are shared with other species of ape. These findings, taken together, unequivocally show evidence of behaviours spontaneously reoccurring, through individual learning, in closely related species, suggesting a ZLS shared between phylogenetically related species.

These studies represent two interesting, but different, cases of the shared ZLS. The picking behaviour described here is similar, in behavioural form, to many other techniques of extractive foraging, where a stick is used to extend the individual's reach where limbs and digits are unsuitable. The only 'technique' required is to insert a stick into an opening containing a food source. As extractive foraging is a fairly common form of enrichment for captive apes, it is highly unlikely that naïve individuals could be found. Of those individuals naïve to extractive foraging (our subjects are not included in this) concerns could be raised about how deprived (Henrich & Tennie, 2017) their existence has been and the resultant effect on their behavioural phenotype (van Schaik & Burkart, 2011).

It is highly unlikely that there is a specific cognitive module for 'picking' or indeed any specific behaviour. It is instead more likely that this resultant shared ZLS is the product of a shared general cognitive capacity that allows apes to use tools in extractive foraging. This is likely to be a remnant of shared behaviours from the last common ancestor of all extant ape species; all extant species show evidence of picking. However, it is also plausible that this finding and therefore the general ability of extractive foraging is the product of convergent evolution. This becomes likely when one considers that the subjects here used a stick to extract a reward from where their bodies could not reach, an ability shared with some corvids (Hunt, 1996; Rutz et al., 2016). A combination of these two explanations is also highly likely.

Scooping, however, has been noted to be an uncommon behaviour in the wild, given the apparent rarity of the algae species within chimpanzee habitats (Whiten et al., 1999). When exposed to the materials required and motivation to perform naïve chimpanzees (Bandini & Tennie, 2017), humans (Reindl et al., 2016), orangutans and potentially gorillas are capable of reinnovating the very specific required motor patterns: the swivelling motion of the wrist (Humle et al., 2011). Though, the substrate used here (bread) often broke up when saturated in water for extended periods, it is possible that by using a more stable substrate more individual, trial and error, learning could have resulted in a full reinnovation of successful scooping.

Similar to picking, it is *possible* that that scooping is a latent solution in all species of great ape, though bonobos should be excluded from this until evidence is found contrary to this study. Bonobo's failure to reinnovate scooping could simply be a result of lower motivation to engage with tool use (Koops, Furuichi, & Hashimoto, 2015) or simply that the size of the mesh made the task more challenging or even impossible in this sample. However, this behaviour may also not be a latent solution in bonobos but given the capacity for bonobo tool use in the right conditions (Gruber & Clay, 2016), this seems unlikely. Thus, further samples of bonobos should be tested for this behaviour.

From the evidence presented here and in previous studies (e.g., Bandini & Tennie, 2017, 2019; Motes-Rodrigo et al., 2019), it is possible that the last common ancestor of all modern great apes was likely *capable* of, at least some, stick tool use; that is, it was within the species ZLS. However, it is also possible that this behavioural capacity did not manifest itself into a phenotypical trait; meaning that it could be a case similar to that of bonobos

(Furuichi et al., 2015), where tool use is clearly within the species capacity (Gruber & Clay, 2016) but is not utilised. This may have been due to a lack of ecological need (Fox, Sitompul, & van Schaik, 1999) or other selection pressures.

The results, and discussions, above clearly speak to a partially shared ZLS most parsimoniously explaining the similar patterns of behaviour found amongst the great apes. Even the most distantly related species of great apes (*Pan* and *Pongo*) share aspects of their behavioural capacity. Individual learning here is the mechanism responsible for the emergence of these behaviours, whereas, social learning may simply act as a catalyst, harmonising them within (and between) communities. Simply providing apes with the materials and motivation results in the spontaneous reinnovation of behaviours previously considered as putative cases of culture dependent traits.

CHAPTER 4: TESTING THE INDIVIDUAL AND SOCIAL LEARNING ABILITIES OF CAPTIVE, TASK-NAÏVE, CHIMPANZEES (PAN TROGLODYTES SP.) IN A NUT-CRACKING TASK

This chapter, largely in its current form, is being revised, following minor revisions, for publication in PeerJ as:

Neadle, D., Bandini, E., & Tennie, C. (Submitted). Testing the individual and social learning abilities of captive, task-naïve, chimpanzees (*Pan troglodytes sp.)* in a nut-cracking task. *PeerJ*.

The changes made from the submitted manuscript are largely aimed at reducing overall length, per the prescribed word count, and allowing the manuscript to flow with the rest of the thesis by excluding theoretical points which have been discussed in previous sections of this thesis.

The author contribution statement, as presented to PeerJ for publication was:

Conceptualization: EB, CT
Data Collection: DN
Investigation: DN
Methodology: DN, EB, CT
Formal analysis: DN
Project administration: DN
Resources: DN
Supervision: CT
Writing – original draft: DN
Writing – review & editing: DN, EB, CT

This study had been conceptualised by EB and CT before my starting my PhD in the "Tools and Culture Among Early Hominins" lab. However, no data had been collected and the methodology needed to be finalised, the study was only conceptualised at this time ethical permission had to be sought by myself with Twycross Zoo before the study taking place. The methodological design was a collaborative effort between all three authors; however, I designed the apparatus and collected/analysed the data alone. I wrote the first working manuscript; EB, CT and myself took turns reviewing/editing drafts.

4.1 Introduction

Amongst animals, chimpanzees are, for now, the ‘most cultural’ species, at least in terms of known numbers of cultural traits (Whiten et al., 1999). An increase in the number of cultural traits a population shows is known as accumulation (Dean et al., 2014). However, accumulation should not be confused with cumulation; i.e., the cultural change of the traits themselves along with the transmission, thus cumulative culture (Dean et al., 2014). Only the latter is the result of the ‘ratchet effect’ (Tomasello, Kruger, et al., 1993), which underlies cumulative culture (Boyd & Richerson, 1996).

Whilst chimpanzees’ accumulation of cultural traits is impressive, for those concerned with human cultural evolution, the presence or absence of CDTs in chimpanzees is of more interest. CDTs are not always more complex than other cultural traits (though they may be; Reindl et al., 2017). This said, trait complexity can serve as a starting point to identify at least candidate CDTs; specifically, those that have ‘ratcheted up’ in complexity via cultural transmission (Tennie et al., 2018). Complexity is hard to define and measure. Complexity can be depicted using stepwise flow-diagrams (*sensu* Byrne, Corp, & Byrne, 2001) or “cognigrams” (Haidle, 2012). It can refer to the number of parts within a final artefact/behaviour (techno-units; Oswalt, 1976), the goals and sub-goals of an action (Read & Andersson, 2019), the manual dexterity of an action (Foucart et al., 2005) and the number of “rules” necessary to describe the behaviour (Sirianni, Mundry, & Boesch, 2015), amongst other metrics (see Vaesen & Houkes, 2017 for further discussion of complexity). Indeed, even apparently highly complex behaviours may not require cultural transmission (Byrne, 2007).

For example, naïve bower birds can make their nests without requiring any cultural transmission of knowledge (Collias & Collias, 1984).

Nut-cracking is regarded as one of the most complex behaviours expressed by any wild ape, as it requires a high level of dexterity (Foucart et al., 2005) and involves several objects, to be used in several steps following a specific sequential order to produce the desired effect (Biro et al., 2003; Boesch et al., 2019; Inoue-Nakamura & Matsuzawa, 1997; Read & Andersson, 2019). Perhaps unsurprisingly given its relative complexity, nut-cracking is rare across wild communities only being documented in two geographically separate and culturally unconnected populations to date: two geographically similar communities in West Africa (Bossou, Guinea and Taï Forest, Côte d'Ivoire Whiten et al., 2001) and another in Ebo Forest, Cameroon (Morgan & Abwe, 2006).

The number of steps, alongside the manual dexterity and use of multiple objects in conjunction required for this behaviour, suggests that nut-cracking is most likely a complex behaviour for chimpanzees. When distilled down to the basics, the behavioural form of nut-cracking consists of the following four sequential steps:

1. Place nut on an anvil
2. Pick up a hammer (unless already picked up)
3. Lift the hammer
4. Drop/push the hammer onto a nut (all may be repeated).

Perhaps due to this apparent complexity, nut-cracking is often assumed to be culturally transmitted (Boesch & Boesch-Achermann, 2000; Lycett, Collard, & McGrew, 2007, 2010), with some researchers arguing that action copying (imitation) must be the mechanism responsible for its acquisition. For example, Boesch (1996) claimed that chimpanzees learn how to crack nuts “by individual and social learning, including imitation” (Boesch, 1996, p. 418). Similarly, Biro et al. (2003, p. 220) argue that when nut-cracking “infant chimpanzees are driven not by a motivation for food but to produce a copy of the mother’s actions”. Others agree, claiming that nut-cracking (amongst other chimpanzee traits) are difficult to explain “by social learning processes simpler than imitation” (Whiten et al., 1999, p. 685). More recently, it has been argued that chimpanzees rely on mother to infant “teaching” to acquire the skills required to crack nuts, at a rate consistent with that of others within their community (Boesch et al., 2019). Overall, the behaviours underpinning nut-cracking have been argued to require social learning (in particular action copying and/or unspecified variants of teaching). It, therefore, follows that nut-cracking is assumed to be outside of chimpanzees’ ZLS, making nut-cracking a CDT. If true, it can be expected that, given a demonstration of the behaviour, chimpanzees should be capable of learning nut-cracking. This would provide evidence that social learning is sufficient for nut-cracking to occur. However, to determine whether social learning is necessary, whether nut-cracking can occur even in the absence of social learning, needs to be ascertained through a baseline test.

In its purest form, the ZLS hypothesis (Tennie et al., 2009) posits that all non-human great ape cultural behaviours can be reinnovated by naïve apes. Similarly, Hayashi, Mizuno and Matsuzawa (2005) suggested that nut-cracking could be individually reinnovated by chimpanzees. This is supported by some wild case studies, e.g., a report of nut-cracking in Cameroon (Morgan & Abwe, 2006) passes the ‘information barrier’ of the N’Zo-Sassandra River (McGrew, Ham, White, Tutin, & Fernandez, 1997). These results suggest that nut-cracking was reinnovated in two, culturally separate, wild communities (Tennie et al., 2009, p. 2406). If nut-cracking were reinnovated by a naïve, captive, chimpanzee in a culturally separate "island" of individuals (Tennie, Braun, Premo, & McPherron, 2016; Tomasello, 1999a) then the behaviour would cease to be a putative example of an ape CDT. Such data would support the ZLS hypothesis and would determine that chimpanzees are capable of individually learning all four of the steps underpinning nut-cracking; suggesting that social learning is not required for the behavioural form (these steps in succession) to emerge. This would mean that similar to other chimpanzee behaviours, a combination of individual learning and non-copying variants of social learning would suffice to explain the geographic patterns of nut-cracking in the wild.

This chapter compares the relative efficacy of the CDT hypothesis (Section 1.2.4.2.1), assuming that nut-cracking is a CDT (Boesch et al., 2019; Whiten et al., 1999) and the ZLS hypothesis (Section 1.2.4.2.2) positing that nut-cracking can be reinnovated, but may nevertheless be mediated by non-copying variants of social learning. Raw material selection is likely influenced by non-copying variants of social learning. For example, wooden or stone anvils are used in the wild to keep the nut in place and wooden or stone hammers are used to crack it (Sirianni et al., 2015). Whether stone or wood is used, the form of the behaviour is the same (see above), and only material selection has changed. Accordingly, this chapter focusses on the behavioural form, which is the aspect of the behaviour pertinent to the question of whether nut-cracking is a CDT.

4.2 Methods

4.2.1 Subjects

The subjects were 13 chimpanzees (M_{age} = 31.08; SD = 1; female = 9, male = 4; Table 4.1). All subjects lived within a single group, except for one individual (HO), that, due to group transfers within the zoological institution throughout the duration of this study, was introduced into the group before the start of the second condition (thus, HO did not participate in the baseline condition). The subjects were housed in two different enclosures throughout the course of the study. Between June 2017 and April 2018 subjects were housed in the "conversion" enclosure, from April 2018 until the end of the study subjects were housed in the "Eden" enclosure. Both enclosures consisted of two indoor areas and an outdoor area, with separate management areas. Subjects could be observed through glass panes in all public areas and mesh in management areas. Within the main enclosures, subjects had access to enrichment devices, such as climbing frames/ropes, hanging feeders and nesting baskets. Other enrichment devices are regularly provided by keepers.

Table 4.1. Details of subjects included in the study. Subject HO is displayed in italics as she was only included in the study after the baseline condition.

ID	DoB	Sex	Rearing	Location of birth
RO	30/04/1976	Female	Hand	Twycross, UK
JM	09/06/1982	Male	Hand	Twycross, UK
FY	25/10/1986	Male	Hand	Twycross, UK
VC	18/08/1990	Female	Hand	Twycross, UK
JO	28/12/1990	Male	Hand	Twycross, UK
TU	10/08/2007	Female	Parent	Twycross, UK
GE	25/05/1995	Female	Hand	Twycross, UK
TJ	17/06/1977	Female	Undetermined	Wild
JS	20/02/1988	Female	Hand	Dudley Zoo, UK
CO	01/01/1965	Female	Undetermined	Wild
ND	14/12/1971	Female	Undetermined	Wild
KB	05/12/2003	Male	Parent	Bremerhaven, Germany
HO	*27/12/1982*	*Female*	*Parent*	*Twycross, UK*

4.2.2 Prior experience questionnaire

As in Chapter 3, the data set from the questionnaire distributed by EB was initially consulted to assess naivety. However, given the fact that the questionnaire was over 2 years old at the start of this study follow up interviews were carried out with keepers. The relevant aspect of the questionnaire was the question of the presence of the following behaviour:

> *"Using one object to bang on, or hit, another: usually, this means the use of a hard object to bang on or hit another, often hard, object. This may be with the aim to crack or break open the latter object, or to remove a substrate. Here, we are interested in any hammer-like behaviours, regardless of the objects involved".*

This definition encompasses nut-cracking and similar actions, such as hammering behaviours. No instances of nut-cracking were reported in the questionnaire; however, in the questionnaire, a keeper described how one individual (TU; F; age 9 at the time of the questionnaire) used a stone to tap on the glass of the outdoor enclosure; given that the results presented here are ‘negative’ this behaviour did not influence the findings. However, should TU have expressed nut-cracking it would be possible that this tapping behaviour could be considered an antecedent behaviour. All but one keeper reported that the chimpanzees were frequently witnessed using their teeth to crack nuts such as walnuts or peanuts. These findings were confirmed by later follow up interviews.

4.2.3 Ethical statement

All participation in this study was voluntary, and subjects were allowed to leave the testing area at any point throughout the session. Subjects’ usual feeding and cleaning routines were followed, minimising disruption to the apes. The experimental phase of this study was ethically reviewed and approved by the University of Birmingham AWERB committee (UOB 31213) and by an internal committee at the testing location, following guidelines provided by SSSMZP, EAZA, BIAZA, WAZA on animal welfare and research in zoological institutions; this study also received a letter of support from BIAZA. This study adhered to legal requirements of the UK, where the research was carried out, and adhered to the ASP principles for the Ethical Treatment of Primates.

4.2.4 Motivation tests

This phase took place between 13th June and 27th September 2017. Before starting experimental testing, it was important to ensure that the subjects were sufficiently interested and motivated to access the novel food reward (macadamia nuts) used in this study. To motivate the chimpanzees to try the nut kernels when first presented, the first stage involved a trusted individual (KW; head ape keeper, who had worked with the subjects for more than five years) first eating a portion of familiar food in front of the subjects (here we used dried raisins and berries). Throughout motivation testing, subjects were in their normal groups. KW attracted the subject's attention by calling their name, and then ate a single item of the familiar food (i.e., one raisin) in view of them. This process was repeated until each individual had observed the demonstration. The subjects were then provided with the same food and were required to eat it before moving onto the next step, every individual ate the familiar food.

The next stage was to introduce the novel food (macadamia nut kernels without their shells). Again, KW ate a single macadamia kernel in the same way as with the familiar foods. Each individual was first given a demonstration, within the group context. Once each individual had observed the consumption of the nuts at least once, they were provided with their macadamia kernel. This process was designed to increase the likelihood that the subjects would eat the novel food (Visalberghi, Yamakoshi, Hirata, & Matsuzawa, 2002) as the trusted keeper ate and introduced edible and safe food. Thus, increasing the likelihood that the chimpanzees would be motivated to eat the kernels. We required at least half of the chimpanzees to eat the novel nuts before starting testing, this was to ensure that the preference testing did not go on for too long, as these tests were carried out within a group context, it was likely that lower-ranking individuals would never be allowed access to the nut kernels.

4.2.5 Test conditions

Each trial was video recorded, this began when the subjects were given access to the testing apparatus. Trial times were the period between the first morning feed and the afternoon feed; this was chosen to compliment the daily routine of the keepers and apes whilst providing the maximum testing time possible. The timings changed once the chimpanzees moved enclosure as the keepers were able to provide the afternoon feed without needing to move the subjects outside the testing area. Average trial length in “conversion” was 3 hours (n = 8) and in “Eden” was 5 hours 41 minutes (n = 12). Overall, there was a total of 92 hours and 18 minutes of observation time ($M_{\text{trial length}}$ = 4 hours 37 minutes). The experimenter (DN) was present throughout each trial.

This study used a result dependent design, where each condition (see Figure 4.1) was followed by the next, if the behaviour was not expressed in the previous condition, after five trials. For example, the "End state" condition was only implemented if the behaviour was not reinnovated in the "Baseline" condition. The study ended once the subjects had participated in all trial up to and including 5 trials with full action demonstrations.

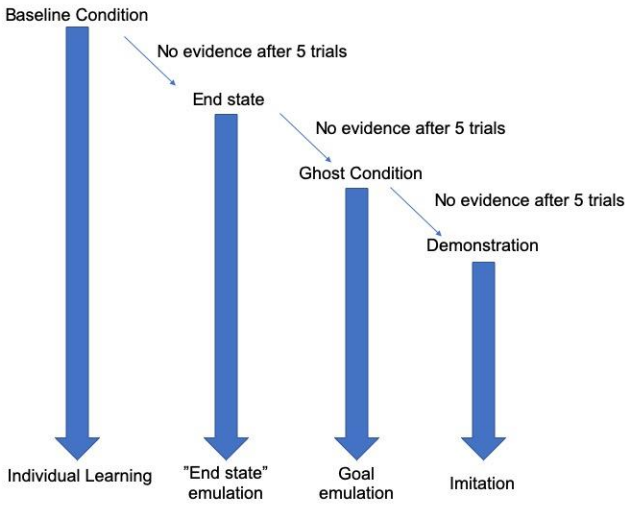

Figure 4.1. Decision tree depiction of the result dependent conditions. If, at any stage, evidence of nut-cracking was encountered then testing would have ceased. Each condition was continued for five trials before moving onto the next condition.

In all of the conditions, behaviours were first live coded using the ethogram in Table 4.2. Video recordings were focused on the experimental hammer and anvil set up, described below, however, DN was present at all times to observe any behaviours which might have occurred outside of the camera frame.

Table 4.2. Coding ethogram used during the live coding procedure; this was added to throughout live coding as behaviours of interest were observed. This ethogram was provided to the second coder for reliability coding.

Behaviour	Description
Place nut	The subject places one/several nuts on the surface of the anvil. This is also coded if the subject drops the nut onto the anvil. The nut may roll off the anvil after being "placed" this is acceptable as it is likely due to the nut's shape and the angle of the anvil's surface.
Hold hammer	The subject picks up the hammer – with the nut on the anvil, by holding the wood itself or the securing attachment.
Raise hammer	The subject lifts the hammer above the nut – this may be at/below/above head height for the subject.
Drop hammer	The subject brings the hammer down onto the nut, which must be resting on the anvil. The hammer can be dropped or held in the hand the entire time. This behaviour can be repeated until the nut is cracked. The behaviour is coded each time the behaviour occurs – i.e., each time the nut is struck.
Eat nut	The subject takes the kernel of the, now broken nut and eats it. Note, this must have followed cracking of the nut by the subject.
Stamp	The subject uses their foot to stand on the nut, which has been placed on the anvil.
Throw	The subject, whilst sitting on the anvil, throws the nut in any direction.

4.2.6 Materials

The same apparatus set up was used in all conditions, and any changes to these conditions are noted in the relevant section. To set up the apparatus, DN entered the enclosure and secured a large wooden log (50cm tall x 40cm diameter), that would serve as an "anvil", to an upright portion of the climbing frame (which had a horizontal crossbeam, to ensure that the anvil could not be removed; see Figure 4.2). The anvil was secured to the upright climbing frame using two 1m long, 8mm thick, PVC coated, steel rope passed through two (12mm diameter) holes drilled through the anvil (located ¼ and ¾ of the way down the log).

Both ends of the rope had a loop (secured by five 'clips' at each point, 'clips' used two, 8mm, nuts and bolts (tightened using an electric drill), which was too large to pass through the hole in the anvil, and a steel padlock attached the two ends. Two of these securing attachments were used as a failsafe measure (see Figure 4.3).

Figure 4.2. Hammer and anvil set up within subjects' enclosure. Note, the two securing attachments are passed through separate holes within the anvil and the hammer is less than 1m from the anvil (this was ensured by the length of the securing attachment of the hammer to the anvil).

A wooden "hammer" was also attached to this structure (wooden, rather than stone, hammers were chosen as they were more secure in their attachment to the rope). The hammer consisted of a 30cm long x 15cm diameter log – approx. weight 2.5 kg – with a 12mm hole drilled through half way along (see Figure 4.3). The hammer was attached to the anvil's own securing attachment by creating another looped end in another (1.5m) length of the same steel rope; the loop was passed onto the top securing attachment (of the anvil) and the loose end was secured to the hammer (by passing the loose end through the drilled hole and then securing with another five clips). The hammer was then moved less than 1m from the anvil (see Figure 4.2).

Figure 4.3. Securing attachment of the hammer.

Keepers then scattered three macadamia nuts (in their shell) per individual (i.e., 3 nuts x 13 individuals = 39 nuts) throughout the enclosure, avoiding a 2m radius around the hammer and anvil set-up. The macadamia nuts were distributed at the same time as a regular scatter feed (mainly consisting of vegetables with some fruit), just prior to the subjects being released into the outdoor enclosure. The unshelled weight of the nuts (around 1g average across 10 measurements) was taken from the chimpanzees' usual allowance of nuts for the week (this was to maintain the dietary health of the subjects, at the testing institution's request). Once the attachments had been checked by DN and at least one keeper, all humans exited the enclosure and the chimpanzees were allowed in the enclosure. Just prior to the chimpanzees being allowed access, video cameras (SONY HDR-CX330e), set at two points framing the apparatus (to better capture various angles), on tripods, were set to record. DN was also present to live code relevant behaviours (see above).

4.2.7 Conditions

4.2.7.1 *Baseline condition*

This test condition took place between 15th October 2017 and 30th November 2017.

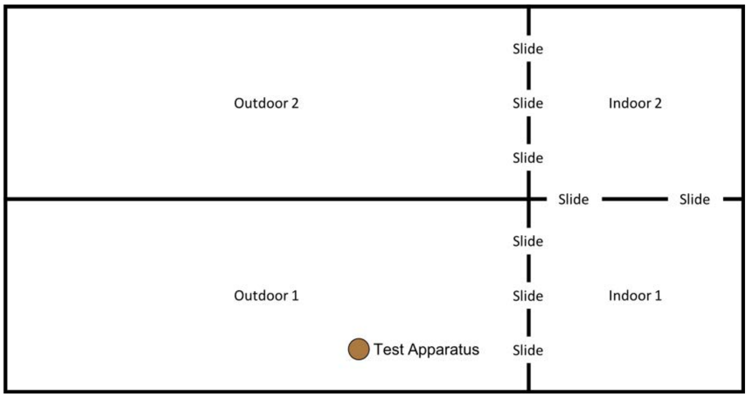

Figure 4.4. Experimental set up for baseline condition in "conversion"; note, the same set up was used for the first two trials of the "end-state" condition, prior to the enclosure move (see below).

In order to examine whether the subjects would individually reinnovate the target nut-cracking behaviour, it was necessary to test subjects without providing any social information beforehand. All sessions began between 10 am and 12 noon, when keepers provided the chimpanzees' scatter feed. All sessions were conducted in the "Outdoor 1" section of the enclosure (see Figure 4.4); however, subjects had access to both indoor areas throughout the session.

4.2.7.2 ***End state condition***

This phase of the study was completed between 15th January 2018 and 18th May 2018. However, after the first two trials (15th January 2018 and 17th January 2018) the weather conditions at the testing institution became so harsh that the subjects would often refuse to leave the indoor enclosure. Thus, testing was paused until 14th May 2018, after which the final three trials were completed on the 14th, 16th & 18th May. Between testing in January and May subjects were moved from “Conversion” (their previous enclosure) to a new enclosure: “Eden” (see Figure 4.5); subjects were therefore given one month after moving to the new enclosure before testing resumed.

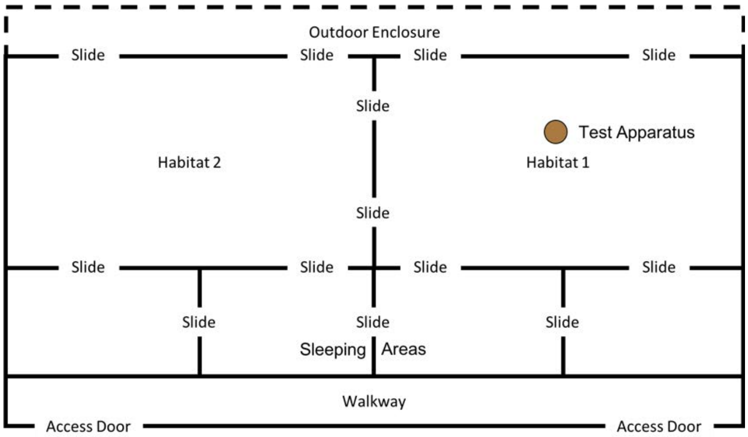

Figure 4.5. Experimental set up for “end-state” condition in “Eden”. Note, subjects had access to the entirety of this enclosure throughout these trials, however, the outdoor section of the enclosure was still under construction.

In this condition, we placed three macadamia nuts, shells and kernels, which had been split in half (see Figure 4.6) on top of the anvil (in the “Conversion” enclosure this was in “Outdoor 1” and in “Eden” this was in “Habitat 1”). This condition represents a partial emulation condition, where the subjects are presented with the ‘end state’ of the object after the behaviour has occurred, but without demonstrators present. This condition replicates a scenario where a prior individual has cracked nuts at the location and left some broken nuts with kernels in the vicinity of the anvil.

Figure 4.6. Left panel: Macadamia nuts, sawn in half (with kernels left whole) for the end-state emulation condition. Right panel: Nuts placed atop the anvil as described in text.

This condition was carried-out as the chimpanzees failed to individually reinnovate the nut-cracking behaviour in the baseline. During the design process the study originally included an extra condition between the "Baseline" and "End state" conditions, called "Local Enhancement". In this condition it would have been made clear to the subjects that a kernel is inside the macadamia nut and therefore that it constitutes a food source by shaving half of the nut shell away to reveal the kernel inside (see Bandini and Tennie, 2018). However, some of the chimpanzees in this study cracked the shells of the macadamia nuts with their teeth and subsequently consumed the kernels (see Figure 4.7), rendering this condition unnecessary as the contents of the nuts were clear.

Figure 4.7. Adult male chimpanzee (JO) cracking a macadamia nut with his teeth, then eating the kernel.

4.2.7.3 ***Ghost condition***

This phase of the study was completed between 19th July 2018 and 10th August 2018 and involved a significant increase in the level of social information provided to the subjects. In this condition, the hammer and anvil set-up were still present inside the enclosure, along with three macadamia nuts per individual (scattered throughout "Habitat 2"; Figure 4.8) and a further three nuts (this time whole, uncracked nuts, inside the shell was provided) placed on top of the anvil. Additionally, a replica of the equipment inside the enclosure (i.e., a hammer and anvil set up) was placed outside the enclosure, visible through the mesh near the subjects' sleeping area (see Figures 4.8 & 4.9); DN was also present, standing to the left of the anvil.

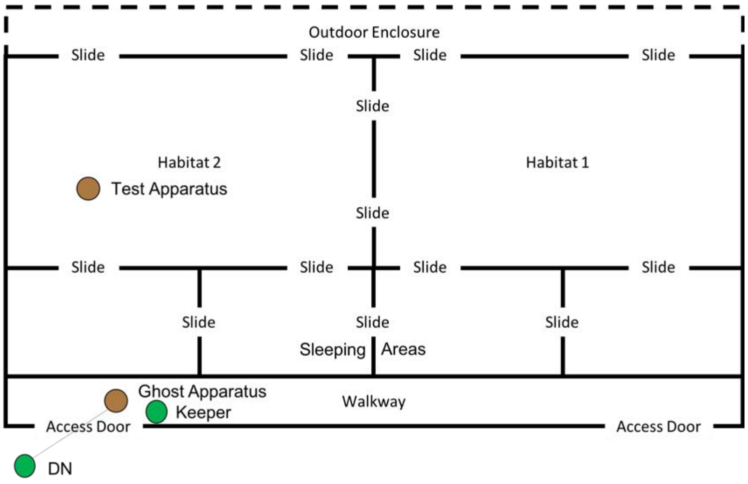

Figure 4.8. Experimental set up for "Ghost" condition in "Eden". Note, subjects had access to the entirety of this enclosure throughout these trials including the outdoor enclosure.

A reel of clear fishing line (0.65mm diameter; 18.14kg break strain) was attached to the hammer and passed through a section of mesh, allowing the hammer to be raised (between 80 and 50cm) above the anvil, via a pulley-like system. Once the subject was clearly attending the apparatus (the subjects' attention was gained by calling their names), the hammer was dropped onto a nut (which was placed in a groove in the centre of the anvil), cracking the nut open. A keeper then approached the anvil and gave the subject (which watched the demonstration) the cracked nut. The device was then rebaited with a new nut in the centre of the anvil. This procedure was repeated for a further 29 nuts (equalling a total of 30 demonstrations; with the exception of trial 4; where an equipment malfunction (the fishing line broke) – forced the trial to end after 17 nuts had been cracked.). Subjects had access to the testing apparatus during the course of the ghost trials. One camera was used to record the subjects' interactions with the test apparatus, whilst the other was used to record subject's observing the ghost demonstrations. In both this condition and the Full Action Demonstration condition observing subjects were considered to be those in the enclosure immediately in front of the demonstration area (far left sleeping area in Figure 4.8) oriented towards the apparatus/demonstrator (i.e., not with their back turned).

Figure 4.9. Experimental set up of "Ghost Condition" apparatus. Note the hammer is suspended by fishing line, and a single nut is in the centre of the anvil.

This ghost condition (inspired by Hopper, Lambeth, Schapiro, & Whiten, 2008) fulfils the primary stipulation of learning by emulation (Tomasello, Kruger, et al., 1993); i.e., the learner should not copy the motor patterns of the demonstrator (see Section 1.2.1.1). In this condition, the motor patterns required for nut-cracking were not demonstrated, making it impossible for the chimpanzees to copy the actions (Heyes, 1994).

4.2.7.4 ***Full action demonstration condition***

This phase of the study was completed between 16th August 2018 and 6th September 2018. The full action demonstration condition was the first condition that for the first time allowed for the possibility of action copying. In this condition DN was positioned outside the enclosure (in the same location as the ghost condition). An anvil was placed in the same location as in the ghost condition (see Figure 8), with a hammer placed 1m from the anvil (both pieces of wood were identical to those in the subject's enclosure). The researcher then attracted a subjects' attention by calling their name and proceeded to crack a nut, on top of the anvil, using the hammer. Note, it was not possible to exclude the fact that multiple subjects may attend to the call of one individual – subjects attending to a demonstration were coded from videos. The experimenter used the hammer in a vertical manner, thus matching the hammer orientation from the ghost condition (see Figure 4.10), raising it to eye level and then hitting down onto the nut, resulting in the nut breaking open. The kernel was then provided to the subject by a keeper (see Figure 4.10D) and the device rebaited with another nut. A total of 30 nuts were cracked using this procedure in each trial; a nut was not cracked until DN considered that the target subject was attending to the demonstration. A maximum of 30 nuts were used based on advice from keepers that not all subjects would attend to, or even approach, the demonstrations; therefore, trials could have continued indefinitely and would have quickly become unfeasible.

Figure 4.10. DN performing demonstrations. Panel A: subjects' attention is gained by calling their given name; panel B: hammer is raised to eye-level and brought down on the nut as many times as required until it cracks (panel C); panel D: cracked nut (both shell and kernel) are provided to the target subject by a keeper. The keeper rolled the nut to JS in panel D (hand feeding, even by keepers, is not permitted at the testing institution).

