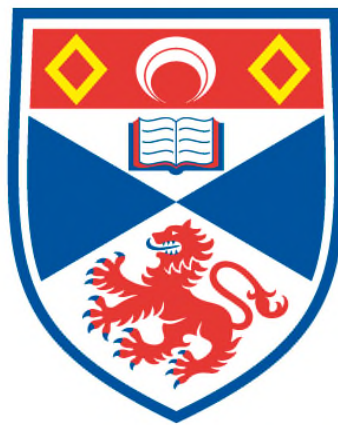


# **FACTORS SHAPING SOCIAL LEARNING IN CHIMPANZEES**

**Stuart K. Watson**

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



**2018**

**Full metadata for this item is available in  
St Andrews Research Repository  
at:**

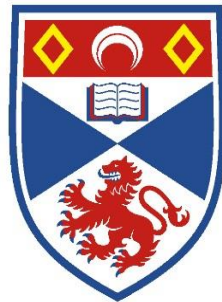
**<http://research-repository.st-andrews.ac.uk/>**

**Please use this identifier to cite or link to this item:**

**<http://hdl.handle.net/10023/12781>**

**This item is protected by original copyright**

# **FACTORS SHAPING SOCIAL LEARNING IN CHIMPANZEES**



University of  
St Andrews

**Stuart K. Watson**

Thesis submitted for partial fulfilment of the degree of PhD at the  
University of St Andrews

September, 2017

# DECLARATIONS AND PERMISSIONS

## 1. Candidate's declarations:

I, Stuart Watson, hereby certify that this thesis, which is approximately 40,000 words in length, has been written by me, and that it is the record of work carried out by me, or principally by myself in collaboration with others as acknowledged, and that it has not been submitted in any previous application for a higher degree.

I was admitted as a research student in September, 2014 and as a candidate for the degree of PhD in September 2014; the higher study for which this is a record was carried out in the University of St Andrews between 2014 and 2017.

Date ..... signature of candidate .....

## 2. Supervisor's declaration:

I hereby certify that the candidate has fulfilled the conditions of the Resolution and Regulations appropriate for the degree of PhD in the University of St Andrews and that the candidate is qualified to submit this thesis in application for that degree.

Date ..... signature of supervisor .....

## 3. Permission for publication: *(to be signed by both candidate and supervisor)*

In submitting this thesis to the University of St Andrews I understand that I am giving permission for it to be made available for use in accordance with the regulations of the University Library for the time being in force, subject to any copyright vested in the work not being affected thereby. I also understand that the title and the abstract will be published, and that a copy of the work may be made and supplied to any bona fide library or research worker, that my thesis will be electronically accessible for personal or research use unless exempt by award of an embargo as requested below, and that the library has the right to migrate my thesis into new electronic forms as required to ensure continued access to the thesis. I have obtained any third-party copyright permissions that may be required in order to allow such access and migration, or have requested the appropriate embargo below.

The following is an agreed request by candidate and supervisor regarding the publication of this thesis:

### PRINTED COPY

- a) No embargo on print copy

### ELECTRONIC COPY

- a) No embargo on electronic copy

### ABSTRACT AND TITLE EMBARGOES

If you have selected an embargo option indicate below if you wish to allow the thesis abstract and/or title to be published. If you do not complete the section below the title and abstract will remain embargoed along with the text of the thesis.

- |    |   |     |
|----|---|-----|
| a) | I agree to the title and abstract being published | YES |
| b) | I require an embargo on abstract                  | NO  |
| c) | I require an embargo on title                     | NO  |

Date ..... signature of candidate ..... signature of supervisor .....

## ACKNOWLEDGEMENTS

I would like to take this opportunity to thank all of the animals (human and otherwise) who have contributed towards the completion of this thesis and my own well-being in the act of doing so.

First, I would like to thank my supervisor, Andrew Whiten, for the generosity with which he has shared his time and expertise, the freedom and independence with which he has allowed me to pursue my interests and of course for giving me the opportunity to come to St Andrews in the first place. I could not have asked for a better or more supportive supervisor.

Thanks to my parents and family for their emotional and financial support throughout my education. I know that without them I would not be in the incredibly fortunate position of beginning a career in academia, studying the thing that fascinates me most. Thanks in particular to my Mum, Lynda, for always encouraging me to seek work that I love, even if the route to find it is longer and harder.

At times a PhD can feel like a great, hulking, many-limbed beast that one must grapple with. This task was made incomparably easier with the support and companionship of my partner and best friend, Phoebe, who filled the last two and a half years with more fun, joy, love, board-games and gull-watching than I had ever hoped for.

Thanks to my friends for their love, laughter, inspiration and commiserations: Matt, Mark, Rachel, Jenny, Lotty, Sumir, Kate, Camille, Kirsty, Elena, James, Amy, Mary-Catherine, Gill, Lisa, Sarah, Jess, Murillo, Dan, Dan, Keelin, Joe, Lewis and Lara.

Thanks to Susan and Mike Pavonetti for being such wonderful hosts and friends during my time in Texas, where I carried out the bulk of the research for this thesis. Thanks also to all of the staff at MD Anderson who provide such excellent care for the animals. The love and dedication these individuals have for their animals was a daily treat to observe, and made everything in this thesis possible. Thanks in particular to Steven Schapiro for his instrumental role in making all of the research at MD Anderson possible.

I remain grateful to Dr Katie Slocombe for her supervision and friendship during my Master's degree, where my journey as a primatologist began. Thanks also to Dr Erica van de Waal for taking me on as a field assistant at the Inkawu Vervet Project, where I honed a skill most key to primatology – patience.

My thanks always to the other animals who have touched my life and inspired the curiosity that led me to this point. Gary, Cleo, Max, Hamish, Chester, Daisy, Jake, Odie, Bliksem, Shimmy, Andrea and Mary. Honourable mentions to two un-named Cayuga ducks, the monkeys of Mawana, the chimpanzees of Edinburgh Zoo, the herring gulls of St Andrews and one concussed Texan armadillo (sorry).

Finally, I owe a debt of gratitude to all of the chimpanzees I have had the enormous fortune and pleasure of working with over the last three years. Chapter 4 of this thesis is in particular, for me, a celebration of just a small chunk of the contribution that these individuals have made to science, and the important role they have played in the lives of the many scientists to have worked at MD Anderson.



Figure 0.1. '*Waiting for Jane*', 2017, Lynda Watson, oil on canvas, (72 x 83 cm)

## ABSTRACT

Culture is an important means by which both human and non-human animals transmit useful behaviours between individuals and generations. Amongst animals, chimpanzees live particularly varied cultural lives. However, the processes and factors that influence whether chimpanzees will be motivated to copy an observed behaviour are poorly understood. In this thesis, I explore various factors and their influence on social learning decisions in chimpanzees. In turn, the chapters examine the influence of (i) rank-bias towards copying dominant individuals, (ii) majority and contextual influences and finally (iii) individual differences in proclivity for social learning. In my first experiment, I found evidence that chimpanzees are highly motivated to copy the behaviour of subordinate demonstrators and innovators in an open-diffusion puzzle-box paradigm. In contrast, behaviours seeded by dominant individuals were not transmitted as faithfully. This finding has important implications for our understanding of the emergence of novel traditions. In my second experiment, I found that some chimpanzees are highly motivated to relinquish an existing behaviour to adopt an equally rewarding alternative if it is consistently demonstrated by just one or two individuals within a group context, but not in a dyadic context. This contrasts with prior studies which argue that chimpanzees are highly conservative and may hint at a hitherto unrecognised process by which conformity-like behaviour might occur. Finally, I performed a novel type of 'meta' analysis on 16 social learning studies carried out at our research site to determine whether individuals demonstrated consistency in their social learning behaviour across experimental contexts. Strong evidence for individual differences in social information use was found, with females more likely to use social information than males. No effect of age, research experience or rearing history was found. This presents a promising new method of studying individual differences in behaviour using the accumulated findings of previous work at a study site.

# TABLE OF CONTENTS

<b>DECLARATIONS AND PERMISSIONS</b> .....	2
<b>ACKNOWLEDGEMENTS</b> .....	3
<b>ABSTRACT</b> .....	5
<b>TABLE OF CONTENTS</b> .....	6
<b>CHAPTER 1</b> .....	9
<b>CULTURE IN NON-HUMAN ANIMALS</b>	
<b>ABSTRACT</b> .....	10
<b>INTRODUCTION</b> .....	11
<b>WHAT DO ANIMAL CULTURES LOOK LIKE?</b> .....	12
<b>CORE CULTURAL CONCEPTS</b> .....	16
<b>WHY IS CULTURE USEFUL?</b> .....	17
<b>SOCIAL LEARNING PROCESSES</b> .....	19
<b>SOCIAL LEARNING BIASES</b> .....	22
<b>CUMULATIVE CULTURE</b> .....	26
<b>SUMMARY</b> .....	28
<b>REFERENCES</b> .....	30
<b>THESIS OUTLINE</b> .....	30
<b>CHAPTER 2</b> .....	40
<b>SOCIALLY TRANSMITTED DIFFUSION OF A NOVEL BEHAVIOUR FROM SUBORDINATE CHIMPANZEES</b>	
<b>ABSTRACT</b> .....	41
<b>INTRODUCTION</b> .....	42
<b>METHODS</b> .....	44
<i>Study Site</i> .....	44
<i>Apparatus</i> .....	47
<i>Procedure</i> .....	48
<i>Statistical analyses</i> .....	49
<i>Network-based diffusion analysis</i> .....	50
<i>Generalised linear mixed effects models</i> .....	51
<i>Video Coding</i> .....	51
<b>RESULTS</b> .....	52
<i>Network-based Diffusion Analysis</i> .....	55
<i>GLMMs</i> .....	56
<i>An Innovation</i> .....	57

DISCUSSION .....	58
REFERENCES.....	63
<b>CHAPTER 3</b> .....	<b>68</b>
<b>CHIMPANZEES PRIORITISE SOCIAL INFORMATION OVER PRE-EXISTING BEHAVIOURS IN A GROUP CONTEXT BUT NOT IN DYADS</b>	
ABSTRACT .....	69
INTRODUCTION .....	70
METHODS.....	73
<i>Participants and study site</i> .....	73
<i>Apparatus</i> .....	74
<i>Experimental procedure</i> .....	74
<i>Group condition</i> .....	75
<i>Stage 1: Training</i> .....	75
<i>Stage 2: Open-access</i> .....	77
<i>Stage 3: Solo sessions</i> .....	77
<i>Stage 4: Final open-access session</i> .....	78
<i>Dyad condition</i> .....	78
<i>Asocial condition</i> .....	79
<i>Statistical analyses</i> .....	79
RESULTS.....	80
<i>Analysis 1: Group condition</i> .....	80
<i>Analysis 2: Dyad and Control conditions</i> .....	85
<i>Analysis 3: Group and Dyad conditions</i> .....	86
DISCUSSION .....	87
REFERENCES.....	93
<b>CHAPTER 4</b> .....	<b>98</b>
<b>CHIMPANZEES DEMONSTRATE PERSISTENT INDIVIDUAL DIFFERENCES IN SOCIAL INFORMATION USE</b>	
ABSTRACT .....	99
INTRODUCTION .....	100
METHODS.....	104
<i>Study site</i> .....	104
<i>Data collation</i> .....	105
<i>Analysis</i> .....	108
RESULTS.....	110
DISCUSSION .....	113
REFERENCES.....	117



<b>CHAPTER 5</b> .....	124
<b>GENERAL DISCUSSION</b>	
<b>SUBORDINATE CHIMPANZEES CAN EFFECTIVELY SEED FORAGING INNOVATIONS</b> .....	124
<b>CHIMPANZEE SOCIAL LEARNING IS INFLUENCED BY SOCIAL CONTEXT</b> .....	131
<b>INDIVIDUAL DIFFERENCES IN CHIMPANZEE PROPENSITY FOR SOCIAL LEARNING</b> .....	137
<b>CONCLUDING REMARKS</b> .....	141
<b>REFERENCES</b> .....	143
<b>APPENDIX A – ETHICAL APPROVAL</b> .....	150
<b>APPENDIX B – PUBLISHED WATSON ET AL. (2017)</b> .....	151

# CHAPTER 1

## CULTURE IN NON-HUMAN ANIMALS

This introductory chapter has been accepted for publication in The Encyclopaedia of Animal Cognition and Behaviour and is currently in press. The version presented in this thesis, being unconstrained by publisher limits on the reference list, includes additional details and references that do not accompany the published version. The authorship list for the published version is as below.

Stuart K Watson<sup>1</sup>, Andrew Whiten<sup>1</sup>

*Affiliation*

<sup>1</sup>Centre for Social Learning and Cognitive Evolution, and Scottish Primate Research Group, School of Psychology and Neuroscience, University of St Andrews, UK

## **ABSTRACT**

Once a controversial subject, it is now broadly accepted that many non-human animals may live cultural lives, sometimes entailing significant complexity. This can involve substantial within-species and between-group variation in behaviour as a result of social learning. Behaviour transmitted in this way is taxonomically widespread and involves variation across a broad range of domains of behaviour, including but not limited to vocal, sexual and foraging behaviour. This chapter provides an overview of the history of the study of culture in non-human animals and investigations of the processes and transmission biases that underpin social learning, upon which subsequent chapters in this thesis will build.

## INTRODUCTION

The word 'culture' may evoke many different meanings depending on the audience. Such interpretations might refer to language, national identity, table manners, a style of cooking, art or literature, for example. Consequently, a broad definition of the term is necessary to encompass everything that a diversity of writers describe as cultural. One such definition is that culture is a package of traditions, with traditions being behaviour patterns common to more than one individual in a group which are transmitted between individuals by social learning (Hoppitt & Laland, 2013). Another important feature of culture is that it is at least somewhat enduring, as opposed to the transmission of transient social information such as "The building is on fire!"

Culture may be 'horizontally' transmitted, such as teaching a friend to sew, or 'vertically' transmitted, such as offspring observing their parents' hunting techniques. Humans are, of course, highly dependent on culture. In many societies this is emphasised by the enormous importance placed upon formal education for children and juveniles until a mandatory age, a recognition of the difficulties one can face in those societies without this baseline of cultural capital. Of course, our absorption of social information doesn't end at leaving school. Friends, family, colleagues, media and now the internet all present a constant barrage of social information that we often cannot help but incorporate into how we perceive the world and act within it. But complex cultures have of course arisen also in societies that lack formal schooling or writing, whether in present times or more universally in earlier times.

Human culture has been recognised to be uniquely complex as a result of our capacity for 'cumulative culture' (Dean, Vale, Laland, Flynn, & Kendal, 2014), the ability to modify learned behaviours such that they become more complex and/or efficient, then be transmitted and further improved by others until eventually a level of complexity is attained that could not have been achieved by a single individual. However, the capacity to pass traditions through multiple generations of social learners is not uniquely human.

In fact, current evidence would suggest that it is ubiquitous in vertebrates and perhaps larger swathes of the animal kingdom (Whiten, 2017).

## **WHAT DO ANIMAL CULTURES LOOK LIKE?**

One of the earliest signs of culture in non-human animals (hereafter “animals”) was reported in Japanese macaques. A group of monkeys on Koshima Island in Japan was regularly provisioned with sweet potatoes to supplement the natural diet and researchers noticed that one individual, a juvenile female named Imo, had started washing her potatoes before eating them (Kawai, 1965). This behaviour involved dipping them in water with one hand and brushing away sand with the other, presumably to make them more palatable. In the subsequent five years, this behaviour spread to 15 of the 19 other individuals in her group. Consistent with social transmission, this behaviour did not arise randomly in other individuals but rather followed lines of social affiliation. This crucial detail makes it likely that individuals copied others that they were close to rather than each independently discovered potato washing behaviour. A potentially problematic issue with this finding is that sweet potatoes are not a natural part of Japanese macaques’ diet, and so it is not demonstrable from this study alone that they would develop cultural variants under natural conditions. However, it was enough to spark an interest in primate cultures and several other naturally occurring traditions have now been attributed to Japanese macaques.