4.2.8 Coding/analysis of behaviours

4.2.8.1 *Coding procedure*

Trials were live coded using the ethogram in Table 4.2. Following live coding, a formal coding procedure from the videos was followed. DN coded each trial in turn and a second coder (MT), naïve to the hypothesis of this study, second coded 100% of the behaviours identified (N=31) along with an equal number of "dummy" clips where a subject was in the frame but DN did not identify a behaviour occurring. To assess inter-rater reliability (acceptable Kappa would be 0.6; Cohen, 1968; calculated using R package "irr" v.0.84.1; Gamer, Lemon, Fellows, & Singh, 2019). Note that the behaviours in Table 4.2 rely on the previous behaviour for them to be coded; e.g., if the subject picked up the hammer without first placing a nut on the anvil then the hammer behaviour would not be coded. This was to attempt to parse hammer centred play/exploration from attempts at nut-cracking.

4.2.8.2 ***Analyses***

After a single reinnovation of the behaviour, social facilitation cannot be excluded as a potential reason for the behaviour's continued emergence (Bandini & Tennie, 2018; Tennie & Hedwig, 2009). Given an N of 1, it is not possible to perform inferential statistics on acquisition times or rates between individuals. Instead, descriptive statistics were used, all descriptive statistics were produced using R v.3.5.2 (R Core Team, 2013).

4.3 Results

4.3.1 Motivation test

During the motivation test, seven subjects (54% of sample; FY, GE, JS, TJ, JO, KB & HO) consumed at least one macadamia nut provided by the keeper, leading to the conclusion that macadamia nuts were a) palatable and b) desirable to most of subjects included in this study (although note that dominance hierarchies/individual personality characteristics may have interfered with certain individual's ability/motivation to access the nuts).

4.3.2 Reliability analysis

The results of Cohen's Kappa analysis revealed a strong level of agreement between coders ($\kappa = .85$, $p<.001$).

4.3.3 Attempts at nut-cracking

None of the individuals in this study attempted to crack open the nuts using a tool in any of the conditions described above; as there was never any evidence of nut-cracking or approximations of it, all conditions were completed (as explained in Section 4.3.3).

4.3.3.1 ***Attempts recorded within the ethogram***

The coding procedure identified the following behaviours from the ethogram: place (*n* = 26; first occurring during baseline condition trial 2 but distributed across baseline (*n = 7)*, end state (*n = 15)* and ghost (*n = 4)* conditions), hold (*n* = 1; occurring during baseline condition trial 2), stamp (*n* = 2; occurring during baseline condition trial 2) and throw (*n* = 2; occurring during baseline condition trial 2). Recordings of "place" were identified in C5 (*n* = 7), C6 (*n* = 18) and C7 (*n* = 1) across all conditions apart from full demonstration. In only one instance did a "hold" event follow "place", this concerned C6 during baseline condition trial 2; who was also the only individual to "stamp" on or "throw" the nuts. It is unclear whether throwing was an active effort to break the nut or simply an act of frustration/play as it did not appear that the throws were aimed at any hard surface, nor were there ever attempts to retrieve the nuts afterwards by the throwers.

4.3.3.2 ***Alternative techniques***

Anecdotally, the majority of subjects (if not all) were witnessed, at least once, attempting to crack the nuts with their teeth (with some individuals succeeding; see Figure 4.7). Male chimpanzees (n = 4) were the only individuals observed (by DN) successfully accessing the nut kernel using this method. The teeth cracking technique was first observed in the baseline condition and persisted throughout the study. These behaviours were not captured on the main videos as the cameras were facing the apparatus throughout the trial (to ensure that any attempts at using the apparatus to crack the nuts were captured), also some subjects were not visible throughout; therefore, any attempt to quantify these behaviours would be inaccurate as it would likely present only part of the actual series of events.

4.3.4 Observers: Ghost and Full Action Demonstration Conditions

Occasionally the identity of the observer could not be ascertained from video footage; in these cases, the individuals were not included in the calculations below. Furthermore, as participation in the study was voluntary, and subjects were free to approach and interact with the testing apparatus whenever they chose, not all subjects observed all the demonstrations provided. Some subjects (n = 2; JO & ND) never observed the demonstrations in either condition; whilst other subjects never observed demonstrations in the ghost (n = 3; JO, HO & ND) or full demonstration conditions (n = 4; JO, ND, RO, CO). However, 77% of subjects (n=13) were coded as observers in the ghost condition and 69% (n=13) were coded as observers the full demonstration condition; there was an average of 2.48 observers per ghost demonstration and 2.99 observers per full demonstration.

4.4 Discussion

We found no evidence of nut-cracking with a tool, or any approximation at this, at any point during the course of this study. Thus, our sample of 13 naïve chimpanzees failed to reinnovate or socially learn the behavioural form of nut-cracking. At first, it would seem our findings support the CDT hypothesis, in that nut-cracking behaviour was not reinnovated in our initial baseline condition. However, our study also consisted of various social learning test conditions – including one that demonstrated the necessary action patterns for nut-cracking to the chimpanzees. This condition allowed for the possibility of action copying being a requirement of the behaviour, as has recently been claimed (Estienne, Cohen, Wittig, & Boesch, 2019). Even so, nut-cracking was not acquired by the subjects. Therefore, our study does not provide conclusive evidence for either the CDT or the ZLS hypothesis. Below we discuss three possible explanations for our null result and the general disparity in studies of chimpanzee nut-cracking.

4.4.1 Conspecific models

The findings of this study raise the question as to why some chimpanzee populations in the wild regularly crack nuts (on average 270 nuts per day for as long as 2 hours 15 minutes in Taï Forest; Boesch & Boesch-Achermann, 2000) whereas captive chimpanzees (in this sample and others; Funk, 1985) seem to rather consistently fail to acquire the behaviour, even after demonstrations. A first possibility for the disparity between wild and captive data is that nut-cracking is indeed a CDT and requires the learner to imitate a conspecific demonstrator (Boesch, 1996). In this study we used human demonstrators, which may not have been considered 'good' enough models for the chimpanzees. Indeed, some research has shown that chimpanzees are more proficient social learners from conspecific models as compared to videos or human models (Hopper, Lambeth, Schapiro, & Whiten, 2015). However, in contrast, others have instead claimed that it is possible for chimpanzees to "learn" nut-cracking from human demonstrators (see findings of Ross, Milstein, Calcutt, & Lonsdorf, 2010 but also review of other related studies Table 3 (p. 230) of Ross et al. 2010).

Concurrently, other studies have found that, even with conspecific demonstrators, sometimes captive chimpanzees fail to acquire complex behaviours such as nut-cracking (Funk, 1985) or behaviours which strictly require imitation (Clay & Tennie, 2018; Tennie, Call, & Tomasello, 2012; Tomasello et al., 1997). Although it might have been interesting to observe the chimpanzees' reaction to a conspecific demonstrator in this study, we did not have the resources to train a chimpanzee to act as a demonstrator, but we encourage interested researchers who do have the resources to replicate this study, and include a conspecific demonstrator to observe whether this affects the findings presented here.

4.4.2 Behavioural flexibility

An alternative explanation for the fact that nut-cracking did not emerge in this study is that the chimpanzees were hindered by their lack of behavioural flexibility, a commonly recorded phenomenon in chimpanzees (e.g., Harrison & Whiten, 2018). The chimpanzees in the current study seemed to become fixated on one solution to open the nuts: i.e., the use of their teeth. The chimpanzees may have relied on this technique due to their pre-existing knowledge on how to crack softer-shelled nuts (such as peanuts and walnuts), which they are often provided during their feeds at the testing institution. These nuts are easily cracked open by apes using teeth (DN; personal observation, keeper reports and see also Visalberghi et al., 2008 for measurements on the required force for different types of nuts). The heuristic (Marsh, 2002) in this case may be that nuts (in general) *can* be opened with teeth – and indeed our macadamia nuts were no exception. Chimpanzees have been shown to be reluctant to display behavioural flexibility in abandoning a previously successful solution (see Harrison & Whiten, 2018; Hrubesch, Preuschoft, & van Schaik, 2009; but see also Manrique, Völter, & Call, 2013). Thus, it is possible that the first individual to successfully crack a nut with the use of teeth (see Figure 7), facilitated this behaviour within the group and/or that other individuals independently converged on this method. Following this, the subjects were inhibited in their ability to innovate a new method, even if cracking the nuts with a tool would have been mechanistically easier/more efficient (this possibility is also in line with cultural founder effects; Tennie et al., 2009).

4.4.3 Sensitive learning period

Based on the literature, the most likely explanation for the findings in this study is that the chimpanzees may have simply been outside of their sensitive learning period for nut-cracking. Previous studies on nut-cracking in wild chimpanzees have reported that before 3.5 years, juvenile chimpanzees are unable to express the full nut-cracking behavioural form (Inoue-Nakamura & Matsuzawa, 1997; Matsuzawa, 1994). However, juvenile chimpanzees (as young as 1.5 years old) that had been exposed to the materials required for nut-cracking at various ages/developmental stages were able to perform the basic actions of the behaviour (put, hold, hit and eat), but not combine them in the required order to perform the full nut-cracking behaviour (Inoue-Nakamura & Matsuzawa, 1997). Indeed, recent research in wild chimpanzees shows an exponential increase in nut-cracking between 5 and 6 years of age, though the first signs were observed in 3-4-year-old individuals (Estienne et al., 2019) in line with the concept of maturation (Corp & Byrne, 2002). This finding suggests a certain level of developmental prowess required to express nut-cracking, perhaps somewhere between maturation effects of the body and the brain.

In addition to this lower age limit for the acquisition of nut-cracking, there also appears to be an upper limit (more relevant for the current study). A 13 year longitudinal study by Biro et al., (2003) found that wild chimpanzees who did not learn the basic nut-cracking skills before five years old seemed unable to acquire the behaviour later on in adulthood (a similar case has been documented recently for stone tool-use in long-tailed macaques; Tan, 2017). The subjects tested in the current study were all outside of the hypothesised sensitive learning period for nut-cracking, as the youngest subject in our sample was already 10 years old at the time of testing. The youngest individual however was the only subject to display the "hold" behaviour (stage two of four) in the behavioural form of nut-cracking. Our findings, coupled with those described here suggest that a sensitive learning period may be a decisive factor for whether a chimpanzee will start to crack nuts or not (leaving open the question how this is learned, i.e. whether it is a CDT or a latent solution).

Given the fact that wild chimpanzees engage in an extended process of acquisition before expressing nut-cracking (Matsuzawa et al., 2008), we suggest that future work considers applying an even longer study time than the one employed here. It is possible that chimpanzees may then individually, or socially, learn the behaviour. The social learning opportunities that we present here were fewer compared to the wild; in wild populations that express the behaviour, individuals have more and longer (and perhaps also more varied) opportunities to observe nut- cracking. Equally, given the potential importance of a sensitive learning period in explaining the emergence patterns of chimpanzee nut-cracking (discussed in this section) we suggest that the next logical test of this behaviour should aim to test younger chimpanzees between the ages of 3 and 10 years (Ross et al., 2010 suggest between ages 3-7); either way, these individuals should once again be selected from populations that have not been observed previously to crack nuts.

Though we used a within-subject design throughout our result-dependent design, we would reccomend that (wherever feasible) a between-subject design be used in future tests (one group for each of the conditions). By doing the latter, it is possible to control for and measure the time of exposure required for chimpanzees to express nut-cracking, and it would exclude potential carry-over effects. However, this project would likely be an overly large undertaking for any one research group, so therefore may be better suited to large scale colaborative projects (e.g., the ManyPrimates project).

4.4.4 Conclusions

Although no chimpanzees in this study demonstrated nut-cracking using tools, two geographically separate populations in the wild have seemingly converged on the same method for cracking nuts using tools (West Africa; Whiten et al., 2001 and Cameroon; Morgan & Abwe, 2006). As these populations do not have access to each other, logically they must have independently reinnovated nut-cracking (Byrne, 2007). However, the data from Cameroon is based on procured nut cracking tools and auditory assumptions and so are an inference rather than direct observations. It is possible that these tools were actually from modern human nut-crackers and may not be considered evidence of chimpanzee nut-cracking in multiple populations. Thus, to date, there is only concrete evidence of one culturally independent wild population expressing nut-cracking. As the data from this study and wild data do not unequivocally support either the ZLS or the CDT hypothesis, both remain in contention.

In addition to the wild data and that presented here, one chimpanzee in an experimental study spontaneously reinnovated nut-cracking when provided with all the materials (Marshall-Pescini & Whiten, 2008). The individual (Mawa) acquired the nut-cracking behaviour seemingly without requiring any copying variants of social learning (Marshall-Pescini & Whiten, 2008). However, Marshall-Pescini & Whiten (2008) fail to note the importance of these findings, by assuming, based on the speed of acquisition, that "Mawa" had prior experience of nut-cracking. It is worthy of note however that unlike this study and that of Funk (1985), no claim was made about the naivety of the subjects. Indeed, Mawa was kept as a pet prior to residing at the sanctuary where Marshall-Pescini and Whiten (2008) carried-out their study. Mawa arrived at the sanctuary when he was approx. three years old with wounds from a rope where he was tied up (Ferdowsian et al., 2011). As a result of this potential enculturation, or at the very least deprivation, these data should be treated with caution; indeed, the generalisability of such individuals to wild chimpanzees is questionable (Henrich & Tennie, 2017).

Excavations of chimpanzee nut-cracking sites suggest that the basic behavioural form has remained constant for at least 4,000 years, and likely even longer (Mercader et al., 2007). Similarly, excavations of capuchin nut-cracking sites have demonstrated that their nut-cracking form has remained the same for 3,000 years, with only the tools (hammerstones) changing in shape over time (Falótico, Proffitt, Ottoni, Staff, & Haslam, 2019). Indeed, if the behavioural form of nut-cracking were being copied between individuals, we would expect to see some changes to its form over time due to copying error alone (see Eerkens & Lipo, 2005). Therefore, social learning may not be fully responsible for the emergence of nut-cracking in chimpanzees (especially given the results of the current study, in which the chimpanzees did not acquire the behaviour even after full demonstrations were provided). We acknowledge that the chimpanzees in this study were captive and therefore are not subject to the same ecological pressures as their wild conspecifics; that is, they would have less ‘necessity’ to reinnovate the behaviour (Fox, Sitompul & van Schaik, 1999). Therefore, (parts of) this study could perhaps be replicated in a wild sample, naïve to nut-cracking.

Therefore, the results of this study do not support nut-cracking as the first evidence of a CDT in chimpanzees (see also Byrne, 2007), yet they also do not fully support nut-cracking as a latent solution in chimpanzees. Instead, we conclude that the behaviour may not have emerged here due to interplay of factors, including a certain level of behavioural conservatism and, crucially, the fact that all the subjects were already out of their sensitive learning periods for nut-cracking. We believe it is unlikely that our use of human demonstrators was the reason for the failure of all our subjects to express nut-cracking, given the results of previous studies, discussed above. Accordingly, we propose that future studies should adopt the methodology presented here, but test unenculturated infant/juvenile chimpanzees, naïve to nut-cracking *and* to opening nuts with their teeth, to remove the confounds of the sensitive learning periods and conservatism (ideally tested in isolation in order to increase effective sample size). Under these conditions, it is plausible that some naïve chimpanzees will reinnovate nut-cracking. Yet, on the other hand, given the extended trial-and-error learning process that young wild chimpanzees engage in (Matsuzawa et al., 2008) it is possible that under the relatively short term test conditions, the full form of nut-cracking may still fail to emerge spontaneously, although some of the pre-requisite steps to the behaviours may still develop.

So far, the current state of knowledge does not support the view that nut-cracking *has* to be reliant on social learning as it has potentially been reinnovated in two culturally distinct populations, therefore, it seems unlikely that it is a CDT. However, it is also possible that even chimpanzees within their sensitive learning period would continue to fail to individually acquire the skills required to crack nuts and therefore could be considered a CDT. The data at hand suggest that the behavioural form of nut-cracking may only be acquired through an interplay of ecological and developmental factors, i.e., chimpanzees must be in a location with appropriate nuts and tool materials, during or before, their sensitive learning period. Therefore, it remains possible that nut-cracking is within the species level ZLS of chimpanzees. Despite this, not all individuals may realise this potential within their lifetime if they were not exposed to the required ecological conditions or individual prerequisites (note that these were termed by Tennie et al. (2009) as the “right” conditions that may be required). It is yet to be determined whether nut-cracking’s acquisition is best described as being due to, and requiring, social learning (culture-dependent) or is due to socially mediated reinnovation (latent solution). Further research should consider the importance of the ecological factors explored here in addressing this question.

CHAPTER 5: NON-HUMAN GREAT APES FAIL TO SPONTANEOUSLY COPY NOVEL ACTIONS EVEN WHEN ACTION DEMONSTRATORS FORM A MAJORITY

This chapter, largely in its current form, is being prepared for submission to Nature as:

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Conceptualization: DN, CT
Data Collection: DN
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Formal analysis: DN
Project administration: DN
Resources: DN, ZC
Supervision: CT
Writing – original draft: DN
Writing – review & editing: DN, CT, JC, ZC

The changes to this chapter from that submitted to Nature are generally the addition of information, which was excluded from the Nature manuscript in the interest of brevity. However, I have placed the OSF registration for this chapter in Appendix B. This registration contains details of planned conditions that could not be carried out because the stipulations of the result-dependent design were not met.

5.1 Introduction

It has been claimed that one of the most important social learning mechanisms fuelling cumulative culture is the ability to copy actions (imitation; Galef, 1992; Tennie, Call, & Tomasello, 2009; Tomasello, 1996). In other variants of social learning (with the exception of action-based teaching and direct moulding) the behavioural form shown by observers is instead essentially a reinvention of the wheel (Tennie et al. 2009) rather than a learned sequence of behaviours.

Other variants of copying, in particular copying physical results in the environment (emulation), may lead to cumulative culture in the physical domain (Caldwell & Millen, 2009; Reindl et al., 2017). Though, some argue that such approximations at cumulative culture are not all they seem, meaning that the comparatively simple approximations of culture, used in a laboratory setting, do not speak to the complexity of cumulative culture in reality (Miton & Charbonneau, 2018; Section 1.2.3.3.2). Regardless, action copying is necessary for many aspects of human cumulative culture; cultural practices that are largely, or entirely, based on actions, with little to no environmental results, such as dances, some rituals, and gestural language (Legare & Nielsen, 2015) could not occur or be maintained without action copying. As a consequence, it is difficult to over-emphasise the utility of action copying in explaining modern human behaviour.

One way to tackle the question of the evolution of action copying is to look for evidence for this ability in our closest extant relatives, apes. The debate around this topic have been covered at length already in this thesis (see Section 1.2.1.2). In summary, it has often been claimed that, ape culture (like human culture) is based on action copying (e.g., Boesch, 1991; Byrne, 2007, 2009; Whiten, 2000; Whiten et al., 1999; Whiten, Horner, & Marshall-Pescini, 2003). However, this conclusion is not universally accepted. The ensuing debate is known as the "culture war" (Kendal, 2008; McGrew, 2002) and those sceptical about the existence of ape copying represent the other side of the debate (e.g., Clay & Tennie, 2017; Galef, 1976; Tennie et al., 2009; Tomasello, 1996; Tomasello et al., 1993).

While there are clear population differences in (some) ape behavioural repertoires, these differences may merely represent culture in a "minimal" sense; where action *frequencies*, but not the actual action *forms*, are under social learning control (Neadle, Allritz, & Tennie, 2017). This is because these behaviours are not reliant on social learning, particularly copying variants of social learning, and therefore should not be considered as CDTs (*sensu* Reindl et al., 2017). Until such a times as these behavioural variations are confirmed to be the product of copying variants of social learning, we cannot assume that apes are capable of copying in a way comparable to humans. In this sense, the presence of minimal culture cannot be seen to identify action copying abilities in a way that has previously been inferred in the ape culture literature (e.g., Whiten et al., 1999). Evidence of true action copying is necessary before connecting wild ape culture with action copying, i.e., succeeding in a task where other social learning variants are rendered useless.

It is important to note that apes would need to demonstrate the ability to copy actions *without the assistance of humans*. While it is known that apes can copy actions (albeit in a crude manner) after intensive human training (Custance, Whiten, & Bard, 1995; Hayes & Hayes, 1952), it is also known that such training changes brain structures in the trained apes (Pope, Taglialatela, Skiba, & Hopkins, 2018). Wild apes have no access to human training, therefore, only data collected from untrained and unenculturated apes can be seen to have ecological relevance to questions concerning spontaneous or natural abilities (Henrich & Tennie, 2017).

Thus far only three studies have tested directly for true spontaneous action copying in relatively unenculturated and untrained apes. Across these studies, a total of 69 apes have been tested, exclusively in *Pan* species: Tomasello et al. (1997b; Chimpanzee; *n*=20); Tennie et al. (2012; Chimpanzee; *n*=3); and Clay & Tennie (2017; Bonobo; *n*=46). The results of these studies showed no evidence of spontaneous action copying, outside of the apes' existing behavioural repertoire.

All contrasting claims for spontaneous action copying in apes are either anecdotal (e.g., Russon & Galdikas, 1993), from enculturated subjects (e.g., Call, 2001; Tomasello, Savage-Rumbaugh, & Kruger, 1993) or derived from confounded methodologies (such as "two-target" tasks, see Tennie et al., 2012 for detailed discussion of the methodological issues surrounding these). These tasks allow for the possibility of learning mechanisms other than action copying, in particular results copying (emulation; Whiten, Horner, Litchfield, & Marshall-Pescini, 2004). Indeed, apes have demonstrated some ability to solve these kinds of tasks in the complete absence of action information through so-called ghost conditions (Hopper, Lambeth, Schapiro, & Whiten, 2008; but, see also Chapter 4). The results from confounded tasks can be dismissed when considering the question of true imitation, as it is not clear which social learning variants are driving the observed behaviours. Furthermore, results from enculturated or trained individuals are interesting for the question of *potential* in apes but are of little use when informing the variants underlying ape culture in its natural state.

Here, we used an unconfounded novel action copying task (previously used in bonobos; Clay & Tennie, 2018) with an addition of applying social learning biases. The introduction of these biases was intended to provide the apes with the highest likelihood to show (hitherto perhaps unelicited) action copying. Towards this goal, we utilised the power of various social learning biases which have been found to be present in apes (see Laland, 2004 for an overview). It was unclear which of the social learning biases would be most applicable to this task. Therefore, this study applied several social learning biases at once in order to maximise the likelihood that one or more such biases would elicit the elusive phenomenon of spontaneous action copying in apes. Furthermore, for the first time, we tested all four species of non-human ape in a single study.

Social learning biases have been argued to be the mechanisms by which species capable of socially learning, ‘attempt’ to avoid learning maladaptive behaviours or traits (Laland, 2004). That is, these ‘biases’ may select for behaviours that are likely to benefit the individual learner; such a mechanism would be responsible for avoiding the phenomenon of so-called ‘blind’ imitation/mimicry , which could be potentially costly for an individual (Tomasello, 1998a). Laland (2004) provided one of the most complete reviews of the social learning bias literature to date, he divides biases (which he refers to as strategies) into “when” and “who”; the former influencing at what point the learner will socially learn and the latter influencing which individual the learner will acquire information from.

Here, we utilised some of the social learning biases also used in previous action copying tests in *Pan* species (Clay & Tennie, 2018; Tennie et al., 2012; Tomasello et al., 1997). Observers may copy actions because the *goal* of an action is unclear, that is, the behaviour is opaque (Csibra & Gergely, 2009), relating directly to the social learning bias described by Laland (2004) of copy-when-uncertain. Specifically, in our study, the actions performed during the demonstrations appeared functional in opening our puzzle-box. However, owing to the design of the box these behaviours were unsuccessful in subjects, therefore were causally opaque to observers (to copy these would be known as over-imitation; e.g., Lyons, Young, & Keil, 2007). In addition, we also applied "copy when established behaviour is unproductive" (as the puzzle-box would not open), "copy when uncertain" (as the box was new to the apes), "copy successful individuals" (as demonstrators had reliable success with the demonstrated actions), "copy if better" (as the typical ape approach would fail), "copy if dissatisfied" (as the apes were motivated to get to the bait; see Laland, 2004 for a review of these social learning biases) . These were also applicable to the other tests of true action copying (Clay & Tennie, 2018; Tennie et al., 2012; Tomasello et al., 1997).

In addition to the social learning biases that applied to previous studies, our study added two previously unapplied social learning biases to test. The first was a 'sex-bias' (Coussi-Korbel & Fragaszy, 1995); across the two prior tests of true action copying in chimpanzees, both sexes were used as demonstrators (a male in Tennie et al., 2012; two females in Tomasello et al., 1997). However, our study is was the first of the true action copying studies in apes to include both sexes of demonstrators, within a single study. We used demonstrators of both sexes to preserve the majority influence in terms of sex. This meant, no matter the sex of the (single-tested) subject, the demonstrator's sex was *always* a majority, covering both potential 'sex-biases' (Laland, 2004) in a single study. All of our demonstrators identified as 'cisgender', meaning that their gender matched their sex at birth, thus excluding this potential confound.

The second bias we applied was 'copy the majority' (Laland, 2004). Ours is the first true action copying study in apes to use this bias. The majority bias can be subdivided into 'copy the demonstrator majority' and 'copy the behavioural majority' (Morgan, Acerbi, & van Leeuwen, 2019). 'Majority influence' can be considered an umbrella term for various social learning biases. The first of these is 'conformity, where a previously adopted behaviour is abandoned in favour of that displayed by the majority (Asch, 1956). A similar phenomenon is 'conformist transmission', where observers copy a majority of individuals if they do not have any preconceived behavioural solution at time of demonstration (Watson, Lambeth, Schapiro, & Whiten, 2018).

Evidence of conformity has been reported in various species, e.g., fruit flies (Danchin et al., 2018), sticklebacks (Pike & Laland, 2010) and great tits (Aplin et al., 2015). Of special importance here is that these claims extend to primates, namely vervet monkeys (E. van de Waal, Borgeaud, & Whiten, 2013), and especially chimpanzees (Luncz & Boesch, 2014; Luncz et al., 2012). Given the apparent prevalence of majority influence in the animal kingdom and its apparent effect on the social learning in so many species, we supposed that the introduction of this social learning bias might elicit novel action copying in apes. In the first stage of this study we focused on the conformist transmission element of majority influence; later conditions were planned to tease apart which aspect of majority influence facilitated action copying (but these did not occur as action copying was never identified).

Majority influence can be further divided into two forms: behavioural majority or demonstrator majority. The demonstrator majority is the number of demonstrators in relation to the number of observers. In order to produce this bias, we used a ratio of 4:1 (demonstrator: observer) during demonstrations, based on the findings of previous studies (Haun, Rekers, & Tomasello, 2014). All demonstrators remained present throughout the trial to attempt to present ‘normative pressure’ (Hoehl et al., 2019) in copying the demonstrated actions. Normative pressure is the social influence that a demonstrator can have on a learner through simply their continued presence; i.e., the pressure of something akin to expectation that might be felt by a learner, having just observed a demonstration, to copy said demonstration. We also applied the behavioural majority bias in terms of frequency of demonstrated actions (*sensu* Morgan, Acerbi, & van Leeuwen, 2019) by ensuring that the demonstrations were carried-out multiple times prior to subjects being given access to their box; meaning, the most common action was that which we demonstrated.

In the non-human literature, there is convincing evidence both from theoretical models (Kendal, Giraldeau, & Laland, 2009) and controlled tests in captive populations (Kendal et al., 2015) that social learning biases are not restricted to humans. We considered, by implementing several social learning biases at once and testing ape species not tested previously in true action copying studies, that action copying may be finally elicited spontaneously in apes. Such a finding would constitute the first recorded case of *spontaneous* novel action copying in apes. If several apes of a given species copied actions in our setup, this would provide strong evidence that their respective species' wild-type cultures may indeed be based on action copying. If most, or all, apes of one or all species failed to copy actions in our setup, this would indicate that their respective wild ape culture(s) is/are unlikely to be based on action copying.

5.2 Method

No major methodological deviations from our registered plan (Neadle, Chappell, Clay, & Tennie, 2018; Appendix B) were required. Our registered study was designed to follow a result-dependent design: the methods included a decision tree, such that the particular protocol implemented depended on whether or not evidence of action copying was identified (and when). No such evidence was found, therefore only the first of the preregistered conditions (i.e., "Conformist Transmission" at the top of Figure 5.1) needed to be implemented. All other conditions, as they would have been carried-out, are described in the registration.

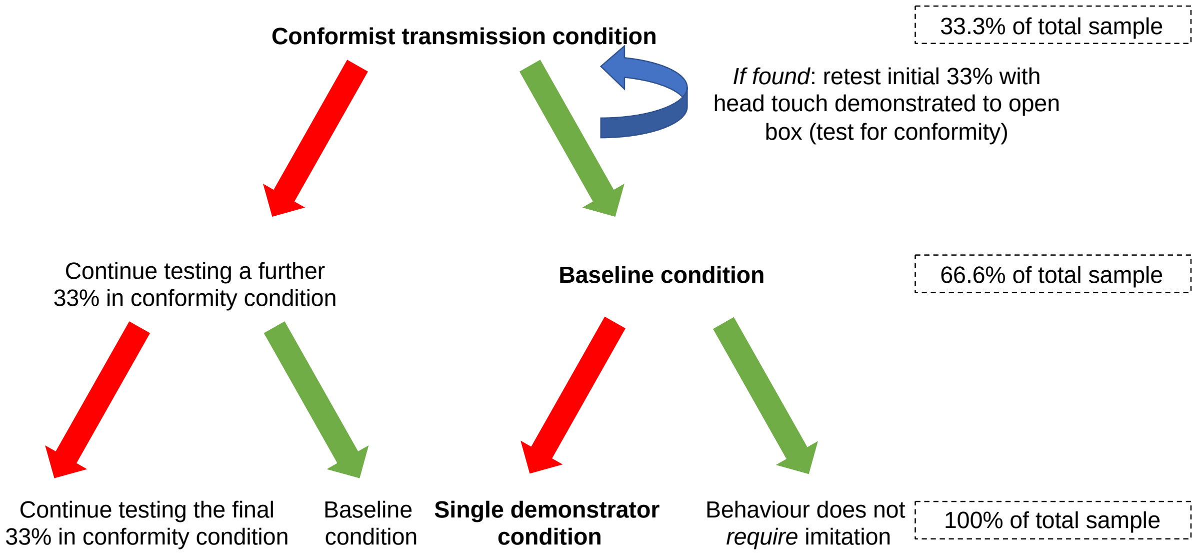


Figure 5.1. Taken from Registration. Green arrows represent successful display of the behaviour at that stage, and red arrows represent failure to display the behaviour. Note that at each stage the additional subjects are still naïve to the behaviour. The pathway through the decision tree that allows for each condition to be implemented is displayed in bold. See below for coding.

5.2.1 Design

As a part of the result-dependent design, the duration of trials was directly influenced by the performance of the subjects in the task. In our study, apes were exposed to demonstrators performing causally irrelevant actions before opening a ‘puzzle-box’. Demonstrators provisioned the subjects with the reward that was kept in the box. Subjects were provided with their version of the box (test box) which was designed to look identical to the demonstrator’s box, but in fact, could not be opened. Subjects were observed and recorded for a *maximum* of 5 minutes whilst they interacted with their box. If subjects relinquished contact with their box 30 seconds before three, four or five minutes had passed (depending on the stage of testing, see Figure 5.2) the trial ended once the next whole minute was reached.

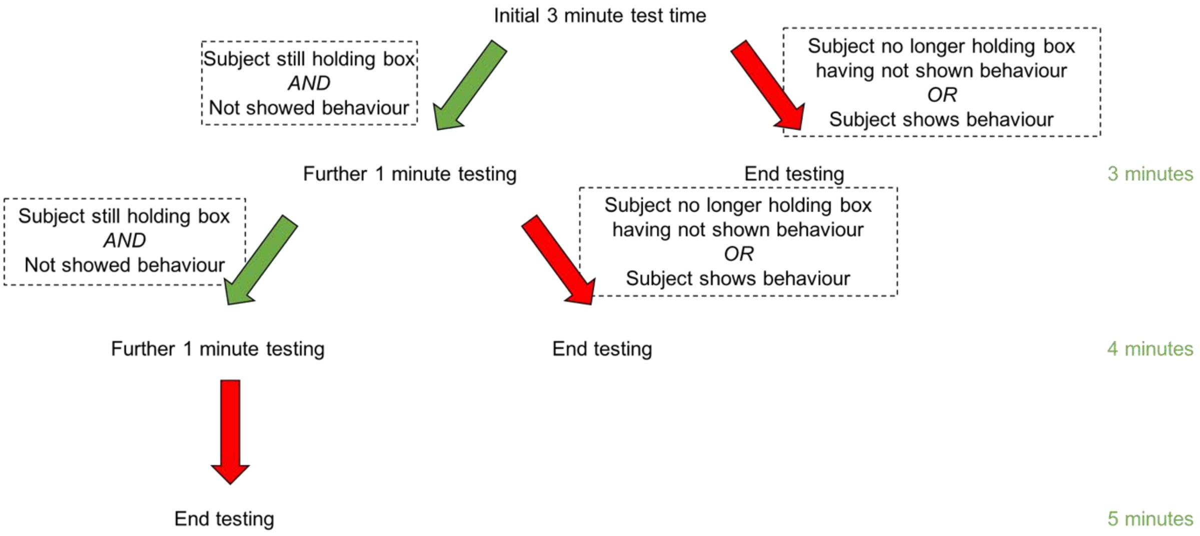


Figure 5.2. Taken from Registration. Decision tree for each stage of testing, green arrows relate to testing continuing, red arrows relate to testing ceasing.