Later, McGrew and Tutin (1978) discovered that one community of chimpanzees was displaying a novel method of social grooming, in which the grooming partners clasp hands above their heads and groom with the other hand (‘hand clasp grooming’). This behaviour was found to be common in one chimpanzee group in Tanzania but yet absent in a second group whose territory lay only 50km away. Given that the two groups belonged to the same sub-species, and due to their geographic proximity were likely to have interbred in the recent past, the authors concluded that this behavioural difference

was likely to be cultural rather than genetic in its origin. Another observational study of chimpanzees found that while one frequently used stone hammers and anvils to crack nuts, the behaviour was absent in a neighbouring community (Boesch, Marchesi, Marchesi, Fruth, & Joulain, 1994). The availability of relevant nuts and tool materials does not differ greatly between these two areas, so the authors argue that the difference is likely to be cultural. Determining the presence of culture by examining behavioural differences between communities and whether they can be accounted for by ecological differences, such as availability of materials in the case of tool-use behaviours, is known as the 'exclusion' method. This method was later applied on a much larger scale (Whiten et al., 1999, 2001) to collate observational data from seven long-term chimpanzee field sites. The researchers identified 39 behaviours which were common in some groups and absent in others (Figure 1.1). These examples ranged from variation in foraging behaviours such as nut-cracking and termite fishing, to social behaviours such as hand-clasp grooming. The unique patterning of these traditions in each community means that one could identify the group to which an individual belongs simply by examining their behavioural repertoire, just as one might make inferences about a human's cultural identity based on their social customs. Similar approaches have since been applied to other members of the primate order, finding that orangutans (Van Schaik et al., 2003), gorillas (Robbins et al., 2016), capuchins (Perry et al., 2003) and spider monkeys (Santorelli, Schaffner, & Aureli, 2011) all exhibit a great deal of behavioural diversity between groups that can be attributed to culture (though with fewer different traditions than chimpanzees).

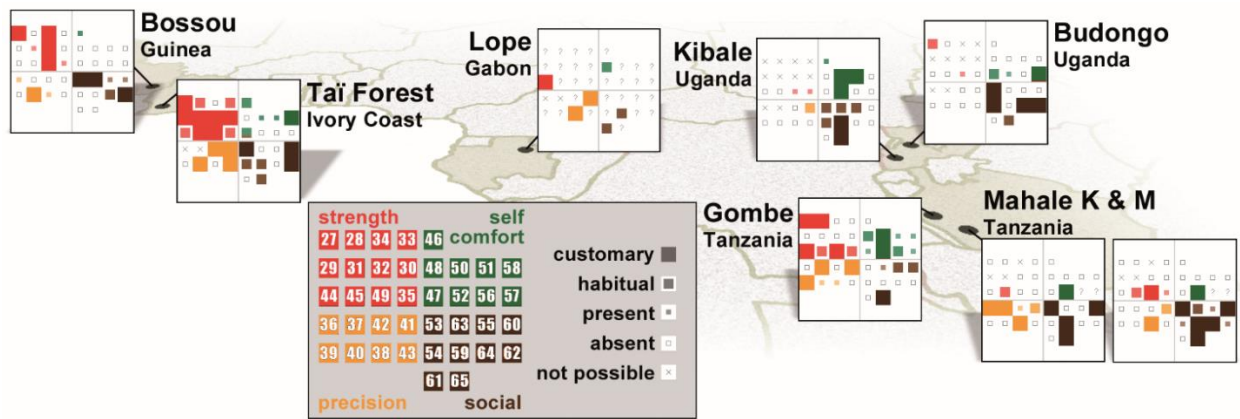


Figure 1.1. The putative cultures of wild chimpanzees. ‘Customary’ acts are those typical in a community, ‘habitual’ are less frequent but consistent with social learning. Numbers identify behaviour patterns in the catalogue attached to Whiten et al. (1999).

However, there is some uncertainty over how conservative such counts of cultural variation are. For example, while the tools necessary for nut-cracking may be available to multiple chimpanzee communities, it is not implausible that other foods are in sufficient abundance in certain locations that the many years required to master nut-cracking skill is not a worthwhile time investment. Genetic factors are also difficult to completely rule out. Langergraber and Vigilant (2011) identified a correlation between the cultural variation between chimpanzee communities and their genetics. However, with the geographic distances involved one might predict this correlation regardless of whether behavioural variation is cultural or genetic in origin. Indeed, cultural variation may well drive such genetic differences. For example, in humans the cultural practice of cattle farming in certain human population appears to have led to the evolution of lactose-tolerance in adults. Similarly, it has been found that cultural variation in foraging specialisms may have led communities of killer-whales to occupy different ecological niches for long enough that they are now demonstrating incipient speciation (Riesch et al., 2012). Indeed, if a particular cultural variant is adaptive and persists for long enough then it will inevitably have an effect on genetic selection, which in turn may influence the

development of future traditions. A classic example of this in humans is the cultural practice of cattle farming in certain human population leading to the evolution of lactose-tolerance in adults (Laland, Odling-Smee, & Myles, 2010). This feedback process is known as 'gene-culture coevolution' or 'dual inheritance theory' (Richerson & Boyd, 1978).

That a significant portion of the behavioural repertoires of some non-human primate species is seemingly shaped by cultural inheritance presents a key point of commonality between these species and ourselves, and seems likely to characterise our shared ancestry (Whiten, Hinde, Laland, & Stringer, 2011). However, this commonality extends far beyond the primate order, with compelling evidence for cultural transmission existing in a diverse range of species. For example, in meerkats researchers have found that neighbouring groups differed in the time of day they would emerge from their burrows, despite frequent dispersal between groups (thus controlling for genetic differences) and a lack of any known environmental correlates (Thornton, Samson, & Clutton-Brock, 2010). Furthermore, some of the most compelling evidence for animal culture is found in the study of marine mammals. In 1980, a single humpback whale was recorded as using a novel foraging method known as 'lobtail fishing'. Over three decades, researchers observed this behaviour diffuse between closely associated individuals in a manner consistent with social learning (Allen, Weinrich, Hoppitt, & Rendell, 2013). Further evidence of complex culture in humpback whales comes from studies of their vocal communication. Depending on where they live, humpbacks have acoustically distinct songs. However, following the migration of small numbers of individuals between two communities of whales, researchers found that their new group quickly and comprehensively changed their song to match that of the newcomers (Noad, Cato, Bryden, Jenner, & Jenner, 2000). This last example introduced culture in the domain of vocal behaviour. As well as other marine mammals such as orcas (Yurk, Barrett-Lennard, Ford, & Matkin, 2002) and sperm whales (Rendell, Mesnick, Dalebout,



Burtenshaw, & Whitehead, 2012), there is a large body of research demonstrating vocal dialects in a variety of bird (Catchpole & Slater, 1995) and primate species (de la Torre & Snowdon, 2009). Though less often discussed than non-communicative traditions, these are particularly interesting in that the primary function appears to lie in identifying and facilitating social relationships. This illustrates that social learning may allow individuals not only to optimise their use of their physical environment (e.g. learning to exploit a food resource), but also their social environment.

## **CORE CULTURAL CONCEPTS**

Although the typical measures by which culture in animals is quantified refers to patterns of behaviour, it may be useful to think in more nuanced terms. In humans, cultural anthropologists have suggested that we should think of culture in terms of core concepts or 'cultural cognitions' which may or may not elicit a range of related behaviours. A human example of this would be the emphasis placed on collectivism as opposed to individualism in Eastern cultures relative to Western ones, and the ways in which these concepts manifest themselves in behaviours common to each these culture (Nisbett, Peng, Choi, & Norenzayan, 2001). Discussing 'concepts' with regards to animals is inherently problematic insofar as we cannot examine such states as we might through conversing with human participants. However, careful examination of animal behaviour can allow us to draw useful inferences. One example of how differences in 'core cultural cognitions' might manifest in non-human animals comes from observation of stick-tool use behaviour in two different Ugandan groups of chimpanzees. One of these communities (the 'Kanyawara' group) frequently uses stick-tools to access a variety of resources, such as termites. In another community ('Budongo'), stick-tool use is entirely absent. Knowing this, researchers (Gruber, Muller, Strimling, Wrangham, & Zuberbühler, 2009) introduced a novel resource, artificial honey-filled holes, to see how these two different cultures would respond. Just as with similarly located resources, the

Kanyawara chimpanzees gathered stick-tools to retrieve the honey, whereas the Budongo community used leaf sponges. Even when appropriate stick-tools were provided next to the honey holes a similar pattern prevailed. Kanyawara chimpanzees stripped the sticks of their leaves and used the sticks as usual, whereas Budongo chimpanzees ignored the stick and kept the leaves for sponging (Gruber, Muller, Reynolds, Wrangham, & Zuberbühler, 2011). This carrying over of a particular *type* of solution from pre-existing behaviours to a novel problem is perhaps suggestive that culture runs deeper than any individual behaviour. Another interesting example of culture as a 'mind-set' rather than a specific behaviour comes from a longitudinal study of aggression in a troop of olive baboons (Sapolsky & Share, 2004). During the 1980's, the most aggressive males of this group died of tuberculosis as a result of contact with human waste. As a result, the rate of aggressive encounters in the group was dramatically reduced, physiological measures of stress dropped in young males and a higher than normal rate of inter-sex grooming and affiliation was recorded. Critically, this 'pacific' culture persisted even after the remaining original males of the group had migrated elsewhere, and was adopted by new males who joined the group from other communities.

## **WHY IS CULTURE USEFUL?**

Individual, or 'asocial' learning is one means by which animals can adapt their behavioural repertoire to best suit their environment. It is potentially costly however, requiring a significant amount of time or energy investment to explore different options. In more urgent scenarios, such as predator avoidance, experimenting with behaviours that have an unknown payoff may cost an individual their life. Copying the behaviour of other individuals allows one to bypass this process to arrive at useful behaviours without paying these costs. Furthermore, when individuals do arrive at a novel and productive behaviour, this allows for benefit not only to themselves but also for it to be passed on to

kin and allies, enhancing their fitness. That cultural information may be passed through multiple generations to shape behaviour in a similar manner to genetic inheritance has led social learning to be referred to as “Nature’s second inheritance system” (Whiten, 2005; 2017). However, not all cultures emerge as a result of innovations to adapt to a physical environment. Innovations may also maximise the benefits of the social environment, such as facilitating social bonding (as in cultural variations of grooming behaviour in chimpanzees) or identifying oneself as a member of a group (such as group-wide convergence in vocal dialects). There is much evidence, both scientific and historical, that humans may give preferential treatment to those who share their language, appearance and culture (Carpenter, Uebel & Tomasello, 2013; Van Baaren, Holland, Kawakami, & Van Knippenberg, 2004), but whether animals also demonstrate such ‘in-group’ bias based on cultural practices is not yet known. However, in species with extended periods of parent-offspring directed social learning, or high within-group relatedness, culture may function as a useful cue for identifying kin. Some animals may even purposefully diverge from the behaviour of out-group individuals in order to make the difference clear, as suggested by the fact that captive pygmy marmosets changed the acoustics of their vocalisations to diverge from a newly introduced neighbouring group (Elowson & Snowdon, 1994).

The importance of complementary experimental work, such as the honey-hole chimpanzee study described above, to check and verify field observations is illustrated by studies into the tool-making practices of New Caledonian crows. Crows from different regions of New Caledonia are known to construct different types of tools for foraging, despite similar apparent availability of tool-materials and prey. It has therefore been suggested that this may be an example of cultural variation, and even cumulative culture (Hunt & Gray, 2003). However, it was later found that hand-raised crows would spontaneously manufacture and use similar tools (Kenward, Weir, Rutz, & Kacelnik, 2005), suggesting that while social learning may well facilitate the learning of this

behaviour in the wild, it is not essential. This example highlights an important issue with studying culture in wild animals, which is that one is often having to make post-hoc inferences about an existing distribution of behaviour. One can collect data consistent with a behaviour being either socially learned or developmentally fixed, but without direct observation of the propagation of a behaviour (as with the cetacean examples above) or experimental intervention, it is difficult to draw firm conclusions and its cultural status. Experimental work in both captivity and the wild allows us to systematically determine a species' capacity for social learning, as well as how exactly a behaviour progresses from being an idiosyncrasy to a full-fledged group-wide tradition. Questions over how culture is transmitted can be usefully split as to whether they concern social learning *processes* or social learning *biases*. Processes refer to how information is transmitted between two individuals, and biases refer to the factors that guide when and towards whom individuals choose to copy. The sections below will summarise the literature on each of these topics.

## **SOCIAL LEARNING PROCESSES**

Social learning processes are differentiated in terms of what information is being utilized by social learners, and how it is dealt with cognitively. For example, local enhancement is one such process, whereby individuals learn by focussing their attention on a location that others preferentially acted upon. If many conspecifics are feeding in an area, this suggests an abundance of food there and it makes functional sense for the learner to focus in a similar way (Waite, 1981). Stimulus enhancement is very similar, except that attention is drawn to certain objects rather than locations.

Researchers have distinguished between two principal higher level processes: imitation and emulation. Imitation refers to copying the bodily actions of an individual, for example the technique with which they manipulate a tool to achieve a goal, such as using a saw to cut a piece of wood in half. Emulation, on the other hand, refers to learning the outcome of a behaviour and finding one's own path to achieving it. For example, breaking

a piece of wood over one's knee instead of using the saw that the individual observed had used. The key difference is copying the *result* rather than the *form* of an action. Depending on the task, a learner's pre-existing knowledge and the range of options available, they may well end up using essentially the same method as the demonstrator even if learning was not imitative, making disambiguation difficult. Of the two processes, imitation is commonly considered to be the most sophisticated form of social learning, since it allows for high-fidelity transmission of complex behaviours and requires the demanding translation of visual (or vocal) patterns seen in another individual's actions into commands in one's own motor system, to bring about the correspondence between the two despite a quite different perspective.

Whether and/or which animals are capable of imitation has long been a contentious issue. Tomasello, Davis-Dasilva, Camak, and Bard (1987) found that although young chimpanzees faced with an out-of-reach reward did not precisely copy a sequence of tool-use behaviours used by a conspecific to retrieve it, they did learn something of the *function* of stick-tools for reaching such objects and this was later described as emulation. In another study (Whiten, Horner, & De Waal, 2005) a single chimpanzee in each of two different groups was trained on alternative methods of using a stick tool to operate parts of a foraging device, which would release a food reward. These alternative techniques spread throughout the models' respective groups to become recognisably different traditions, and while some individuals did explore other methods, they were found to eventually re-converge on the behaviour most common to their group. That the group-mates of these demonstrators converged on their methods is suggestive of imitative learning. 'Ghost' experiments in which the movements of the device were made without any chimpanzee responsible, so could be replicated only by emulation, failed to lead to success, reinforcing this conclusion (Hopper, Lambeth, Schapiro & Whiten, 2008).

Long-term care staff of captive apes frequently have a long list of anecdotes about their animals copying the behaviour of their carers, such as brushing one's teeth or scrubbing floors. These behaviours, which serve no purpose for the ape, are difficult to explain without imitative learning but were common in the diaries of researchers studying home-reared chimpanzees in particular. Some evidence for imitation has also been found in species as diverse as marmosets (Voelkl & Huber, 2000, 2007), dolphins (Kuczaj & Yeater, 2006) and pigeons (Zentall, 2004).

A social transmission process that is thought to particularly characterise humans is teaching (Kline, Boyd, & Henrich, 2013). Even pre-school children have been found to engage in spontaneous teaching behaviour by verbally instructing their peers on how to solve an experimental problem (Dean, Kendal, Schapiro, Thierry, & Laland, 2012). Together with imitation, teaching has been proposed as a critical high-fidelity process of cultural transmission that allows for the unique complexity of human culture (Galef, 1992). However, whether teaching can be considered uniquely human is highly dependent on how one defines the term. A popular 'functional' definition of teaching in comparative studies is that it is a behaviour in which an individual modifies their own behaviour only in the presence of an observer, which both facilitates learning in the observer and does not benefit the actor (Caro & Hauser, 1992). Using this definition, researchers have identified a broad range of species for whom there is evidence for teaching. For example, meerkats bring home scorpions in which they first remove the sting, but later present scorpions decreasingly disabled, allowing pups to progressively discover the skills necessary to hunt this dangerous prey in a safe and structured way (Thornton & McAuliffe, 2006). Evidence for teaching defined in this functional way has also been offered in bees (Seeley, Mikheyev, & Pagano, 2000), ants (Franks & Richardson, 2006), birds (Raihani & Ridley, 2008), cats (Caro, 1980) and golden-lion tamarins (Rapaport & Ruiz-Miranda, 2002), but seems strikingly absent in the great apes. It may be that the lack of teaching found in apes may be due to long periods of immaturity

which allow juveniles instead to learn necessary skills through extended observational learning.

## **SOCIAL LEARNING BIASES**

Culture benefits an individual only insofar as the benefits outweigh those of learning individually (asocially). If an individual copies every novel behaviour it observes conspecifics performing, then they may end up copying maladaptive behaviours or replacing perfectly useful methods with less efficient ones (Kendal, Coolen, van Bergen, & Laland, 2005). Consequently, in order to maximise the benefits of social learning it has been proposed that species with an evolved propensity for social learning are likely to also have evolved a suite of biases that guide when and towards whom it should be deployed. Understanding these biases is crucial to improving our understanding of how culture emerges and propagates, as well as the contexts in which it is most useful. They can be usefully categorised into 'who' and 'when' biases.

'Who', or 'Model-based biases' direct individuals towards copying specific individuals (such as one's mother) or categories of individuals (such as kin). Humans demonstrate a number of such biases, such as children directing their social learning towards older (Rakoczy, Hamann, Warneken, & Tomasello, 2010) and more prestigious individuals (McGuigan, 2013). Some animals also appear to be selective in their preferential sources for social information. For example, in an experiment where the method of opening a puzzle-box was introduced to chimpanzee groups by trained models, it was found that naïve individuals preferentially directed their attention towards dominant knowledgeable demonstrators (Kendal et al., 2015). A tendency to copy dominant individuals, or 'rank bias' has been proposed as a key factor in chimpanzee social learning. It may explain why so few chimpanzee innovations are recorded as going on to become group-wide traditions (Nishida, Matsusaka, & McGrew, 2009), since many innovations come from subordinate individuals (Reader & Laland, 2001). Dominant

individuals typically also enjoy the greatest amount of reproductive success (Pusey, Williams, & Goodall, 1997) in a group and so are perhaps likely to be good role models. If their success is a result of their behavioural preferences, then copying them might bestow those same benefits on the learner. In many cases, the characteristics that make an individual dominant, such as physical prowess or being the offspring of a dominant individual, cannot be directly copied. In this case, converging on their behaviour must serve another purpose. One possibility is that behavioural similarities facilitate social bonding between individuals, in which case copying the behaviour of dominant individuals may serve an additional function of improving one's social standing. However, when researchers seeded groups with a method of opening a puzzle-box by either alpha male or subordinate female chimpanzees (i.e. only one model was available, whether of high or low rank), it was found that observers were highly motivated to copy the behaviour of subordinate models (Watson et al., 2017 – see Chapter 2). It may be then that individuals are motivated to learn visibly productive foraging behaviours from whomsoever they observe demonstrating them since learning this can only be beneficial, whereas transmission of more 'arbitrary' traditions does indeed flow primarily from dominant models.

A bias towards copying one's own kin appears to be common. For example, brown capuchin monkeys do not copy individuals based on their relative rank, but do demonstrate a bias towards copying related models (Dindo, Leimgruber, Ahmed, Whiten, & de Waal, 2011). The vocal production behaviour of killer-whales is also known to be largely transmitted within matrilineal lines (Yurk et al., 2002). The capacity for kin-bias to shape cultures is neatly illustrated in vervet monkeys. It has been found that, within the same group of monkeys, multiple distinct methods of cleaning food before consumption were present in the group and were differentiated along matrilineal lines (van de Waal et al. 2012). Also, vocal behaviour of killer-whales is known to be largely transmitted through matrilineal lines (Miller & Bain, 2000). In some species, kin-bias may only manifest during



specific developmental windows. For example, observations of wild chimpanzees suggest that infants are significantly more likely to observe the nut-cracking behaviour of related individuals than juveniles or adults. There are many possible reasons for a kin bias in social learning. The simplest would be that if one is raised by kin, they provide the most opportunities for social learning. Kin-specific traditions could also help related individuals identify one another, which may be useful for avoiding them when choosing a mate or banding together to form social alliances.

On the other hand, if one's parents have had a particularly stressful life this may indicate that they are not behaviourally well-suited to the current environment and therefore make poor role models. Experimentally elevated stress hormones in zebra finch nestlings caused them to switch from the developmentally typical strategy of copying their parents to exclusively copy unrelated adults (Farine, Spencer, & Boogert, 2015). This finding emphasises that social learning biases may vary greatly within a species according to an individual's own life history. Dominant chimpanzees, for example, are less likely to use social information than subordinate individuals (Kendal et al. 2015). Furthermore, young white-headed capuchins are more likely to be influenced by social information than older individuals, but both old and young monkeys are influenced by the relative pay-offs of the behaviours they observe (Barrett, McElreath & Perry, 2017). These facts demonstrate that social learning biases vary not just between species, or between individuals, but also within individuals during their own lifetime. More often than not, culture is therefore likely to be the result of a tapestry of interacting biases.

Computer modelling of social learning behaviour predicts that a very effective way of getting reliable social information is, instead of targeting specific individuals, to simply copy the behaviour of the majority of one's group. This tendency to be disproportionately likely to copy the behaviour of a majority (as opposed to the likelihood of copying the behaviour if choosing a model at random) is known as 'majority biased transmission'. This is occasionally conflated with 'conformity', but a useful distinction is

that while majority bias is something naïve individuals may do, conformist behaviour requires the additional feature of relinquishing an existing behaviour to converge on a majority preference. Both of these biases have been proposed as being crucial for stable, long-term culture, as without some process causing individuals to converge on a group 'norm', traditions may be eroded through copying errors and novel behaviours (Tennie, Call, & Tomasello, 2009). Consequently, these biases have received considerable research attention.

The study of conformity behaviour has its roots in social psychology. A seminal series of experiments carried out by Solomon Asch in the 1950's (Asch, 1951) tasked small groups of people with judging which of three lines of varying lengths was the same length as a fourth line. Unbeknownst to the sole participant, every other individual in the group was a confederate of the experimenter tasked with unanimously giving the same incorrect answer. Even though this answer was obviously incorrect, around 30% of participants gave the same answer when it was their turn. However, often they did not do so when able to give their answer in private. This is suggestive of a powerful motivation in humans to conform to the normative behaviour of those around us, an effect which has been replicated across cultures and age groups (Bond & Smith, 1996; Haun & Tomasello, 2011). Given that this behaviour is so widespread in humans, there has naturally been interest in whether animals behave similarly.

There is evidence for conformity in nine-spined stickleback fish, who after learning the relative payoffs of two artificial feeders, relinquished their trained preference in favour of feeding at the same location as a group of individuals (Pike & Laland, 2010). Further evidence for animal conformity comes from male vervet monkeys. After migrating to different groups, these monkeys have been found to conform to the food preferences of their new group, even though they had previously found that food to be unpalatable (van de Waal, Borgeaud, & Whiten, 2013). Conformity has also been identified in great tits, who learned one of two methods of opening a puzzle box and then migrated to

groups who used the alternative method. It was found that many of these individuals gave up their original behaviour to adopt that of their new group (Aplin et al., 2015b). However, a criticism of these studies, and a general difficulty with investigating conformist behaviour, is that it is often challenging to differentiate the outcomes of so-called 'conformity' from other social learning biases or even random-copying (Acerbi, Van Leeuwen, Haun, & Tennie, 2016; Haun, Van Leeuwen, & Edelson, 2013; Van Leeuwen & Haun, 2013, 2014; Van Leeuwen, Kendal, Tennie, & Haun, 2015) (c.f. Whiten & van de Waal, 2016; Aplin et al., 2015a). Great methodological care is required to disentangle these alternative explanations.

Despite the apparently wide taxonomic distribution of conformist behaviour discussed above, evidence in chimpanzees is mixed. Observations of wild chimpanzees have recorded females who migrate between communities converging on the materials chosen for nut-cracking used by their new group, despite no difference in availability of (Luncz & Boesch, 2014, Luncz, Wittig, & Boesch, 2015). However, experimental studies have repeatedly failed to demonstrate such conformity. On the other hand, naïve chimpanzees preferentially copy a token-exchange behaviour demonstrated once each by three individuals rather than a single individual demonstrating an alternative method three times (Haun et al., 2013), revealing a majority bias.

## **CUMULATIVE CULTURE**

Although most researchers would now agree that culture is a widespread phenomenon across the animal kingdom, there is something strikingly unique about human culture in the way in which it continues to grow in scope and complexity over time, with each generation of learners modifying and adding to the body of knowledge that came before them. The complexity of these accumulated modifications has continued to ratchet up until most of the artefacts and processes we engage with on a daily basis could not have been invented by a single naïve person even if they spent a

lifetime attempting to do so. It is this capacity to 'stand on the shoulders of giants' that has allowed humans to thrive in almost every habitat on Earth, and it is known as 'cumulative culture'. In this capacity, humans are unquestionably pre-eminent. However, the jury is still out on whether this is a difference in quantity or kind.

Candidates for any degree of cumulative cultural evolution are rare in animals and it may surprise some that perhaps the most compelling example to date comes from homing pigeons. Researchers found that groups of homing pigeons that had individuals replaced over time successively built on the efficiency of their homing route to the extent that the group would home more efficiently than solo individuals or groups with fixed membership (Sasaki & Biro, 2017). Several candidates for cumulative culture have also been proposed in wild chimpanzees. Perhaps the most convincing of these is one community's method of termite fishing. Rather than fish horizontally at large mounds, as most chimpanzees do, this group uses a selection of stick tools to dig under-ground. This process involves selecting a particularly robust stick to penetrate the earth (often using a foot to provide extra force, just as one might with a spade) and several slimmer stems for insertion down the resulting tunnel, which must be stripped of leaves and pulled through their teeth to produce a 'comb-like' end (Sanz, Call, & Morgan, 2009). Though impressive, these examples still pale in comparison to the complexity of human cumulative culture.

Direct comparisons of three-to-four year old children and chimpanzees have shed some light on this. In a 3-step task designed to require cumulative cultural learning to reach the final, most rewarding step, chimpanzees typically failed to progress beyond the first step whereas almost all children reached step 3 (Dean et al., 2012). One critical difference lies in our unique capacity for language, as children have been found to quickly engage in verbal teaching in complex tasks, allowing them to a) inform others they have the solution, b) impart this to them and c) correct any copying errors. Another potential road block for chimpanzees in particular appears to be behavioural inflexibility. There is

some evidence that chimpanzees tend to get 'stuck' on a method they have learned for solving a particular problem, thereby preventing them from 'ratcheting up' the complexity of these methods in a cumulative fashion. This behavioural conservatism might also explain the lack of conformist behaviour in chimpanzees described above. However, there is some evidence that chimpanzees are motivated to relinquish an existing behaviour when it becomes sufficiently inefficient and a more productive alternative is demonstrated in front of them (Davis et al., 2016). One thing to consider in such investigations is that although contemporary human culture changes at an unprecedented rate, our technological progress was in fact relatively static for most of the *Homo* genus' history. For instance, while stone 'flaking' technology dates back to between 2.6 and 3.3 million years ago, the first known cumulative development from stone flakes to more advanced 'Acheulian' hand axes did not occur until around 1.8 million years ago, followed by relatively little progression for another million or so years, which corresponds to hundreds of thousands of generations. In light of these time scales, identifying instances of cumulative culture in animals is likely to be difficult – wild chimpanzees, for example, have been studied for only 3-4 generations, by comparison.

## **SUMMARY**

Once thought to be a uniquely human trait, culture is now demonstrably widespread in the animal kingdom, incorporating a range of behavioural domains including foraging, communicative and social behaviours. With a suite of biases to guide its adaptive use, social learning allows individuals to benefit from the hard-won knowledge of their conspecifics while paying relatively few of the costs. This capacity allows for rapid adaptation to changing environments or selective pressures that complements and has a reciprocal relationship with genetic inheritance, as use of social learning is both shaped by genes (giving us the capacity for social learning in the first place) and may shape their further evolution. The study of culture and cultural

transmission in animals is therefore critical not only in understanding this phenomenon, but also for our understanding of the broader evolutionary processes that have shaped animal life. Complementary studies of both captive and wild populations, using a combination of experimental and observational methods, are yielding an increasingly detailed understanding of cultural transmission in animals. Through comparisons with humans, this also informs us about our own evolutionary history with regard to what has made human culture unique and what common roots it developed from.

## REFERENCES

- Acerbi, A., Van Leeuwen, E. J., Haun, D. B., & Tennie, C. (2016). Conformity cannot be identified based on population-level signatures. *Scientific Reports*, *6*.
- Allen, J., Weinrich, M., Hoppitt, W., & Rendell, L. (2013). Network-based diffusion analysis reveals cultural transmission of lobtail feeding in humpback whales. *Science*, *340*(6131), 485-488.
- Aplin, L. M., Farine, D. R., Morand-Ferron, J., Cockburn, A., Thornton, A., & Sheldon, B. C. (2015a). Counting conformity: evaluating the units of information in frequency-dependent social learning. *Animal Behaviour*, *110*, e5-e8.
- Aplin, L. M., Farine, D. R., Morand-Ferron, J., Cockburn, A., Thornton, A., & Sheldon, B. C. (2015b). Experimentally induced innovations lead to persistent culture via conformity in wild birds. *Nature*, *518*(7540), 538-541.
- Asch, S. E. (1951). Effects of group pressure upon the modification and distortion of judgments. In H. Guetzkow (Ed.), *Groups, Leadership, and Men* (pp. 177-190): Pittsburgh: PA Carnegie Press.
- Barrett, B. J., McElreath, R. L., & Perry, S. E. (2017). Pay-off-biased social learning underlies the diffusion of novel extractive foraging traditions in a wild primate. *Proceedings of the Royal Society B: Biological Sciences*, *284*(1856)
- Boesch, C., Marchesi, P., Marchesi, N., Fruth, B., & Joulain, F. (1994). Is nut cracking in wild chimpanzees a cultural behaviour? *Journal of Human Evolution*, *26*(4), 325-338.
- Bond, R., & Smith, P. B. (1996). Culture and conformity: A meta-analysis of studies using Asch's (1952b, 1956) line judgment task. *Psychological Bulletin*, *119*(1), 111.
- Caro, T. M. (1980). Predatory behaviour in domestic cat mothers. *Behaviour*, *74*(1), 128-147.
- Caro, T. M., & Hauser, M. D. (1992). Is there teaching in nonhuman animals? *The quarterly review of biology*, *67*(2), 151-174.

- Carpenter, M., Uebel, J., & Tomasello, M. (2013). Being mimicked increases prosocial behavior in 18-month-old infants. *Child development*, *84*(5), 1511-1518.
- Catchpole, C., & Slater, P. (1995). *Bird song: Biological themes and variations*. Cambridge University Press.
- Davis, S. J., Vale, G. L., Schapiro, S. J., Lambeth, S. P., & Whiten, A. (2016). Foundations of cumulative culture in apes: improved foraging efficiency through relinquishing and combining witnessed behaviours in chimpanzees (*Pan troglodytes*). *Scientific Reports*, *6*, 35953.
- la Torre, S., & Snowdon, C. T. (2009). Dialects in pygmy marmosets? Population variation in call structure. *American Journal of Primatology*, *71*(4), 333-342.
- Dean, L. G., Kendal, R. L., Schapiro, S. J., Thierry, B., & Laland, K. N. (2012). Identification of the social and cognitive processes underlying human cumulative culture. *Science*, *335*(6072), 1114-1118.
- Dean, L. G., Vale, G. L., Laland, K. N., Flynn, E., & Kendal, R. L. (2014). Human cumulative culture: a comparative perspective. *Biological Reviews*, *89*(2), 284-301.
- Dindo, M., Leimgruber, K., Ahmed, R., Whiten, A., & de Waal, F. (2011). Observer choices during experimental foraging tasks in brown capuchin monkeys (*Cebus apella*). *American Journal of Primatology*, *73*(9), 920-927.
- Elowson, A. M., & Snowdon, C. T. (1994). Pygmy marmosets, *Cebuella pygmaea*, modify vocal structure in response to changed social environment. *Animal Behaviour*, *47*(6), 1267-1277.
- Farine, D. R., Spencer, K. A., & Boogert, N. J. (2015). Early-life stress triggers juvenile zebra finches to switch social learning strategies. *Current Biology*, *25*(16), 2184-2188.
- Franks, N. R., & Richardson, T. (2006). Teaching in tandem-running ants. *Nature*, *439*(7073), 153-153.
- Galef, B. G. (1992). The question of animal culture. *Human Nature*, *3*(2), 157-178.