Owing to the result-dependent design of this study participants would only have been subjected to the later conditions (see registration; Neadle et al., 2018) if evidence of action copying was identified (which did not happen). This decision was made to maximise sample sizes, whilst retaining even sample sizes across conditions.

5.2.2 Subjects

Subjects (N=33) were housed at the Wolfgang Köhler Primate Research Center (WKPRC), Leipzig, Germany (as part of the Max Plank Institute for Evolutionary Anthropology, also in Leipzig). All species at the WKPRC were tested between 11th June and 9th July 2018; ages correct at time of testing (see Table 5.1 for full details): bonobos (n=6; Male:Female - 2:4; M_{age}=19.83; SD_{age}=8.28), chimpanzees (*n*=19; 5:14; M_{age}=29.42;

SD_{age}=12.26), western lowland gorillas (*n*=2; 1:1; M_{age}=16.5; SD_{age}=3.54) and Sumatran orangutans (*Pongo abelii*; *n*=6; 2:4; M_{age}=23.16; SD_{age}=10.65).

Coupled with this large and varied sample, these populations were chosen as the apes had previously been reported as able to copy in the kind of emulation-confounded tasks (two-target tasks; Tennie, Greve, Gretscher, & Call, 2010), which are frequently claimed to show imitation skills. This allowed us to directly test for ‘pure’ action copying in a population that have previously been claimed to copy actions, through confounded tasks. Participation in our study was voluntary: animal doors were opened; the subjects were called by caretakers to enter and either they entered or not (and those who entered were released as soon as they showed signs of stress). One orangutan "Dokana" was deemed too unwell to participate in one trial, however, recovered sufficiently for the remaining two; another orangutan refused to enter the testing room in one of the trials. Owing to exhibiting signs of distress, the trials of two gorillas, “Kumili” and “Diara”, were terminated and as a result, no data could be collected on these two individuals. One bonobo, “Lexi”, gave birth during the study period. As a result, she was excluded from testing for a week following the birth and therefore was not present during one of her three trials. Also, one bonobo "Jasongo" was never tested as only one male could be tested within the time constraints of the study.

Table 5.1. Demographic details and rearing histories of the subjects in this study.

Name	Species	Sex	Date of birth	Place of birth	Breeding
Bambari	*Pan troglodytes hybrid*	F	08/12/2000	Ostrava, CZ	Parent
Corrie	*Pan troglodytes verus*	F	12/12/1976	Rijswijk, NL	Hand Reared
Dorien	*Pan troglodytes verus*	F	22/10/1980	Rijswijk, NL	Hand Reared
Fraukje	*Pan troglodytes verus*	F	06/04/1976	Rijswijk, NL	Hand Reared
Frodo	*Pan troglodytes verus*	M	28/11/1993	Rijswijk, NL	Parent
Kisha	*Pan troglodytes verus*	F	04/03/2004	Osnabrück, DE	Parent
Lobo	*Pan troglodytes verus*	M	21/04/2004	Leipzig, DE	Parent
Lome	*Pan troglodytes verus*	M	11/08/2001	Leipzig, DE	Parent
Natascha	*Pan troglodytes verus*	F	28/03/1980	Rijswijk, NL	Hand Reared
Riet	*Pan troglodytes hybrid*	F	11/11/1977	Rijswijk, NL	Hand Reared
Robert	*Pan troglodytes verus*	M	01/12/1975	Rijswijk, NL	Hand Reared
Sandra	*Pan troglodytes verus*	F	09/06/1993	Rijswijk, NL	Parent
Swela	*Pan troglodytes verus*	F	19/10/1995	Basel, CH	Parent
Tai	*Pan troglodytes hybrid*	F	12/08/2002	Leipzig, DE	Parent
Alex	*Pan troglodytes*	M	10/03/2001	Plaisance, FR	Hand Reared
Daza	*Pan troglodytes verus*	F	1986	Unknown	Unknown
Frederike	*Pan troglodytes hybrid*	F	1974	Unknown	Unknown
Hope	*Pan troglodytes hybrid*	F	14/12/1990	Jerusalem, IL	Parent
Jeudi	*Pan troglodytes hybrid*	F	1966	Unknown	Unknown
Gemena	*Pan paniscus*	F	07/11/2005	Twycross, GB	Parent
Joey	*Pan paniscus*	M	13/12/1982	Antwerp, BE	Hand Reared
Kuno	*Pan paniscus*	M	26/11/1996	Wilhelma, DE	Hand Reared
Lexi	*Pan paniscus*	F	13/09/1999	Jacksonville, FL	Hand Reared
Luiza	*Pan paniscus*	F	27/01/2005	Leipzig, DE	Parent
Yasa	*Pan paniscus*	F	27/08/1997	Twycross, GB	Parent
Bimbo	*Pongo abelii*	M	20/09/1980	Duisburg, DE	Hand Reared
Dokana	*Pongo abelii*	F	31/01/1989	Dresden, DE	Parent
Padana	*Pongo abelii*	F	18/11/1997	Leipzig, DE	Parent
Pini	*Pongo abelii*	F	30/06/1988	Leipzig, DE	Parent
Raja	*Pongo abelii*	F	26/09/2003	Leipzig, DE	Parent
Suaq	*Pongo abelii*	M	14/05/2009	Leipzig, DE	Parent
Abeeku	*Gorilla gorilla*	M	05/05/1999	Rotterdam, NL	Parent
Kibara	*Gorilla gorilla*	F	13/01/2004	Leipzig, DE	Parent

Three trials were attempted with each subject, though due to the voluntary nature of this study, sometimes fewer trials were attained as apes refused to participate or were excluded for medical/husbandry reasons. Subjects were called into the testing rooms as often as possible during the period of the study, however, certain subjects did not choose to participate in all three trials (see above). The data for these individuals were omitted from subsequent analyses. Multiple trials were carried out to allow subjects to recall knowledge of how to solve the task from previous demonstrations.

Subjects were tested individually in most cases; where possible, except for mothers with dependent offspring and any individuals that were uncomfortable being individually separated. Cases where individual separation was not possible were noted, had these apes shown evidence of action copying, the data set would have been analysed both with and without these cases (but, given the null results, no analysis of copying attempts was not necessary).

Individual separation ensured an effective demonstrator majority to maximise the effect of majority influence (in 25 subjects out of 33 this was achieved at least in one trial). An effective majority is 3:1 (Bond & Smith, 1996; Haun, Leeuwen, & Edelson, 2013), and here we used a 4:1 ratio to also include potential effects of demonstrator sex majority. When subjects were tested in dyads an overall ratio of 2:1 was the maximum that could be achieved.

5.2.3 Stimuli

Our study used a ‘puzzle-box’ that shared the same design as previously used in an action copying study with bonobos and human children (Figure 5.3). We used two variants of this box: the ‘demonstration’ box and the ‘test’ box.

Figure 5.3. Photographs of puzzle-box. Left panel contains demonstrator's box ('demonstration box'), opened to reveal hidden compartment, right panel contains subject's box ('test box'), showing the apparent divide between the two "halves" of the box, note that this box could not be opened as the divide was simply a line scored into the wood.

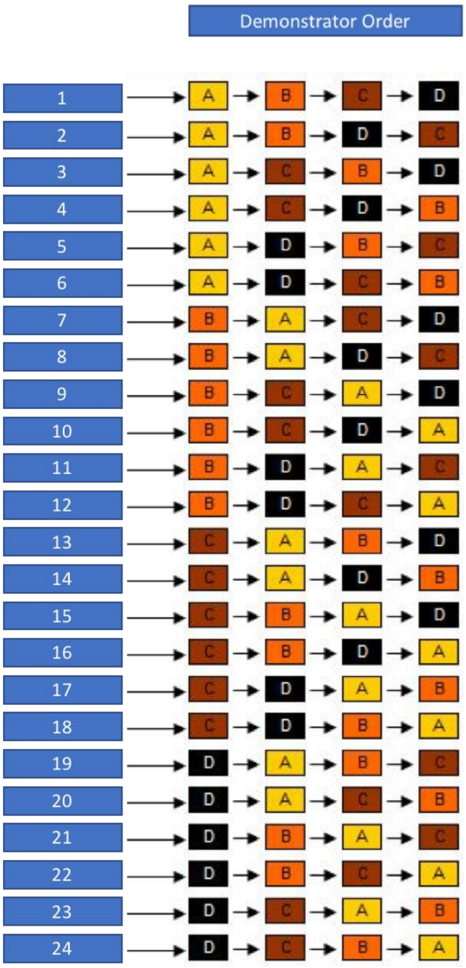
To remain consistent with the previous study, the 'demonstration box' was made from a piece of wood, cut in half, with a small depression cut into the centre of both halves (see Figure 5.3). This 'demonstration box' was only used by the demonstrators (humans) and was never provided to any of the subjects.

The 'test box', provided to the subjects, looked identical to the demonstration box but could *not* be opened, as it only featured horizontally scored lines in place of a true opening (see Figure 5.3). The logic behind the test box was that, as the subject would attempt, and fail, to open the box directly, by attempting to pull the two halves apart, they should then fall back on (copy) the observed actions, helped by the social learning biases we applied.

5.2.4 Demonstrations

Before testing, all human demonstrators were trained on the following procedure to ensure consistency across demonstrators; training lasted for approximately 1 hour. Before this training, each demonstrator was provided with a video of DN modelling the demonstration, meaning the demonstrator could watch the video as many times as possible to match the actions of DN. Demonstrators were required to copy both the form and speed of the actions, using DN's as a template, which was modelled after the demonstrated actions from Clay and Tennie (2018). ZC instructed and commented on the training videos before them being provided to demonstrators. DN and CT observed each demonstrator's performance in person before the start of testing, to confirm that their demonstrations were proficient. The demonstrator's production of actions was assessed continually throughout the study, had discrepancies occurred additional training would have been provided.

All demonstrators (N=2 male; N = 2 females) were human adults between the ages of 23 - 30, none of whom were zoo staff. To reduce possible order effects, subjects were randomly allocated to each possible iteration of demonstrator order (see Figure 5.4 and Section 5.2.4). The same demonstrators were used throughout the study, and demonstrators remained in the room with subjects throughout each trial to attempt to maintain the majority influence/normative pressure throughout the course of the trial (similar to Haun et al., 2014). Further details of the demonstrators are available in Appendix C.



	Demonstrator Order			
1	A	B	C	D
2	A	B	D	C
3	A	C	B	D
4	A	C	D	B
5	A	D	B	C
6	A	D	C	B
7	B	A	C	D
8	B	A	D	C
9	B	C	A	D
10	B	C	D	A
11	B	D	A	C
12	B	D	C	A
13	C	A	B	D
14	C	A	D	B
15	C	B	A	D
16	C	B	D	A
17	C	D	A	B
18	C	D	B	A
19	D	A	B	C
20	D	A	C	B
21	D	B	A	C
22	D	B	C	A
23	D	C	A	B
24	D	C	B	A

Figure 5.4. Table used to define the order of demonstrators before each trial, this was done using a random number generator app

5.2.4.1 ***Target actions to copy***

Similar to Clay & Tennie (2017), demonstrators performed two actions either on, or next to, the demonstration box (depending on the action). They did so whilst standing in the keeper/researcher side of the subjects' management area. Demonstrations were visible to the subjects through plexiglass and metal mesh. Both actions were preceded by demonstrators extending their arms forwards away from their bodies at a roughly 90° angle, whilst holding the demonstrator box, and performing the actions with their arms extended.

For the ‘Rub’ action, the demonstrator rubbed the back of the right hand in a consistent, but slow, circular, clockwise, motion across the top of the demonstrator box, in contact with the box, four times (1 second per rotation, 4 seconds total). For the ‘Rotate’ action, the demonstrator raised the right hand and rotated it, at the wrist, in a clockwise motion – not in contact with the demonstrator box, four times (1 second per rotation, 4 seconds total). The demonstrator then opened the demonstrator box, showed the contents of the box (a grape) to the subject and gave the grape to the subject[2].

5.2.5 Procedure

Demonstrators stood in a line, facing the enclosure, out of reach of the subjects (see Figure 5.5). Once all demonstrators moved into the testing room and cameras were turned on, the demonstration phase of the trial began. Movement of demonstrators before trials represents a minor deviation from the registration, as, in the methods registered, they were due to be present in the testing room before the subject entering. However, during the first trials, it became evident that keepers would sometimes need to be undisturbed when calling subjects into the testing room, therefore, in the interest of standardisation this procedure was implemented throughout the study; even when not required.

Subjects had the opportunity to observe at least eight full demonstrations of the actions: one per demonstrator (one by one), followed by a simultaneous additional demonstration by each of the four demonstrators. Each subject was given up to five

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[2] Video demonstration available at http://tiny.cc/k996bz

demonstrations of the Rub-Rotate action by each demonstrator and the test box was rebaited after each. If the subject did not see at least one iteration of each action (i.e., Rub or Rotate) during any demonstration, up to four repeats were given until the subject had either seen both Rub and Rotate or five attempts were given by that demonstrator. As a result, as many as 20 repeats could have occurred for a subject that never attended to the demonstrations (i.e., an initial four and 16 repeat demonstrations).

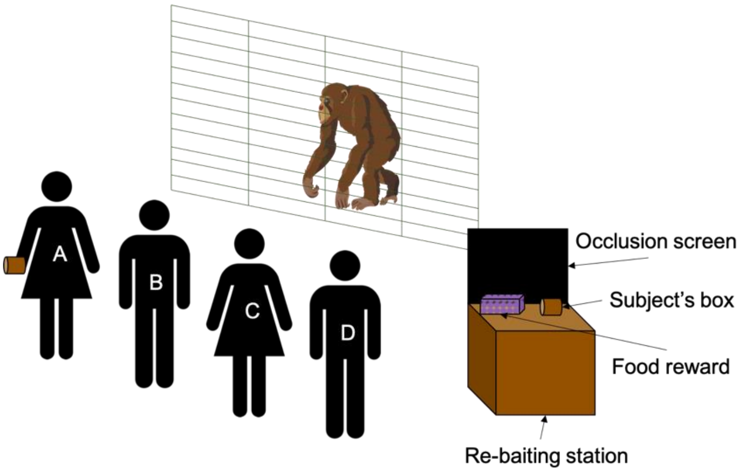


Figure 5.5. Pictorial representation of experimental set up, subjects were unable to observe demonstrators using the re-baiting station due to the occlusion screen, the subject's test box was retrieved from behind the occlusion screen as though the demonstration box was being rebaited again. Chimpanzee image by Jose R. Cabello from Pixabay and is permitted for use under the "Pixabay licence" agreement.

Demonstrators performed the actions individually following a predefined, randomly selected, order (see Figure 5.4). A random number between 1 and 24 was generated before each trial, these numbers related to the pre-defined demonstrator order in Figure 5.4 and dictated demonstration order (i.e., the order of A, B, C and D in Figure 5.5).

Once each demonstrator had individually demonstrated the actions, and these had been sufficiently witnessed by the subject, all four demonstrators additionally performed a simultaneous group demonstration of both actions.

Several measures were put in place to ensure that subjects witnessed the demonstrations and that the demonstrators could confirm that the subject had seen the demonstration. First, demonstrators faced subjects throughout. Second, each demonstrator wore a GoPro Hero Session 5 camera, mounted to their chest. This was used to allow us to later verify that the subject was attending to the demonstrator before performing the actions. We defined attending as having looked at the box or demonstrator for one second or more. Third, all demonstrators were permitted to call the subject's name to gain their attention as often as required before and throughout the demonstration. Once the subject was attending (defined as head oriented towards the demonstrator), a demonstration began.

After observing the subject during the demonstration, all demonstrators reported out loud (yes/no for each action, in demonstrator order) whether the subject observed *none, part of* or the *whole* demonstration. Thus, a subject having seen only one action would be called yes/no or no/yes, both would be yes/yes and none no/no. If less than three of the demonstrators replied with a yes to either of the actions the respective demonstrator repeated their demonstration (up to a maximum of five times; see above). The next demonstrator followed the same procedure, and so on until the subject clearly had observed the full demonstration of both actions *at least* four times (across all demonstrators). The number of repeat trials required to attain agreement was recorded after the study was completed, by reviewing the video footage. It became apparent, upon viewing video footage, that it was difficult to reliably code the percentage of the demonstrations observed, as subjects were regularly out of line-of-sight of the camera. A more attentive subject, i.e., one that observed the demonstrations, in full, the first time would have required fewer repeats. Thus, the number of repeat trials needed before an agreement was reached was used as a proxy for attention, where higher numbers of repeat trials indicate less attentiveness to the demonstrations.

Each subject was then tested. The final demonstrator then took the demo box behind the occlusion screen and swapped it for the test box whilst behind the screen. The subject was given the test box by the demonstrator, who placed it into a ‘food chute’ that allowed items to be passed between researchers and apes without physical contact. Once the subject was allowed access to the box, they had a maximum of five minutes to copy the actions demonstrated (Figure 5.2). All trials were video-recorded using two cameras (Panasonic HC-V777) mounted on tripods at either end of the line of demonstrators, in addition to the demonstrator-mounted GoPro cameras.

5.2.6 Behavioural Coding & Analysis

Behaviours were live coded and to ensure reliability, after each trial, each demonstrator independently wrote down whether they considered any of the subject’s actions during the trial to constitute action copying (i.e., whether these actions, in their opinion, were similar to the demonstrated action; see Table 5.2). The paper on which the live coders independently wrote their decision was then folded in half and placed into a container. These verdicts were counted by DN, after the trial. A positive case of copying would have been recorded if more than half (i.e., 3 or 4) of the demonstrators had considered that the subject had copied at least one of the demonstrated actions. Demonstrators were instructed to note any approximation at action copying (see Table 5.2 and Neadle et al., 2018). For example, even a subject copying the Rub action with the left hand and for a half rotation and without attempting a Rotate action would be considered as having copied the Rub action for the result dependent design (see Figure 5.1). These approximations would have been further analysed *post hoc*.

Table 5.2. Description of behaviours as provided to demonstrators several days before the first trial, after demonstrators had received training on the actions from DN. These instructions were later reiterated, immediately before the first testing session.

Behaviour	Description
Rub	The subject places the back of their hand (either hand), on top of (or close above) the box and rubs it in a circular motion (regardless of direction).
Rotate	The subject raises their hand (either hand) and rotates it – for a minimum of 180˚ at the wrist (regardless of direction).
Rub-Rotate	The subjects performs the "Rub" behaviour, and this is followed by the "Rotate" behaviour
Rotate-Rub	The subjects performs the "Rotate" behaviour, and this is followed by the "Rub" behaviour
No relevant behaviour	The subject performs none of the actions described here

Furthermore, we analysed the attention paid to demonstrations**.** To do so, we used the number of demonstrations required as a proxy for attention to the demonstrations, where a higher number of repeats indicates a less attentive subject. We used a one-way ANOVA to compare differences in attention across species and rearing history, and a Mann Whitney Wilcoxon (also termed Mann Whitney-U) test was used to compare sex.

Using video analysis, we calculated the mean time an individual spent interacting with the test box, which we used as a proxy for motivation to engage with the test box. As each subject had either a three, four or five-minute trial (see Figure 5.2); the total number of seconds that the subject was in contact with the test box was divided by the total trial time (in seconds), resulting in a percentage of "motivation". The data were bounded, due to them being percentages, between 0% and 100% so a logarithmic transformation was used to make the data appropriate for use using a GLM. We used Welch's correction for a one-way ANOVA for data which failed to meet the assumption of homogeneity of variance (Moder, 2007, 2010) to compare motivation across species and rearing history. A Mann Whitney Wilcoxon test was again used to compare differences in motivation across sexes.

All analyses and data-based figures were produced in R (version 3.4.3; R Core Team, 2013) and R-Studio (version 1.1.423; RStudio Team, 2016). During the analyses/visual representation of the results the following packages were utilised: ggplot2 (version 3.1.0), ggpubr (version 0.2.0), psych (version 1.8.10), car (version 3.0-2), cowplot (version 0.9.3), multicomp (version 1.4-8), ggsignif (version 0.4.0), pastecs (version 1.3.21) Additional analyses (see Neadle et al., 2018 registration) were not performed given the null findings (again, our method, including our analysis, was preregistered and designed to be result-dependent). Data were transformed for analyses and then un-transformed for graphical representation.

5.2.6.1 ***Interrater reliability***

Interrater reliability for subjects' attentiveness to the demonstration was assessed during trials. In the case that even a single potential instance of action copying was identified during live coding, a naïve second coder would have been required for *post hoc* coding from a naïve coder. However, as no cases of action copying were observed, a second coder was not required. There were always four independent witnesses to any given event. As a result, a four-way instantaneous interrater reliability was possible, using the paper on which demonstrators recorded any observed behaviours.

Demonstrators did not communicate during the trials and, immediately after the trial, completed a coding sheet determining whether or not a behaviour from the predefined ethogram had occurred. As there were no cases in which one of the demonstrators suggested that any action had been approximated at by any of the tested apes, there was no need for further interrater reliability checks, and so none were performed.

5.2.7 Ethics

Per ethical recommendations, all subjects were housed in semi-natural indoor and outdoor enclosures containing climbing structures, such as ropes and platforms; and natural features, such as vegetation, trees and streams. They received their regularly scheduled feedings, primarily consisting of vegetables, had access to enrichment devices including shaking boxes and poking bins, and water *ad-lib*. Subjects were never food or water-deprived for this study. All research was conducted in the subjects sleeping rooms.

The study was ethically approved by an internal committee of the Max Planck Institute for Evolutionary Anthropology (director, research coordinator), the Leipzig zoo (head keeper, curator, vet) and the University of Birmingham AWERB committee (reference no. UOB 31213). No medical, toxicological or neurobiological research of any kind is conducted at the WKPRC. The research was non-invasive and strictly adhered to the legal requirements of Germany. Animal husbandry and research comply with the "EAZA Minimum Standards for the Accommodation and Care of Animals in Zoos and Aquaria", the "WAZA Ethical Guidelines for the Conduct of Research on Animals by Zoos and Aquariums" and the "Guidelines for the Treatment of Animals in Behavioral Research and Teaching" of the Association for the Study of Animal Behavior (ASAB). Institutional Animal Care and Use Committee approval was not necessary to conduct this research.

5.3 Results

We did not find any evidence of action copying or any approximations of action copying in any of the apes tested in this study (total N= 33). This finding is reliable, as it was confirmed using our four-way independent live coding system (see above). This result held even for hand-reared individuals.

An analysis of the attention paid to demonstrations revealed a substantial degree of variation between subjects; with a range = 0 – 14 repeats. An average of 4 repeat demonstrations were required across all subjects, 20% of the possible repeats, indicating good attention. There were no significant species differences in number of demonstrations required ($M_{bonobo} = 6.56$, $SD_{bonobo} = 4.59$, $M_{chimpanzee} = 5.06$, $SD_{chimpanzee} = 3.44$, $M_{gorilla} = 3.17$, $SD_{gorilla} = 3.06$, $M_{orangutan} = 3.38$, $SD_{orangutan} = 4.30$; F(1, 92) = 1.20, p =.28); each species contained individual(s) that required no repeat demonstrations for at least one of their trials ($N_{bonobo} = 2$, $N_{chimpanzee} = 4$, $N_{gorilla} = 1$, $N_{orangutan} = 3$). There were also no significant differences in attentiveness as a function of rearing history ($M_{hand} = 5.27$, $SD_{hand} = 3.82$, $M_{parent} = 4.60$, $SD_{parent} = 4.04$, $M_{unknown} = 5.89$, $SD_{unknown} = 3.41$; F(2, 91) = 0.58, p =.57) or sex ($M_{male} = 5.63$, $SD_{male} = 3.68$, $M_{female} = 4.66$, $SD_{female} = 3.98$; W = 756.5, p =.22); see Figure 5.6.

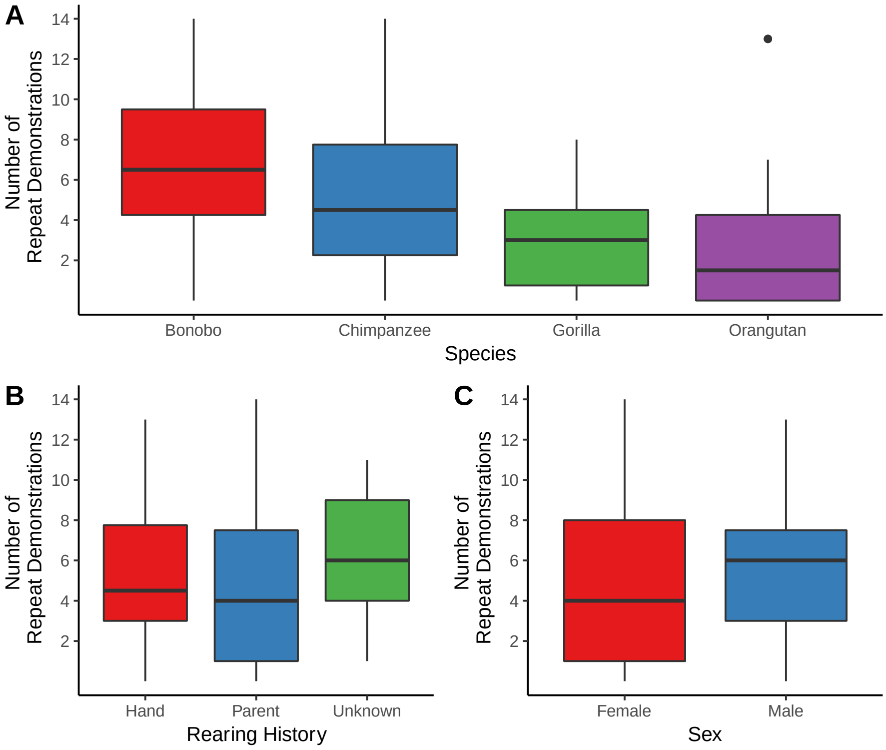


Figure 5.6. Box plots depicting the data used in the attention paid to demonstrators' analyses. Number of repeat demonstrations required as a function of A) Species B) Rearing History C) Sex. Central bar represents median value, upper and lower hinges correspond to 75th and 25th percentiles, upper and lower whiskers extend to largest or smallest value (no further than 1.5 times the Inter Quartile Range (IQR) from the hinge, data beyond 1.5 times IQR are displayed as ● and plotted individually.

Subjects varied substantially in their motivation, with a range = 0 – 100%, i.e. in some trials subjects never retrieved the box and in other trials they maintained contact with the box until the trial was ended by the experimenters. Across all species, subjects spent 40% of trials interacting with the box. Species differed in the time spent interacting with the test box ($F(3, 16.64) = 9.36$, $p<.001$, $\Omega^2 = 0.25$). Gorillas (M=2.37, SD=0.86) and chimpanzees (M=3.32, SD=0.95) showed the lowest mean interaction followed by orangutans (M=4.01, SD=0.58) and bonobos (M=4.19, SD=0.67) see Figure 5.7. In addition, each species, with the exception of gorillas, had individual(s) that maintained contact with the box until the trial was ended by experimenters, for at least one of their trials ($N_{bonobo} = 6$, $N_{chimpanzee} = 8$, $N_{orangutan} = 6$). The analyses showed no significant variation in the percentage of interaction time between subjects of different rearing histories ($M_{hand} = 3.68$, $SD_{hand} = 1.25$, $M_{parent} = 3.57$, $SD_{parent} = 0.85$, $M_{unknown} = 3.46$, $SD_{unknown} = 0.99$; F(2, 12.02) = 0.09, p =.91) or sexes ($M_{male} = 3.86$, $SD_{male} = 0.88$, $M_{female} = 3.47$, $SD_{female} = 0.97$; W=442.5, p =.07).

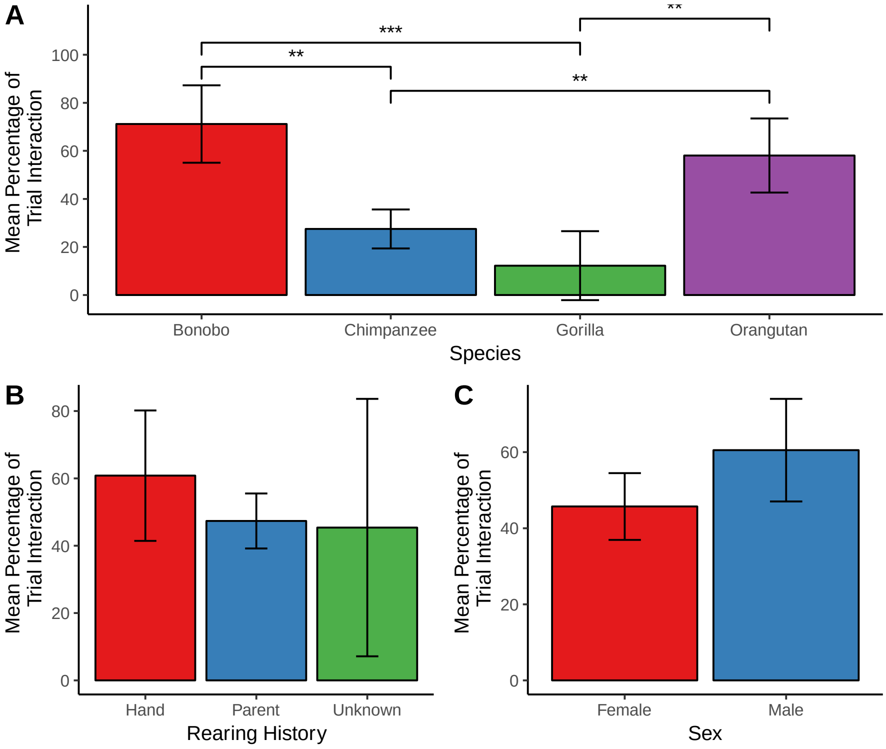


Figure 5.7. Bar charts depicting the data used in the percentage of trial interaction ("motivation to engage") analyses outlined above, these data are untransformed. Percentage of trial interaction as a function of A) Species B) Rearing History C) Sex. Error bars indicate ± 1 SE of the mean. Note, "" indicates p<.05, "**" indicates p<.01 and "***" indicates p<.001.*

5.4 Discussion

This chapter has presented the results of, to the best of our knowledge, the most comprehensive study of spontaneous ape copying to date. Despite testing four species of apes and applying a wide variety of social learning biases, in particular majority influence and sex-bias, all designed to increase the motivation for action copying, none of the 33 tested apes copied any of the novel actions. The observed absence of action copying was unlikely due to a lack of attentiveness or motivation, as demonstrated by the results of the attention and motivation checks. Our conclusion, based on the evidence to date, is that unenculturated apes do not spontaneously copy novel actions.

Not only was ours the most comprehensive study ever performed to test for spontaneous action copying in apes (testing four species), but to our knowledge, ours is also the first ape action copying study that enlisted a majority influence bias (see van Leeuwen, Kendal, Tennie, & Haun, 2015 *and* Watson et al., 2018 for discussion of terminology) whilst also enlisting both demonstrator based sex-biases in a single study. As only the first condition in our result dependent design was completed, as per our registration, we only tested the conformist transmission aspect of majority influence.

Despite an apparent motivation to interact with the puzzle-box, no ape spontaneously copied any of the demonstrated actions. Due to the new, and fuller array of social learning biases that were enlisted in our test (Section 5.1) it is unlikely that we missed the elusive ‘key’ social learning bias which would finally ‘unlock’ spontaneous action copying in apes. However, as in any negative result, the theoretical possibility remains that certain biases or other variables we did not include could have produced positive findings.