- Gruber, T., Muller, M. N., Reynolds, V., Wrangham, R., & Zuberbühler, K. (2011). Community-specific evaluation of tool affordances in wild chimpanzees. *Scientific Reports*, 1, 128.
- Gruber, T., Muller, M. N., Strimling, P., Wrangham, R., & Zuberbühler, K. (2009). Wild chimpanzees rely on cultural knowledge to solve an experimental honey acquisition task. *Current Biology*, 19(21), 1806-1810.
- Haun, D. B., & Tomasello, M. (2011). Conformity to peer pressure in preschool children. *Child Development*, 82(6), 1759-1767.
- Haun, D. B., Van Leeuwen, E. J., & Edelson, M. G. (2013). Majority influence in children and other animals. *Developmental Cognitive Neuroscience*, 3, 61-71.
- Hopper, L. M., Lambeth, S. P., Schapiro, S. J., & Whiten, A. (2008). Observational learning in chimpanzees and children studied through 'ghost' conditions. *Proceedings of the Royal Society of London B: Biological Sciences*, 275(1636), 835-840.
- Hoppitt, W., & Laland, K. N. (2013). *Social learning: an introduction to mechanisms, methods, and models*: Princeton University Press.
- Hunt, G. R., & Gray, R. D. (2003). Diversification and cumulative evolution in New Caledonian crow tool manufacture. *Proceedings of the Royal Society of London B: Biological Sciences*, 270(1517), 867-874.
- Kawai, M. (1965). Newly-acquired pre-cultural behavior of the natural troop of Japanese monkeys on Koshima Islet. *Primates*, 6(1), 1-30.
- Kendal, R. L., Coolen, I., van Bergen, Y., & Laland, K. N. (2005). Trade-offs in the adaptive use of social and asocial learning. *Advances in the Study of Behavior*, 35, 333-379.
- Kendal, R. L., Hopper, L. M., Whiten, A., Brosnan, S. F., Lambeth, S. P., Schapiro, S. J., & Hoppitt, W. (2015). Chimpanzees copy dominant and knowledgeable individuals: implications for cultural diversity. *Evolution and Human Behavior*, 36(1), 65-72.

- Kenward, B., Weir, A. A., Rutz, C., & Kacelnik, A. (2005). Behavioural ecology: Tool manufacture by naive juvenile crows. *Nature*, 433(7022), 121-121.
- Kline, M. A., Boyd, R., & Henrich, J. (2013). Teaching and the life history of cultural transmission in Fijian villages. *Human Nature*, 24(4), 351-374.
- Kuczaj, S. A., & Yeater, D. B. (2006). Dolphin imitation: Who, what, when, and why? *Aquatic Mammals*, 32(4), 413.
- Laland, K. N., Odling-Smee, J., & Myles, S. (2010). How culture shaped the human genome: bringing genetics and the human sciences together. *Nature Reviews Genetics*, 11(2), 137-148.
- Langergraber, K. E., & Vigilant, L. (2011). Genetic differences cannot be excluded from generating behavioural differences among chimpanzee groups. *Proceedings of the Royal Society of London B: Biological Sciences*, rspb20110391.
- Luncz, L. V., & Boesch, C. (2014). Tradition over trend: Neighboring chimpanzee communities maintain differences in cultural behavior despite frequent immigration of adult females. *American Journal of Primatology*, 76(7), 649-657.
- Luncz, L. V., Wittig, R. M., & Boesch, C. (2015). Primate archaeology reveals cultural transmission in wild chimpanzees (*Pan troglodytes verus*). *Phil. Trans. R. Soc. B*, 370(1682), 20140348.
- McGrew, W. C., & Tutin, C. E. (1978). Evidence for a social custom in wild chimpanzees? *Man*, 234-251.
- McGuigan, N. (2013). The influence of model status on the tendency of young children to over-imitate. *Journal of Experimental Child Psychology*, 116(4), 962-969.
- Miller, P. J., & Bain, D. E. (2000). Within-pod variation in the sound production of a pod of killer whales, *Orcinus orca*. *Animal Behaviour*, 60(5), 617-628.
- Nisbett, R. E., Peng, K., Choi, I., & Norenzayan, A. (2001). Culture and systems of thought: holistic versus analytic cognition. *Psychological review*, 108(2), 291.

- Nishida, T., Matsusaka, T., & McGrew, W. C. (2009). Emergence, propagation or disappearance of novel behavioral patterns in the habituated chimpanzees of Mahale: a review. *Primates*, *50*(1), 23-36.
- Noad, M. J., Cato, D. H., Bryden, M., Jenner, M.-N., & Jenner, K. C. S. (2000). Cultural revolution in whale songs. *Nature*, *408*(6812), 537-537.
- Perry, S., Baker, M., Fedigan, L., Gros-Louis, J., Jack, K., MacKinnon, K. C., . . . Rose, L. (2003). Social conventions in wild white-faced capuchin monkeys. *Current Anthropology*, *44*(2), 241-268.
- Pike, T. W., & Laland, K. N. (2010). Conformist learning in nine-spined sticklebacks' foraging decisions. *Biology Letters*, rsbl20091014.
- Pusey, A., Williams, J., & Goodall, J. (1997). The influence of dominance rank on the reproductive success of female chimpanzees. *Science*, *277*(5327), 828-831.
- Raihani, N. J., & Ridley, A. R. (2008). Experimental evidence for teaching in wild pied babblers. *Animal Behaviour*, *75*(1), 3-11.
- Rakoczy, H., Hamann, K., Warneken, F., & Tomasello, M. (2010). Bigger knows better: Young children selectively learn rule games from adults rather than from peers. *British Journal of Developmental Psychology*, *28*(4), 785-798.
- Rapaport, L. G., & Ruiz-Miranda, C. R. (2002). Tutoring in wild golden lion tamarins. *International Journal of Primatology*, *23*(5), 1063-1070.
- Reader, S. M., & Laland, K. N. (2001). Primate innovation: sex, age and social rank differences. *International Journal of Primatology*, *22*(5), 787-805.
- Rendell, L., Mesnick, S. L., Dalebout, M. L., Burtenshaw, J., & Whitehead, H. (2012). Can Genetic Differences Explain Vocal Dialect Variation in Sperm Whales, *Physeter macrocephalus*? *Behavior Genetics*, *42*(2), 332-343.
- Richerson, P. J., & Boyd, R. (1978). A dual inheritance model of the human evolutionary process I: Basic postulates and a simple model. *Journal of Social and Biological Structures*, *1*(2), 127-154.

- Riesch, R., Barrett-Lennard, L., Lance, G., Ellis, G. M., Ford, J. K., & Deecke, V. B. (2012). Cultural traditions and the evolution of reproductive isolation: ecological speciation in killer whales? *Biological Journal of the Linnean Society*, *106*(1), 1-17.
- Robbins, M. M., Ando, C., Fawcett, K. A., Grueter, C. C., Hedwig, D., Iwata, Y., . . . Stoinski, T. S. (2016). Behavioral Variation in Gorillas: Evidence of Potential Cultural Traits. *PLoS One*, *11*(9), e0160483.
- Santorelli, C. J., Schaffner, C. M., & Aureli, F. (2011). Universal behaviors as candidate traditions in wild spider monkeys. *PLoS One*, *6*(9), e24400.
- Sanz, C., Call, J., & Morgan, D. (2009). Design complexity in termite-fishing tools of chimpanzees (*Pan troglodytes*). *Biology Letters*, rsbl. 2008.0786.
- Sapolsky, R. M., & Share, L. J. (2004). A pacific culture among wild baboons: its emergence and transmission. *PLoS Biology*, *2*(4), e106.
- Sasaki, T., & Biro, D. (2017). Cumulative culture can emerge from collective intelligence in animal groups. *Nature Communications*, *8*, 15049.
- Seeley, T. D., Mikheyev, A. S., & Pagano, G. J. (2000). Dancing bees tune both duration and rate of waggle-run production in relation to nectar-source profitability. *Journal of Comparative Physiology A*, *186*(9), 813-819.
- Tennie, C., Call, J., & Tomasello, M. (2009). Ratcheting up the ratchet: on the evolution of cumulative culture. *Philosophical Transactions of the Royal Society of London B: Biological Sciences*, *364*(1528), 2405-2415.
- Thornton, A., & McAuliffe, K. (2006). Teaching in wild meerkats. *Science*, *313*(5784), 227-229.
- Thornton, A., Samson, J., & Clutton-Brock, T. (2010). Multi-generational persistence of traditions in neighbouring meerkat groups. *Proceedings of the Royal Society of London B: Biological Sciences*, *277*(1700), 3623-3629.
- Tomasello, M., Davis-Dasilva, M., CamaK, L., & Bard, K. (1987). Observational learning of tool-use by young chimpanzees. *Human Evolution*, *2*(2), 175-183.

- Van Baaren, R. B., Holland, R. W., Kawakami, K., & Van Knippenberg, A. (2004). Mimicry and prosocial behavior. *Psychological Science*, *15*(1), 71-74.
- van de Waal, E., Borgeaud, C., & Whiten, A. (2013). Potent social learning and conformity shape a wild primate's foraging decisions. *Science*, *340*(6131), 483-485.
- van de Waal, E., Krützen, M., Hula, J., Goudet, J., & Bshary, R. (2012). Similarity in food cleaning techniques within matrilineal groups in wild vervet monkeys. *PLoS One*, *7*(4), e35694.
- Van Leeuwen, E. J., & Haun, D. B. (2013). Conformity in nonhuman primates: fad or fact? *Evolution and Human Behavior*, *34*(1), 1-7.
- Van Leeuwen, E. J., & Haun, D. B. (2014). Conformity without majority? The case for demarcating social from majority influences. *Animal Behaviour*, *96*, 187-194.
- Van Leeuwen, E. J., Kendal, R. L., Tennie, C., & Haun, D. B. (2015). Conformity and its look-a-likes. *Animal Behaviour*, *110*, e1-e4.
- Van Schaik, C. P., Ancrenaz, M., Borgen, G., Galdikas, B., Knott, C. D., Singleton, I., . . . Merrill, M. (2003). Orangutan cultures and the evolution of material culture. *Science*, *299*(5603), 102-105.
- Voelkl, B., & Huber, L. (2000). True imitation in marmosets. *Animal Behaviour*, *60*(2), 195-202.
- Voelkl, B., & Huber, L. (2007). Imitation as faithful copying of a novel technique in marmoset monkeys. *PLoS One*, *2*(7), e611.
- Waite, R. (1981). Local enhancement for food finding by rooks (*Corvus frugilegus*) foraging on grassland. *Ethology*, *57*(1), 15-36.
- Whiten, A. (2005). The second inheritance system of chimpanzees and humans. *Nature*, *437*(7055), 52-55.
- Whiten, A. (2017). A second inheritance system: The extension of biology through culture. *Interface Focus*, *7*(5), 20160142.

- Whiten, A., Goodall, J., McGrew, W. C., Nishida, T., Reynolds, V., Sugiyama, Y., . . . Boesch, C. (1999). Cultures in chimpanzees. *Nature*, 399(6737), 682-685.
- Whiten, A., Goodall, J., McGrew, W. C., Nishida, T., Reynolds, V., Sugiyama, Y., . . . Boesch, C. (2001). Charting cultural variation in chimpanzees. *Behaviour*, 138(11), 1481-1516.
- Whiten, A., Hinde, R. A., Laland, K. N., & Stringer, C. B. (2011). Culture evolves. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 366(1567), 938-948.
- Whiten, A., Horner, V., & De Waal, F. B. (2005). Conformity to cultural norms of tool use in chimpanzees. *Nature*, 437(7059), 737-740.
- Whiten, A., & van de Waal, E. (2016). Identifying and dissecting conformity in animals in the wild: Further analysis of primate data. *Animal Behaviour*, 122, e1-e4.
- Yurk, H., Barrett-Lennard, L., Ford, J., & Matkin, C. (2002). Cultural transmission within maternal lineages: vocal clans in resident killer whales in southern Alaska. *Animal Behaviour*, 63(6), 1103-1119.
- Zentall, T. R. (2004). Action imitation in birds. *Learning & Behavior*, 32(1), 15-23.

## THESIS OUTLINE

As discussed in my introductory review of the key relevant literature in **Chapter 1**, there are many unanswered questions about the social learning processes that underlie the emergence and transmission of animal cultures. In this thesis, I shed light on the respective influences of model-bias, social context and individual differences upon social learning decisions of chimpanzees.

In my first empirical study, **Chapter 2**, I investigated claims that a bias towards copying dominant individuals may constrain the diffusion of novel behaviours demonstrated by subordinate chimpanzees. I report evidence that individuals from groups with a subordinate model who demonstrated a novel method of opening a puzzle-box were highly motivated to copy the seeded behaviour, whereas those from groups with dominant models were markedly less so.

In **Chapter 3**, I set out to determine whether chimpanzees behave in a conformist manner when confronted with a unanimous majority of their group-mates demonstrating an alternative behavioural preference to themselves. Instead, it was found that individuals rapidly switched from their first-learned method before having observed the majority of their group-mates (just one or two individuals). Individuals who made a similar number of observations in a dyadic learning condition did not deviate from their learned behaviour, so I conclude that social context is a critical factor in motivation for social learning.

In **Chapter 4** I investigated individual differences in chimpanzee social learning behaviour. This was carried out through a novel and ambitious form of analysis, examining the performance of individual chimpanzees across 11 years of social learning experiments carried out at the study site. I provide evidence for consistent individual differences in chimpanzees across experimental contexts, and that these differences are

predicted to a degree by sex, but not rearing history, age or research experience. Nor is it a strongly heritable trait.

Finally, in **Chapter 5**, the findings of all three previous chapters are discussed in further detail as well as their implications for the field more broadly. I also make suggestions for future research based on the findings and methods of these studies.

This thesis is presented in publication format. Each data chapter therefore includes a separate introduction, method, results, discussion and reference section. The status of publication is indicated at the beginning of each chapter except **Chapter 5**.

Ethical approval from the University of St Andrews for my two experimental chapters (**Chapters 2 and 3**) can be found in **Appendix A**.



## CHAPTER 2

### **SOCIALLY TRANSMITTED DIFFUSION OF A NOVEL BEHAVIOUR FROM SUBORDINATE CHIMPANZEES**

This chapter was published by the *American Journal of Primatology* in January, 2017  
(See **Appendix B** for published version) with the authorship listed below.