The results presented here strongly suggest that two-target tasks do not test for action copying but rather emulative copying. Some of the apes tested in this study have previously been shown to copy in two-target tasks (Tennie, Greve, et al., 2010); however, when the possibility for emulative learning is removed, and only pure action copying leads to success, all unenculturated apes tested to date fail to copy novel actions. Here, we support and extend the findings of the three previous pure action copying studies which also found that unenculturated apes do not spontaneously copy such actions (Clay & Tennie, 2018; Tennie et al., 2012; Tomasello et al., 1997). For the first time, results of true action copying, in unenculturated individuals, can extend outside of the *Pan* genus. Meanwhile, we have shown that previous, negative, results of ape action copying were not due to a lack of testing/demonstrator majority or sex-based social learning biases.

It may be argued that these null results were due to using human instead of conspecific demonstrators. However, while human demonstrations may be argued to be less effective overall than conspecific demonstrations (Hopper, Lambeth, Schapiro, & Whiten, 2015), the overwhelming pattern in previous studies is that human demonstrators are attended to and that this translates into social learning (Horner & Whiten, 2005; Whiten, 1998). The difference here is therefore simply that the demonstrations were of a type that apes simply cannot or do not spontaneously copy. Furthermore, our results are consistent with other tests of true action copying even when conspecific demonstrators were used (Tennie et al., 2012; Tomasello et al., 1997). Therefore, human demonstrators can be considered a time-effective and valid way to test claims for social learning abilities in apes. Our entirely negative results, in all four species of apes (N=33), are therefore very unlikely to be the result of using human, rather than ape demonstrators, but instead, show a lack of spontaneous action copying in apes.

The demonstrated actions here were novel, i.e., not in the usual behavioural repertoire of any of the tested ape species (Clay & Tennie, 2018). Any species capable of action-based cumulative culture that goes beyond the reach of the individual (Boyd & Richerson, 1996;

Reindl et al., 2016; Tomasello, 1999a) must be able to copy such actions. Indeed, humans have been shown to copy novel actions in similar conditions (Clay, Over, & Tennie, 2018; Clay & Tennie, 2018). It could be argued that the actions we used were too abstract or artificial for apes. Even if this claim were accurate it would further substantiate a difference between human and animal action copying and resultant cultures (Tomasello, Kruger, et al., 1993); humans can and do learn from seemingly arbitrary actions.

However, research has shown that, when unsure of the causality of an action, apes will copy arbitrary behaviours (Horner & Whiten, 2005); however, Horner and Whiten lacked the necessary controls to ensure that only imitation could be applied. This said, it is important to consider, when apes understand which aspects of a behaviour are irrelevant they do not to copy these steps (Horner & Whiten, 2005). Our results should be caveated by the fact that it is possible that out subjects understood that the demonstrated actions had no causal utility and therefore failed to copy them. This represents an important limitation of using an over-imitation paradigm to test for imitation alone.

Overall, it can be concluded that unenculturated, and by extension wild, apes are unlikely to copy actions. In turn, the idea that wild ape cultures are based on action copying should be reconsidered. Indeed, the results of this study are not at odds with what we currently know about wild ape behaviour. In wild populations, there is no evidence that any part of the ape behavioural repertoires requires action copying for social or technical reasons. This claim is affirmed by captive data that documents the spontaneous reappearance of several of these behavioural forms in naïve individuals through LS tests (e.g., Bandini &

Tennie, 2017; Byrne et al., 2017; Motes-Rodrigo et al., 2019; Neadle et al., 2017; Tennie, Hedwig, Call, & Tomasello, 2008; Sections 2 and 3).

Based on the data presented here, the hypothesis that wild ape culture is dependent on action copying (e.g., Horner et al., 2006; Whiten et al., 1996, 1999) should be reconsidered; along with the notion that the last common ancestor of apes and humans copied actions. Given this, it is an open question when (and also why) action copying evolved in our lineage (e.g., Tennie et al., 2017).

CHAPTER 6: OBJECT MANIPULATION IN BONOBOS: A CASE FOR THE IMPORTANCE OF ECOLOGY IN EXPLAINING BEHAVIOURAL PHENOTYPE

This chapter is currently in preparation for submission to Scientific Reports. This chapter is co-authored with Dr Zanna Clay as senior author, Samin Gokcekus as the middle author and Damien Neadle as the first author. The contribution statement, as it stands at the time of submission, is as follows:

Conceptualization: DN, ZC
Data Collection: ZC
Investigation: DN
Methodology: DN, ZC
Formal analysis: DN
Project administration: DN
Resources: ZC
Supervision: ZC
Writing – original draft: DN
Writing – review & editing: DN, ZC, SG

This study was designed to utilise some hitherto unused video data that ZC collected whilst in the Democratic Republic of Congo at Lola ya Bonobo sanctuary. This data was initially collected to analyse aggression and reconciliation at the sanctuary. The design of this study was entirely novel and was a collaborative effort between DN and ZC. SG was an undergraduate student in ZC's lab at the time of the study taking place, she acted as a secondary coder on this dataset and participated in one round of edits of a prior version of this chapter. In its current form, this chapter contains very little of the edits from SG. AS, another student in the lab, also acted as a secondary coder, however, chose to not participate in any further engagement with this research.

6.1 Introduction

Bonobos have been described as ‘particularly poor’ in terms of tool use (Gruber et al., 2010), it has also been suggested that bonobos might be intrinsically less motivated to manipulate objects than chimpanzees (Koops et al., 2015). In spite of these suggested differences, captive studies reliably report that captive bonobos are competent tool users (Gruber et al., 2010 citing Gold, 2002; Jordan, 1982; Toth, Schick, Savage-Rumbaugh, Sevcik, & Rumbaugh, 1993). It is yet unclear as to the exact factors influencing this disparity between wild and captive conspecifics.

The obvious differences between captive and wild subjects are their environmental surroundings, social settings and their possible degree of enculturation (Tomasello, Kruger, et al., 1993). Some or all of these factors, in combination, lead to what has been described as a “captivity effect” (Forss, Schuppli, Haiden, Zweifel, & van Schaik, 2015). This captivity effect describes the contrast in the behaviours of wild and captive apes highlighting possible effects of reduced neophobia, increased neophilia, and less predation/selection pressures and risk in captivity (Forss et al., 2015). This effect is supported by findings in orangutans, which show that exploration times between captive and wild subjects are largely equal once wild subjects overcome their neophobia. Encounters with novel objects in captivity are almost exclusively positive and novel objects are usually “food or playthings” (Forss et al., 2015, p. 10), thus reducing perceptions of risk, this is potentially not so in wild conspecifics. Furthermore, the opportunity to observe human models interacting with anthropomorphic artefacts may increase levels of exploration and object manipulation in captivity (van Schaik et al., 2016).

The captivity effect suggests that ‘intrinsic motivation’ may not be the sole determinant in the observed differences in *Pan* and indeed, given the disparity between wild and captive bonobo tool use, might explain the within species differences. Captive and wild chimpanzees show a similar pattern of behavioural acquisition of the most complex wild chimpanzee tool use behaviours (nut cracking). Some captive chimpanzees, as with some wild chimpanzees, fail to acquire the nut-cracking behaviour, in spite of repeated demonstrations (see Chapter 4). It is plausible to assume, that chimpanzees are already at the upper end of the non-human great ape ‘complexity scale’, meaning the captivity effect can do little to further bolster their repertoire. Therefore in the ‘naturally’ less tool proficient species (bonobos, gorillas and orangutans; Damerius, Graber, Willems, & Schaik, 2017) the captivity effect is more noticeable (Boysen, Kuhlmeier, Halliday, & Halliday, 1999; Forss et al., 2015; Gruber et al., 2010) than in chimpanzees. This is not to say that full-scale human interference, i.e., enculturation or training, cannot push these individuals beyond their ZLS (Tennie, 2019a).

Whilst it is most likely that the captivity effect is responsible for differences in the behavioural phenotypes of captive and wild bonobos, it is yet to be determined which factors directly influence the degree to which *captive* bonobos manipulate objects. If chimpanzees *are* restricted by their ZLS (a sort of ceiling effect) bonobos susceptibility to the captivity effect could be due to variations in the environment. Therefore, it remains a possibility that in the “right” conditions (*sensu* Tennie et al., 2009) bonobos will express their full potential repertoire.

In one of the most recent and in-depth studies of bonobo tool use, Koops et al. (2015) question whether bonobos might have “lost” their capacity for tool use, this seems unlikely based on the captive data discussed already. However, it remains possible that on a phylogenetic level bonobos remain naturally less motivated to engage with tools and that this is overcome over time, as the social learning biases begin to influence the behavioural phenotype. If this were true, it could be attributed to social learning of object manipulation tendencies within groups, perhaps facilitated by social learning biases, e.g., majority influence (see Chapter 5 for discussion of this phenomenon ; see also Luncz et al., 2012 for evidence of this phenomenon in wild subjects). In this case, we would expect those individuals exposed to the influence of conspecific object manipulation for longer to be more likely to engage in such behaviours; thus, the older the individual the more tool use one would predict.

Equally, should the idea of a social model overcoming the claimed genetic predisposition against object manipulation be accurate, we would expect those subjects raised by their mothers to be more prolific object manipulators. This is because apes have been claimed to undergo an intensive period of social learning during formative years with a primary social model being the mother (with some even claiming this to be that of a mater/apprentice relationship; Matsuzawa et al., 2008), which would go on to shape the resulting behavioural phenotype. However, it could be argued that, those individuals reared by humans, carers might have served as effective social models (*sensu* Ross et al., 2010) to the extent that they would simulate the mother and might even reduce the learner’s inhibitions in a way reminiscent of the captivity effect (*sensu* van Schaik et al., 2016). Thus, we supposed some level of difference between orphaned and mother reared subjects, but the direction of this difference is unclear.

The study that follows is a largely exploratory one, which aimed to uncover potential differences between subjects within an object-rich environment. Prior research has assessed the rates of manipulation in wild subjects and has resulted in bonobos being considered intrinsically less motivated than their sister species, chimpanzees. However, given the captive data to date, it appears bonobos are, in fact, highly capable motivators in the 'right' environment. This study aims to clarify the effect that individual differences in bonobo development and rearing might have on their resulting behavioural phenotype. Additionally, to compare these data with that collected in a wild population (Koops et al., 2015) in an attempt to further demonstrate the importance of environmental considerations in future theoretical studies.

6.2 Methods

6.2.1 Study site and subjects

All data used in this study were collected from Lola ya Bonobo Sanctuary in Kinshasa, Democratic Republic of Congo between June and September 2016. The sanctuary at Lola ya Bonobo is 30ha in size and consists of three separate enclosures (1: 10ha, 2: 15ha, 3: 5ha), surrounded by fencing. Each enclosure contains an indoor sleeping area where subjects sleep in voluntary subgroups in an attempt to replicate the natural fission-fusion system of wild conspecifics (Gruber & Clay, 2016). In the outdoor areas of the enclosure, there is a combination of forest, open grassland and swamp; each enclosure also contains a freshwater source (lake, stream or pool) where individuals can drink *ad libitum* (keepers provide additional water, juice or tea). Subjects are fed regularly throughout the day with vegetables, fruits, plant protein sources and eggs.

The total population at Lola ya Bonobo at the time of the study was 65 individuals (24 adults, 20 adolescents, 15 juveniles and 6 infants; see Table 6.1) these individuals are split between three groups; here only data for juveniles and infants across the three groups were considered, resulting in a total possible sample size of 21 individuals. Due to sampling restrictions, data was not collected from three individuals (BM, GR & SI), resulting in a sample of 18 individuals (M age = 4.00; SD = 2.47; $n_{\text{male}} = 4$; $n_{\text{female}} = 14$, $n_{\text{orphan}} = 4$). Age groups were classified based on a system described by Hashimoto (1997), this system is more fine-grained, rather than simply classifying individuals as an infant or juvenile (e.g., Badrian & Badrian, 1984) age groups are subdivided into four total groups. Importantly, this system has an advantage, in terms of our data, because it distinguishes between young infants (<2) and older infants (2-4). Prior to the age of 2 years old infant bonobos generally stay very close to their mothers and are often in contact with them (with their hands and feet; de Lathouwers & van Elsacker, 2006), as a result the ability of these infants to manipulate objects as readily as other immature individuals is drastically impaired. Importantly, for later analyses, at Lola ya Bonobo at the time of testing, *all* orphaned individuals came under the category of Juvenile-II.

Table 6.1. Individuals at Lola ya Bonobo, during the study period, that were within the sample parameters of this study.

ID	Group	Age (y)	Age Group	Sex	Rearing
KIT	1	<1	Infant-I	F	Mother
JUU	1	1	Infant-I	M	Mother
KM	1	7	Juvenile-II	F	Mother
LY	1	6	Juvenile-II	F	Mother
KI	1	6	Juvenile-II	F	Orphan
NJ	1	6	Juvenile-II	F	Orphan
NDO	2	<1	Infant-I	F	Mother
MVL	2	2	Infant-II	F	Mother
MOS	2	4	Juvenile-I	F	Mother
NYO	2	5	Juvenile-I	F	Mother
MG	2	6	Juvenile-II	F	Orphan
MAY	2	6	Juvenile-II	M	Mother
MV	2	<7	Juvenile-II	F	Orphan
MOL	3	<1	Infant-I	F	Mother
MIN	3	2	Infant-II	M	Mother
ELO	3	4	Juvenile-I	F	Mother
BOL	3	5	Juvenile-I	M	Mother
SZ	3	6	Juvenile-II	F	Mother

6.2.2 Data

6.2.2.1 *Data collection*

Data were collected using animal focal sampling (Altmann, 1974), where single individuals were recorded for 10 minutes at a time. These video recordings were collected by ZC and a field assistant (SK), throughout the daylight hours using high definition cameras

(Panasonic HC-V77) mounted on tripods. Videos were collected from outside the enclosures and the researchers would move alongside the exterior fence to ensure that the focal individual remained in the frame. During the recordings, the researcher would commentate on the other individuals within one and five meters of the focal individual at six time points (start, two, four, six, eight and ten minutes). The activity and proximity scan data were recorded by the primary coder.

6.2.2.2 ***Coding***

6.2.2.2.1 Full data set

The coding was divided between three coders (DN=86; SG=55; AS=55), each coder was provided with a copy of the ethogram (see Table 6.2) before coding beginning. After training, each coder completed a reliability test to ensure that the coding was consistent between individuals. Coders were provided with a total of 200 clips, 50% (*n*=100) of the clips contained randomly selected behaviours described in the ethogram (see Table 6.2), the other 50% were "dummy" clips, as per previous chapters. Provided this reliability test reached an acceptable level ($\kappa \geq 0.6$; Cohen, 1988), each coder then independently coded their proportion of the data.

Table 6.2. Ethogram used when coding object manipulation types in BORIS. Note, only object manipulations were coded, an ethogram with additional notes, as provided to coders is available in Appendix C

Behaviour	Definition
Play	Manipulating object with no apparent immediate goal, including repetitive movements, alone or together with other individuals (alone/social), may be associated with a play face.
Tool-use	Manipulating a detached (?) object as a means to achieve an end (e.g. nut crack, branch drag, drink).
Bite	Biting or chewing object without ingestion.
Break	Breaking (off) a substrate; this includes pulling grass up.
Carry	Carrying object in hands, feet or mouth.
Drag	Pulling object along the ground with hands
Throw	Throwing object or intentionally dropping object from an elevated position.
Support	Using an object to partially support the weight of the subject, i.e., holding onto a root when sitting on a steep hill.
Day nest building	Creating a nest out of sticks and leaves (tree or ground). During this process, the subject may break or bite several sticks and put them over their head or wrap them around the body.

Table 6.3. Ethogram used when coding object types in BORIS

Object Type	Description
Leaf	Non-woody vegetation
Stick	Woody vegetation or branches, with or without leaves attached
Stone	A stone, pebble or rock
Food	Fruits or vegetables provided to the subjects by caregivers
Fruit-shell	Shells of foods provided by caregivers – this can include nut shells or fruit shells (i.e., passionfruit outer).
Man-made	Any non-natural item within the enclosure
Grass	A leafy vegetation growing from the ground – as opposed to from a branch/stick
Other	Any item that does not fit the above categories: e.g., moss, seeds, seedpods, bird's nests, sand, or dirt.

The full data set (N=196 focal samplings) was coded using an open-source, event logging software designed for behavioural ecology studies (BORIS; v. 5.0.1) developed by Friard and Gamba (2016). See Appendix D for details of BORIS settings. Behaviours were initially coded as an instance of manipulation separated from its predecessor by a period of two or more seconds, wherein the same object type (see Table 6.3) was manipulated in the same way; i.e., the same behaviour in the ethogram above. To align this coding system with that used by Koops et al (2015) behaviours were nested within bouts, following Koops et al's definition, where a bout consisted of the same behaviour, involving the same object, with a break of no more than two minutes between behaviours. R (version 3.4.3; R Core Team, 2013) and R-Studio (version 1.1.423; RStudio Team, 2016) were used multiply ten-minute data by six to give bouts per hour, rendering them comparable with related research (i.e. Koops, Furuichi, & Hashimoto, 2015). This was achieved by counting the number of unique bouts within each file combining this data with the number of unique files in the entire data set to provide the "bouts per focal" measure. These data were then indexed by the focal animal in each file and a mean "bouts per focal" measure was aggregated per individual. All these data were combined into a single data frame used for further analyses.

Duration data was used to assess how long subjects engaged in object manipulation for, bouts per hour were used as a measure of the frequency (or rate) of object manipulation. Both measures, in tandem, provide a richer picture of the data. Simply using duration would omit important information about frequency, whereas only including bouts per minute may ignore the importance of extended object manipulation bouts. Thus, the analysis section is divided between duration and bouts per hour.

6.2.3 Statistical analyses

6.2.3.1 *Comparison to previously collected wild data*

Here we harvested data, collected in a wild population (Koops et al., 2015), using data visualisation technology (WebPlotDigitiser, V4.0; Rohatgi, 2018) and combined these data with our own to present a comparison between wild and sanctuary reared individuals. Our data were first plotted against those presented by Koops et al. to present a descriptive level comparison. Following this, a Mann-Whitney Wilcoxon test was performed on the data, which were highly positively skewed, to assess differences between wild and sanctuary reared populations in terms of their rates of object manipulation. As Koops et al. do not report duration data it is not possible to compare the data sets on this level.

6.2.3.2 *Comparison of object manipulation bout duration and frequencies*

6.2.3.2.1 Age

The data were first compared as a function of age group. This was to determine whether there was an effect of development on the duration of object manipulation bouts, however, in order to control for the potential effect of rearing history on this comparison the orphaned subjects were removed from these analyses. Given that both datasets were subject to a substantial positive skew, the decision was made to use non-parametric statistics to compare the age groups, i.e., a Kruskal Wallis test. The results of this analysis were followed up with Dunn Tests, as a post-hoc analysis strategy to determine the exact nature of any potential differences highlighted by the Kruskal Wallis tests.

6.2.3.2.2 Rearing

As any variation in rearing history was restricted to the Juvenile-II sample (see Section 6.2.1) specific analyses were conducted with this sample, comparing the mother reared individuals with orphaned individuals of the same age group. This meant that the dataset was smaller than for the age analyses (Section 6.2.3.2.1), however, the data remained heavily positively skewed therefore non-parametric analyses were applied. In order to assess the influence of rearing history on the duration and frequency of object manipulations a Mann-Whitney Wilcoxon test was applied.

6.3 Results

6.3.1 Interrater reliability

Acceptable interrater reliability was achieved by both AS ($\kappa = 0.73$, $p<.001$; $\kappa = 1.00$, $p<.001$) and SG ($\kappa = 0.67$, $p<.001$; $\kappa = 0.63$, $p<.001$) with DN as a primary coder for manipulation type and object type respectively. In addition, both AS & SG achieved acceptable interrater reliability ($\kappa = 0.85$, $p<.001$; $\kappa = 0.63$, $p<.001$) with one another for manipulation type and object type, respectively.

6.3.2 Descriptive statistics

This study provides an account of the object manipulation behavioural phenotype expressed by sanctuary housed bonobos, the results of the observations show that the bonobos most frequently manipulated objects by playing with them (this included social and solitary play) or by carrying them (Figure 6.1A), sticks were the objects most frequently manipulated in this study (Figure 6.1B). However, here data are also present for the duration of these bouts where the longest bouts were those of nest building and tool use (Figure 6.1C); it is worthy of note that the majority of these tool use bouts were nut-cracking, however in this study we did not divide tool use and therefore these data are not available in anything other than anecdote. The duration of bouts divided by object type did not yield such stark differences (Figure 6.1D), however man-made objects and stones were manipulated for the longest durations. Worthy of note within these statistics is the 'throw' category of object manipulation, this was an instantaneous even and therefore cannot have a duration, it is included in Figure 6.1 for the sake of completeness.

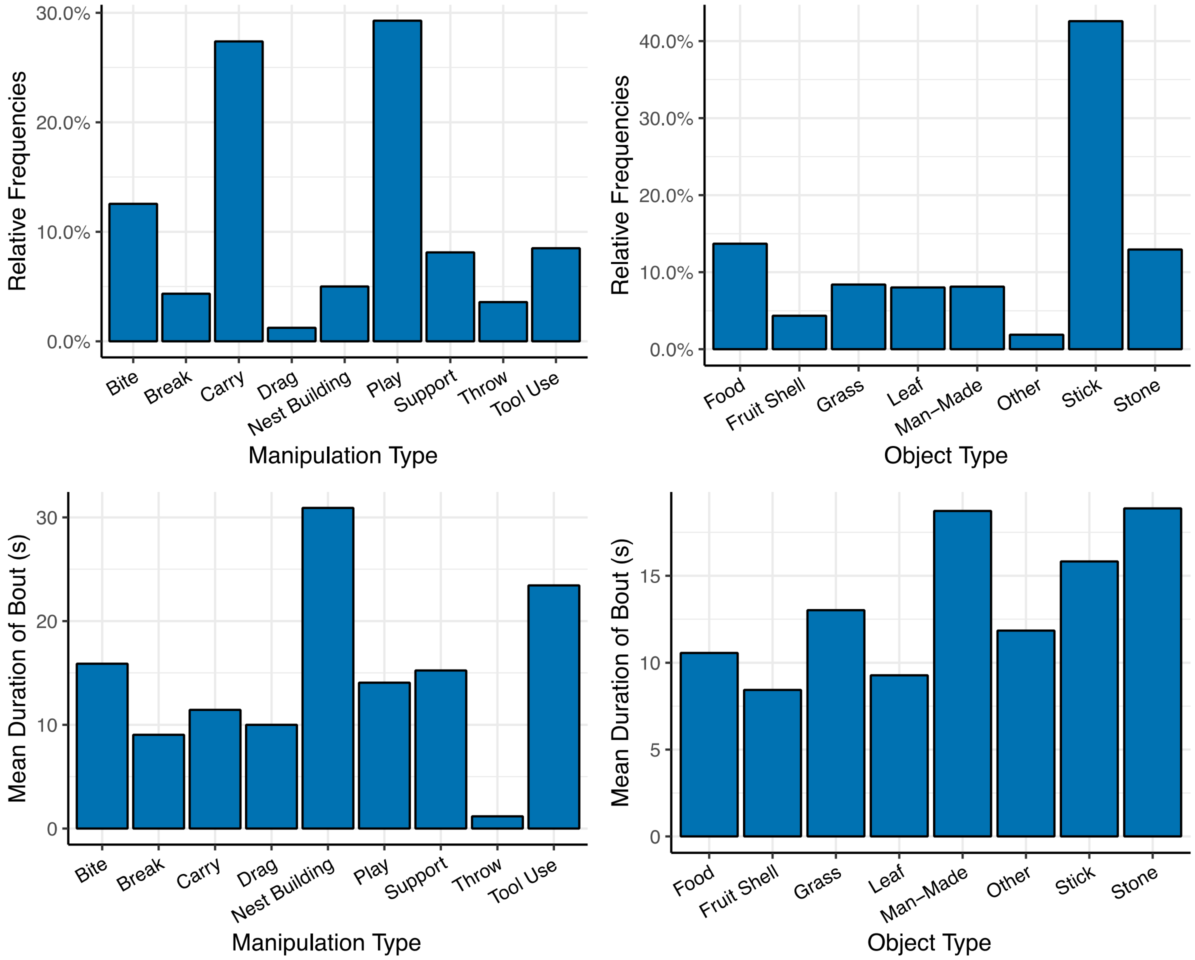


Figure 6.1. Descriptive statistics showing the frequency (A & B) and duration (B & C) of object manipulation bouts by manipulation type (A & C) and mean duration (B & D).

In addition to describing the patterns of behaviour in the present sample, it is possible to compare the rates of object manipulation with wild conspecifics. However, the wild data were collected using data visualisation technology (WebPlotDigitizer, V4.0; Rohatgi, 2018) therefore they only contain the data reported in the source paper (bouts per hour; Koops et al., 2015). Our data were scaled to align them with the data presented in this article (our 10-minute focals were multiplied by 6 to provide a 'bouts per hour' figure). These data can therefore be directly compared with those described by Koops et al., accordingly we have presented them in Figure 6.2A alongside our own for comparison. A statistical representation of this comparison can be seen in Figure 6.2B, where our data (sanctuary reared; Mdn=27.00, SD=11.39) present significantly higher (W=270, $p<.001$, $r=.85$) bouts per hour than those reported by Koops et al. (wild; Mdn=0.43, SD=0.47).

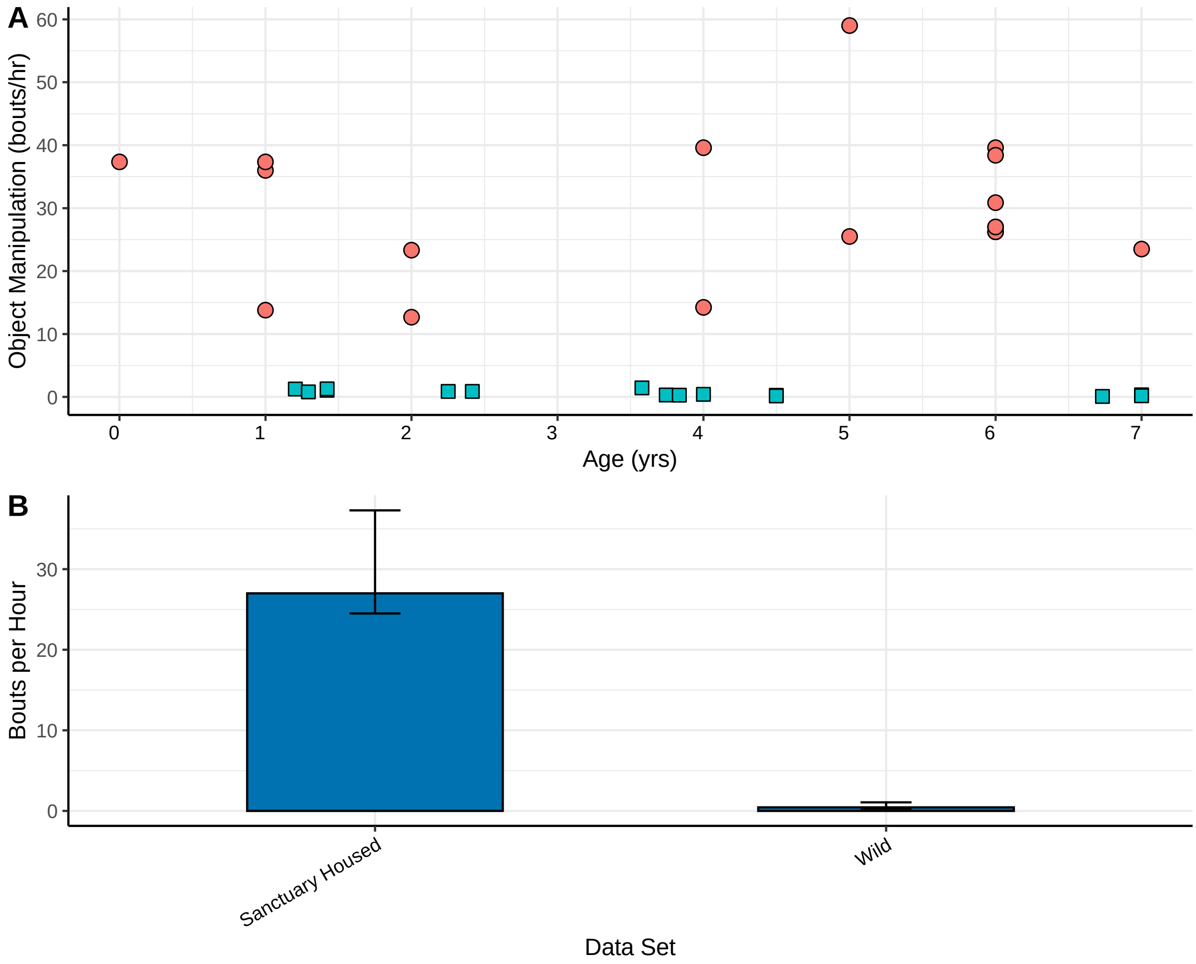


Figure 6.2. (A) Data presented in this study (coral circles) plotted against those collected, using WebPlotDigitizer, from Koops et al. (2015; teal squares). (B) Comparison of the median bouts per hour from the present data set and Koops et al.'s, the statistical comparison of these data are presented in text. Error bars represent 95% confidence intervals.

6.3.3 Duration data comparisons

The results of a Kruskal-Wallis test indicated significant differences in object manipulation durations in this sample of sanctuary housed, mother reared, bonobos with a small effect size ($\chi^2(3) = 48.24$, $p < 0.001$, ε^2=.05). Despite the effect size (which implies that the results should be interpreted with a degree of caution), post-hoc analyses were conducted with these data, in the form of a Dunn test with Bonferroni correction, the results indicate significant differences between all age groups apart from Infant-II and Juvenile-I (see Table 6.5 and Figure 6.3A).

Table 6.4. Test statistics for post-hoc comparisons using a Dunn test with Bonferroni correction following a Kruskal-Wallis test assessing differences in the durations of object manipulation bouts as a function of age group

Pairwise Comparison	Z	Adjusted *p*
Infant-I - Infant-II	2.43	<.001
Infant-I - Juvenile-I	3.68	<.001
Infant-II - Juvenile-I	0.90	1.00
Infant-I - Juvenile-II	-1.89	<.001
Infant-II - Juvenile-II	-4.59	<.001
Juvenile-I - Juvenile-II	-6.48	<.001

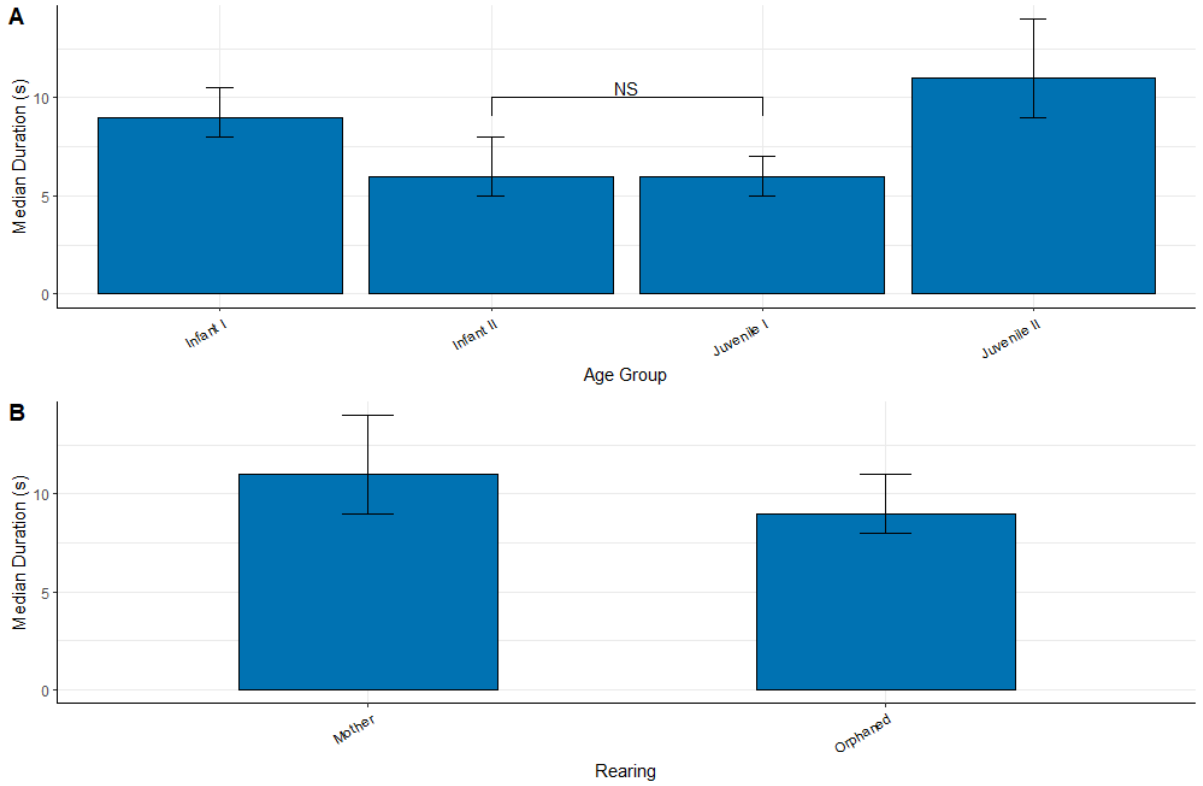


Figure 6.3. (A) Median duration of object manipulation bouts, divided by age group, all groups are significantly different (p>.001) with the exception of the marked groups (Infant II & Juvenile I). Error bars represent 95% confidence intervals. (B) Median duration of object manipulation bouts, divided by rearing history, difference is significant (p<.01), error bars represent 95% confidence intervals.