Stuart K Watson<sup>1</sup>, Lisa A Reamer<sup>2</sup>, Mary Catherine Marenò<sup>2</sup>, Gillian Vale<sup>1,2</sup>, Rachel A  
Harrison<sup>1</sup>, Susan P Lambeth<sup>2</sup>, Steven J Schapiro<sup>2,3</sup>, Andrew Whiten<sup>1</sup>

#### *Affiliations*

<sup>1</sup>Centre for Social Learning and Cognitive Evolution, and Scottish Primate Research Group, School of Psychology and Neuroscience, University of St Andrews, UK

<sup>2</sup>National Center for Chimpanzee Care, Department of Veterinary Sciences, Michale E. Keeling Center for Comparative Medicine and Research, UT MD Anderson Cancer Center, Bastrop, TX USA

<sup>3</sup>Department of Experimental Medicine, University of Copenhagen, Denmark

## ABSTRACT

Chimpanzees (*Pan troglodytes*) demonstrate much cultural diversity in the wild, yet a majority of novel behaviours do not become group-wide traditions. Since many such novel behaviours are introduced by low-ranking individuals, a bias toward copying dominant individuals ('rank-bias') has been proposed as an explanation for their limited diffusion. Previous experimental work showed that chimpanzees (*Pan troglodytes*) preferentially copy dominant over low-rank models. We investigated whether low ranking individuals may nevertheless successfully seed a beneficial behaviour as a tradition if there are no 'competing' models. In each of four captive groups, either a single high-rank (HR,  $n=2$ ) or a low-rank (LR,  $n=2$ ) chimpanzee model was trained on one method of opening a two-action puzzle-box, before demonstrating the trained method in a group context. This was followed by eight hours of group-wide, open-access to the puzzle-box. Successful manipulations and observers of each manipulation were recorded. Barnard's exact tests showed that individuals in the LR groups used the seeded method as their first-choice option at significantly above chance levels, whereas those in the HR groups did not. Furthermore, individuals in the LR condition used the seeded method on their first attempt significantly more often than those in the HR condition. A network-based diffusion analysis revealed that the best supported statistical models were those in which social transmission occurred *only* in groups with subordinate models. Finally, we report an innovation by a subordinate individual that built cumulatively on existing methods of opening the puzzle-box and was subsequently copied by a dominant observer. These findings illustrate that chimpanzees are motivated to copy rewarding novel behaviours that are demonstrated by subordinate individuals and that, in some cases, social transmission may be constrained by high-rank demonstrators.

## INTRODUCTION

It is now generally accepted that social learning is widespread in the animal kingdom and that socially transmitted traditions ('cultures') are found in a wide range of vertebrates (Laland & Galef, 2009; Laland & Janik, 2006; Whiten, 2005). However, the processes by which a novel behaviour propagates to become a group-wide tradition remain unclear (Rendell et al., 2011). Indiscriminately copying the behaviours of conspecifics is often not an optimal strategy, as the learner runs the risk of copying costly behaviours or wasting energy on those that are not productive (Kendal, Coolen, van Bergen, & Laland, 2005; Rendell et al., 2010). Accordingly, a number of adaptive 'biases' in social learning have been proposed as possible influences on whether individuals choose to utilise social information and who they get it from, for example 'when uncertain, copy the majority' (Claidière & Whiten, 2012; Henrich & McElreath, 2003; Laland, 2004; Van Leeuwen & Haun, 2014). Due to their cultural diversity (Whiten et al., 1999) and propensity for social learning, chimpanzees have been a favoured model species for studying these social learning biases. Chimpanzees also present an interesting paradox in that although innovations are not an uncommon occurrence, at one field site where researchers made an attempt to quantify their fate it was found that a majority of innovations failed to become group-wide traditions (Nishida, Matsusaka, & McGrew, 2009). The factors that determine whether a novel behaviour diffuses throughout a group or remains limited to one or a minority of individuals are largely unknown. The direct payoff of a behaviour does not seem sufficient to explain this, given reported instances of the spread of 'arbitrary' traditions with no apparent functional benefits. A striking example of this is described by Van Leeuwen, Cronin, and Haun (2014), who report a single chimpanzee placing a piece of grass in its ear to no discernible benefit - a 'fashion' which was soon adopted by the rest of the group. Conversely, Hopper, Schapiro, Lambeth, and Brosnan (2011) found in a token-exchange task that most chimpanzees chose the same tokens as those selected by a trained model, even when the alternative token choice

resulted in a more preferred food reward, presenting an interesting example of copying a behaviour which is visibly less beneficial than alternatives.

Many novel behaviours enter both wild and captive chimpanzee communities through the lower end of the dominance hierarchy – whether this be from subordinate innovators (Reader & Laland, 2001) or migrant females importing their native behavioural repertoire to their host group (Nakamura & Uehara, 2004; O'Malley, Wallauer, Murray, & Goodall, 2012). A bias toward copying dominant over subordinate individuals has been shown and proposed to explain the relative rarity of these novel behaviours becoming traditions (Kendal et al., 2015). One might suppose that this would occur for strategic reasons (dominant individuals are successful, so copying them might be an adaptive option), due to normative effects (copying the dominant individual facilitates social cohesion) or simply as a result of an attentional bias towards these individuals (e.g. dominant individuals are central in the social network). In capuchin monkeys it has been found that subordinate individuals tend not to demonstrate acquired token-exchange behaviours in a group context (Addessi, Paglieri, & Focaroli, 2011) or in the presence of a dominant individual (Lonsdorf et al., 2016), which means there is an inherent rank-bias in the source of social information available to observers. Although it has also been found that capuchins preferentially observe older, more dominant and more proficient nut-crackers in the wild, suggesting a more active learning bias (Coelho et al., 2015). One or all of these may play a part in restricting the flow of social information from subordinate individuals and cause a group-wide convergence on the behaviour of dominant individuals. To date, two studies have offered evidence for a rank-bias in chimpanzees. Kendal et al. (2015) seeded a method of opening a two-action puzzle box into two groups of chimpanzees using mid-ranking female models (and allowed two other groups to explore the task without trained models), and through complex analysis of attention states during demonstrations found evidence that individuals preferentially attend to dominant and/or knowledgeable demonstrators. Horner, Proctor, Bonnie, Whiten, and

de Waal (2010) also concluded that when presented with demonstrations from both a 'high prestige' (high rank and track record as a model) and 'low prestige' (low rank) individual on a token-exchange task, chimpanzees preferentially copied the method demonstrated by the high prestige individual (Horner et al., 2010). However, there remains the question of whether or not low-ranking individuals, who demonstrate a productive novel behaviour, will be copied if there are no more dominant models available. This question is important for our understanding of how innovations become traditions, and how traditions proliferate across communities.

Accordingly, we compared the diffusion of alternative methods of opening a two-action puzzle-box seeded by either a low- (female) or high-ranking (male) individual in four different groups of chimpanzees. In this context, based on prior work indicating a rank-bias in chimpanzee social learning, we predicted that either (a) social transmission of the seeded method will *only* occur in the groups with high-ranking models (we shall call this the '*hard* rank-bias hypothesis'), or (b) behaviour will be socially transmitted in *both* conditions, but the effect will be stronger in groups with high-ranking models ('*soft* rank-bias hypothesis').

## **METHODS**

### *Study Site*

This study was carried out at the National Center for Chimpanzee Care (NCCC) located at the Michale E. Keeling Center for Comparative Medicine and Research of The University of Texas MD Anderson Cancer Center in Bastrop (UTMDACC), Texas. Data was collected between April and August, 2015. A total of 38 chimpanzees (21 female) participated in the study, aged from 13 to 53 years of age. Most individuals were captive-born, but some (n=5) were wild-born. All individuals have participated in a wide range of previous behavioural research studies, some of which included puzzle-box tasks, but we

have designed our apparatus to require different manipulations to those of earlier studies, as noted below. The participants include both nursery-reared and mother-reared individuals. Following previous studies (Hopper, Kurtycz, Ross, & Bonnie, 2015; Hopper, Lambeth, Schapiro, & Whiten, 2015; Horner et al., 2010; Kendal et al., 2015), the social rank of each individual was determined by surveying the judgments of 5 staff members (behavioural researchers, trainers and management) who had been working with these animals for at least 5 years each. Freeman et al. (2013) found that human assessment of dominance in chimpanzees has good predictive validity for relevant behavioural measures of dominance such as aggression and displacement. Each staff member was asked to rank the individuals in the group linearly from '1' (highest rank) to N (lowest rank) without discussing their rankings with other staff. Agreement between observers was high (>80%), but where disagreements occurred the mode rank for each individual was used. From these rankings we determined the 'alpha' male for each group in the HR condition and chose a subordinate (averaging in the lower third of the hierarchy) female to act as the model for each group in the LR condition. All groups have access to two or more den areas (14m<sup>2</sup> each) and either an outdoor habitat or dome (dome: 90m<sup>2</sup>, habitat: 400m<sup>2</sup>) with a range of enrichment devices and activities, and a variety of climbing and swinging structures to promote species-typical behaviours. Testing generally occurred indoors, but access to outdoor enclosures was not restricted. The full demographic and housing information for each participating individual can be found in Table 2.1. Ethical approval for this study was granted by the School of Psychology & Neuroscience at the University of St Andrews and the IACUC of UTMDACC, adhering to all the legal requirements of US law and the American Society of Primatologists' principles for the ethical treatment of non-human primates. All subjects voluntarily participated in the testing procedures.

<b>ID</b>	<b>CONDITION</b>	<b>SEX</b>	<b>WILD BORN?</b>	<b>DOB</b>	<b>REARING</b>	<b>HOUSING</b>
RAD	LR (1)	M	N	14/01/1990	MOTHER	HABITAT
ANG*	LR (1)	F	Y	01/01/1975	UNKNOWN	HABITAT
CHE	LR (1)	F	N	09/12/1990	NURSERY	HABITAT
KIH	LR (1)	F	N	06/08/1988	NURSERY	HABITAT
MAH	LR (1)	M	N	26/10/1988	MOTHER	HABITAT
NAH	LR (1)	F	N	04/07/1990	NURSERY	HABITAT
AKI	LR (2)	M	N	09/02/1980	NURSERY	DOME
CEC*	LR (2)	F	N	24/02/1991	MOTHER	DOME
HAA	LR (2)	M	N	30/12/1991	MOTHER	DOME
MAR	LR (2)	F	Y	01/01/1966	UNKNOWN	DOME
MART	LR (2)	F	Y	01/01/1965	UNKNOWN	DOME
TAS	LR (2)	F	N	18/11/1992	MOTHER	DOME
ZOE	LR (2)	F	N	13/04/2002	MOTHER	DOME
BRI	HR (1)	F	N	31/08/1995	MOTHER	DOME
CHI	HR (1)	M	N	25/08/1988	MOTHER	DOME
MAG	HR (1)	M	N	24/07/1992	MOTHER	DOME
MAN	HR (1)	F	N	08/09/1984	MOTHER	DOME
NIC*	HR (1)	M	N	07/04/1988	MOTHER	DOME
BER	HR (2)	F	N	18/02/1978	NURSERY	DOME
JUD*	HR (2)	M	N	26/08/1990	NURSERY	DOME
KOB	HR (2)	M	Y	01/01/1972	UNKNOWN	DOME
QUI	HR (2)	F	Y	01/01/1971	UNKNOWN	DOME
TUL	HR (2)	F	N	01/05/1980	MOTHER	DOME
TOD	CONTROL	F	Y	01/01/1971	UNKNOWN	DOME
SAB	CONTROL	F	Y	01/01/1968	UNKNOWN	DOME
PEP	CONTROL	F	Y	01/01/1967	UNKNOWN	DOME
ALP	CONTROL	F	N	08/11/1984	MOTHER	DOME
BET	CONTROL	F	N	23/06/1994	MOTHER	DOME
BIL	CONTROL	M	N	16/06/1993	MOTHER	HABITAT
BO	CONTROL	M	N	16/05/1993	MOTHER	HABITAT
JOE	CONTROL	M	Y	01/01/1972	UNKNOWN	DOME
MAY	CONTROL	F	Y	01/01/1965	UNKNOWN	DOME
MOO	CONTROL	M	Y	01/01/1971	UNKNOWN	DOME
GRE	CONTROL	M	Y	01/01/1970	UNKNOWN	DOME
AJA	CONTROL	M	N	01/01/1978	UNKNOWN	DOME
LUL	CONTROL	F	N	16/01/1982	MOTHER	DOME
TAB	CONTROL	M	N	25/08/1991	MOTHER	DOME
KUD	CONTROL	M	N	07/12/1982	MOTHER	DOME

Table 2.1. Demographic information for all participating individuals. Condition: HR = High rank model, LR = Low-rank model. Asterisk next to name indicates individual was the trained model for their group.

## Apparatus

This study employed a two-action, sliding-door puzzle-box (the 'Vert', see Figure 2.1), a vertical variation we designed to require different actions to those common to earlier social learning studies (Aplin et al., 2015; Hopper, Lambeth, Schapiro, & Whiten, 2008; Kendal et al., 2015).

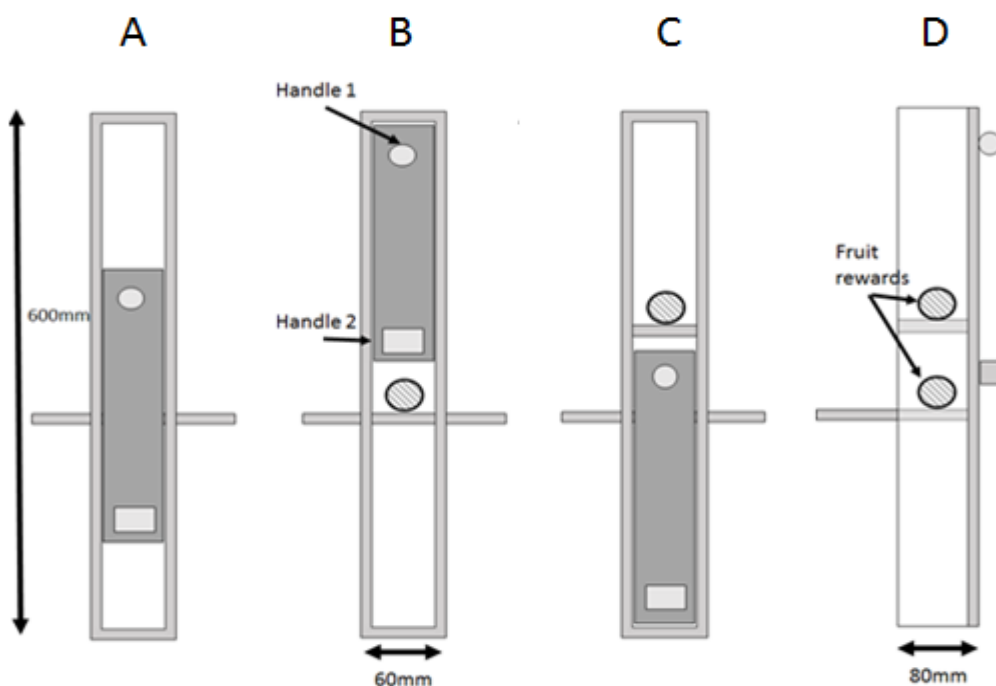


Figure 2.1. The 'vertical artificial vegetable' (the 'Vert') could be opened to reveal a food reward either by sliding the door entirely upwards (B) or entirely downwards (C). The resting position on presentation is shown in (A). The side-profile is shown in (D). Upon a completed opening, the door locked so as to restrict access to the alternative reward. The anchor platform was attached to a trolley with vice clamps.

Sessions were recorded using a Panasonic HC-X920 video camera. All videos were coded using BORIS, version 2.05 ([www.http://penelope.unito.it/boris](http://penelope.unito.it/boris)). All analyses



were carried out using R Statistical Package Version 3.2.3 (2017) with R Studio Version 0.99.491 (R Studio Team, 2015).

### *Procedure*

For Condition LR (low-rank), in two groups (n=6, 7), a low-ranking female individual was voluntarily separated and trained to open the door by either sliding the door up or down. Likewise in the HR (high-rank) condition, the dominant male of each of two groups (n = 5, 5) was trained on a method of opening the Vert. Females were used for Condition LR and males for Condition HR to maximise the rank disparity between these individuals. Since males are almost always of higher social rank than females in chimpanzee communities, in some groups it would not have been possible to select a high-ranking female to act as a model. However, Kendal et al. (2015) found no bias in whether male or female chimpanzees were preferentially attended to during their experiments, so we would not anticipate sex acting as a confound here. Nevertheless, below we include an analysis of audience sizes during demonstrations of the present study in order to explore whether males and females may differently tolerate observers. LR and HR conditions differed only in the choice of model.

Training began by presenting the baited Vert to the test subject with one of the slide-directions locked so it could not be used. Once a reward had been retrieved successfully 10 times in a row, the alternative method was unlocked and baited for all further trials. Models were considered to be 'trained' once they completed a total of 30 sequential uses of the trained method without deviation.

After being trained, the model was reintroduced to the group and given access to the Vert in a group context. Two 20-minute demonstration sessions were carried out on subsequent days, during which only the model had access to the box. The Vert was gently pulled out of reach if another individual displaced the model. This was to ensure a roughly equal number of demonstrations between dominant and subordinate models

and make the methods comparable with previous work on rank-bias and social learning (Hopper, Lambeth, et al., 2015; Horner et al., 2010; Kendal et al., 2015)

The demonstration period was followed by 8 hours of open-diffusion in which unrestricted access to the Vert was provided. Open-diffusion occurred across multiple sessions, typically of 60 minutes but varying between 45 minutes (due to unforeseen interruptions) and 120 minutes in length (group HR2 had an unavoidably condensed test period, resulting in longer sessions to make up time).

Once any individual in the demonstration or open-diffusion phase had retrieved a reward, the Vert was withdrawn one metre, the door was reset and the reward chamber re-baited. When re-setting the door, the Vert was covered with a cloth to avoid possible directional cues from the experimenter.

To determine whether an inherent directional bias may have influenced which method individuals from experimental groups chose to use, 15 individuals were selected from non-experimental groups to participate in an asocial control condition. Individuals were selected based on advice from care staff about their willingness to voluntarily separate from the group and engage with research procedures. Individuals separated voluntarily from their group and were then presented with the Vert for a period of 20 minutes each. Both reward chambers were baited and both methods of opening the door were unlocked. If an individual completed a successful manipulation of the Vert, the Vert was reset and baited as described above.

### *Statistical analyses*

We used binomial tests to determine whether the number of individuals in the control condition to use each method on their first trial differed significantly from chance (50%), which would indicate an inherent directional bias that would have acted as a confound. We then used Barnard's exact test, an alternative to Fisher's exact test with greater

power for small sample sizes (Mehta & Senchaudhuri, 2003), to test whether individuals from high or low rank conditions were significantly more likely to use the seeded method on their first successful trial. Binomial tests were subsequently used to determine whether the proportion of individuals in each condition who used the seeded method on their first successful trial differed significantly from chance (50%). Finally, we applied the same tests to a more conservative, truncated form of the experimental data set. In order to mitigate the possibility that individuals had learned from individuals not of direct interest to the research question, for example a dominant female who had asocially learned the same method as the subordinate model, we only analysed data (for this analysis only) from individuals in both conditions who had *only* observed their group's model demonstrating. This resulted in 11 individuals being excluded from this model, leaving  $n=8$ .

### *Network-based diffusion analysis*

Network-based diffusion analysis (NBDA) is a powerful method of determining whether an observed pattern of acquisition of behaviours is consistent with the predictions of a group's social network (Allen, Weinrich, Hoppitt, & Rendell, 2013; Franz & Nunn, 2009; Hobaiter, Poisot, Zuberbühler, Hoppitt, & Gruber, 2014; Hoppitt, Boogert, & Laland, 2010). In this case, the social network was created using the number of times Individual A observed Individual B using the seeded method before Individual A first demonstrated this method. Because we were able to record the exact times at which an individual first used the method, we used the Time of Acquisition Diffusion Analysis (TADA) variant of NBDA (Hoppitt et al., 2010). Times entered into the model were the number of seconds which the group had been exposed to the Vert before a given individual first opened it using the seeded method.

We used an information theoretic approach (Burnham & Anderson, 2004), using Akaike's information criterion corrected for sample size (AICc) from which total Akaike

weights ( $\sum w_i$ ) for each model were calculated. Total Akaike Weights were then used to create model averaged estimates for the factor by which individuals' learning rates are increased per observation of the seeded method. Models were constructed based on the predictions outlined by the rank-bias hypothesis and the necessary conditions for refutation (above).

This analysis was carried out using the NBDA R Script Version 1.2.11 (available at <http://lalandlab.st-andrews.ac.uk/freeware/>).

### *Generalised linear mixed effects models*

We used two sets of generalised linear mixed effects models (GLMMs) to determine whether the sex of a demonstrator was a useful predictor in determining how many individuals were likely to be in proximity (<3m) on any given trial. The first set of models considered audience size as an absolute value, whereas the second considered it as a proportion of group size. In all models, 'individual' was fit with random intercepts and random slopes to account for multiple measurements from each individual. We took an information theoretic approach to inference, using akaike's information criterion corrected for small sample sizes (AICc) to estimate model fit. From this we calculated total akaike weights ( $\sum w_i$ ) and use these to compute model-averaged estimates of parameter coefficients, allowing us to estimate the effect of a parameter while taking into account model uncertainty. Due to the use of model-averaging, rather than use p-values to determine whether a parameter had an important effect on the output variable, this was established according to whether its 95% confidence intervals overlapped with 0.

### *Video Coding*

The method used by any individual who successfully opened the box was coded, as well as the identities of any individual within 3 meters. Any individuals within 3m whose

heads were oriented towards the Vert and did not have their view obstructed was recorded as having observed the opening. Videos were coded by SKW. Inter-observer reliability was carried out with RAH on the method ('up' or 'down') used and who was observing each demonstration in 30 clips of individuals opening the Vert, with 100% agreement.

## RESULTS

Although the raw data from the control condition (Figure 2.2) are somewhat suggestive of a greater tendency for pushing down than lifting up the door, the number of individuals who chose either method did not differ significantly from chance (Up:  $n = 3$ ,  $P = 0.343$ , 95% CI = 0.07-0.65; Down:  $n = 7$ ,  $P = 0.343$ , 95% CI: 0.35-0.93). Nevertheless, the direction of the seeded method was counterbalanced across groups in the experimental condition. Furthermore, five out of 15 control individuals failed to open the box at all, from which we may infer that the two methods of opening the door were not so salient that every chimpanzee was easily capable of opening it without the use of social information.

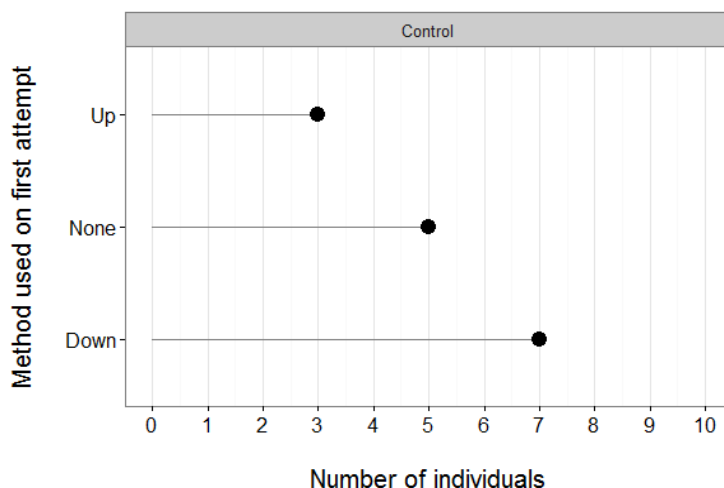


Figure 2.2. Method used on first opening of the Vert by individuals in the control condition, and number of individuals who failed to open the box.

A Barnard's exact test found that individuals in the low-rank condition used the seeded method on their first successful trial significantly more often than individuals in the high-rank condition ( $X^2 = 2.09$ ,  $N=19$ ,  $P=0.048$ , see Figure 2.3). Exact binomial tests found that individuals in the low-rank condition used the seeded method significantly more often than chance ( $n = 11$ ,  $P=0.032$ ,  $95\% \text{ CI}=0.53-1.0$ ) but high-rank condition did not ( $n=8$ ,  $P=0.855$ ,  $95\% \text{ CI}=0.111 - 1.0$ ).

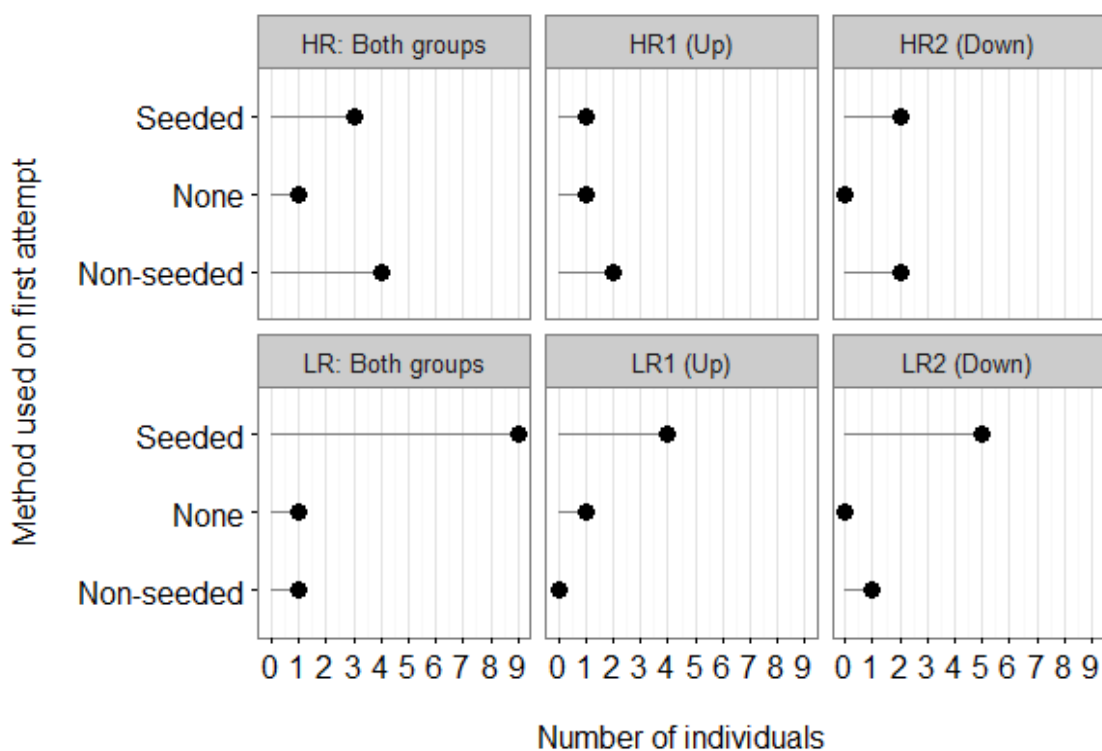


Figure 2.3. Column 1 - Methods used on first opening of the box for each condition. Columns 2 and 3 - Methods used on first opening of the box in each group. Directionality of trained method indicated for each group in brackets.

Using a truncated data set (Figure 2.4: procedure and rationale for exclusion detailed above), there remained a significant difference between low and high-rank conditions in the number of individuals who used the seeded method on their first trial

(Barnard's exact test:  $X^2=2.19$ ,  $n=8$ ,  $P=0.047$ ). However, it is worth noting that two of the four individuals in HR condition (see HR2 in Table 2.2) who first used the non-seeded method later switched to consistently use the seeded method. No other individuals in any group persistently switched to a method other than their first-learned, with the exception of the innovation described in detail below. Both individuals who did not solve the task were males. Neither individual tried any other method of interacting with the door (e.g. hitting, pushing, pulling, etc.), indicating that they lacked the motivation to engage with the task.

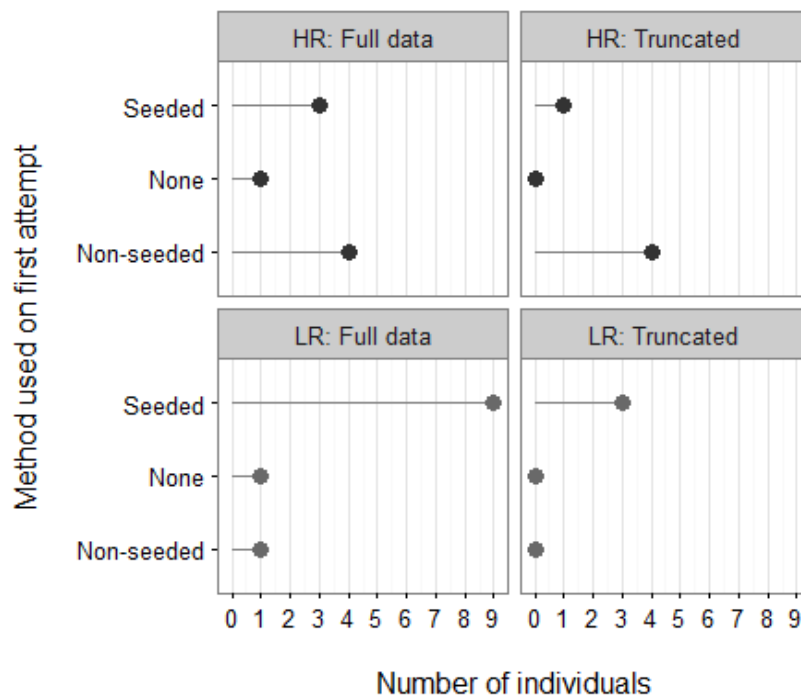


Figure 2.4. Counts for methods used on first opening of the box in the original 'full' data set, side-by-side with 'truncated' data set.

ID	Group	First method as seeded?	Total trials	Total trials as seeded
JUD	HR1	Y	730	720
BER	HR1	N	69	0
TUL	HR1	Y	234	214
QUI	HR1	N	1	0
KOB	HR1	n/a	0	0
NIC	HR2	Y	535	463
CHI	HR2	N	109	108
MAN	HR2	N	54	48
MAG	HR2	Y	106	66
BRI	HR2	Y	9	6
CEC	LR1	Y	170	170
MAY	LR1	Y	185	184
ZOE	LR1	Y	123	121
AKI	LR1	N	171	3
TAS	LR1	Y	166	163
MAR	LR1	Y	34	34
HAA	LR1	Y	138	138
ANG	LR2	Y	146	146
CHE	LR2	Y	115	108
KIH	LR2	Y	326	133
NAH	LR2	Y	188	162
RAD	LR2	Y	13	13
MAH	LR2	n/a	0	0

Table 2.2. Summary table of each individual's interactions with the puzzle box. Where individuals discovered the "improved method" (see below), this was counted as one use of the seeded and one use of non-seeded method in the 'total trials as seeded' column.

### *Network-based Diffusion Analysis*

There was most support for models (Table 2.3) in which there was an effect of social transmission ( $S$ ) in the LR condition but not HR, with  $S$  varying between groups ( $\Sigma w_i = 0.75$ ). Model-averaged estimates for  $S$  indicate that each observation increased an average individual's learning rate by 3% in LR1 and 15% in LR2. Model averaged estimates for  $S$  indicate that each observation increased an average individual's learning rate in HR1 and HR2 by 0.1% per observation. Models based on the hard rank-bias hypothesis were not well supported ( $\Sigma w_i = 0.002$  and  $\Sigma w_i = 0.009$ ). A model allowing for the soft rank-bias hypothesis had some support ( $\Sigma w_i = 0.078$ ), but contrary to the predictions of this hypothesis, the effect of  $S$  was estimated as being greater in the LR condition ( $S = 0.08$ ) than HR ( $S = 0.00$ ). Individual-level variables (sex, age and rearing



history) were added to the best fitting model, but there was little support for any of them improving the model (Table 2.4).

<b>Model</b>	<b>AICc</b>	<b>Delta AICc</b>	<b>Total weighted AICc (<math>\Sigma w_i</math>)</b>
*S only in HR, varies between HR groups	334.1	11.91	0.002
S in all groups	331	8.74	0.009
*S only in HR, constant between HR groups	331	8.74	0.009
S varies between all groups	328.6	6.38	0.027
No S in any group	328.3	6.05	0.036
**S varies between LR and HR	326.8	4.53	0.078
S only in LR, constant between LR groups	326.5	4.28	0.088
S only in LR, varies between LR groups	322.2	0	0.75

\* 'Hard' rank bias hypothesis

\*\* 'Soft' rank-bias hypothesis candidate

Table 2.3. AICc, delta AICc and Total Akaike Weights ( $\Sigma w_i$ ) for each model. 'S' = social transmission.