The results of a Mann Whitney Wilcoxon comparison suggest further differences in object manipulation durations as a function of rearing history with a small effect size (W=64109, *p*<.01, *r*=-.09). Here, orphaned subjects (Mdn=9, SD=28.91) manipulated objects for significantly longer than mother reared subjects (Mdn=8, SD=19.88), again these results should be interpreted with caution given the effect size.

6.3.4 Frequency data comparisons

The results of a Kruskal-Wallis test indicated that there were significant differences in the frequency of object manipulations in the sample of sanctuary housed, mother reared bonobos as a function of age; this result had a small-medium effect size ($\chi^2(3) = 11.00$, $p < 0.05$, $\varepsilon^2=.08$). These results were followed-up with post-hoc analyses, in the form of a Dunn test, with Bonferroni correction. The results of the Dunn test suggest that the effect was being driven by differences between the Infant-I and Infant-II groups along with between the Infant-I and Juvenile-I groups (see Table 6.6 and Figure 6.4A).

Table 6.5. Test statistics for post-hoc comparisons using a Dunn test with Bonferroni correction following a Kruskal-Wallis test assessing differences in the frequency of object manipulation bouts as a function of age group

Pairwise Comparison	Z	Adjusted *p*
Infant-I - Infant-II	-2.76	<.05
Infant-I - Juvenile-I	-2.81	<.05
Infant-II - Juvenile-I	0.40	1.00
Infant-I - Juvenile-II	-1.80	0.43
Infant-II - Juvenile-II	1.12	1.00
Juvenile-I - Juvenile-II	-2.76	1.00

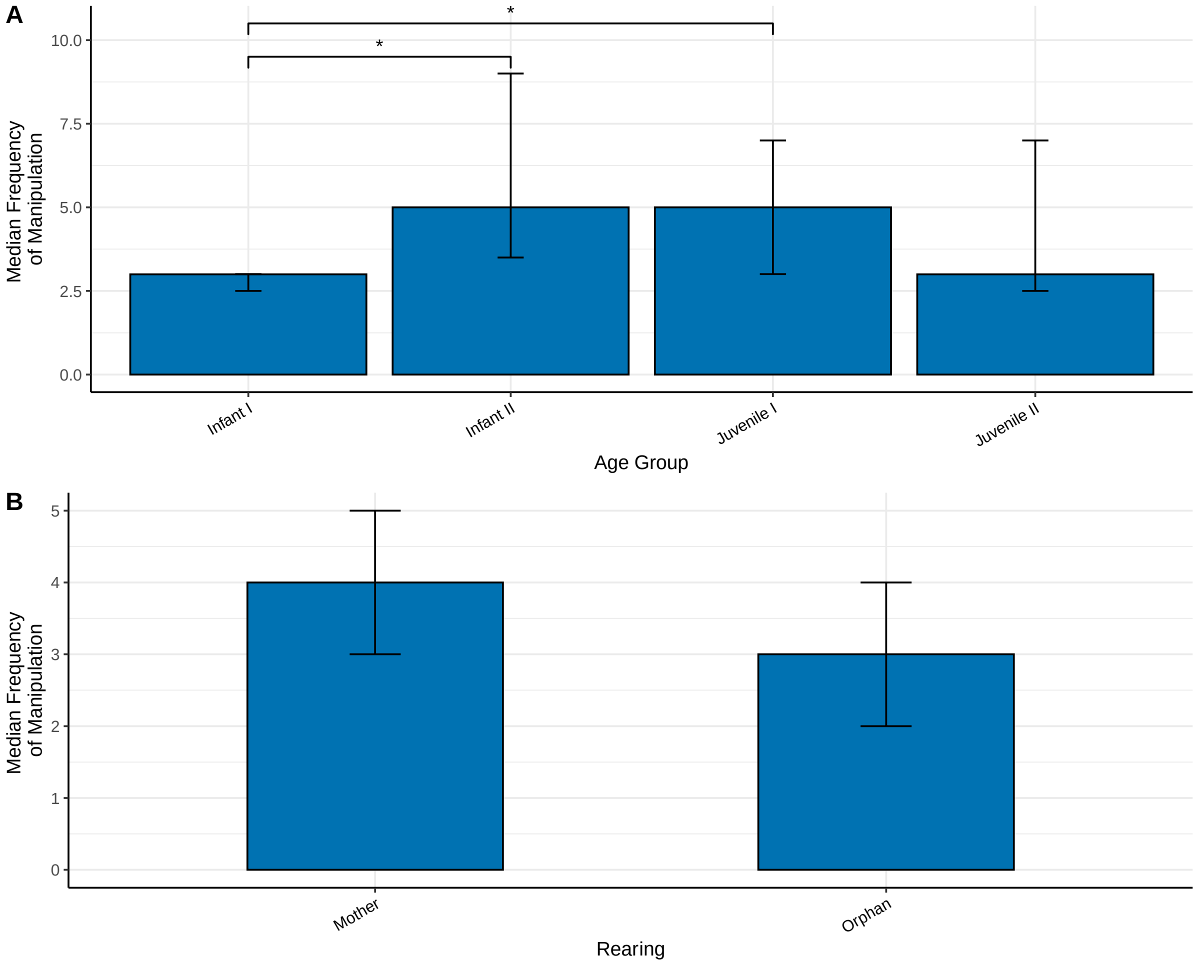


Figure 6.4. (A) Median frequency of object manipulation bouts, divided by age groups, statistically significant results are marked (=p<.05). Error bars represent 95% confidence intervals. (B) Median frequency of object manipulation bouts, divided by rearing history, difference is not significant, error bars represent 95% confidence intervals.*

The results of a Mann Whitney Wilcoxon comparison suggest that there are no differences in the frequency of object manipulation rates as a function of rearing history (W=2444, *p*=.051). However, it is worth noting that these results do approach significance, given the small effect sizes reported here it is possible that a larger sample could tip these results towards significance. This said, throughout the remainder of this chapter and this thesis these results will be treated as not significant.

6.4 Discussion

The results of this study show, in a semi-natural captive environment, bonobos display a rate of object manipulation over 50x greater than wild conspecifics. When the data were considered as a function of age we found that manipulation durations were lowest in the middle stages of development, whereas the frequency of object manipulations appeared lowest whilst the bonobos were youngest – with little change across the course of development. Our data also present an interesting dichotomy between duration and frequency as a function of rearing history, mother reared individuals appear to manipulate objects for shorter periods, but more frequently. Thus, it is unclear as to the relationship between rearing, development and object manipulation though it appears one does exist. These results are discussed here in relation to prior research and in the context of this thesis.

One of the clearer findings is the disconnect between duration and frequency as a measure of object manipulation. From our data it can be seen that each of these constructs measures a very different aspect of behaviour, therefore both were influenced differently by our predictors. This result has a bearing on future comparative studies, which should be clear on the measure used and the reasons for choosing this measure. Our count measure may relate more closely to the level of motivation that an individual has to initially approach, touch and first manipulate an object (*sensu* Koops, Furuichi, & Hashimoto, 2015), whereas, duration most likely codes for a more sustained level of attention (or perseverance). Indeed, both measures, considered together, may also allow researchers to consider reactions to novelty; a highly neophillic individual would presumably approach more objects in a given period. Furthermore, the neophillic individual would most likely have prolonged exposure to those objects and therefore a greater likelihood of innovation, sometimes considered a proxy for "intelligence" (Reader, Morand-Ferron, & Flynn, 2016). However, as the subjects in our study were familiar with the objects concerned we suggest that a future endeavour is to introduce a novel object to both captive and wild bonobo populations and contrast the responses (*sensu* Forss et al., 2015).

On the other hand, it is also possible that individuals with a high count of bouts possess both high neophilia and neophobia. As Reader (2015) suggests in his discussion of innovation, individuals who have both high neophobia and high neophilia are more likely to engage, disengage and re-engage with an object. This is because an initial neophilia results in the individual engaging with the object; once engaged the individual is influenced by their neophobia, resulting in them disengaging. The cycle continues, however each time the novelty of the stimuli reduces and so does the neophobia; as the cycle progresses, individuals may be more likely to notice, appraise, or attend to the various characteristics and parts of the object at hand. Therefore, giving them a better opportunity to consider the functional aspects of an object or how it can be manipulated. Considering bouts per hour and bout duration together allows for a more complete picture of a species' behavioural phenotype, the remainder of this chapter will compare and contrast the results from both perspectives.

When considering the age level comparisons, it becomes important to be mindful of the different utilities of duration and frequency in terms on object manipulation. In the duration dataset the lowest rates of duration were within the Infant-II and Juvenile-I groups. In terms of the frequency measures, the Infant-II and Juvenile-I groups exhibited the highest rates of object manipulation; however, owing to large variance in the Juvenile-II sample, the pattern of the duration data was not mirrored as clearly. After an initial low (during early infancy, when infants are still attached to their mothers and nursing) the frequency of object manipulation appeared to stabilise; though, given the high degree of variability in the Juvenile-II data these finding require further data to confirm. This could be explained as the youngest infants have no obvious need to explore alternate sources of food whilst their mothers are providing nourishment, therefore, as the necessity hypothesis (Fox et al., 1999) predicts and has demonstrated recently (Grund, Neumann, Zuberbühler, & Gruber, 2019) it occurs less. Through a normal period of development, as the need for food arises, exploratory play behaviour would be expected to rise also.

However, from other data presented here, the effect of rearing history becomes clear, within the Juvenile-II group there is a clear divide between orphans and mother reared individuals, it appears that orphans behave like the youngest mother reared infants; despite obvious age differences. Perhaps because humans have acted as a mother figure for these orphans, constantly providing nourishment; this provider has never left, so orphans may never need to begin to explore in the same way as mother reared conspecifics.

Though many explanations are possible for the above patterns, outside of human interference, two seem most likely. It has been suggested that mother/infant interactions are integral in the development of certain aspects of chimpanzee object manipulation, i.e., nut cracking (Boesch & Boesch-Achermann, 2000). Perhaps the orphans in this study lacked a social model and therefore, rather than expressing multiple behaviours, they apply a more select repertoire of behaviours than their mother reared counterparts. However, it has been suggested that as chimpanzees develop, maternal interactions give way to other social models

(Hirata & Celli, 2003; Inoue-Nakamura & Matsuzawa, 1997). This suggestion would, therefore, lean towards an explanation of a ‘sensitive learning period’, i.e., motherly interactions (before social models shift) *are* important in the development of a full group typical repertoire (Biro et al., 2003; Section 4.4.3). This hypothesis *would* explain the low number of bouts recorded in mother reared individuals whilst also accounting for their higher durations of object manipulation.

A second potential explanation for these results is that orphaned individuals are not gaining the same access to objects as mother reared individuals, it is plausible that other group members are gaining preferential access to objects. Some studies have suggested that apes that have suffered an early maternal loss might be characterised by social deficits throughout their lifespan (Kalcher-Sommersguter et al., 2015). This lack of sociality and resultant lack of alliances may hinder individuals ability to access and therefore learn the physical properties of objects (Flemming, Rattermann, & Thompson, 2007).

This said, the aim of the present study was not only to explain the behaviours of our sample, but to test the hypothesis put forward by Koops et al. (2015) that lower intrinsic motivation in bonobos is responsible for their characteristic lack of tool use, compared to their closes extant relatives (Gruber & Clay, 2016). One particularly striking feature of our data is the substantially higher number of bouts of object manipulation observed in our study using captive bonobos when compared to wild bonobos studied by Koops et al. (2015). Koops et al., report data which suggest a maximum bouts per hour rate of ~1.4 in wild bonobo; our data show as many as 59 bouts per hour when figures are scaled up from our 10-minute recordings.

One potential explanation for the disconnect between wild and captive object manipulation in bonobos is the differing ecologies of the conspecific groups, in this sense, the term ecologies refers to physical and social ecologies. Clearly, the social ecologies and cultures between captive and wild individual are different; our data show tool use in various forms often for foraging (i.e., nut-cracking), whereas reports from wild bonobos suggest that "bonobos at Wamba use tools only in a non-feeding context, e.g. twig as a rain hat or branch drag in display" (Koops et al., 2015, p. 2). Therefore, it is highly likely that the bonobos in our sample had substantially greater access to social models of tool use behaviours, these models would likely facilitate the use of tools within the community, harmonising behaviours between individuals (Tennie et al., 2009). This study cannot distinguish between the various social learning variants, therefore we would only suggest that these 'cultures' can be classified in a minimal sense (*sensu* Neadle et al., 2017).

However, outside of the social domain, it appears wild bonobos and chimpanzees are comparable in ecological opportunities for object manipulation (Koops et al., 2015). The natural materials required for tool use are comparable between the species; most, if not all, wild chimpanzee tool use concerns stones, sticks or leaves (Whiten et al., 1999), all of which are freely available across the bonobo range. Indeed, as our sample of bonobos were housed in a semi-natural environment, a fence erected around an area of Congolese forest (their natural habitat), they have similar access to materials. Equally, the density of invertebrate prey (often accessed by chimpanzees through tool use (Nishie, 2011; Whiten et al., 1999) is largely equal between the species in the wild (Koops et al., 2015). Invertebrate tool use was not observed in our sample, however, there were no "*Macrotermes* mounts" and it is unclear as to the density of army ants; as a result, we would consider this absence an ecologically explained one (sensu Whiten et al., 1999).

Equally, regarding the captivity effect (Forss et al., 2015), the bonobos' survival needs are met by their caregivers. There is little to no risk for the bonobos at Lola ya Bonobo: food availability is consistent; their predation pressures are substantially reduced and there is no risk of poaching. These individuals have a decreased need for survival-related activities that require substantial vigilance, time, and energy in the wild, like gathering food, travelling and hiding from predators (Inogwabini & Matungila, 2009). Regardless of the season, bonobos at Lola ya Bonobo are fed a balanced diet at similar times with little variation in location. The abundance of food and relative safety afforded by captivity may leave individuals with more neural resources (due to the "lower cognitive load") and energy more generally, allowing for enhanced curiosity, creativity, and exploration (Damerius et al., 2017; van Schaik et al., 2016).

Captive individuals are more likely to spend prolonged periods exploring their surroundings, manipulating objects, and playing. Kahrs and Lockman's (2014) claim that tool use development in human infants is based on two factors; the ability to explore objects and the ability to learn how objects change the properties and capabilities of the limbs. By exploring objects through manipulation and play, individuals understand how objects enhance or change the actions and motions that they are capable of and can subsequently tune their motor behaviours (Kahrs & Lockman, 2014, p. 90). The heightened levels of these activities at Lola ya Bonobo, in addition to the observation of human models, may help to explain the increased object manipulation and tool use rates observed in this population. This conclusion suggests that, while Koops et al. (2015) speculate that intrinsic motivation is the factor separating chimpanzees from bonobos; in fact, bonobos are capable of engaging in chimpanzee type tool use behaviours, given the required environment and ecological circumstances. Whilst this remains a plausible explanation, the possibility remains that a true captive replication of Koops et al's findings, which compares age and environment matched captive chimpanzees and bonobos, may yield results in favour of intrinsic differences. Future research should consider a comparison of the object manipulation rates in young, captive, bonobos and chimpanzees with the view to detect intrinsic differences whilst controlling for the ecological and rearing conditions between species.

From the data presented here, it can be seen that age is a factor which influences the length of time that captive bonobos engage in object manipulation for, it is possible that age also influences the frequency of that object manipulation, however, due to the tentative nature of this result replications in other populations would be required before any such claim could be asserted. Our data also show that the effect of age in our models may be confounded by rearing history, suggesting additional importance for the effect of ontogeny on behavioural phenotype. Also, the data presented here provide a much-needed view into the object manipulation tendencies (outside of cognitive experimental tasks) of sanctuary living bonobos; taken alone, the data from the wild or our data are incomplete, taken together, they present an interesting dichotomy of bonobo object manipulation.

To dismiss all differences between chimpanzee and bonobo object manipulation and tool use as a function of intrinsic motivation would be overly reductionist. Although wild populations of these sister species seem to exhibit radical differences in the frequencies and types of ‘cultural’ behaviours, the same cannot be found in captive populations. We suggest that differences in the social (the availability of models) and physical ecology (a reduction in risk and an abundance of resources) may interact with differences in motivation (increased neophilia, play, and exploration) *and* genetic predispositions. Therefore rendering the picture of bonobo object manipulation altogether more complex (see Call, 2017) than simply genetically determined intrinsic motivation (Koops et al., 2015), *sensu* triple inheritance theory (Tennie et al., 2016). These findings highlight the need for future collaboration between researchers studying wild and captive populations, to gain a better understanding of how and why individuals use and manipulate objects, and which internal and external factors may mediate these effects.

CHAPTER 7: GENERAL DISCUSSION

7.1 Overview

Throughout this thesis, I have attempted to explore the genetic predispositions, social learning capacities and ecological sensitivities of unenculturated apes and their interdependent, combined relation to ape material culture. This final chapter will serve as a summary of the results and conclusions of the previous chapters; meanwhile, setting these findings in the context of the relevant literature and acknowledging the theoretical and methodological limitations. Finally, I will outline some future research directions based on these findings.

7.2 Chapter summaries

7.2.1 Chapters 2 and 3: culture without copying

In the ape tool use literature there are two prevailing hypotheses (referred to here as the CDT and ZLS hypotheses: Whiten et al., 1999, 2001; Tennie et al., 2009). These hypotheses differ in the extent to which they assume copying is necessary for the emergence of ape culture. However, *both* acknowledge the importance and existence of *some* social learning in ape cultures. Chapters 2 and 3 asked the question: can supposed cultural traits exist without copying variants of social learning?

Chapter 2 focused on a relatively simple, yet unconfirmed, putative cultural trait: food cleaning in gorillas. The results of this chapter show that food cleaning is not reliant on copying and therefore it is not a CDT. Also, upon consideration, it became clear that restricting ‘culture’ to those species capable of CDTs would be remiss. Therefore, we published a new classification of culture: minimal culture (Neadle et al., 2017). In minimal culture, one only need assume that social learning mediates the frequency of a behavioural form, caveated by the fact that the form *could* also occur in full in absence of any social learning (as evidenced in Chapter 2). I proposed in this chapter that many aspects of ape culture fall under the minimal classification and that this should be a first stage in attributing cultural status to a behaviour, only ‘increasing’ the claim when appropriate evidence is found.

In Chapter 3, I used LS tests to determine the presence of chimpanzee behaviours in genetically similar species, to test the ‘shared ZLS’ hypothesis. The results of a previous study (Bandini, 2018) confirmed that the behavioural form ‘picking’ (Whiten et al., 1999) is unlikely to be an example of a CDT, as it was spontaneously expressed in full in two samples of culturally unconnected chimpanzees. With the addition of data presented in Chapter 3 (and data from Reindl et al., 2016 showing picking in human children), it is possible to conclude that the behavioural form of ‘picking’ is a likely a shared Latent Solution throughout the *Hominid* clade, thus lending support to the suggestion that the last common ancestor of all extant *Hominids* was also capable of tool use to some degree. By extension, this chapter lends support to the ZLS hypothesis and contributes evidence contrary to the CDT hypothesis.

7.2.2 Chapter 4: the outer limits of the ZLS

This chapter utilised the ‘extended’ LS testing methodology (using incremental social information to attempt to facilitate the expression of a behaviour), suggested by Bandini and Tennie (2018), and applied it to chimpanzee nut-cracking. Chapter 4 showed that captive chimpanzees may fail to reinnovate or socially learn nut-cracking. This has several potential explanations, each perhaps contributing to the somewhat contradictory findings in chimpanzee nut-cracking in the literature.

It was proposed that chimpanzees have a ‘sensitive learning period’ in which they must learn certain material properties or even behaviours integral to the subsequent development of nut-cracking, assuming they are ever to develop it. Previous wild reports have suggested that chimpanzees begin to acquire the skills needed for nut-cracking from the age of around 1.5 years (Inoue-Nakamura & Matsuzawa, 1997). These skills are continually refined (and/or mature; Corp & Byrne, 2002) until the age of approximately 5 years old, after which point it appears difficult (if not impossible) for chimpanzees to express the behavioural form (Biro et al., 2003). Our results showed that in adult chimpanzees, >10 years old, social information (including full action demonstrations from a human) are not sufficient to catalyse the expression of nut-cracking.

The possibility remains that nut-cracking is within chimpanzees’ ZLS and therefore should not be classed as a CDT. However, if copying forms of social learning were responsible for the expression of nut-cracking it would be plausible to expect some ‘ratcheting’ of the behaviour over time (Tennie et al., 2016), contrary to archaeological evidence (Mercader et al., 2007). Furthermore, if nut-cracking were truly culture dependent it seems unlikely that it would be expressed in two culturally unconnected wild communities (Boesch & Boesch-Achermann, 2000; Sanz & Morgan, 2007), given its low relative probability of occurrence (Tennie et al., 2009). Although nut-cracking ‘failed’ this application of the LS method, it can be seen to have passed the ‘natural’ LS test by virtue of these facts (though this needs confirmation in a captive sample). Thus, nut-cracking has partially fulfilled the “single case standard” (Bandini & Tennie, 2017), but this standard may need further expansion to consider the effects of ontogeny on an individual’s ZLS (Tennie et al., in press). Accordingly, this chapter provides somewhat equivocal evidence concerning the ZLS and CDT hypothesis, thus requiring further investigation.

7.2.3 Chapter 5: apes really don’t ape

This chapter focused on the social learning capacity of unenculturated apes. The empirical chapters up until this point demonstrated that social learning (of any variant) is not *required* for at least some aspects of ape culture to develop; though, social learning is likely to catalyse the expression of many behaviours and harmonise these behaviours within communities. Chapter 5 though was concerned with what is possible, in the ‘perfect storm’ of social learning conditions. Here, we adapted a task, previously used in bonobos and children to attempt to elicit ‘true’ action copying. Previous studies have shown that apes consistently fail to imitate the actions of single conspecific or allospecific demonstrators (Clay & Tennie, 2018; Tennie et al., 2012; Tomasello et al., 1997).

This study used a design whereby four demonstrators provided action models, thus providing a behavioural majority over the naïve subject (in terms of frequency of behaviours *and* demonstrators). Previous studies have indicated that primates, including apes, are susceptible to this form of social learning bias (e.g., Luncz & Boesch, 2014; van de Waal, Borgeaud, & Whiten, 2013) but these earlier studies were unable to pinpoint action copying. Therefore, it was considered plausible that apes would show a hitherto supressed capacity for imitative learning (action copying) when this bias is present. The results of this study show that apes, even in these arguably optimal conditions, fail to spontaneously imitate pure action forms.

7.2.4 Chapter 6: the importance of the environment

The focus of this chapter is how the three factors in the so-called ‘triple inheritance theory’ interact. The three ‘engines’ of this theory (Tennie et al., 2016) are genes (e.g., genetic predispositions), culture (cultural or social factors) and environment (the ecology of the individual). Only the former two are included in the theory’s predecessor ‘dual inheritance theory’ (Boyd & Richerson, 1985), which was, therefore, lacking an important factor. To consider the importance of all three factors together it was important to address the question of how, by changing one of these factors, it was possible to demonstrate the phenotypical potential of a species.

Recently, it was claimed that two species of *Pan* differ on a key fact, this being their intrinsic motivation to engage in object manipulation (Koops et al., 2015); this claim suggested that genetic (i.e., intrinsic) predispositions were able to ‘trump’ the other two engines, thus having a more prominent influence on the behaviour of the individual. Considering the apparent effect of ecological opportunity (demonstrated in Chapters 2 and 3) it was thought possible that intrinsic factors *could* be overcome or mitigated by ecological variation, thereby supporting triple inheritance theory highlighting the importance of ecology in a species’ expression of their latent capacities.

One clear finding from this study is the difference in behavioural phenotype between the sanctuary housed individuals in our sample and the wild individuals in Koops et al.’s (2015) study in the types, but most notably frequencies of the behaviours expressed. Our subjects showed a maximum rate of object manipulation bouts of 59 bouts per hour, the wild data yielded 1.4. The effect of captivity was sufficient to overcome any genetic predispositions that may have held up wild bonobo tool use. Therefore, the results of this study speak to the importance of the social and ecological environment of an individual and the influence that the captivity effect can have on the behaviour of affected individuals. With the data collected here, it is not possible to determine whether social or ecological influences were the primary driving force behind this difference; however, both are important (alongside genetic predispositions), when considering the behavioural phenotype of subjects.

7.3 Support for the ZLS hypothesis

7.3.1 On the relationship between the CDT and ZLS hypotheses

Historically, the ZLS hypothesis (Tennie et al., 2009) has been considered as a somewhat extreme explanation of ape culture, one that highlights the importance of individual learning, to the exclusion of social learning. However, in recent years and indeed partially through the works presented in this thesis, the ZLS account can now be seen as somewhat less extreme and more inclusive of the importance of social learning. Rather than considering all behaviours as the products of pure individual reinnovation, as has been assumed by various researcher, more recent literature on the ZLS hypothesis considers the importance of socially mediated serial reinnovations (Bandini & Tennie, 2017). This becomes important as an example of how the ZLS approach is beginning to make clear the importance of non-copying variants of social learning in explaining the patterns of ape behaviour observed within and between wild communities. In this sense, the two theoretical perspectives begin to merge, moving towards the ever elusive ‘academic middle ground’.

However, the absence of social learning within the ZLS account is more the result of misinterpretations than a theoretical difference; from its formulation the ZLS hypothesis was clear in acknowledging that social learning, though the variant is undefined, is important in explaining the ‘spread’ of behaviours within communities (Tennie et al., 2009). A clear difference between the two hypotheses is the perceived probability of copying, in particular action copying. This appears to be a somewhat irreconcilable difference between the two hypotheses; though, it is sometimes painted as a straw-man argument put forward by ZLS theorists. Classically (Whiten et al., 1999), and even in very recent pieces (Boesch et al., 2019), advocates of the CDT hypothesis have considered that copying variants of social learning are potentially responsible for the observed behavioural patterns. This difference then represents one of theoretical capacity, under a pure ZLS framework, apes are considered incapable of action copying, instead relying on non-copying variants of social learning (with the possible exception of some emulative capacity; Tennie, Call, & Tomasello, 2010; Tennie et al., in press).

This thesis presents data that generally favour the ZLS hypothesis: evidence of behaviours being reinnovated by naïve individuals, individuals failing to socially learn behaviours within their species’ behavioural repertoire and a demonstration of apes failing to copy action-level information, in the absence of results. However, here I have also presented some importance caveats to the ZLS account: not all individuals appear to have the same innovative capacity, individual learning is not always sufficient for reinnovations to occur and the importance of the ‘right’ conditions. The way in which this thesis, in particular, supports the ZLS hypothesis is discussed at length below.

The results presented in this thesis generally support the ZLS hypothesis (Tennie et al., 2009), including its latest iteration (Tennie et al., in press). In particular, they provided further examples of independent reinnovations (Chapters 2 and 3; where reinnovation is inconsistent with the CDT hypothesis). They also provided further evidence that no matter the circumstances and motivations, apes do not appear to copy actions (Chapter 5; where the supposed presence of action copying in apes instead is an important aspect of the CDT hypothesis). Finally, the results also show the importance of ecology in influencing the degree to which a species will express their potential behavioural repertoire, which is most likely the result of socially mediated reinnovations.

The conclusions drawn here suggest that the method of exclusion is a useful first stage in identifying putative cases of culture; however, in contrast to some applications of the method of exclusion (Whiten et al., 1999), I hesitate to assume that copying is necessary for ape culture. Instead, one should assume (upon identifying a putative case of culture) that this is an example of minimal culture (Chapter 2), facilitated and harmonised within communities (i.e., increased in frequency) via non-copying social learning variants (Chapter 3). The expression of particular cultural behaviours is predicted by the individual (Chapter 4), social (Chapters 4 and 6) or ecological (Chapter 6) factors influencing the individual. It seems unlikely, based on the findings from Chapter 5, that copying, especially imitation (action copying) is the social learning variant underpinning ape cultures; instead, non-copying variants are likely at the heart of ape culture. These qualifications present a very different picture of ape culture compared to human culture; these differences may also represent one of the key differences in the behavioural phenotypes between our species and other extant species of apes. Simply, the data presented here are inconsistent with the CDT hypothesis, leaving one to assume that the ZLS hypothesis is the more accurate and therefore satisfactory account of ape culture.

7.3.2 Reinventing the wheel

Chapters 2 and 3 suggest that the majority of ape cultural behaviours can be explained through socially mediated serial reinnovations (Bandini & Tennie, 2017), i.e., each individual can and does ‘reinvent the wheel’. A common critique of the ZLS hypothesis is that its seeming devotion to individual learning ignores the importance of social learning in ape cultures (e.g., Gruber et al., 2012). Works since the initial formulation of the ZLS (Tennie et al., 2009) have attempted to address this claim by making clear that social learning is consistent with the ZLS account and plays a large role in explaining the cultural patterns observed in the wild (e.g., Bandini & Tennie, 2017; Neadle, Allritz, & Tennie, 2017; Tennie et al., in press). A key difference between the ZLS and CDT accounts is that the former assumes that this social learning constitutes only non-copying variants. These non-copying social learning mechanisms act to harmonise frequencies of individual reinnovations across subjects within affected communities. The likelihood of being affected in this way also correlates stochastically with the environment the population is in (Tennie et al., 2009; in press).

Through this, it becomes possible to explain the geographic variations observed in wild populations of apes (Hohmann & Fruth, 2003; Robbins et al., 2016; van Schaik et al., 2003; Whiten et al., 1999). As a concrete example, if a given individual were to reinnovate a behaviour (within their ZLS), for example the sponging of water using leaves (e.g., Hobaiter, Poisot, Zuberbühler, Hoppitt, & Gruber, 2014), the expression of this behaviour would be made more likely in further individuals within the community (e.g., through enhancement; see Chapter 1). However, where there are multiple methods by which a problem can be solved, such as in the case of sponging (where moss can also be used as a sponge), the first method to be innovated would gain an advantage, therefore reducing the relative probability of the second method's occurrence (Bandini & Tennie, 2018; Tennie et al., in press), this was referred to by Tennie et al. (2009) as the 'cultural founder effect'. This is likely influenced by non-copying social learning mechanisms biased by social learning strategies (Laland, 2004); together these factors would lead to a harmonisation of the first behaviour (leaf sponging) within the community. This would lead to patterns of behaviour where the relative probability of leaf sponging is increased in certain populations whilst remaining at baseline in others. This could lead to the sorts of geographic variations shown by the method of exclusion, without needing to *rely* on social learning as an explanatory tool; thus, conforming to the findings of this thesis.

It is possible that later reinnovations of the *alternative* behaviour may occur, provided that the alternative behaviour is also within the species ZLS (which we can assume here given that moss sponging *has* been reported in chimpanzees and bonobos; Hobaiter et al., 2014; Hohmann & Fruth, 2003). Whether these later reinnovations are maintained within the community is likely to depend on the individual that innovates them (rank, sex or even location) and perhaps factors that may influence the other individuals within the community.

For example, older individuals may be inhibited in their ability to reinnovate a behaviour within their species repertoire due to behavioural inflexibility/conservativism (as may have occurred in Chapter 4).

7.3.3 Waiting for the 'right' time

In its initial formulation, the ZLS hypothesis states:

> *Our claim is thus that the behaviours one sees as part of chimpanzee culture are all things that individual chimpanzees could invent on their own fairly readily if all of the external and internal conditions are right. While some such behaviours will be highly likely for all groups (like making nests), others will need more environmental input (which sometimes can take an indirect route via physiology) in order to develop—perhaps even in the right order and at the right time—and these will then necessarily be relatively rare behaviours or 'inventions'.* (Tennie et al., 2009, p. 2407)

Some have claimed that the ZLS hypothesis lacked some degree of operationalisation (Schofield et al., 2018), one of the issues with the initial formulation was the use of the term "right". Here I will operationalise the "right" conditions into individual, social and ecological factors, relating to the studies presented. Each of these may influence the probability of reinnovation and thus the expression of latent solutions.

7.3.3.1 ***Individual factors***

Both double (Boyd & Richerson, 1985) and triple (F. J. Odling-Smee, Laland, & Feldman, 2003; Tennie et al., 2016) inheritance theory acknowledge the importance of genetic influences on the expression of behavioural phenotypes. I would include these genetic predispositions under the banner of individual factors, as they influence each individual within a species. However, across this section, I aim to discuss ontogenetic factors, as they influence the capacity of an individual within the species as a whole, rather than phylogenetic ones. Therefore, whilst I acknowledge the importance of genetic, therefore bio-evolutionary effects, here I will focus mainly on those factors influencing specific individuals.

An individual lacking the required incentives to engage with a particular task may not follow through with the required amount of individual, trial and error learning to reinnovate the task. For example, during Chapter 3, Study 1, individuals were provided with the simulated bones, required for the picking behaviour, alongside other food sources, i.e., their regular scatter feed. There was a successful reinnovation in all species, however, the orangutan reinnovation did not occur for over 10 minutes, bonobos did not reinnovate until the second trial and gorillas did not reinnovate until the third. In this sense, the “right” condition refers to a subject that desires food or whatever reward available upon task completion; this said, food desire can be further subdivided into desires for specific aspects. Even then, desire for food reward is subject to the Yerkes-Dodson law (Yerkes & Dodson, 1908), whereby too much desire might lead to a lack of inhibition, resulting in the behaviour not being expressed (e.g., Coolidge & Wynn, 2005). This may be because subjects fail to inhibit initial desires, e.g., putting nuts in the mouth to crack them, rather than using tools, which might be more efficient.

Another individual factor is that of enculturation. Human interference (even with positive intent) may alter the behavioural phenotype (even physiology and perhaps resultant cognition; Pope, Taglialatela, Skiba, & Hopkins, 2018) of a subject substantially. It was for this very reason that, in Chapter 5, I excluded "Alex" from the main data set, as he is a hand reared male that was even trained in the "do-as-I-do" paradigm (Custance et al., 1995) according to Hribar, Sonesson and Call (2014). Alex was raised by humans before the training, this may have influenced him in later years. In the case of Alex and Chapter five, this exclusion proved an unnecessary precaution as Alex also failed to copy the action demonstration. Within the scientific literature there are cases of apes going well beyond their species' natural behaviour to demonstrate language-like abilities; e.g., Kanzi (Savage-Rumbaugh, McDonald, Sevcik, Hopkins, & Rupert, 1986), Chantek (Call, 2001; Miles, 1994) and Koko (Patterson, 1978). These individuals are not representative of their respective species, in their natural, i.e., unenculturated (*sensu* Henrich & Tennie, 2017) states. It is for this reason that Henrich and Tennie (2017) consider experiments with enculturated, trained or deprived subjects to lack ecological validity and therefore dismiss them. Note, Chapter 6 contains data from potentially deprived subjects, orphaned bonobos deprived of their mothers; however, this study is directly concerned with the potential influence of the captivity effect and not the wild-type behaviours of these individuals, these data are provided by Koops et al. (2015). Thus, the call to set aside data from enculturated or deprived individuals only applies to those studies that seek to answer questions of wild-type behaviour, not those concerned with directly comparing captive vs. wild subjects.

Outside of full enculturation, one must consider the other effects of human interference; for example, by removing ‘risk’ and adding ‘time’, captive individuals can go far beyond their wild conspecifics; this is, in essence, the factor underlying the so-called captivity effect (*sensu* Forss, Schuppli, Haiden, Zweifel, & van Schaik, 2015). Through this, the probability of behavioural reinnovation is substantially higher in captive populations compared to wild conspecifics. The results of this effect are clear from studies of captive bonobos (Gruber & Clay, 2016; Chapter 6), which have been demonstrated to use tools and manipulate objects in a way far removed from wild conspecifics (Koops et al., 2015). In this sense, the effects of human enculturation can greatly contribute towards the “right” conditions, however, the question of how valid it is to generalise from these subjects to entire populations from is questionable. Equally, some might suggest that captive apes are insufficient models for wild apes, this will be discussed in greater detail in section 7.4.

The "right" individual conditions can, consequently, be summarised as the subject who feels motivated, not distracted (instead: attracted) nor at risk. These conditions can be influenced by factors external to the individual, e.g., food scarcity may increase motivation for extractive foraging through increased need (Fox et al., 1999) thus resulting in a physiological change. According to the assumptions of the ZLS, the "right" conditions shouldn’t need to include any human interference, however, this may mediate and catalyse the expression of some behaviours. There may also be behaviour specific conditions; for example, Chapter 4 suggested that, in the case of nut cracking, chimpanzees may need to be within the ‘sensitive learning period’ when first discovering the material and physical properties of nut cracking. The lack of these "right" conditions may have also contributed to the fact that gorillas and bonobos didn’t successfully reinnovate scooping in Chapter 3.

7.3.3.2 ***Social factors***

In addition to those factors only influencing the subjects themselves, individual factors may also influence the subject’s behavioural phenotype, which may, in turn, affect their social relationships. In a novel approach, Ferdowsian et al. (2011) applied the diagnostic criteria for human depression and anxiety to chimpanzees that have suffered deprivation; the results suggested that these individuals suffered from a phenomenon similar to human post-traumatic stress disorder, resulting in distinct behavioural phenotypes. Thus, *any* trauma may hamper the ability of an individual to express their full potential behavioural repertoire. Therefore, at the very least, subjects should not have suffered any mistreatment or trauma, e.g., as a result of human intervention. Note that trauma can occur independent of human captivity (e.g., Leendertz et al., 2004), therefore these effects are likely to influence wild and captive populations alike.

Chapter 6 provided evidence for the captivity effect bolstering the rate of object manipulation in captive bonobos compared to wild conspecifics. However, these individuals were exposed to both allsospecific and conspecific models throughout their tenure at the sanctuary. Prior research suggests that apes reared in social isolation, e.g., in medical research laboratories, are neophobic (Menzel, 1962), thus suggesting a sort of ‘anti-captivity effect’. It is possible that our subjects in Chapter 6 were also party to this effect; however, other studies have shown that this effect is reversible with subsequent social integration (Reimers, Schwarzenberger, & Preuschoft, 2007), this may explain why we failed to note a difference between mother reared and orphaned individuals. Apes are social beings that socially learn via their mothers in the early years of life. Being without a model in these early years is likely to influence later behaviour, rendering the affected individuals not representative of their species as a whole.

In this sense, it is possible to level critique toward the ZLS hypothesis; it has long been an example that individuals raised on a ‘desert island’ would develop their entire species repertoire, given the ‘right’ conditions (*sensu* Tennie et al., 2016; see Section 1.2.4.2.2). This is not a suggestion and is only a metaphor; however, the data presented in this thesis do not support this supposition, instead, I suggest that the metaphor be restructured. In addition to taking an infant and placing them on an island, where their nutritional and individual needs are met, their social needs must be also met, this may involve the presence of a mother figure, and potentially even other social agents. The necessity of this caveat to the ZLS account suggests an interesting interplay between the ZLS and CDT hypotheses, which may be the root of the assumption that certain behaviours are CDTs. This thesis suggests that the behaviours themselves are unlikely to be CDTs. However, apes (at the very least) can be considered as ‘socially dependent beings’ that *require* social interactions to function in a way representative of their species. Thus, it is impossible to separate apes and sociality.

7.3.3.3 ***Ecological factors***

As is to be expected within a ‘triple inheritance’ framework (F. J. Odling-Smee et al., 2003; Tennie et al., 2016), all three of the factors influencing the ‘right’ conditions for a species’ ZLS to be expressed interact with one another. Therefore, the individual conditions of the subject may be predicted by their environment. A subject's motivation may be directly influenced by food availability in their ecology (an individual factor), but also the ecology of the subject may influence their ability or propensity for engaging in certain behaviours. For example, in Chapter 2 it was suggested that it is unlikely that the absence of food cleaning in mountain gorillas but its presence in lowland gorillas (Robbins et al., 2016) is a result of genetic differences between the subspecies. Instead, it was predicted that mountain gorillas, placed within the same ecological situation as lowland gorillas would behave similarly, as a result of the phylogenetic similarities and resultant shared ZLS (Chapter 3). This suggests that the ecology of the individual has a large influence on the final behavioural phenotype. This is essentially the logic underlying the LS testing methodology (*sensu* Tennie & Hedwig, 2009), that, provided the ecological opportunity, and 'right' motivations, a typically developing and naïve subject would express the same behaviours as a wild conspecific, whose behaviours were facilitated by social learning.

Whilst ecological variations can be sufficient to facilitate the expression of behaviour within a species specific ZLS, they can also be sufficient to alter the expressed behavioural repertoire of a population (Chapters 3 and 6). Wild bonobos have rarely been observed to spontaneously use tools (Gruber & Clay, 2016; Gruber et al., 2010); however, in Chapter 6 it was shown that in a stimulus rich and risk devoid environment, where the individual's nutritional needs are met, object manipulations (even tool use) are frequent and occur at a rate much higher than wild populations. Such is the influence of the captivity effect (Forss et al., 2015).

Therefore, through the use of captive experiments (where some ecological conditions are optimal; i.e., nutritional needs are catered for, there is no risk of predation or poaching and subjects are rarely exposed to aversive stimuli), it is possible to explore the outer limits of a species' ZLS. However, it should be noted that these 'optimal' conditions might not, and often do not, represent the conditions that wild populations exist under. Despite this, through captive studies it is possible to discover the extent to which 'cognitive cladistics' (*sensu* Haun, Rapold, Call, Janzen, & Levinson, 2006) are responsible for behavioural similarities between genetically similar species. From this information, it is possible to infer the behavioural phenotypes of extinct species, i.e., the last common ancestor between humans and apes.

7.3.3.4 ***The 'right' conditions***

In sum, although the terminology used by Tennie et al. (2009) may appear imprecise or lacking operationalisation (according to Schofield et al., 2017; but see Tennie et al., in press for a more precise version) it highlights the somewhat fluid nature of the required conditions for behavioural expression. Although there is no 'recipe' for a species ZLS, it is plausible that by providing something approaching the 'right' conditions a given individual would express their full potential. However, as Ferdowsian et al. (2011, p. 9) make clear "Chimpanzees cannot clearly articulate their thoughts, feelings, and experiences to humans", therefore to attempt to fully quantify the 'right' conditions is futile. Instead, researchers should take into account the individual, social and ecological conditions outlined and evidenced throughout this thesis when considering *some* of the factors influencing great ape cultural behaviours.

7.4 Limitations of this work

Although every effort was made throughout this work to ensure that it maintained the utmost scientific integrity, limitations do exist. In this section, I will acknowledge some of these and reflect on how they could have been addressed, with the benefit of hindsight.

7.4.1 Theoretical

The Zone of Latent Solutions hypothesis offers one of the more elegant accounts of ape cultures, assuming very little of ape capabilities whilst acknowledging their ability to acquire behaviours through trial and error (individual) and even insight learning and for these behaviours to be harmonised within communities through non-copying social learning mechanisms. However, the ZLS hypothesis (Tennie et al., 2009) has been argued to be overly conservative in its attribution of CDTs. Stout et al. (2019) argue that in its conservativism the ZLS may begin to reject cases of CDTs that are yet to ‘ratchet up’ beyond the capacity of any one individual with their lifetime. It is following this logic that Stout et al. argue that the ZLS is asking the “wrong question” (2019, p. 312); rather than considering whether social learning is necessary, they argue research should focus on whether it occurs. In this sense, they hope to demonstrate that more behaviours are ‘cultural’ by the presence of social learning. However, Stout et al. fail to acknowledge some of the more recent contributions to the ZLS theoretical standpoint (Bandini & Tennie, 2017, 2018; Tennie et al., in press) including my work (Neadle et al., 2017). These papers demonstrate that, for the ZLS, the presence of social learning in the facilitation of many behaviours, in a social species such as apes, is beyond question. This is only to be expected given that social learning is widespread in the whole animal kingdom

(Boyd & Richerson, 1996) and therefore, its absence in apes would be surprising in any account, including the ZLS. Stout et al.'s criticism, therefore, misses its target. It is to address these very objections that the term 'tradition' (*sensu* Galef, 1976) was abandoned (Neadle et al., 2017; Chapter 2) in favour of a more minimal classification of culture, with the hope that this term is more palatable across fields (Neadle & Tennie, 2019).

Theoretically then, the very questions that this thesis asks could be challenged, such a challenge would follow the rhetoric of: "why would we be interested in what is *possible*? It is far more important to know what is *happening*". There is little or no question that all aspects of ape culture involve social learning, this is no longer an 'open question'. Rather, the important (and open) question is: which of these resultant behaviours *require* it? Even 'hardwired' behaviours such as yawning, which require no social learning for "reinnovation" across subjects (Tennie, 2019b; Yoon & Tennie, 2010), are facilitated in their frequency by social learning; i.e., if individual A yawns around individual B then B is more likely to yawn. Thus, the yawn was socially mediated by A's actions (yawn contagion; Provine, 1986, 2005). If it is accepted that social learning mediates behavioural frequencies as genetically fixed as a yawn, then the open question is which behavioural forms *require* social learning; i.e., which behaviours cannot occur in the absence of social learning, this then logically excludes yawning. If evidence of these behaviours (CDTs) were found in extant ape species, outside our own, it would be necessary to reconsider the assumption that cumulative material culture is unique to humans. The data presented in this thesis, and that reported elsewhere suggest that ape culture, as we know it today, is better explained through socially mediated reinnovations than CDTs (e.g., Bandini, 2018; Bandini & Tennie, 2017, 2019; Menzel, Fowler, Tennie, & Call, 2013; Motes-Rodrigo et al., 2019; Sherry & Galef, 1984; Tennie, Hedwig, Call, & Tomasello, 2008). Therefore, at present, CDTs and the process of cumulative cultural evolution can continue to be considered “uniquely human” (Tomasello, 1998b) owing to our reliance on copying and ability to ‘ratchet’ beyond the capacity of any single individual.

7.4.2 Methodological

7.4.2.1 *The LS methodology*

The LS methodology has undergone two major revolutions since its initial formulation (Bandini & Tennie, 2017, 2018). The first saw the introduction of two “standards”: the single or double case (Bandini & Tennie, 2017) and the second involved the introduction of incremental levels of social learning information (Bandini and Tennie, 2018; Chapter 4). The double case standard went against the initial "one size fits all" logic of the LS test, which assumed the reinnovation (or reinvention as it was then termed) of a behaviour in a single individual within a population is sufficient to assume that the entire species was capable of such a reinnovation. Instead, the double case standard requires two independent reinnovations (Bandini & Tennie, 2017), i.e., a reinnovation in two separate populations. The introduction of this standard was in response to critiques that single reinnovations are insufficient to assume species wide patterns of behaviour.

However, even with the addition of this double case standard, some behaviours demonstrated using the LS methodology can still be considered as latent solutions following a single reinnovation. Bandini and Tennie (2017) argue that behaviours should be exempt from the stipulations of the double case standard if they are relatively complex, though this definition lacks universal qualification. This means that, based on the current framework, it is not possible to empirically predict which behaviours would be exempt from these standards, they instead need to be assessed on a case-by-case basis. These authors cite nut-cracking as a sole example of where the double case standard would not be applicable as the behaviour "requires a specific technique performed in a predetermined order and several objects in conjunction" (Bandini & Tennie, 2017, p. 5). Based on this, in the currently known chimpanzee tool use repertoire (Whiten et al., 2001), only nut-cracking would qualify for exemption from the double case standard. Thus, a universal qualification of what is needed before a trait is exempt from the double case standard is required; however, this would need a universal definition of complexity, such a feat is far beyond the scope of this thesis.

As there appeared to be no universal qualification of when practitioners should withhold the double case standard, throughout this thesis I took each behaviour on a case-by-case basis. Despite the assumption of naivety inherent in the LS method (Tennie & Hedwig, 2009), Chapter 2 tested for a behaviour which was already likely to be present within the target population (indeed all populations given its simplicity see Chapter 2 for further discussion; Neadle et al., 2017). As the populations were culturally independent and there were reinnovations of the target behaviour in our captive population and the wild, it can be seen that the double case standard was upheld. It is likely, according to Tennie et al. (2009), that the three wild populations documented to show this behaviour did so via individual learning, perhaps mediated by non-copying social learning, however, the data provided by Robbins et al. (2016) cannot confirm this. Given the relative simplicity of this behaviour (i.e., the fact that no tool use needed, and its behavioural form requires only one step) and its seeming universality in the wild, we applied the double case standard.

However, the double case standard was not upheld throughout this thesis, Chapter 3 looked outside of the tested species' naturally occurring repertoires. It was therefore assumed that the behaviours might represent a relatively complex solution in these species, the wild conspecifics of which express little to no foraging related tool use (Hohmann & Fruth, 2003; Robbins et al., 2016; van Schaik et al., 2003). Thus, the double case standards were suspended. Finally, in Chapter 4 we also suspended the double case standard, as nut-cracking in chimpanzees is considered a behaviour with a low relative probability of occurrence (Bandini & Tennie, 2017; Tennie et al., 2009).

Therefore, as with many findings in science, the results presented here should be replicated before they are assumed to be 'fact'. However, when replicating such results, it is necessary to recall the factors influencing cultural behaviours outlined in Section 7.3.2.4. Should a population fail to reinnovate a behaviour, it is possible that they are not exposed to the "right" conditions. Equally, it is possible that the populations that I have reported here, for example, the chimpanzee sample in Chapter 4, were not exposed to these "right" conditions and/or in the right state (age) and this can explain the results. The LS methodology has limitations, primarily its reliance on the assumption that a small number of individuals can be generalised to an entire species. However, to date, it is the only method by which we can test for the ability of a species to reinnovate a behaviour whilst excluding the confound of social learning. Therefore, by considering the backgrounds of tested subjects and applying the double case standard where appropriate, it is possible to mitigate the effects of this limitation on the resulting data.

7.4.2.2 ***Allospecific demonstrators***

Chapters 4 and 5 considered the social learning capacities of the great apes; this was achieved by using demonstrations to attempt to facilitate the expression of a novel behaviour in captive apes. Chapter 4 began the demonstrations with ‘ghost conditions’, which allow the subjects social information about the results of a behaviour, even the pathways that the objects must follow to result in this end state but not the bodily actions (Heyes, 1994; Hopper, 2010). In this sense, the ‘ghost condition’ uses many social learning mechanisms (Whiten et al., 2004) to the exclusion of imitation. The final condition of Chapter 4 used a full action demonstration from a human demonstrator; similarly, Chapter 5 used a full action demonstration from a group of demonstrators (N=4). It could be argued that it would have been better to utilise conspecific demonstrators; i.e., train a conspecific to perform the target actions and have this individual complete these actions in front of conspecifics. This suggestion has some validity, indeed Hopper et al. (2015) showed that apes are more likely to copy other apes than humans. However, studies of ‘true’ action copying, i.e., those without the confound of other social learning mechanisms, suggest that no matter the demonstrator species, apes appear to fail in imitating novel bodily actions (e.g., Clay & Tennie, 2018; Tennie et al., 2012; Tomasello et al., 1997). Additionally, in practice, it would have been nearly impossible to recreate the conditions of this study (multiple serial demonstrations followed by one coordinated simultaneous demonstration) with ape demonstrators.

7.4.2.3 ***Measures by proxy***

Throughout this thesis, I have had to use indirect measures to assess phenomena that I cannot be sure to have occurred, i.e., measures by proxy. This was necessary either because to measure the actual phenomenon required specialist equipment or would have required me to use techniques that, whilst valid, were tangential to the aims of the particular study.

Firstly, I considered that when performing demonstrations to subjects, e.g., in Chapters 4 and 5, it was necessary to ascertain the attention paid by subjects to the demonstrations, to eliminate the possibility that subjects did not imitate because they simply did not pay attention. In these chapters, I attempted this using body-mounted cameras on the demonstrator(s), along with another camera on a tripod behind the demonstrator(s). It was soon clear that ascertaining eye-gaze was next to impossible at such a distance, to do so would require much higher definition and close up footage. Therefore, it became necessary to measure, by proxy, those individuals who were oriented towards and in clear view of the demonstrator, therefore, were deemed to have observed the demonstration.

This measure was far from perfect and in hindsight might have been better accomplished using eye-tracking techniques such as those employed by Myowa-Yamakoshi, Scola and Hirata (2012). Such a technique *was* considered; however, it has two important limitations itself. Firstly, using this methodology only video demonstrations can be provided, thus falling short of ‘full’ demonstration as previous LS studies (Bandini & Tennie, 2018) have shown that primates pay limited attention to these demonstrations. Equally, it could be argued that the captive subjects are ‘used to’ observing humans interacting with objects and, if the copying assumption of the CDT hypothesis were correct (e.g., Byrne & Tanner, 2006), would thus copy the live human action demonstration, if sufficiently motivated. Therefore, the second limitation of eye-tracking tools becomes relevant, in that the cost-benefit ratio of using this technology becomes highly weighted towards forgoing the more expensive option. Undoubtedly, if the research question is centred on *where* an ape is attending, there is no substitute for eye-tracking. However, in the case of this research, the costs far outweighed the benefits. As a result, the results of this measure should be interpreted with caution. I attempted to improve on this measure in Chapter 5 by designing a four-way ‘on the spot’ reliability measure that required a majority of demonstrators (i.e., at least three out of four) agreed the subject had observed an action demonstration. I believe this measure presents a good balance between cost and utility, in a study that does not focus on the locations observed, whilst attempting to mitigate some of the limitations

This leads to the second major measure by proxy: attempting to unravel subjects’ motivations. In Chapter 5, I attempted to quantify subjects’ motivation to engage with the apparatus by measuring, as a percentage of available testing time, the time subjects spent in contact with the ‘test box’. This measure is limited by the fact the subject could simply hold the box for the entire trial without attempting to open it once and would receive 100% ‘motivation’. Equally, a subject could spend the entire trial throwing the box at a wall in an attempt to open it and they would receive <100% ‘motivation’. This said, to quantify subjects’ motivations when psychometric assessments are limited, is always going to leave some degree of validity to be desired. Thus, I simply acknowledge that this remains a limitation of my work and temper claims based on this data accordingly.

7.4.2.4 ***Captive subjects***

Throughout this thesis the data presented have been collected from captive individuals, or, at the least, those in the care of humans. The captive environment offers some important advantages over a wild one; however, this also leads to limitations, which must be acknowledged before drawing conclusions from the data. This section will consider these limitations and therefore set the context for the later conclusions, which need to be somewhat tempered in the light of them. Also in this section justifications will be made to consider why, in spite of the limitations, captive populations were used throughout this thesis.

Wild and captive apes react differently to novel stimuli (Forss et al., 2015); potentially as a result of this, research often observes substantive differences in the behavioural repertoires of these conspecific groups (e.g., Gruber & Clay, 2016). It could be considered that this 'captivity effect' may have influenced the likelihood of the apes in Chapters 3 and 4 to initially approach or engage with the novel apparatus/food sources. It is possible that, due to increased neophobia (Forss, Motes-Rodrigo, Hrubesch, & Tennie, 2019; Forss et al., 2015), wild populations may be less likely to reinnovate behaviours outside their population's repertoire. This would mean that some of the results reported in this thesis might not be as likely to occur, had I chosen to use wild subjects in data collection. This might have resulted in, for example, not all species of apes reinnovating 'picking'.

Furthermore, other research has found that captive baboons (*Papio anubis;* Laidre, 2008) and spotted hyenas (*Crocuta crocuta*; Benson-Amram, Weldele, & Holekamp, 2013) are more proficient problem solvers than their wild conspecifics. It is possible that this would explain why orangutans in Chapter 3 successfully reinnovated the 'scooping' behaviour.

However, these results were not replicated in either the gorilla or bonobo samples, therefore it is possible that other, group specific factors (see Section 7.3.2) are also involved. As discussed at length in Chapter 6, the captivity effect is a likely explanation for the disparity between wild and captive bonobo populations' differences in object manipulation rates. Though, given that Chapter 6 directly investigated these differences, the collection of data from captive subjects is not a limitation of this study.

However, it is also possible that the data reported here underrepresent the capacities of the species investigated. Wild apes undergo a substantive period of maturation and learning, through interactions with their environment, conspecifics and exploration; this is a function of the elongated juvenile period of this clade (even compared to other organisms of similar body size; Russon & Begun, 2004). Russon and Begun also suggest that the consistent provisioning of apes with the required nutritional sources might delay the development of their innovative abilities. However, they go on to express that, in the wild, mothers begin to withdraw the crutch of provisioning as the juvenile develops, through a weaning process; thus, developing a necessity for innovative means to access food sources (Fox et al., 1999; Laland & Reader, 1999). However, in captive populations, this necessity never arises, subjects are consistently provisioned with sufficient food sources that require little to no processing, though enrichment devices are often given in modern captivity. In spite of this, the apes, from which these data are collected, have likely only experienced an approximation of the maturation process that wild conspecifics undergo; accordingly, they should be treated as approximations of their wild conspecifics. However, more recent research has suggested that the necessity hypothesis, whilst valid, does not have clear predictive utility, in terms of apes falling back on ‘difficult to access foods’ during staple food scarcity (Koops et al., 2013). Regardless, findings from captivity should be replicated in wild populations before strong conclusions are drawn from them.

In spite of the clear limitations, described above, inherent to a captive sample, this thesis presents a case for the potential capacities of the concerned species. Accordingly, at times the data presented might go beyond what would be expected, or even is typical, of wild populations; for example, wild gorilla and bonobo tool use does occur on occasion (Breuer, Ndoundou-Hockemba, & Fishlock, 2005; Ingmanson, 1996), but this thesis presents these species as comparable, at times, to chimpanzees and orangutans (Chapter 3). Contrastingly, the chimpanzees in Chapter 4 were outside of their sensitive learning period for nut cracking, this chapter concluded that this, in combination with a lack of behavioural flexibility, was responsible for the sample failing to reinnovate or learn the behavioural form. However, wild data suggest that migrant females might be able to adapt their behavioural repertoires to more closely resemble that of the new group (Luncz et al., 2012). The data presented here have allowed me to isolate specific social learning variants, something that would have been exceptionally challenging in a wild population; as well as assume, with very little doubt, that subjects are naïve to behavioural processes of interest prior to conducting research of their acquisition. For these reasons, the data presented here have benefited from collection in a captive population. However, as always, they should be complimented by wild data yet to be collected; therefore being postfaced by the notion that captive apes are simply models of wild conspecifics, the accuracy of these models requires further determination.

7.5 Future research directions

7.5.1 Resetting the null

Based on the results presented in the earlier chapters, I suggest here that future research takes this opportunity to ‘reset the null’ hypothesis of ape culture in a way similar to that suggested in early human stone tool cultures (Tennie et al., 2017). That is, research following this thesis should consider that socially mediated reinnovations *may* be sufficient to explain the patterns of behaviour observed in wild populations. In so doing researchers should reconsider the anthropomorphised assumption that action copying is integral to ape culture. This should be upheld at least until a time that spontaneous ‘true’ imitation (such as that described in Chapter 6) is documented outside our lineage. This is not to suggest that the ‘search for imitation’ should stop here, but rather the search should begin anew, setting aside data from enculturated individuals and restricting studies of imitation to those that exclude the possibility of other social learning variants. Following this, experimental studies with wild apes should be conducted, those that exclude the possibility of social learning mechanisms other that imitation, in order to assess whether any potential for imitation is a product of captivity and/or enculturation.

7.5.2 Stringent imitation studies

Accordingly, research should develop on the studies presented here in using conspecific demonstrators, to assess the claim that conspecifics *are* better demonstrators than allospecifics (Hopper et al., 2015). By using conspecific demonstrators, it can be made clear not only which species is the ‘best’ demonstrator but also whether apes have any capacity for action copying. Importantly, these demonstrations should be of behaviours that are outside of the individual's ZLS, thereby ensuring that the behaviour constitutes a CDT thereby excluding individual learning. It is for this reason that I suggest a result dependent design in studies of 'true' action copying, such as that used in Chapter 5. However, based on the findings of Tennie et al., (2012) it appears unlikely that such results would yield anything different from those presented here.

7.5.3 The ZLS project

An ongoing project should also be to subject each putative case of culture to an LS test. This would ensure that claims of 'culture' are given the most accurate cultural label. Those cases which 'pass' the LS test, i.e., are shown to be CDTs through several, valid, populations failing to reinnovate the behaviour, should be further subjected to the extended LS method (as applied in Chapter 4) to ascertain which social learning variant is necessary for the emergence of the trait. Those behaviours which 'fail' the LS test should be considered as cultural in the minimal sense (outlined in Chapter 2) and can be placed within the species' ZLS. Through testing behaviours in this way, it will be possible to build up species-specific repertoires and infer the degree to which the resulting ZLSs overlap. I suggest that such an endeavour would be better placed using a more large-scale collaboration similar to the "ManyPrimates" project (Bohn et al., 2019), rather than the single methods used in this thesis, to maximise sample sizes and the reliability of resultant conclusions.

7.6 Conclusions

This thesis contains a new classification of culture (minimal culture), based on the results of captive experiments (Chapter 2), the first application of the LS testing methodology outside of the behaviour's intended species (Chapter 3), the first attempt to classify chimpanzee nut-cracking as a CDT or a latent solution (Chapter 4), the first test of 'true' imitation to make use of majority influence (Chapter 5) and a report of the capabilities of bonobos in the domain of object manipulation (Chapter 6). A recurring theme throughout this entire thesis is that the assumptions of the ZLS hypothesis appear largely accurate; specifically, the emergence of, at least some, ape cultural variants can be explained through socially mediated reinnovations. Furthermore, apes appear unable to demonstrate convincing evidence of 'true' imitation, even under optimal conditions.

However, there are some instances where the basic predictions of the ZLS hypothesis appear to not correspond with observed data. In these cases, it is important to consider the external factors that may have influenced this outcome. Consistent with the ZLS hypothesis, these factors should be eclectic, therefore considering individual, social, environmental *and* biological influences. Throughout this thesis, I have attempted to find common ground between the ZLS and CDT hypotheses, whilst also testing the assumptions that cannot be reconciled between the two. Overall, I find support in favour of the ZLS hypothesis, with the caveat that potentially even more emphasis should be placed on the factors influencing the expression of great ape cultural behaviours in future applications of this theory.

A clear undertone throughout this thesis is, whilst individual reinnovations can explain many of the putative cultural traits identified by prior research, social learning and culture are pervasive in the lives of all great ape species. These species should be considered as ‘cultural’, however the degree of this ‘culture’ requires further investigation. Evidence of culture should be identified before behaviours are assumed to not be the product of individual learning; however, absence of appropriate cultural evidence is not evidence of its absence. Thus, both the ZLS and CDT hypotheses remain in contention as explanations for the observed behavioural patterns in wild great apes.

Ape cultures are complex, we are still uncovering evidence of new behaviours and capabilities of our closest extant relatives. However, researchers should consider their own biases when interpreting these data and avoid anthropomorphising where possible. By assuming nothing about the requirements of a behaviour, it is possible to discover the true factors influencing great ape cultural behaviours.

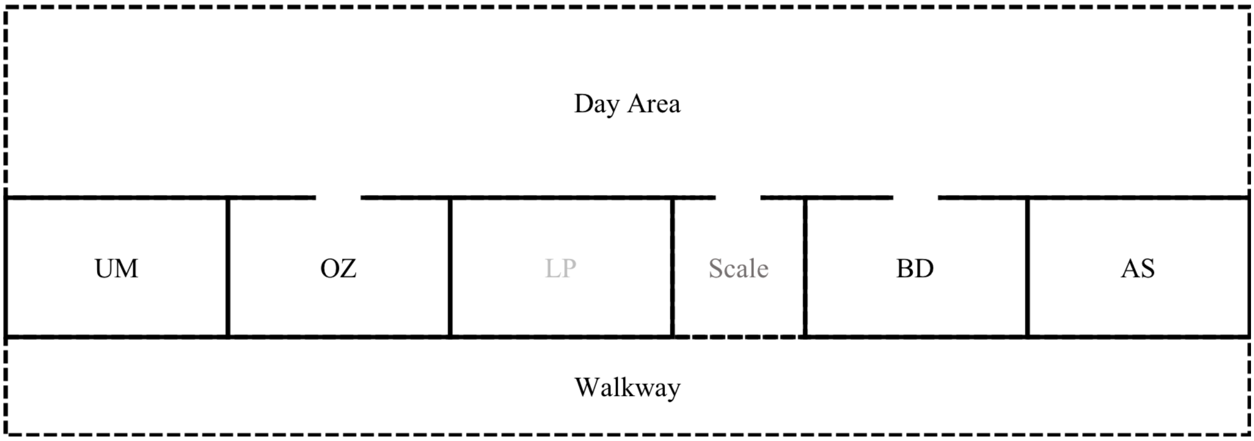
CHAPTER 8: END PAGES

8.1 Appendix

APPENDIX TABLE OF CONTENTS

APPENDIX A: GORILLA SLEEPING AREAS.