<b>Asocial variable</b>	<b>df</b>	<b>AICc</b>	<b>Delta AICc</b>	<b>Total weighted AICc</b>
Sex	4	325.73	3.51	0.07
Rearing	4	323.13	0.91	0.25
Age	4	323.08	0.86	0.26
None	3	322.22	0	0.41

Table 2.4. AICc, delta AICc and Total Akaike Weights ( $\Sigma w_i$ ) for the best fitting model from

Table 2.3 with additional individual-level variables.

### *GLMMs*

A model-averaged estimate (Table 2.5) of the coefficient for the effect of demonstrator sex on audience size when counting absolute number of individuals within 3m was 0.14 (95% CI: -0.23, 0.51), and when considering audience size as a proportion of total group size was 0.02 (95% CI: -0.05, 0.08). We may infer that Sex did not have an important effect as the 95% confidence intervals did not overlap with zero.

Furthermore, as seen in Table 2.5, adding Sex to the models resulted in a considerably higher AICc and therefore poorer fit.

GLMM Set 1: Audience = Number of individuals < 3m from demonstrator

<b>Model</b>	<b>K</b>	<b>AICc</b>	<b>Delta AICc</b>	<b>Total AICc weight</b>
Audience ~ 1 ID	3	9178.19	0	0.94
Audience ~ Sex + Sex ID	6	9183.63	5.44	0.06

GLMM Set 2: Audience = Proportion of group < 3m from demonstrator

<b>Model</b>	<b>K</b>	<b>AICc</b>	<b>Delta AICc</b>	<b>Total AICc weight</b>
Audience ~ 1 ID	3	-2114.53	0	0.94
Audience ~ Sex + Sex ID	6	-2108.95	5.58	0.06

Table 2.5. Model comparison summary statistics for two sets of GLMMs. Sex = Sex of demonstrator. 1|ID = Random intercepts for individual. Sex|ID = random slopes and intercepts for Individual. K = number of effective parameters.

### *An Innovation*

Finally, we report an innovation which occurred in one of the high-rank condition groups. After 7 hours of open-diffusion, a subordinate individual (TUL) discovered a narrow window of motion in which the door can be opened using 'Up', so that a reward can be retrieved, but the locking mechanism is not activated. This allowed her to then also use 'Down' to move the door a second time and obtain a second reward. TUL had not used 'Down' prior to this discovery, but had observed two other females in her group using it on multiple occasions. This suggests TUL combined her first-learned method with previously acquired social information about that used by others to generate a more productive method, although asocial learning cannot be ruled out. Despite the innovator being of low rank, after 11 observations of this improved method the dominant male (JUD) of the group, who to this point had exclusively used the 'Up' method, also began to use the combined form. A similar pattern was observed in a second group. Again, the first individual was a subordinate female (CHE) and the method was subsequently used

by two higher ranking females (KIH, NAH). Due to the limited data available, it is not possible to carry out any formal analyses of these events, but we present them as 'naturally' occurring examples of subordinates' innovations achieving limited diffusion through their groups.

## **DISCUSSION**

Rank-bias has been proposed as a way to account for the relatively rare adoption of innovations to produce traditions within chimpanzee communities (Horner et al., 2010; Kendal et al., 2015). Based on this 'rank-bias hypothesis', we predicted that novel behaviours seeded by subordinates either fail to spread, or motivate a considerably lesser degree of social learning than novel behaviours seeded by dominant individuals. In our study, not only were the group-mates of low-ranking models more likely to use the seeded rather than non-seeded method on their first opening of the box, but they were also substantially more likely to do so than individuals in groups with high-rank models. Furthermore, a NBDA showed greatest support for models in which social transmission of the seeded method was present only in the low-rank condition. Finally, we reported innovations developed by two subordinate chimpanzees in separate groups which built on pre-existing methods and were subsequently used by more dominant individuals, likely as a result of social learning. While one must be cautious in interpreting isolated events, these instances are striking in their pertinence to our research question and in how they contrast with the predictions of the rank-bias hypothesis.

We conclude these findings strongly suggest that the rank-bias identified by previous studies (Kendal et al., 2015; or 'prestige-bias' in Horner et al., 2010), which occurred when observers had a choice between models of various ranks, does not prohibit the successful emergence of group-wide behaviour patterns from subordinate models or innovators when no competing model is present. As well as a rank-bias, Kendal et al. (2015) identified a bias towards copying 'knowledgeable' individuals, which

our results suggest to be the case even when demonstrators are of low social rank. This may make adaptive sense, since if one observes an individual doing something that is rewarding, it is counterintuitive to ignore this information simply on the basis of the demonstrator's low social status. However, this does not preclude the indirect importance of rank in more natural settings. For example, if recent immigrants tend to be spatially peripheral to the group, this would reduce the number of individuals in close enough proximity to observe (and copy) any novel behaviours being used, functionally resulting in a rank bias. By contrast, individuals in the present study could only carry out the behaviour when performing it in a central, commonly used space where the researcher and experiment were set up, making them readily visible to their group. Furthermore, while we did identify comprehensive diffusion of methods seeded subordinate models, it is important to note the difference in group size between the relatively small groups studied here (between 6 and 8 individuals) and wild chimpanzee communities which can have anything from 20 to 150 members (Boesch & Boesch-Achermann, 2000; Goodall, 1986; Nishida, 1990). Communities of larger scale, as well as the presence of fission-fusion social dynamics, may present additional obstacles for behavioural diffusion.

Being raised in captivity and participating in behavioural research for so many years (e.g. Brosnan et al., 2007; Hopper, Lambeth, Schapiro & Whiten, 2008; Dean, Kendal, Schapiro, Thierry & Laland, 2012; Kendal et al., 2015) may also have shaped the study population to be more ready social learners (Carpenter & Tomasello, 1995), further mediating the effects of rank-bias. The influence of such developmental, cultural, environmental and individual differences on social learning are difficult to examine in such long-lived species, but are likely to be critical in our understanding of cultural transmission (Whiten, Caldwell, & Mesoudi, 2016). Nevertheless, this would not explain why there was a greater effect of social transmission in the low-rank condition than in our high-rank condition.

These results contrast with prior studies (Horner et al., 2010; Kendal et al., 2015) in that the effect of social transmission was found to be stronger in our low-rank condition, and a greater proportion of individuals in the LR condition used the seeded method on their first trial than those in HR. One methodological difference between the current study and previous work that might explain this discrepancy is that our high-ranking models were dominant males rather than dominant females. This was an intentional design choice, as males are almost always dominant relative to females, and it was desirable to maximise the rank disparity between model types. However, this may have introduced additional confounds. While males were successfully used as models in Price, Lambeth, Schapiro, and Whiten (2009), the study used video demonstrations and observers were not always from the same group as the model, and were therefore unaware of their rank. Wrangham et al. (2016) found that in a community of chimpanzees where multiple grooming techniques were in use, individuals tended to converge on the method primarily used by their matriline, potentially hinting at a sex bias in chimpanzee social learning. However, the only systematically documented example of an incipient tradition diffusing through a wild chimpanzee community originated in a male chimpanzee (Hobaiter et al., 2014), indicating that males can also make effective models. Furthermore, in a series of GLMM's we examined whether the number of individuals in proximity or attending to an individual's demonstrations could be predicted by that demonstrator's sex, and this was not found to be the case (Table 2.5). From this we may infer that our use of differently sexed models did not introduce an important confound with respect to social tolerance that would explain the contrast between effects of high versus low rank models in our study. In any case, the key finding in our results is not so much the contrast between effects of high versus low ranked models, but that the low ranked female provided an adequate model whose preferred behavioural option was copied by others.

There is already good evidence for an attentional bias toward dominant individuals (Kendal et al., 2015), but it is unclear to what extent this may be vigilance

rather than active social learning. Spatial tolerance between demonstrators and observers is also likely to be crucial in facilitating social learning (Van Schaik, 2003), which may be confounded when highly dominant demonstrators monopolise a resource. The difficulty associated with faithfully copying a socially intolerant individual may explain why two observers in the HR condition first discovered the non-seeded method and then switched to consistently use the seeded method for the remainder of testing. Based on previous work (Hrubesch, Preuschoft, & van Schaik, 2009) we would expect such individuals to fixate on their first-learned method, since the alternative did not provide a greater payoff (Van Leeuwen et al., 2013). It may be that, in this case, the first-used method was an 'accidental' discovery on the route to learning the seeded method.

As previously discussed, capuchin monkeys inhibit demonstration of known behaviours while in the presence of dominant males (Lonsdorf et al., 2016). If the same is true of chimpanzees, then non-dominant individuals having to wait for an appropriate social context to interact with the task may have introduced additional demands on memory that would interfere with accurate copying models in the HR condition. In our experiment, the fact that we removed the Vert when models were displaced in the demonstration phase meant that the resource could not be immediately monopolised. The reason for this was to remain methodologically consistent with prior work on rank-bias (Horner et al., 2010; Kendal et al., 2015), as well as to directly examine the motivation of observers to learn from subordinate models rather than the effects of resource-monopolisation on the diffusion of novel behaviours. Competition over resources remains an unexamined and potentially important influence on the diffusion of chimpanzee traditions.

While this study has shown that chimpanzees are motivated to learn novel methods of accessing a resource from subordinate individuals, it is possible this is not true of forms of imitative behaviour that are thought to be normatively motivated and therefore, perhaps particularly directed toward important social partners. Examples of

this include the fashion of putting grass in one's ear, invented by a high-ranking female, described by van Leeuwen, Cronin and Haun (2013) or vocal convergence resulting from close social affiliation (Fedurek, Machanda, Schel, & Slocombe, 2013; Watson et al., 2015). Further examination of context-specific qualities, such as behavioural-domain, extrinsic motivators (e.g. food or social benefits), ease of monopolisation and how these inhibit or promote particular learning biases, may be a fruitful area of research.

## REFERENCES

- Adessi, E., Paglieri, F., & Focaroli, V. (2011). The ecological rationality of delay tolerance: insights from capuchin monkeys. *Cognition*, *119*(1), 142-147.
- Allen, J., Weinrich, M., Hoppitt, W., & Rendell, L. (2013). Network-based diffusion analysis reveals cultural transmission of lobtail feeding in humpback whales. *Science*, *340*(6131), 485-488.
- Aplin, L. M., Farine, D. R., Morand-Ferron, J., Cockburn, A., Thornton, A., & Sheldon, B. C. (2015). Experimentally induced innovations lead to persistent culture via conformity in wild birds. *Nature*, *518*(7540), 538-541.
- Boesch, C., & Boesch-Achermann, H. (2000). *The chimpanzees of the Tai Forest: Behavioural ecology and evolution*: Oxford University Press, USA.
- Brosnan, S. F., Jones, O. D., Lambeth, S. P., Mareno, M. C., Richardson, A. S., & Schapiro, S. J. (2007). Endowment effects in chimpanzees. *Current Biology*, *17*(19), 1704-1707.
- Burnham, K. P., & Anderson, D. R. (2004). Multimodel inference: understanding AIC and BIC in model selection. *Sociological methods & research*, *33*(2), 261-304.
- Carpenter, M., & Tomasello, M. (1995). Joint attention and imitative learning in children, chimpanzees, and enculturated chimpanzees\*. *Social Development*, *4*(3), 217-237.
- Claidière, N., & Whiten, A. (2012). Integrating the study of conformity and culture in humans and nonhuman animals. *Psychological Bulletin*, *138*(1), 126.
- Coelho, C., Falótico, T., Izar, P., Mannu, M., Resende, B., Siqueira, J., & Ottoni, E. (2015). Social learning strategies for nut-cracking by tufted capuchin monkeys (*Sapajus* spp.). *Animal Cognition*, *18*(4), 911-919.
- Dean, L. G., Kendal, R. L., Schapiro, S. J., Thierry, B., & Laland, K. N. (2012). Identification of the social and cognitive processes underlying human cumulative culture. *Science*, *335*(6072), 1114-1118.



- Fedurek, P., Machanda, Z. P., Schel, A. M., & Slocombe, K. E. (2013). Pant hoot chorusing and social bonds in male chimpanzees. *Animal Behaviour*, 86(1), 189-196.
- Franz, M., & Nunn, C. L. (2009). Network-based diffusion analysis: a new method for detecting social learning. *Proceedings of the Royal Society of London B: Biological Sciences*, 276(1663), 1829-1836.
- Freeman, H. D., Brosnan, S. F., Hopper, L. M., Lambeth, S. P., Schapiro, S. J., & Gosling, S. D. (2013). Developing a comprehensive and comparative questionnaire for measuring personality in chimpanzees using a simultaneous top-down/bottom-up design. *American Journal of Primatology*, 75(10), 1042-1053.
- Goodall, J. (1986). *The chimpanzees of Gombe: Patterns of behavior*. Belknap Press of Harvard University Press.
- Henrich, J., & McElreath, R. (2003). The evolution of cultural evolution. *Evolutionary Anthropology: Issues, News, and Reviews*, 12(3), 123-135.
- Hobaiter, C., Poisot, T., Zuberbühler, K., Hoppitt, W., & Gruber, T. (2014). Social network analysis shows direct evidence for social transmission of tool use in wild chimpanzees. *PLoS biology*, 12(9), e1001960.
- Hopper, L. M., Kurtucz, L. M., Ross, S. R., & Bonnie, K. E. (2015). Captive chimpanzee foraging in a social setting: a test of problem solving, flexibility, and spatial discounting. *PeerJ*, 3, e833.
- Hopper, L. M., Lambeth, S. P., Schapiro, S. J., & Whiten, A. (2008). Observational learning in chimpanzees and children studied through 'ghost' conditions. *Proceedings of the Royal Society of London B: Biological Sciences*, 275(1636), 835-840.
- Hopper, L. M., Lambeth, S. P., Schapiro, S. J., & Whiten, A. (2015). The importance of witnessed agency in chimpanzee social learning of tool use. *Behavioural Processes*, 112, 120-129.

- Hopper, L. M., Schapiro, S. J., Lambeth, S. P., & Brosnan, S. F. (2011). Chimpanzees' socially maintained food preferences indicate both conservatism and conformity. *Animal Behaviour*, *81*(6), 1195-1202.
- Hoppitt, W., Boogert, N. J., & Laland, K. N. (2010). Detecting social transmission in networks. *Journal of Theoretical Biology*, *263*(4), 544-555.
- Horner, V., Proctor, D., Bonnie, K. E., Whiten, A., & de Waal, F. B. (2010). Prestige affects cultural learning in chimpanzees. *PloS One*, *5*(5).
- Hrubesch, C., Preuschoft, S., & van Schaik, C. (2009). Skill mastery inhibits adoption of observed alternative solutions among chimpanzees (*Pan troglodytes*). *Animal Cognition*, *12*(2), 209-216.
- Kendal, R. L., Coolen, I., van Bergen, Y., & Laland, K. N. (2005). Trade-offs in the adaptive use of social and asocial learning. *Advances in the Study of Behavior*, *35*, 333-379.
- Kendal, R. L., Hopper, L. M., Whiten, A., Brosnan, S. F., Lambeth, S. P., Schapiro, S. J., & Hoppitt, W. (2015). Chimpanzees copy dominant and knowledgeable individuals: implications for cultural diversity. *Evolution and Human Behavior*, *36*(1), 65-72.
- Laland, K. N. (2004). Social learning strategies. *Animal Learning & Behavior*, *32*(1), 4-14.
- Laland, K. N., & Galef, B. G. (2009). *The question of animal culture*: Harvard University Press.
- Laland, K. N., & Janik, V. M. (2006). The animal cultures debate. *Trends in Ecology & Evolution*, *21*(10), 542-547.
- Lonsdorf, E., Bonnie, K., Grim, M., Krupnick, A., Prestipino, M., & Whyte, J. (2016). Seeding an arbitrary convention in capuchin monkeys: The effect of social context. *Behaviour*, *153*(5), 633-654.
- Mehta, C. R., & Senchaudhuri, P. (2003). Conditional versus unconditional exact tests for comparing two binomials. *Cytel Software Corporation*, 675.