Used to illustrate that UM & OZ could not have seen one another, owing to an obstruction in the form of the scales. Container was placed into the walkway. Note, although LP’s bed area is marked, he did not have the opportunity to participate in study 2 of chapter 3.



APPENDIX B: PREREGISTRATION

This was placed on the OSF website prior to the study beginning. This is available at DOI: 10.17605/OSF.IO/GPV54 as:

Neadle, D., Chappell, J., Clay, Z., & Tennie, C. (2018, June 15). Effect of Social Learning Biases on Great Ape Imitative Capacities. https://doi.org/10.17605/OSF.IO/GPV54

B.1 Background

Action copying[3] has been argued to be the bedrock on which human (*Homo sapien*) cumulative culture rests (Boyd & Richerson, 1996)[4]. To date, no convincing evidence exists suggesting that action copying – "Learning to do an act from seeing it done" (Whiten & Ham, 1992) – is present in non-human animals. Furthermore, many would agree that action copying is a 'special' form of social learning that makes cumulative culture easier to access – if not, allowing it to develop in the first place (Tennie et al., 2009). Therefore, one would expect chimpanzees (*Pan troglodytes;* and other social animals) to have produced obvious forms of cumulative culture (similar to humans), if they were able to copy actions. As chimpanzees are, genetically, the most similar species to humans (along with bonobos; *Pan paniscus*) it is reasonable to expect that they would have similar abilities to humans (cognitive cladistics). The question then is, *can* chimpanzees spontaneously engage in action copying?

Earlier studies on action copying have neglected the potential for social learning biases. These can be defined as a factor that varies the likelihood of an individual to express a given trait after seeing it in others (Henrich, 2001). Henrich (ibid) identified three forms of social learning (or "transmission") biases: direct, prestige and conformist biases, argued

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[3] Action copying, defined here, is similar to imitation. However, crucially, here we do not assume that action copying requires the copier to understand the goals of the demonstrator, simply, they must show the same actions, hence the distinction. Otherwise, the terms are interchangeable.

[4] This is a contentious conclusion, with some studies suggesting that action copying is in fact *not* required for cumulative culture to occur in humans (Caldwell & Millen, 2009; Reindl et al., 2017).

likely to give social learning, and culture, an *adaptive* direction (Richerson & Boyd, 2005). Conformist biases (or "conformist transmission") should not be confused with conformity (Watson et al., 2018). Conformity is defined as abandoning an existing behaviour in favour of that of the majority (Acerbi, van Leeuwen, Haun, & Tennie, 2016; Haun et al., 2014; Haun & Tomasello, 2011). Whereas, conformist transmission is defined as an individual adopting the behaviour of the majority (this definition makes no stipulations about prior behaviours; Watson et al., 2018); conformist transmission has also previously been termed "majority-biased transmission" (Haun, Rekers, & Tomasello, 2012). Both conformity and conformist transmission will be discussed below, however, conformist transmission is the main focus of this empirical work.

The common factor in any operationalised definition of conformity or conformist transmission is that the learner must adopt the behaviour of the "majority of individuals" (Haun & Tomasello, 2011; van Leeuwen & Haun, 2013). However, it is important to note that it is often difficult for an external observer to determine which demonstrator(s) an observer is learning from (van Leeuwen, Acerbi, Kendal, Tennie, & Haun, 2016). It is important – for the question of conformity or conformist transmission – to determine whether a behaviour has been socially learned, through simple social learning (in any form) or whether a learning bias has acted. For example, van de Waal et al. (2013) argued that their study with wild Vervet monkeys (*Chlorocebus pygerythrus*) showed evidence of conformity, however, it was not possible to confirm that observers were not simply copying a dominant individual, which was a key argument in a later rebuttal (van Leeuwen et al., 2016). Indeed, Galef & Whiskin (2008) showed that it is possible to replicate behavioural patterns, similar to those caused by conformity/conformist transmission, in rats with only a single demonstrator. These cases, where only a single demonstrator is implicated, do not constitute conformity or conformist transmission and are simply caused by social learning. However, more recent research in great apes has shown that chimpanzees and humans (but not orangutans) are more likely to take on the behaviour of a majority – even when the number of demonstrations is matched across a majority and minority condition (Haun et al., 2012); therefore suggesting that the influence of a majority is greater than simply social learning.

There have been claims that conformity is present in several species[5], one of the most commonly cited examples are humans: in human psychology one classical example is Asch's (1956) study. This study showed that participants would adopt a demonstrated viewpoint, that they clearly knew to be (or previously believed to be) false, in order to fit with a majority. Conformity has also been inferred in wild chimpanzees (Luncz, Wittig, & Boesch, 2015), where immigrant females' tool use patterns become more similar to their new group compared to their original group. Immigrant females from one group increased their proportion of stone hammer use – for nut cracking – upon moving to a new group that used stone hammers more often than their previous group. It was shown that the immigrant females were indistinguishable from others in the new group, after just one season of observation[6].

This said, claims of conformity have not been without criticism; with critics often stating that it is difficult (if not impossible) to identify conformity simply from observing behaviour, as it cannot be certain that the behaviour shown by a majority is copied (as opposed to, for example, one salient[7] individual; Acerbi et al., 2016; van Leeuwen et al., 2016; van Leeuwen, Kendal, Tennie, & Haun, 2015). Nevertheless, given that the first evidence for conformity from controlled captive work has been shown in chimpanzees (Haun et al., 2012, 2014), it is possible that chimpanzees indeed conform – to some degree.

Given that there is so far no convincing evidence for true behavioural action copying in untrained and unenculturated great apes (Clay & Tennie, 2018; Tennie et al., 2012), research should aim to test for the possibility that true action copying is within the capabilities of these species after all, using all possible means to do so – in this case we

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[5] Chimpanzees (Whiten, Horner, & de Waal, 2005), orangutans (*Pongo pygmaeus & Pongo abelii;* Whiten & van Schaik, 2007), rats (*Rattus norvegicus*; Galef & Whiskin, 2008), Vervet monkeys (E. van de Waal et al., 2013), sticklebacks (*Pungitius pungitius*; Pike & Laland, 2010) & humans (Haun et al., 2014). Note, that each study represents just one example in each species, and this list is not exhaustive, to produce such a list would be beyond the scope of this empirical work.

[6] It is worthy of note that there are no direct observations from the previous groups. Therefore, artifacts left behind at nut cracking sites were used as a proxy, to determine the tool use proportions in previous groups and therefore infer prior behaviour patterns. These inferences separate the conformity claim from one of conformist transmission.

[7] No assumption is made here about what makes that individual salient.

intend to implement social learning biases, i.e., conformist transmission/conformity. We have noticed that, so far, studies aiming to elicit true action copying in these animals have failed to make use of social learning biases, such as conformist transmission, which have been shown to have an effect over and above that of single demonstrator social learning alone (Watson et al., 2018). However, the introduction of social learning biases (and especially conformist transmission) may be key, it may allow the discovery of true action copying in a sample of untrained, unenculturated, non-human great apes. Here we will fill this knowledge gap. We will adapt parts of the methods of Haun et al's (2012, 2014) studies on conformist transmission and conformity (respectively) in ape's general social learning (Haun et al's studies were not designed to determine or isolate underlying social learning mechanisms; so, local enhancement, for example, might have been implemented). Haun et al. (2014) used an experimental design that exposed three species of great ape (two year-old human children, adult chimpanzees and adult orangutans; all exposed to the same task) to a group of three demonstrators who exhibited a different location strategy (placing an item in one of three locations) from the strategy individually learned by the participant. The results showed that human children were significantly more likely to conform to the demonstrators' location strategy than the other species of great ape tested (which did not significantly differ when compared to one another; however, only one chimpanzee ever switched strategy, and no orangutan ever did). This was interpreted to be evidence of conformity in humans, but not in other species of great ape.

Haun et al.'s general method of using a majority of demonstrators to induce social learning (similar to Asch's (1956) original) will be used in the present study. However, as it remains unknown whether the introduction of conformist transmission will be sufficient to stimulate action copying in a sample of non-human primates, we will also test this here. We combine Haun et al's (2012, 2014) method of social conformist transmission/conformity demonstrations with a task that has been shown to result in *true* action copying in humans. This task was taken from Clay and Tennie's (2018) comparative study of human children and bonobos. It involves the demonstration of novel actions with a novel object that is baited and is opened after demonstrations. As no previous studies have attempted to use social learning biases to act as a catalyst for action copying we cannot make predictions about the results.

However, *if* social learning biases, in this case conformist transmission, can lead to action copying in our task, then this will be evidence that non-human primates *are capable* of action copying, even if this may not occur in other situations.

B.2 Method

B.2.1 Subjects

We will aim to test all species of great ape at the Wolfgang Köhler Primate Research Center, Leipzig, Germany; however, owing to time constraints it is likely that testing only chimpanzees and bonobos will be possible. In case of this, we would aim to use the Sumatran orangutan and Western lowland gorilla (*Gorilla* gorilla) samples at the Wolfgang Köhler Primate Research Center as a "pilot" and their data would be added to supplementary material for reference. This study will operate on a volunteer basis, it is possible therefore that subjects choose not to participate in the study (either by not entering testing rooms or by wanting to leave the room before the test). Individuals will need to be tested separately (mothers and their offspring are acceptable, however, testing dyads will be avoided where possible). Due to the strong dominance hierarchies in many ape species[8], if only one puzzle box is used per demonstration it is possible that only dominant individuals would gain possession. Most importantly, we need to establish a majority influence of demonstrations, in both sexes (see below) and this can only be practically be achieved for single observer subjects (and only partly for testing dyads). If testing dyads the demonstrators can merely achieve a smaller (2:4 as opposed to 1:4) overall numerical majority. Establishing an effective majority (most effective being 1:3 or greater; Bond & Smith, 1996) is essential for testing conformity/conformist transmission. We aim for a minimum of three trials for each individual. Subjects will be randomly allocated to experimental and baseline conditions (though note that a baseline condition would only be necessary if evidence of action copying

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[8] Chimpanzee, gorilla and orangutan dominance hierarchies are patriarchal (Goodall, 2005), i.e., a male is usually at the top of the hierarchy, whereas, bonobos exist within a matriarchal society (Gruber & Clay, 2016). Note, that the finer details of bonobo hierarchies are more complex than this, however for the purpose of this study a more coarse approach shows the differences that may exist between sexes.

is found, so we follow a study design that flexibly adjusts to outcomes; details below). Each subject will be assigned a randomly generated number, subjects will then be tested in ascending numerical order in order to randomly assign subjects to conditions. Each trial should take no longer than 15 minutes from the beginning of the demonstration to the end of testing (see below); thus, a total of 45 minutes testing time would be required with each subject across all trials.

In accordance with the recommendations of the Weatherall report "The use of non-human primates in research" all subjects will be housed in semi-natural indoor and outdoor enclosures containing climbing structures, such as ropes and platforms; and natural features, such as vegetation, trees and streams. They will receive their regularly scheduled feedings, primarily consisting of vegetables, have access to enrichment devices including shaking boxes and poking bins, and water ad lib. Subjects will never be food or water deprived for the purposes of this study. All research will be conducted in the observation rooms.

No medical, toxicological or neurobiological research of any kind is conducted at the Wolfgang Köhler Primate Research Center. This research will be non-invasive and strictly adhered to the legal requirements of Germany, where the study will take place. The study has been ethically approved by the University of Birmingham AWERB committee (reference no. UOB 31213) and by Dr. Daniel Hanus, lab coordinator at the Wolfgang Köhler Primate Research Center, following SSSMZP, EAZA and WAZA protocols on animal research and welfare.

Animal husbandry and research comply with the "European Associations of Zoos and Aquaria Minimum Standards for the Accommodation and Care of Animals in Zoos and Aquaria", the "World Association of Zoos and Aquariums Ethical Guidelines for the Conduct of Research on Animals by Zoos and Aquariums" and the "Guidelines for the Treatment of Animals in Behavioral Research and Teaching" of the Association for the Study of Animal Behavior. IRB approval is not necessary because no special permission for the use of animals in purely behavioural or observational studies is required in Germany.

B.2.2 Stimuli

All trials will centre around a ‘puzzle box’ previously used in an action copying non-majority demonstrator experiment (see Figure 1; Clay & Tennie, 2017). We will use two variants: the “demo” box and the “test” box. In order to remain consistent with the previous study, the demo puzzle box would be made from a piece of non-toxic wood, cut in half, with a small depression (shown in red) cut into the centre of the bottom half (shown in blue in this figure, and indicated by a double headed arrow), and cut horizontally as shown by line A. This demo box (used by the demonstrator humans) would never be provided to any animal. The test box (that will be handed to the apes) would be a cylindrical piece of wood, visually, identical to the demo box. Although this version of the box would be a visual replica of the demo box, in reality the test box cannot be opened, as it is simply a piece of wood (matched in dimensions to the puzzle box) with a line scored horizontally (see right hand image in Figure 1) around the edge. The use of a dummy box for the test box is aimed to imply to the subjects that an additional step may be needed to open the box, therefore potentially acting as a further catalyst for action copying (note a similar setup was used also for children and bonobos by Clay and Tennie (2018)).

Figure 1. The ‘puzzle box’: schematics are shown far left; the demonstrators’ box in the centre and the subjects’ box far right.

B.2.3 Procedure

B.2.3.1 Actions

Demonstrators will be trained on the below demonstration procedure prior to testing. Human training on how to perform the demonstration will last for 1 hour each – with each demonstrator having previously been provided a video of DN modelling the demonstration once (S1), demonstrators will be required to copy DN's actions and speed of performing those actions during demonstrations. DN and CT will observe each demonstrator prior to testing beginning, to determine whether their demonstrations are proficient; videos of each demonstrator (after training) will be published along with the final paper. Demonstrator action consistency checks will also be performed after each week on testing, allowing a retraining procedure to be implemented if necessary.

B.2.3.2 Demonstrators

Half of the human demonstrators (N=4) will be male (n=2) and half will be female (*n*=2). Demonstrators will also be of roughly similar age (all adults between the ages of 25-30). None of the demonstrators will be zoo staff. In order to reduce possible order effects, subjects will be randomly allocated to each possible iteration of demonstrator order or randomised to one demonstrator of the original four (in the single demonstrator condition, see below).

B.2.3.3 Actions to copy

Human demonstrators will perform two actions with/above the demo box whilst standing outside the enclosure; two actions will be demonstrated (based on Clay & Tennie, 2017). Both actions will be preceded by demonstrators extending their arms away from their bodies, holding the box, and performing the following actions with their arms extended. The first action is "Rub", the demonstrator rubbing the back of the right hand in a consistent, but slow, circular, clockwise, motion across the top of the box, four times (Rub lasts 1 second per circle – 4 seconds total). The second action is "Rotate", the demonstrator raises the right hand and rotating it, at the wrist, in a clockwise motion, four times (Rotate lasts 1 second per rotation – 4 seconds total). The demonstrator will then open the box, show the contents of the box (a grape) to the subject and give the grape from inside to the subject through secure "food chutes". This action is used in the conformist transmission condition – see Figure 3.

Action for conformity condition

In order to demonstrate conformity, as opposed to conformist transmission, it is necessary to demonstrate that the subjects are able to abandon a previously adopted behaviour in favour of that displayed by the majority. Therefore, should the subjects adopt the Rub-Rotate behaviour in the conformist transmission condition, human demonstrators will demonstrate, to them, a second action "head touch" – with all other aspects of the demonstration remaining the same[9]: the conformity condition (see Figure 3). The action involves the demonstrator holding the box (top side up) in both hands and raising it to their forehead twice (the action takes 8 seconds total – 4 seconds for each iteration). This is done, before opening the box and providing the subject with the grape, through the "food chutes". Human demonstrators will be trained in the head touch action to the same degree as they were with the Rub-Rotate actions, and in the same way.

This action will also be used in the final 33% of the subjects, if the data shows that the naïve subjects spontaneously express the Rub-Rotate action in the baseline condition (see below). This would then require a test with a novel action (namely head touch).

B.2.3.4 Logistics of testing

To ensure that the subjects have been given the best chance to witness the demonstrations, demonstrators will face subjects (with their head and body) throughout. In addition, two further measures will be put in place. First, each demonstrator will wear a GoPro™ camera[10], mounted to their chest. Prior to performing their demonstration procedure, described above, the demonstrators will ensure that the subject is attending to them – here we define this as having gazed in the general direction of the box (and therefore, the demonstrator) for one second or more. If not, demonstrators will gain the subject's attention by calling their given name – the subject's name may be used to gain their attention

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[9] The difference between the conditions will be the Rub-Rotate action will be substituted for the head touch action.

[10] GoPro Hero Session 5 (4K capable), set to 1080p 60fps video.

as often as is required. Once the subject is attending to the demonstrator (defined as head positioned towards them), each will begin their demonstration. All demonstrators will code inwardly whether the subject was attentive during the demonstration of each individual action (i.e., whether they observed each action for at least one second – which directly relates to one repetition of each action). After the demonstration, all demonstrators will say out loud (in order of demonstration; by simply saying yes/no to each action) whether the subject observed the *whole* demonstration[11]. If the subject did not observe the whole demonstration (to the satisfaction of the majority – i.e. at least ¾ of the demonstrators), then that demonstrator will repeat their demonstration (up to a maximum of five times), the next demonstrator will follow the same procedure, and so on until the subject has had the chance to observe the full demonstration. After the trial, parts of the demonstrations observed (i.e., which actions: Rub/Rotate/Both), along with which demonstrators were successfully observed, will be noted[12].

The second measure will be achieved through post-hoc data analysis, whereby each of the demonstrator’s GoPro footage will be analysed and a percentage of the total demonstration time that the subject attended to the demonstrator will be calculated. This will be measured by the amount of time that the subject spends with their head inclined towards each respective demonstrator (regardless of where the body is facing).

All trials would also be additionally video recorded, using two cameras mounted on small tripods (positioned at either end of the line of demonstrators). These recordings would be stored redundantly on several hard drives and later backed up to Max Plank Institute and University of Birmingham servers at the first opportunity.

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[11] For example, a subject having seen both actions would lead to a call out of “yes, yes”, only seeing the “Rub” demonstration would lead to “yes, no”, etc.

[12] This will be achieved by demonstrators noting inwardly during the trial and then reporting the actions observed after the trial has ended, as with determining how much of the trial has been observed.

B.2.4 Trial

B.2.4.1 Timings

The subject will have, after the demonstration, three minutes to complete the task (defined as at least attempting to reproduce the demonstrated action – see conditions section below). If they complete the task, the trial will end immediately. If they fail to complete the task within three minutes, and were not touching the box in the last 30 seconds, then the trial would end (Clay & Tennie, 2018). Should the subject be touching the box (with any body part) in the last 30 seconds of the initial three minutes, then a further one minute of testing time would be added, and a further one minute would also be added at the end of this minute if the subject was still in recent contact with the box (i.e. within the last 30 seconds of the previous, i.e. fourth minute). This would result in a maximum testing time of five minutes (see Figure 4). If the subject successfully demonstrated the behaviour, at any point during the trial, then they would be given a whole grape (or appropriate food) as a reward.

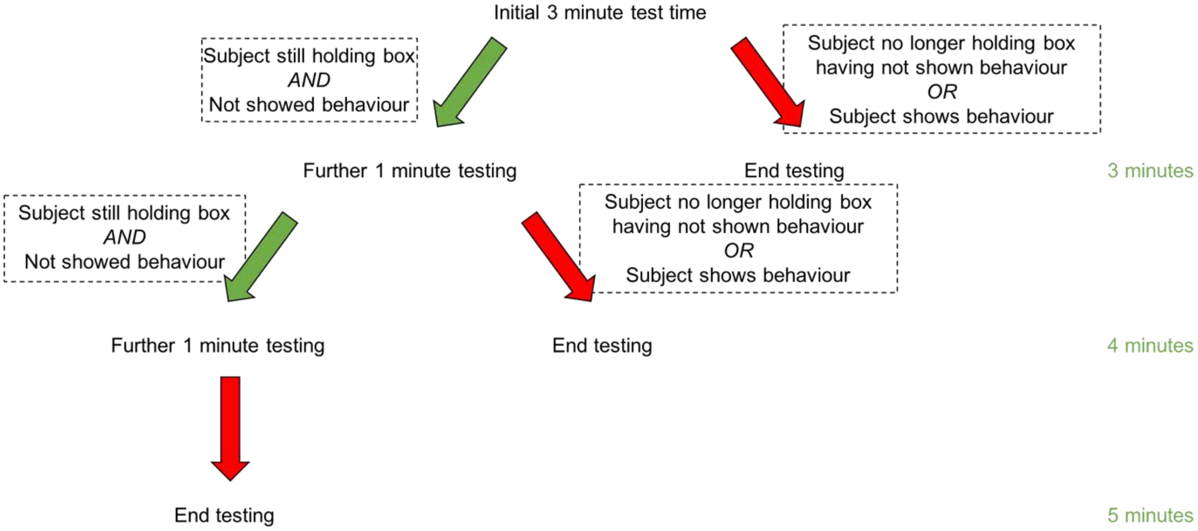

Figure 2. Decision tree for each stage of testing, green arrows relate to testing continuing, red arrows relate to testing ceasing.

B.2.4.2 Retrieval of test box

Whenever the trial stops (regardless of whether this is due to action copying being identified or the allotted time running out) the box will be retrieved. It is possible that the box will be given back to the researchers at the end of the trial (or before this) in which case the box will be accepted and the trial will end. If not, and the trial ends, the ape will be offered half a grape (or 50% of whatever food is used as a reward; in trade) in order to retrieve the box. The addition of a smaller piece of food in trade, even following an unsuccessful trial, is to reduce the chance that subjects do not become trained to assume an equal reward for non-success. Some subjects may hold on to the test box, but the box would need to be retrieved before the subject is allowed to re-join the rest of the group. This would be by way of the subject having to place the test box in the Futterklappe[13]. This might prove difficult and we might need the experienced keepers' help for this. Should a subject refuse to give back the box for a half grape (or half of whatever reward is used in the study), we would increase the

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[13] This is a two way system that allows researchers and subjects at the Wolfgang Köhler Primate Research Center to pass objects between one another safely, without needing to come into direct contact.

quantity/quality of food offered to the subject in order to get the box back, at the rate of half a grape per minute, this would continue until the box is traded for the food. Any time that the subject requires the food trade to be increased in order to retrieve the box the trial will be flagged for potential later analyses[14].

A typical trial should last no longer than 15 minutes from start to finish and would require the demonstrators to all stay throughout the trial (to ensure that that the effect of the aimed social learning bias (if any) is constant throughout the trial (see Haun et al., 2014). We aim to use the same human demonstrators for all individuals, to ensure reliability. During the conformity trials, the demonstrators will remain in their line and during the testing time will stand with their hands clasped at their waist, no less than 1m from the enclosure (or out of arms reach of the subjects; see Figure 5) ; this is to attempt to control for any distractions that the demonstrators may cause.

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[14] This is because there is a possibility that the subjects will become conditioned to doing nothing with the box and simply holding onto it, in order to get a larger reward.

B.2.5 Conditions

B.2.5.1 Flexible design

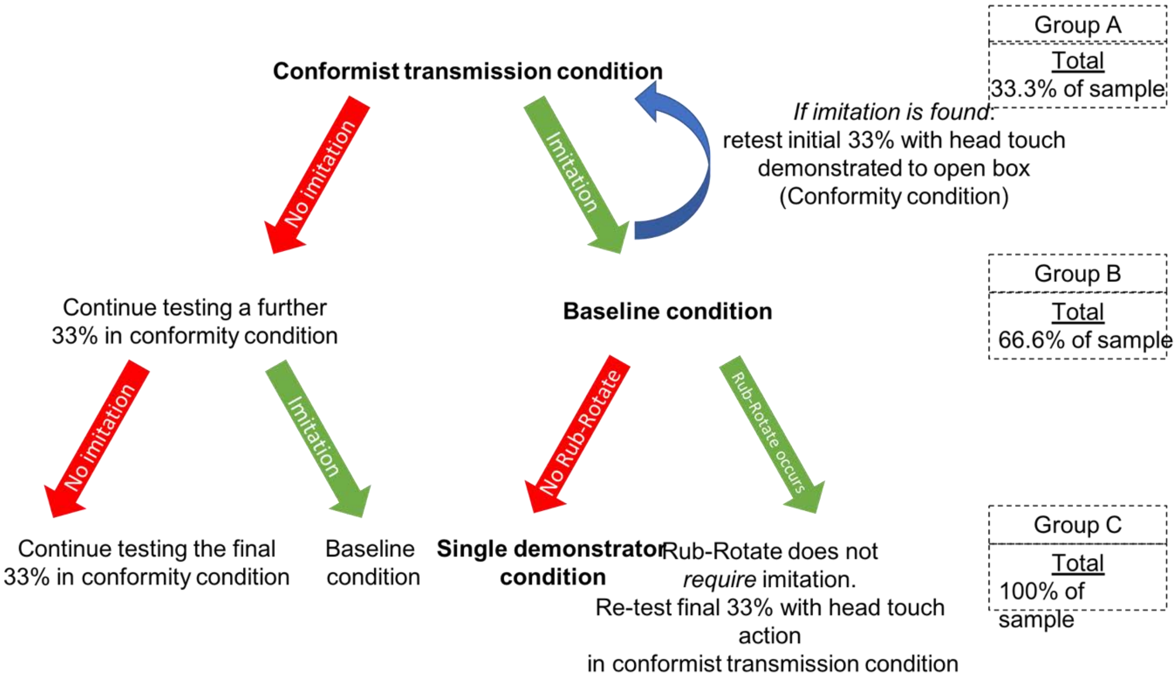

Figure 3. Green arrows represent successful display of the behaviour at that stage, and red arrows represent failure to display the behaviour. Note that at each stage the additional subjects are still naïve to the behaviour, as this is a between subjects design. The pathway through the decision tree that allows for each condition to be implemented is displayed in bold. See below for coding.

Throughout this study we are using a flexible, result-dependent design. This means that unless the relevant behaviour is expressed (see below for criteria) in the previous condition, the next test condition will not be completed. For example, if group A do not express the Rub-Rotate behaviour[15] in the conformist transmission condition (to do so would be considered evidence of action copying) then group B (that would have taken part in the baseline condition had action copying occurred) will be absorbed into the conformist transmission condition (see Figure 3). This is to give the best chance that at least one subject

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[15] Meaning: they express the Rub behaviour, Rotate behaviour or both.

within the sample is likely to express evidence of action copying, with the assistance of conformist transmission.

The only way that all test conditions can be completed is for evidence of action copying to be identified in the first conformist transmission condition (1st 33% of subjects); then, for no evidence of the Rub-Rotate behaviour to be expressed in the baseline condition (2nd 33% of subjects), which would lead to the final 33% of subjects participating in the single demonstrator condition. Each of these conditions is described below.

During testing, behaviours will be live coded to inform the next step based on Figure 3, behaviours will be live coded[16]. This will follow the criteria of Clay and Tennie (2017), being a simple binomial decision, i.e., did the subject sufficiently copy the actions that were demonstrated to them or not? This uses the coarse-grained system described below. However, to ensure reliable live coding, *after* each trial each demonstrator will independently write down whether they considered the subject's actions to constitute action copying (i.e., were they, *according to their view*, the same as the demonstrated action; see Table 1). The paper on which the live coders have written their decision will be folded in half and placed into a box[17]. These will then be counted, after the trial, if more half (i.e., 3 or 4) of the demonstrators agree that the subject displayed action copying then it will be considered that action copying has been found in that trial (and thus, that condition) and the appropriate path on the decision chart above will be followed.

Given that there are at least two distinct actions in this study (i.e., Rub *and* Rotate) approximations (i.e., just one of the two actions) at the demonstration will be live coded as *attempts* at action copying; these will be treated as action copying for the purpose of the decision tree. Demonstrators will be trained on, and provided with a copy of the ethogram (see Table 1), and videos of DN performing each of the behaviours in the ethogram prior to any testing occurring, this is to ensure that all demonstrators are clear on what behaviours

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[16] Meaning that the researchers present will make instantaneous (i.e., in the moment) decisions as to whether the behaviours expressed constitute the behaviours described in the ethogram, and therefore action copying.

[17] This is done independently to avoid the effect of majority influence altering the perception of the demonstrators (Asch, 1956).

count as approximations. This means that any behaviour that is defined in the ethogram (see Table 1) will be considered as "successful", which would allow the study to progress to the next condition in the decision tree. These attempts will be further analysed, from video footage with a reliability coder, after testing is completed to determine to what extent action copying occurred.

Table 1. Ethogram, given to coders, detailing the exact action behaviours. This will be accompanied by videos of DN performing the actions. Note that approximations of these behaviours will also be coded, for example a single "Rub" with the left hand will be considered as an attempt at action copying (this attempt will be qualified in the post-hoc video analyses but will be classified as a "yes" in the binomial code).

Behaviour	Description
Rub	The subject places the back of their hand (either hand), on top of (or close above) the box and rubs it in a circular motion (regardless of direction).
Rotate	The subject raises their hand (either hand) and rotates – for a minimum of 180˚ it at the wrist (regardless of direction).
Rub-Rotate	The subjects performs the "Rub" behaviour, and this is followed by the "Rotate" behaviour
Rotate-Rub	The subjects performs the "Rotate" behaviour, and this is followed by the "Rub" behaviour
No relevant behaviour	The subject performs none of the actions described here

B.2.6 Social learning bias

B.2.6.1 Conformist transmission

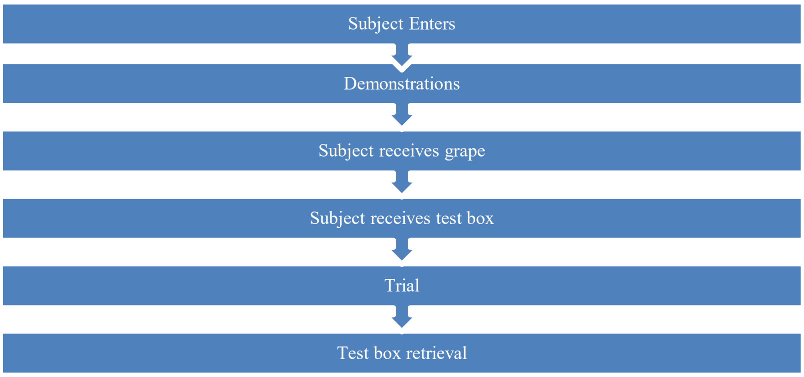


Figure 4. Flow chart of social learning bias transmission conditions (conformist transmission and conformity), demonstration phase is described in more detail above

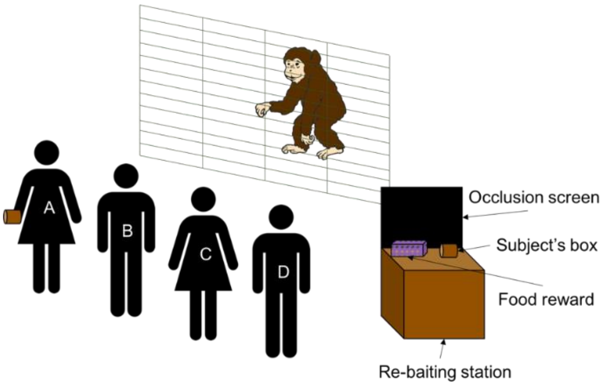
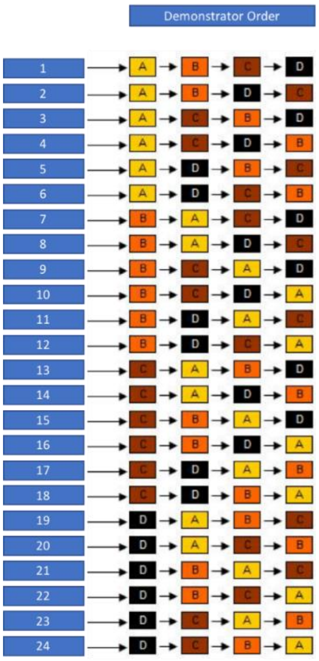


Figure 5. Experimental set up for the conformist transmission condition.

This condition will involve testing at least the first 33% of subjects.

Demonstrators will stand in a line, facing the enclosure, no less than 1m (or out of arms reach of the subjects) from the enclosure prior to the subjects entering the enclosure. Once the subject is inside the enclosure the demonstration phase of the trial will begin. In the conformist transmission condition subjects will have the opportunity to observe eight, full, demonstrations of the actions (see above). Demonstrators will proceed to perform the Rub-Rotate actions (see above) individually, from the demonstrator's left to the demonstrator's right (e.g., in the case of Figure 5, A, B, C, D); the order of the demonstrators will be randomly assigned across subjects with each subject being assigned a random number between 1 and 24, which relates to demonstrator order in Figure 6. Once each demonstrator has individually demonstrated the actions, all four demonstrators will perform a group demonstration. Each subject will then have the initial 3 minutes in order to complete the actions, followed by two additional minutes should they remain in contact with the box (see Figure 2).



Demonstrator Order

1 → A → B → C → D
2 → A → B → D → C
3 → A → C → B → D
4 → A → C → D → B
5 → A → D → B → C
6 → A → D → C → B
7 → B → A → C → D
8 → B → A → D → C
9 → B → C → A → D
10 → B → C → D → A
11 → B → D → A → C
12 → B → D → C → A
13 → C → A → B → D
14 → C → A → D → B
15 → C → B → A → D
16 → C → B → D → A
17 → C → D → A → B
18 → C → D → B → A
19 → D → A → B → C
20 → D → A → C → B
21 → D → B → A → C
22 → D → B → C → A
23 → D → C → A → B
24 → D → C → B → A

Figure 6. Demonstrator orders, each trial will begin with a random number (between 1-24) being generated, which relates to the order of demonstrators to be used in the group demonstration conditions (conformist transmission & conformity).

B.2.6.2 Conformity condition

This condition will involve testing only the subjects that displayed evidence of action copying in the conformist transmission condition; as a result, the number of subjects in this condition could range from 0 to all 8 of the subjects from the conformist transmission condition. This will essentially be a “side condition” where the subjects are retested, the next 33% of the sample will be tested in the baseline condition should action copying arise.

This condition is provisional on evidence of action copying in one group. Should evidence of action copying be found, then we will use this condition to determine whether subjects abandon a previously adopted method in favour of that displayed by the majority (thus fulfilling the definition of conformity described above). In order to test this, a different action will be implemented (head touch, see above). This condition will be exactly the same as the conformist transmission condition, with the only variation being that a different action will be demonstrated.

B.2.6.3 Baseline condition

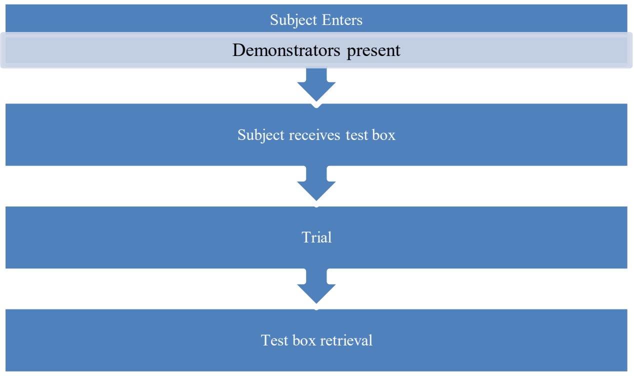


Figure 7. Flow chart of baseline condition, note that although the same demonstrators are present during this condition they do not demonstrate any of the actions described above. This condition is therefore likely to be shorter than the social learning bias conditions.

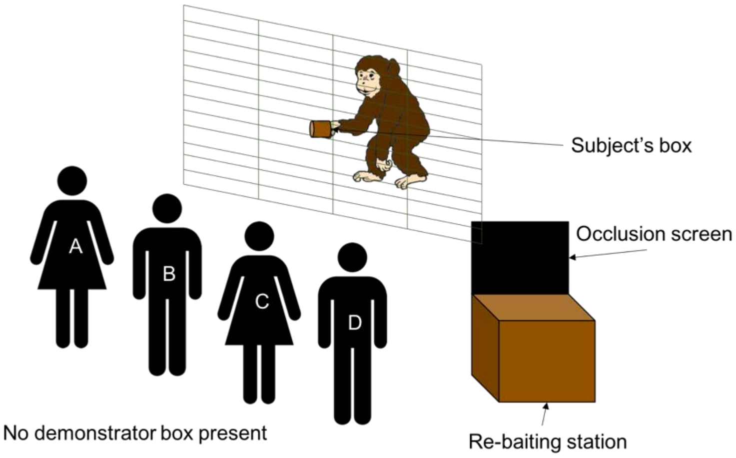


Figure 8. Experimental set up for the baseline condition (after provisioning the ape with the box), note that demonstrator boxes are not present in this condition, this is designed only to test the baseline behaviours, i.e., with no demonstrations.

This condition would involve the next – randomly selected – 33% of the sample (this could be either the second 33% or the final 33% depending on the result of the previous conditions), thus, the subjects in this condition would be different to those in the conformity condition[18]. For the baseline condition we would not provide subjects with any demonstrations. They would still be tested individually. After a sham baiting (same as in the test condition above) subjects would be handed the test box by a demonstrator. Testing times would remain the same as before (i.e. maximum of five minutes, including two possible time extensions). During the baseline trial the same four demonstrators (from the conformity condition) will be present and standing in the same way, but not performing any demonstration; this is to control for a possible effect of social presence. The order of the demonstrators will once again be decided by way of generating a random number and matching it to the chart in Figure 6; the demonstrator closest to the "Futterklappe" will pass the box and rewards to the subject.

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[18] This assumes that evidence for action copying is found in the conformist transmission condition, with the previous group. Should this not be found at all, then this condition would not ever be used. Please see Figure 3 for a decision chart depicting the process of which condition will follow depending on the outcome of the previous condition.

B.2.6.4 Single demonstrator condition

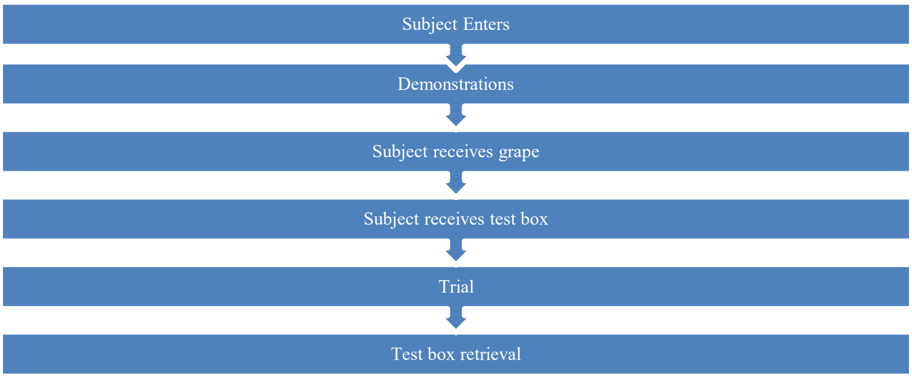

Figure 9. Flow chart of the single demonstrator condition, note that this condition contains the same number of demonstrations as the social learning bias condition, however, all demonstrations will be performed by a single (randomly selected, demonstrator – from the original four.

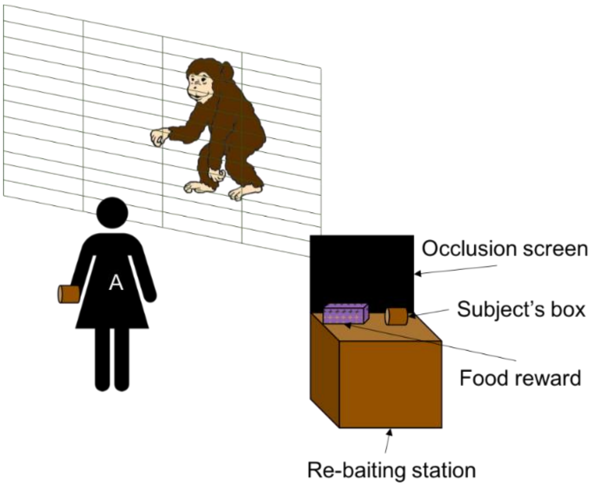

Figure 10. Experimental set up for single demonstrator condition (here with a female experimenter)

This condition would involve the final 33% of the sample. These subjects would not have taken part in either the conformity condition or the single demonstrator condition. In the single demonstrator condition the procedure would be mostly identical to the conformity condition, however a single demonstrator (subjects will be randomly assigned to a demonstrator using a random number generator at the start of each trial) would perform the same demonstration (i.e. Rub-Rotate) for eight successful times to control for the number of demonstrations in the conformity condition (described above). Repeat demonstrations would happen according to the same rule as described in the conformity condition.

Note, bonobos have already been tested in a single demonstrator condition with these very actions and type of box in Clay and Tennie (2018), which demonstrated that bonobos did not display evidence of action copying. As a result the bonobos in our sample will never be tested in this condition, and instead the bonobos will be split 50-50 across the conformist transmission (and conformity if the Rub-Rotate behaviour is found) and baseline conditions. Should evidence of action copying not be found in the first 50% in the conformist transmission condition the final 50% (initially assigned to baseline) will be absorbed into the conformist transmission condition to determine whether the social learning bias of conformist transmission is sufficient to result in action copying, where a single demonstrator has previously failed (Clay & Tennie, 2018).

B.2.7 Analyses

All analyses will be performed in R and R Studio (most recent versions available). Behaviours will be coded in "attempts", where if the subject relinquishes contact with the box (for more than 1 second), the attempt is considered to end, the next "attempt" begins when contact is re-established. An attempt will consist of any behaviour that meets *any* of the criteria in Table 1.

B.2.8 Coding

All videos will be viewed by DN prior to any coding, the video that DN perceives to have the best view of the subjects will be used. Only one video type and angle will be used for coding and later analyses per trial.

B.2.8.1Interrater reliability

Prior to DN coding the entire data set, an independent naïve (to the conditions and hypotheses) second coder and DN will independently code a randomly selected 33% of videos using a “fine grained” *and* “coarse grained” style. This will distinguish between attempts at action copying (coarse grained) and degrees of action copying (fine grained).

Coarse grained

Coarse grained, attempts at action copying, will be described in the most basic terms, this is simply any attempt that relates to any part of the ethogram in Table 1. This will be completed on the first viewing of each video, coders will be required to state (binomially) whether or not the subjects made an approximation at the behaviour(s) demonstrated to them. This will be done using the ethogram above (see Table 1). The observations of DN and the second coder (i.e., which, if any, actions were performed) in the coarse grained coding will be compared to one another using Cohen’s Kappa, a minimum Kappa value of 0.6 (Cohen, 1960; McHugh, 2012) will be required before coding will be considered reliable.

Fine grained

This will be completed after the coarse grained coding, coders will be required to state, in detail, how similar the behaviours, considered at least as “attempts” at action copying, are to the behaviours that were demonstrated. This will include, the order of the behaviours expressed (one behaviour, Rub-Rotate or Rotate-Rub) the hand that is used to perform the action (Left or Right) and the number of iterations of the behaviour(s) expressed (this will be coded separately for Rub and Rotate); see Table 2. Cohen’s Kappa values will be calculated for each of the above coding categories (N=4; Order, Hand, Rub Iterations and Rotate Iterations). A minimum Kappa value of 0.6 will be required for each category, to ascertain reliability (Cohen, 1960; McHugh, 2012) before full coding is considered reliable.

Full dataset

The coding of the complete data set will be performed by DN. This will combine coarse and fine grained coding methods (i.e., was an attempt made *and* how similar was that attempt to the demonstration). Success will be defined as adherence to methods demonstrated, and will be coded using a points system (see Table 2). Attaining even the minimum number of points possible (3; only one action, performed once with the left hand) will be evidence of some degree of action copying – provided that the corresponding action is not identified in a baseline condition. However, the degree of action copying that is expressed by each successful attempt will be scored on a scale of 3-15; where 15 is full, high fidelity, action copying (*both* actions performed, with *4 iterations each*, in the *Rub-Rotate order*, using the *right* hand). Anything less than full action copying will be considered an approximation, the fidelity of which can be measured by the percentage of similarity to the full demonstration (higher percentages = higher fidelity).

Table 2. Points system to be used during the video coding, this will determine the degree of action copying – even a minimum score (3) will be considered as weak evidence of action copying (which remains a novel finding) where a higher score (to a maximum of 15) indicates proportionally greater degrees of action copying fidelity. Note, values in bold signify those that were demonstrated and therefore the "correct" actions.

Fine grained variable	Description	"Score"
Number of Rub iterations	The number of times the individual replicated the Rub action performed 4 times by the demonstrator	0 = 0 points 1 = 1 point 2 = 2 points 3 = 3 points **4 = 4 points** 5 = 3 points 6 = 2 points 7+ = 1 point
Number of Rotate iterations	The number of times the individual replicated the Rotate action performed 4 times by the demonstrator	0 = 0 points 1 = 1 point 2 = 2 points 3 = 3 points **4 = 4 points** 5 = 3 points 6 = 2 points 7+ = 1 point
Hand used for Rub action	The hand that the individual used when replicating the Rub action performed by the demonstrator using the right hand.	Neither = 0 points Left = 1 point **Right = 2 points**
Hand used for Rotate action	The hand that the individual used when replicating the Rotate action performed by the demonstrator using the right hand.	Neither = 0 points Left = 1 point **Right = 2 points**
Actions replicated	Which of the actions were replicated by the subject and in which order; demonstrator used Rub-Rotate	Rotate = 1 point Rub = 1 point Rotate-Rub = 2 points Other order = 2 points **Rub-Rotate = 3 points**
Number of Head Touch iterations[1]	*The number of times the individual replicated the Head Touch action performed by the demonstrator*	*1 = 1 point* *2 = 2 points* *3 = 3 points* ***4 = 4 points*** *5 = 3 points* *6 = 2 points* *7+ = 1 point*

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[1] Note, this variable will only be coded for in the case that the conformity condition is completed. This will not be added to any of the calculations for degree of action copying in the conformist transmission condition.

B.2.8.2 Statistical analyses

The possibility for statistical analyses is limited by the success of the conditions. It is possible that only one individual (or even none) will show any evidence of action copying[19], in which case statistical analyses would not be possible. However, the plan below assumes that all conditions are completed (following the highlighted line in the decision tree) and that sufficient individuals have displayed evidence of action copying in order to perform statistical analyses.

It is possible that no statistical analyses will be appropriate, due to small sample sizes. In which case, we will aim to describe any "attempts" and full replications of actions in detail using photograph and video evidence. Also, we will use descriptive statistics and frequencies to provide an overview of the data.

Degree of action copying

Action copying fidelity

A GLMM, with a binomial error structure[20], will be constructed, with an outcome variable of action copying fidelity (converted to a decimal from percentage; using fine grained coding). Predictors will be condition (conformist transmission or single demonstrator), sex, age, and rearing history (mother reared or human reared – this includes human training outside of that required for normal animal husbandry[21]). Random intercepts will include, the individual ID, as it is likely that each individual will contributed more than one data point per trial. Also included as a random intercept will be trial, because each individual will take part in three trials within each condition. The results of the model will

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[19] To date there is no evidence of action copying in non-human great apes, as a result it is not possible to predict how effective the use of a social learning bias will be in stimulating action copying.

[20] Binomial error structure was chosen as the outcome variable, action copying fidelity, has a minimum of 0 and maximum of 1 (when percentage scores are displayed as decimals).

[21] This will be determined by asking keepers about prior experiences of non-normal zoo training

determine the factors that significantly influenced the fidelity of action copying. The structure of the model is summarised in Table 3.

Table 3. Structure of planned model predicting degree of action copying fidelity (operationalised as % of score of possible 15).

Model	DV	Predictors	Random Intercepts
Fidelity	% of action copying fidelity	Condition, Sex, Age, Rearing history.	Individual, Trial

Latency to attempt to copy actions

A further GLMM, with a Gaussian error structure[22], will be constructed with an outcome variable of latency to copy actions (in seconds; this will be the time from the onset of the trial to the first evidence of action copying approximation – coded using the coarse grained coding). Predictors will be condition (conformist transmission or single demonstrator), sex, age, and rearing history (mother reared or human reared – this includes human training outside of that required for normal animal husbandry). Random intercepts will be individual ID and trial number, for the same reasons explained above. The results of this model will be used to determine which predictors influence speed at which an individual begins to approximate action copying, the structure of the model is described in Table X.

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[22] This assumes that the outcome variable *does* conform to a normal distribution. Should this not be the case an alternative error family will be selected.

Table 4. Structure of model predicting latency to begin action copying (here using the coarse grained coding structure, therefore a very minimal definition of what constitutes action copying).

Model	DV	Predictors	Random Intercepts
Latency	Time taken to approximate action copying (s)	Condition, Sex, Age, Rearing history.	Individual, Trial

B.3 Outcomes and interpretation

Should action copying be reliably identified in the conformity condition (without being identified in the baseline condition) this would be the first evidence, to date, of spontaneous, true action copying in non-human great apes. This finding would be a ground-breaking discovery for the fields of animal behaviour and cultural evolution and would support the supposition that great ape cultures may well be founded on mechanisms of *copying* social learning after all (e.g., action copying; Whiten et al., 1999). Moreover, this would dismiss any claims that great apes are generally unable to imitate novel actions spontaneously (Tennie et al., 2012). The findings of Tennie et al. (2012) when considered alongside that of Clay and Tennie (2017) and this new potential finding, would also make possible the claim: conformity biases are *necessary* for non-human primates to display action copying. This could then explain the geographical pattern of behaviours that have been shown in three of the four species of non-human great apes (Gorillas, Robbins et al., 2016; Orangutans, van Schaik et al., 2003; Chimpanzees, Whiten et al., 2001) using a similar logic to that used in human cases (e.g., in the anthropology of dance culture; Kaeppler, 1978). However, note that none of these conclusions hold if action copying will only be found weakly and or rarely. In that case, only some of the above assumptions will be negated (it would still not be parsimonious to explain whole population wide behaviours in apes by way of action copying).

However, should action copying *not* be identified in the conformity condition, to any degree, non-human great apes may not be able to spontaneously copy behaviours, and conformist transmission does not act as a "catalyst" for action copying. This finding would lend support to the notion that great ape cultures are built on a foundation of individual learning, the results of which are facilitated within cultures by non-copying social learning (e.g., stimulus enhancement). In this case, the idea that these cultures are based on socially mediated serial reinnovation, as is suggested by the Zone of Latent Solutions hypothesis, would have gotten further support (Tennie et al., 2009).

If action copying were to be identified, during the social learning bias conditions, then a baseline condition would follow. This condition is to ascertain whether the behaviour can occur by individual learning alone (thus, action copying is not parsimonious). Based on the results of Clay and Tennie (2017) this is unlikely, as their sample of bonobos failed to display this behaviour, *even when demonstrations were used*; however, given that this study uses bonobos *and* chimpanzees further verification is required. If evidence were identified during the baseline condition then it would be concluded that the Rub-Rotate behaviour *can* occur without action copying; thus the study will retest the conformist transmission condition with the head touch demonstration in the final 33% of subjects. Undemonstrated target actions in baseline would raise questions about the validity of the study by Clay and Tennie (ibid) as a study of copying novel actions, however, the main conclusion of the study would not change much: it would mean that bonobos do not even copy familiar actions (at least not in a non-conformity demonstration condition).

Should evidence of the demonstrated behaviour *not* occur at baseline, then (given that subjects were counterbalanced between conditions) it is unlikely that individual learning is sufficient for non-human great apes to express this behaviour. This would imply that either, great apes *cannot* perform the target behaviour (i.e., they are physiologically limited, this is grossly unlikely but remains a possibility), and/or they are insufficiently motivated (this is also a possibility, however, the provision of a high value food reward is usually sufficient for apes to perform most tasks, even those well outside of their species-typical repertoire; Biro & Matsuzawa, 1999). Should the demonstrated behaviour not be identified during the conformity condition, and again not at baseline then we would conclude that it is not within the capabilities of non-human great apes to imitate the behaviours of humans – even under a conformity demonstration condition; and in doing so, support the Zone of Latent Solutions hypothesis and the notion that spontaneous action copying of novel behaviours is a uniquely human trait (Tennie et al., 2009; Tomasello, 1998b).

Following this result, with the remaining 33% of the sample, we would seek to use the Clay and Tennie (2017) study design (single demonstrator, see above), in a sample of other species of great ape (i.e., gorillas, chimpanzees or orangutans; dependent on time constraints). In this case, we would simply follow the same protocols as the conformist transmission condition, however only use one demonstrator. Should the behaviour still not be identified then the above conclusion would be further strengthened and we would also lend support to the findings of Clay and Tennie (ibid). If the behaviour were to be identified in this condition then this would still serve as evidence of action copying in non-human great apes, and would have equal, if not more, impact to a finding in the conformity condition. The variation being simply that whichever species completed the task seem able to imitate (without the crutch of a social learning bias), whereas bonobos are not (see Clay and Tennie, ibid).

Depending on outcome, this study could substantially help to reset the default assumption in the animal culture literature that social learning is responsible for the emergence of many cultural behaviours, thus equating them with human culture dependent traits (Reindl et al., 2017).

This study may also show that not all social learning is alike: if one finds evidence, e.g. for conformity using one social learning mechanism (e.g. local enhancement in Haun et al.) then this does not mean that this particular social learning bias is equally sufficient to induce other social learning mechanisms in the species in question. Social learning biases are clearly important in the evolution of culture, but so are social learning mechanisms. We need to understand both aspects if we are to make progress in understanding the evolution of culture in humans and animals.

APPENDIX C: FULL DETAILS OF EACH OF THE DEMONSTRATORS, THESE DEMONSTRATORS WERE KEPT CONSISTENT THROUGHOUT TESTING.

Demonstrator 1 was Anna Pietschmann. Anna was, at the time of testing, a student in the psychology department at Leipzig University. Anna, prior to the onset of the study, had no contact with the apes in this study. Anna had no prior experience in testing great apes.

Demonstrator 2 was James Cook, James was, at the time of testing a student in the psychology department at Aston University doing a research internship at the University of Birmingham's psychology department. James, prior to the onset of the study, had no contact with the apes in this study. James had no prior experience in testing great apes.

Demonstrator 3 was Madita Zetzsche, Madita was, at the time of testing, a master's student in the biology department at Leipzig University. Madita, prior to the onset of the study had some contact with the apes used in this study. This was during a placement was the Max-Plank-Institute for Evolutionary Anthropology, this contact included behavioral observations, assisting in cognitive test and animal husbandry. Madita had not been involved in *any* training of subjects to copy the behaviour of a demonstrator. Madita had prior experience (outlined here) testing great apes. Madita had, at some points, worked with *all* of the apes at the WKPRC.

Demonstrator 4 was Damien Neadle, Damien was, at the time of testing, a Doctoral Researcher in the psychology department at the University of Birmingham. Damien, prior to the onset of the study had no contact with the apes in this study. Damien had prior experience testing great apes at other institutions in cognitive tasks of physical cognition, these tasks are included in the various chapters of this thesis. Ethogram from Chapter 6, as provided to coders, including notes.

Behaviour	Definition	Notes
Play	Manipulating object with no apparent immediate goal, including repetitive movements, alone or together with other individuals (alone/social), may be associated with a play face.	Play is only coded as "social" if two individuals are simultaneously manipulating the same object.
Tool-use	Manipulating a detached (?) object as a means to achieve an end (e.g. nut crack, branch drag, drink).	-
Bite	Biting or chewing object without ingestion.	Only coded if the object is not ingested and leaves the individual's mouth.
Break	Breaking (off) a substrate; this includes pulling grass up.	Only coded if the object is not ingested within 30 seconds of breaking it. This was chosen to create a certain, if arbitrary, cut off between manually breaking foods pre-ingestion, as a part of the feeding process, and independent object manipulation.
Carry	Carrying object in hands, feet or mouth.	Only coded if the individual is not feeding on the object and has moved at least their own body length away from their starting position.
Drag	Pulling object along the ground with hands	-
Throw	Throwing object or intentionally dropping object from an elevated position.	-
Support	Using an object to partially support the weight of the subject, i.e., holding onto a root when sitting on a steep hill.	Not coded if the object is holding the *entirety* of the individual's weight.
Day nest building	Creating a nest out of sticks and leaves (tree or ground). During this process the subject may break or bite several sticks and put them over their head or wrap them around the body.	For further description see: St Amant & Horton (2008); Shumaker, Walkup, & Beck, (2011)

APPENDIX D: SETTINGS USED FOR BORIS FOR CODING IN CHAPTER 6.

In BORIS, videos can be opened as raw files, and users simply code to a predefined ethogram (see Table 2). Using the BORIS coding scheme, all behaviour types were set as “state events” with the exception of “throw” which was a “point” event (as throw behaviours were assumed to be instantaneous); each point behaviour was given a default duration of 1 second (the minimum time period our data were accurate to). Independent variables were set as Group (i.e. the enclosure within the sanctuary) and subject ID. Using BORIS, a “coding map” was used to code behaviours (allowing a button press to relate to a single behaviour) with the time format set to seconds only. This allowed the duration of each behaviour (in seconds) to be exported along with the data file. The data file was exported from BORIS as a .csv file and additional demographic information about each subject was added in Microsoft Excel (sex, rearing history, actual age of subject and age group; see Table 1; also see S1 File for raw data in .csv format). This demographic information was added to each focal in turn to allow for the later analyses to control for the effects of these variable and use them as predictors.

APPENDIX E: GLOSSARY OF KEY TERMS

Term	Definition
Behavioural Form	This is the collective term for the steps required for an individual to be said to have performed a behaviour. The form of a behaviour is independent of antecedent behaviours that may alter peripheral aspects of the behaviour. For example, the behavioural form of nut-cracking is independent of material choice, in that the behavioural pathways of nut-cracking are comparable between stone and wooden hammers.
Complexity	A full discussion of complexity is beyond the scope of this thesis, instead readers should consult a recent review by Vaesen and Houkes (2017). In the context of this thesis complexity is broadly defined as an increase in the number of parts (technounits; be they objects or actions; Oswalt, 1976), goals (Read & Andersson, 2019), or 'rules' (Sirianni et al., 2015). In addition, those behaviours that require a higher level of manual dexterity might be considered more complex than those with relatively simple behavioural forms (Foucart et al., 2005).
Culturally Unconnected	Used to describe populations, both captive and wild, that have not had the chance to socially learn from one another. This can be determined through the Method of Exclusion or individual reports in the literature, corroborated with 'stud-book' entries or keeper testimony. In wild populations, to describe subjects/populations as culturally unconnected, substantive 'information' barriers must exist between the two populations (e.g., N'Zo-Sassandra River; McGrew et al., 1997)
Culture Dependent Trait (CDT)	A culture dependent traits, or CDT, (*sensu* Reindl et al., 2017) is a behaviour and/or artefact (trait) that has been shown to be reliant on a copying variant of social learning (see below) in order for it to occur. These traits should not emerge and/or be maintained within culturally unconnected communities and/or within communities (and species) that lack copying variants of social learning.
Cumulative Culture	Cumulative culture is the variant of culture that a species capable of copying can develop. The human species has cumulative culture (in addition to our ZLS). Cumulative culture requires several conditions to be met: The ability to 'ratchet up' traits (Tomasello et al., 1993). The behaviour should show some evidence of cumulated, culturally inherited change (e.g., in complexity and/or in efficiency) across generations with limited 'slippage' across these generations. Cumulative culture must be underlain by copying variants of social learning (see Table 1.1). There is still debate as for the concrete possibilities here, but most discussed are action and environmental results copying – including teaching of these types of information (Caldwell & Millen, 2008; Reindl et al., 2017; Tennie et al. 2009; in press). Traits, which are the product of cumulative culture, should be beyond the capacity of a naïve individual to innovate within a single lifetime (Boyd & Richerson, 1996). Cumulative cultural traits should be outside the ZLS.

Enculturated	Refers to non-human individuals that have been saturated within human culture to the extent that their behavioural phenotype has markedly changed from ‘unenculturated’ conspecifics. For example, Kanzi, a bonobo that was raised by researchers (Savage-Rumbaugh et al., 1986) has been demonstrated to be able to ‘produce’ and use stone tools (Toth et al., 1993), communicate using a ‘lexi-gram’ (Savage-Rumbaugh et al., 1986), understand morality and even express feelings (Savage-Rumbaugh, Fields, Segerdahl, & Rumbaugh, 2005). Kanzi can be considered enculturated, to the extreme, thus, should not be assumed to represent his species.
Facilitated/ catalysed	Behaviours that are facilitated or catalysed are those that did not necessarily *require* social learning (i.e., were not CDTs), however through non-copying social learning variants were increased in frequency within a population. This is distinct from behaviours that are acquired or transmitted between individuals, these terms have connotations of copying.
Ghost Condition	A type of demonstration that shows the movement pathways of an object, without providing information of the bodily actions of a demonstrator/agent. These conditions were first suggested by Heyes et al., (1994) as a mechanism by which researchers can isolate imitative and emulative capacities in subjects.
Hominid	The term used to describe the family of primates, within this is included modern and extinct humans *and* all extinct and extant non-human great apes.
Hominin	The term used to describe modern and extinct humans, i.e., those of the genus *Homo*, excluded from this definition are the non-human great apes.
Innovation	This term lacks universal qualification to date (see Bandini & Harrison, under review; for an overview of relevant literature though). Despite this, the term can be defined as a behaviour that is expressed for the first time, i.e., is novel, within a population, thus adding to that population’s behavioural repertoire (Reader & Laland, 2003).
Latent Solution	These are traits within a species’ ZLS (Tennie et al., 2009), i.e., those traits that every member of that species has the capacity to reinnovate in the absence of social learning and enculturation by another species (Tennie et al. 2009; in press). However, it is important to note that outside of controlled testing conditions (e.g., LS tests) the vast majority (if not all) of these traits are socially influenced in their *frequency* across individuals, by non-copying variants of social learning (e.g., local enhancement).
Latent Solutions (LS) methodology	This is the methodology used to test the claim that a trait should be considered a CDT – where the alternative is that the behaviour is within the species’ Zone of Latent Solutions (ZLS; see below). This methodology involves exposing naïve, motivated subjects at the correct ontogenetic stage to the ecological conditions (i.e., raw materials) required to express the target trait and observing them for a given time period to determine if the trait reappears “from scratch” (Hedwig & Tennie, 2008). Recent versions of the LS methodology differentiate between two ‘standards’, which allow researchers to include behaviours with a low relative probability of reoccurrence (e.g., comparatively complex traits such as nut cracking) in a species’

	ZLS following just one reinnovation (single case standard; Bandini & Tennie 2018).
Method of Exclusion	Also known as the 'ethnographic technique/method' (e.g., Laland & Janik, 2006). This is a method of determining putative cultural traits by taking reports of behaviours observed at various locations across time and classifying them as in Table 1.2. It is possible to attempt to control for the effect of genetic and ecological variation using this technique, practitioners claim it results in cultural variations.
Minimal Culture	Those behaviours that are facilitated or catalysed by social learning, but do not require social learning, in any form, for the behavioural form to be reinnovated (Neadle et al., 2017); compare with CDTs. These behaviours are 'cultural' in the most minimal sense and are distinct from examples of cumulative culture or CDTs. This term is largely similar to 'tradition' *sensu* Galef (1976).
Putative cultural trait	Those traits that have been identified to be potentially culturally dependent (CDT; see below), often through the method of exclusion (*sensu* Whiten et al., 1999). These traits have been shown to be customary or habitual in one geographically distinct community but absent in another.
Reinnovation	Also known as 'reinvention' (e.g., Tennie et al., 2009). These are behaviours that may not be innovations on a species level, but constitutes an innovation for a particular individual within the population. It is therefore possible for multiple individuals within a species, or even population, to engage in innovations. Those innovations facilitated or catalysed by social learning are termed 'socially mediated serial reinnovations' (Bandini & Tennie, 2017).
Sensitive Learning Period	This a range of years or developmental stage, during which an individual must learn the skills required for or full behavioural form of a behaviour in order for them to go on to express the behaviour later in development (Biro et al., 2003). It is possible that individuals do not require copying abilities (see Table 1.1) in order to acquire a behaviour during their sensitive learning period, Tomasello (1998a) suggested that this might occur even though environmental happenstance.
Social Learning	Social learning can be largely defined as the process of an individual being influenced by its perception of traits produced by others. This influence must alter the traits produced by the observer – the observer may then show a decrease or an increase in the frequency of a trait (non-copying variants of social learning) and/or the form of the trait (copying variants of social learning; compare Tennie et al. in press). There are myriads of ways in which social learning mechanisms are currently divided. Whiten et al. (2004) provide an overview of currently used terms (see Table 1.1).
Zone of Latent Solutions (ZLS)	This is the potential repertoire of traits that any typically developing individual within a species has the potential ability to develop 'from scratch'. It is influenced by a range of factors, including genetic predispositions and evolved cognitive skills (Tennie et al., 2009; Section 7.3.2.4). The ZLS of one individual may be 'smaller' than another of the same species and the same is true for single populations of the species (their realised mix of LS is often smaller than the full species ZLS). This is not to say that all species are restricted by their ZLS: a species that can copy traits can move beyond their ZLS (Tennie et al., 2009; Reindl et al., 2017).

8.2 References

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