- Nakamura, M., & Uehara, S. (2004). Proximate factors of different types of grooming hand-clasp in Mahale chimpanzees: implications for chimpanzee social customs. *Current Anthropology*, 45(1), 108-114.
- Nishida, T. (1990). *Chimpanzees of the Mahale Mountains*: University of Tokyo Press.
- Nishida, T., Matsusaka, T., & McGrew, W. C. (2009). Emergence, propagation or disappearance of novel behavioral patterns in the habituated chimpanzees of Mahale: a review. *Primates*, 50(1), 23-36.
- O'Malley, R. C., Wallauer, W., Murray, C. M., & Goodall, J. (2012). The appearance and spread of ant fishing among the Kasekela chimpanzees of Gombe: a possible case of intercommunity cultural transmission. *Current Anthropology*, 53(5), 650-663.
- Price, E. E., Lambeth, S. P., Schapiro, S. J., & Whiten, A. (2009). A potent effect of observational learning on chimpanzee tool construction. *Proceedings of the Royal Society of London B: Biological Sciences*, 276(1671), 3377-3383.
- R Studio Team. (2015). RStudio: Integrated Development for R. Boston, MA: R Studio, Inc. Retrieved from [www.rstudio.com](http://www.rstudio.com)
- Reader, S. M., & Laland, K. N. (2001). Primate innovation: sex, age and social rank differences. *International Journal of Primatology*, 22(5), 787-805.
- Rendell, L., Boyd, R., Cownden, D., Enquist, M., Eriksson, K., Feldman, M. W., . . . Laland, K. N. (2010). Why copy others? Insights from the social learning strategies tournament. *Science*, 328(5975), 208-213.
- Rendell, L., Fogarty, L., Hoppitt, W. J., Morgan, T. J., Webster, M. M., & Laland, K. N. (2011). Cognitive culture: theoretical and empirical insights into social learning strategies. *Trends in cognitive sciences*, 15(2), 68-76.
- Vale, G. L., Davis, S. J., van de Waal, E., Schapiro, S. J., Lambeth, S. P., & Whiten, A. (2017). Lack of conformity to new local dietary preferences in migrating captive chimpanzees. *Animal Behaviour*, 124, 135-144. doi:<http://dx.doi.org/10.1016/j.anbehav.2016.12.007>

- Van Leeuwen, E. J., Cronin, K. A., & Haun, D. B. (2014). A group-specific arbitrary tradition in chimpanzees (*Pan troglodytes*). *Animal cognition*, 17(6), 1421-1425.
- Van Leeuwen, E. J., Cronin, K. A., Schütte, S., Call, J., & Haun, D. B. (2013). Chimpanzees (*Pan troglodytes*) flexibly adjust their behaviour in order to maximize payoffs, not to conform to majorities. *PLoS One*, 8(11), e80945.
- Van Leeuwen, E. J., & Haun, D. B. (2014). Conformity without majority? The case for demarcating social from majority influences. *Animal Behaviour*, 96, 187-194.
- Van Schaik, C. P. (2003). Local traditions in orangutans and chimpanzees: social learning and social tolerance. In D. Fragaszy & S. Perry (Eds.), *The biology of traditions: Models and evidence* (pp. 297-328): Cambridge University Press.
- Watson, S. K., Townsend, S. W., Schel, A. M., Wilke, C., Wallace, E. K., Cheng, L., . . . Slocombe, K. E. (2015). Vocal Learning in the Functionally Referential Food Grunts of Chimpanzees. *Current Biology*, 25(4), 495-499.
- Whiten, A. (2005). The second inheritance system of chimpanzees and humans. *Nature*, 437(7055), 52-55.
- Whiten, A., Caldwell, C. A., & Mesoudi, A. (2016). Cultural diffusion in humans and other animals. *Current Opinion in Psychology*, 8, 15-21.
- Whiten, A., Goodall, J., McGrew, W. C., Nishida, T., Reynolds, V., Sugiyama, Y., . . . Boesch, C. (1999). Cultures in chimpanzees. *Nature*, 399(6737), 682-685.
- Wrangham, R. W., Koops, K., Machanda, Z. P., Worthington, S., Bernard, A. B., Brazeau, N. F., . . . Otali, E. (2016). Distribution of a Chimpanzee Social Custom Is Explained by Matrilineal Relationship Rather Than Conformity. *Current Biology*, 26(22), 3033-3037.

## CHAPTER 3

### CHIMPANZEES PRIORITISE SOCIAL INFORMATION OVER PRE-EXISTING BEHAVIOURS IN A GROUP CONTEXT BUT NOT IN DYADS

This chapter is currently under review at *Animal Cognition* with the authorship detailed below.

Stuart K Watson<sup>1</sup>, Susan P Lambeth<sup>2</sup>, Steven J Schapiro<sup>2,3</sup>, Andrew Whiten<sup>1</sup>

#### *Affiliations*

<sup>1</sup>Centre for Social Learning and Cognitive Evolution, and Scottish Primate Research Group, School of Psychology & Neuroscience, University of St Andrews, UK

<sup>2</sup>National Center for Chimpanzee Care, Department of Veterinary Sciences, Michale E. Keeling Center for Comparative Medicine and Research, UT MD Anderson Cancer Center, Bastrop, TX USA

<sup>3</sup>Department of Experimental Medicine, University of Copenhagen, Denmark

## ABSTRACT

How animal communities arrive at homogenous behavioural preferences is a central question for studies of cultural evolution. Here, we investigated whether chimpanzees (*Pan troglodytes*) would relinquish a pre-existing behaviour to adopt an alternative demonstrated by a unanimous majority of group-mates. In other words, whether chimpanzees behave in a conformist manner. In each of five groups of chimpanzees (N=37), one individual was trained on one method of opening a two-action puzzle-box to obtain food, while the remaining individuals learned the alternative method. Five hours of open-access to the apparatus was provided in a group context, during which it was found that 4/5 'minority' individuals explored the majority method and three of these used this new method in the majority of trials. Those that switched did so after observing only a small subset of their group, thereby not matching conventional definitions of conformity. In a further 'Dyad' condition, six pairs of chimpanzees were trained on alternative methods and then given access to the task together. None of these individuals switched method. The number of observations that individuals in the minority and Dyad individuals made of their non-trained method, was not found to influence whether or not they themselves switched to use it. In a final 'Asocial' condition, individuals (N=10) did not receive social information and did not deviate from their first-learned method. We argue that these results demonstrate an important influence of social context upon prioritisation of social information over pre-existing methods, which can result in group homogeneity of behaviour.

## INTRODUCTION

Culture emerges and is maintained by a suite of social learning processes and biases that govern how social information is transmitted and when individuals choose to prioritise social information over pre-existing methods. Conformity, defined as foregoing personal information in favour of adopting a behaviour demonstrated by a majority of conspecifics (Haun & Tomasello, 2011; Whiten & Van Schaik, 2007), is a well-established bias in humans, occurring across varied cultures and age-groups (Bond & Smith, 1996). However, it is important to note that the term 'conformity' is used differently in some literature, where it is defined as a tendency for individuals to *disproportionately* copy the behaviour of a majority (Boyd & Richerson, 1988; Van Leeuwen & Haun, 2013).

Whether non-human species exhibit conformist behaviour is a topic of recent debate (Claidière & Whiten, 2012). While experimental evidence has been offered for conformist behaviour in nine-spined stickleback fish (Pike & Laland, 2010), great tits (Aplin et al., 2015a), vervet monkeys (van de Waal, Borgeaud, & Whiten, 2013) and chimpanzees (Whiten, Horner, & De Waal, 2005), each of these examples has been critiqued for not systematically ruling out alternative explanations (Acerbi, Van Leeuwen, Haun, & Tennie, 2016; Haun, Van Leeuwen, & Edelson, 2013; Van Leeuwen & Haun, 2013, 2014; Van Leeuwen, Kendal, Tennie, & Haun, 2015). For example, it has been suggested that so-called 'conformist' individuals could have copied the most frequently observed behaviour rather than the behaviour of a majority of individuals (van Leeuwen et al., 2015; c.f. Aplin et al., 2015a) or simply copied one or more individuals at random, which could lead to the same effect of acting like a majority in the group (Acerbi et al., 2016; c.f. Smaldino, Aplin & Farine, 2017). Three further studies have experimentally investigated whether our closest extant relatives, chimpanzees, behave in a conformist way, none of which found evidence to support this claim (Haun, Rekers, & Tomasello, 2014; Vale et al., 2017; Van Leeuwen, Cronin, Schütte, Call, & Haun, 2013). However, each of these studies had a confound that may explain these results. Van Leeuwen et

al. (2013) used minority *sub-groups* rather than lone minorities faced with a unanimous majority, which we know is critical in motivating conformity effects in humans (Asch, 1951). In Haun et al. (2014) and Vale et al. (2017), subjects had prior experience that the majority method was either ineffective or aversive, respectively. This introduced an asymmetry in the likely payoffs of each method, which chimpanzees are sensitive to when making social learning decisions (Van Leeuwen et al., 2013), and may therefore explain the lack of conformist behaviour. Human conformity can be sufficiently strong to override such negative valence associated with the majority method, but only in a minority of humans tested (Asch, 1951; Bond & Smith, 1996) and this is not a critical part of the definition of conformity adopted in our opening paragraph. It therefore remains a possibility that conformity is more readily expressed by animals in contexts that lack this element, and where there is unanimity in the majority responses, a hypothesis we thus explore in the present study.

Consistent with this hypothesis, Luncz and Boesch (2014) offer evidence that, when migrating, wild female chimpanzees conform to the new tool-use behaviours that are most common in the community they transfer to. Similar effects have been reported in migratory vervet monkeys (van de Waal et al., 2013), great tits (Aplin et al., 2015) and possibly meerkats (Thornton, Samson, & Clutton-Brock, 2010). Furthermore, chimpanzees who explored alternative methods after their group was seeded with a method of solving a puzzle box nevertheless converged on homogeneity of behaviour, a disposition the authors suggest may have been conformity to the majority preference (Whiten et al., 2005). However this has been suggested to be explicable by reversion to an individual's first-learned method, a hypothesis that cannot be rejected without further experimental testing (Van Leeuwen & Haun, 2013).

In the present study we investigated whether chimpanzees proficient in a pre-existing minority method (Minority Individual/s = 'MIN-I') of opening a puzzle-box (Figure 3.1), and who were naïve to alternative methods, would be motivated to converge on the



different behaviour demonstrated in a group context by a unanimous majority of group-mates (Majority Individual/s = 'MAJ-I'). This open-diffusion 'Group' condition lasted for a total of five hours. We predicted that if subjects were to demonstrate conformist behaviour, they would maintain their trained behaviour until they had observed a majority of their group-mates demonstrate, at which point they would converge on this majority method. In order to explore whether frequency of observations (as opposed to number of individuals observed, (Van Leeuwen et al., 2015), asocial exploration or random-copying (Acerbi et al., 2016) might account for changes in behavioural preference in the Group condition, we introduced two further conditions. In a 'Dyad' condition, we paired individuals who were trained on alternative methods of opening the apparatus and observed whether either would converge on the behaviour of their partner over one hour of access to the apparatus. We predicted that if frequency of observed behaviour or random-copying can motivate behaviour switching, levels of switching should be similar between the Dyad and Group condition. In an 'Asocial' condition, a single individual was trained on one method to explore whether they would switch to an alternative method without social information during 30 minutes of unrestricted access to the task.

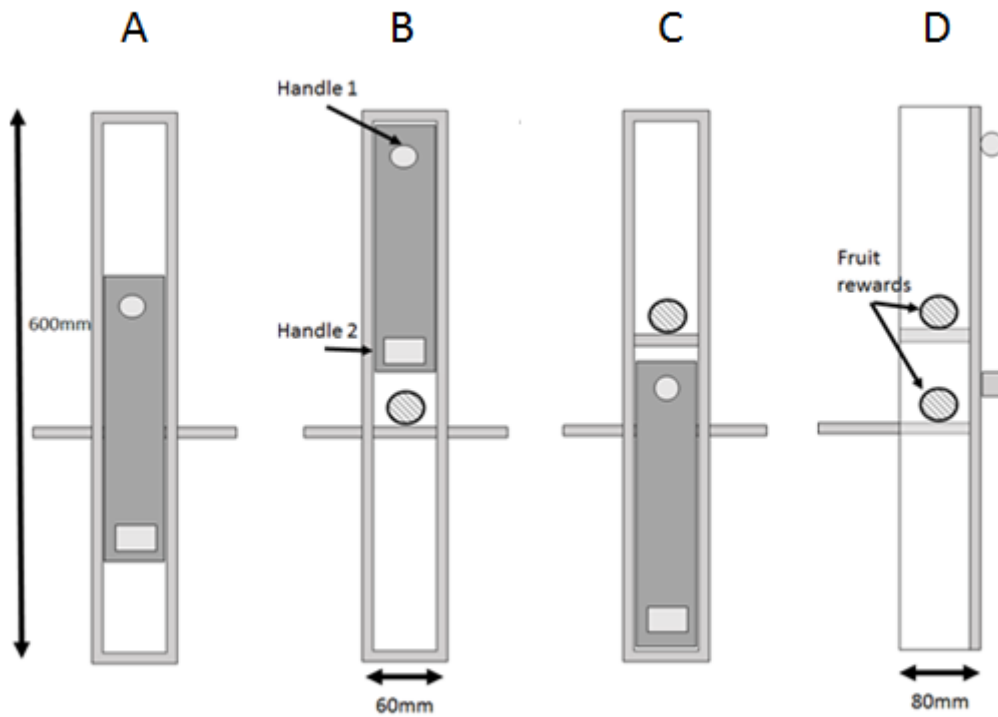


Figure 3.1. The box could be opened to reveal a food reward either by sliding the door entirely upwards (B) or entirely downwards (C). The resting position on presentation is shown in (A). The side-profile is shown in (D). Upon a completed opening, the door locked so as to restrict access to the alternative reward. The anchor platform was attached to a trolley with vice clamps to stabilise the apparatus.

## METHODS

### *Participants and study site*

Participants were 59 chimpanzees (Group condition MIN-I N = 5: all female, Group condition MAJ-I: N = 32, 17 female, Dyad condition N = 12: nine female, Asocial condition N = 10: four female) housed at the National Center for Chimpanzee Care located at the Michale E. Keeling Center for Comparative Medicine and Research of The University of Texas MD Anderson Cancer Center in Bastrop (UTMDACC), Texas. Data were collected

between April and August 2016. All individuals were naïve to the apparatus prior to training except two (BER, KUD) in the Dyad condition who had previously participated in Watson et al. (2017). These individuals were used to provide sufficient partners for the Dyad condition, but were excluded from all analyses. Ethical approval for this study was granted by the School of Psychology & Neuroscience at the University of St Andrews and the IACUC of UTMDACC, adhering to all the legal requirements of US law and the American Society of Primatologists' principles for the ethical treatment of non-human primates. All subjects voluntarily participated in the testing procedures.

### *Apparatus*

This study employed a two-action, sliding-door puzzle-box (Figure 3.1), a design that has been successfully used to examine social learning in previous work (Aplin et al., 2015; Hopper, Lambeth, Schapiro, & Whiten, 2008; Kendal et al., 2015; Watson et al., 2017). Some of the individuals at the study site had previously been exposed to horizontally-oriented puzzle boxes (Hopper et al., 2008; Kendal et al., 2015), and so, in order to minimise directional bias from prior experiments when sampling the same individuals, we gave the apparatus a vertical orientation. All training and experimental sessions were recorded using a Panasonic HC-X920 video camera. Videos were directly transferred in high-definition '.mts' format to an ASUS laptop computer. All videos were coded using BORIS (Behavioural Observation Research Interactive Software) version 2.05 (2015).

### *Experimental procedure*

All three conditions consisted of a training phase followed by open-access. In the Group condition, the single MIN-I for each of five groups voluntarily separated from their group and learned to open the apparatus door by sliding it either up or down (counterbalanced

across groups). At least 80% of the remaining group-members (MAJ-I) were trained on the alternative method. This was followed by five hours (except Group 3, which had four) of open-access to the apparatus, one hour on each consecutive weekday. In order to explore whether behavioural changes persisted without the presence of their group, after open-access finished we retested MIN-I individuals in two 20-minute 'solo' sessions. Finally, during the second week after finishing the open-access phase, we carried out one final hour of open-access testing. This was to determine whether any observed changes in behavioural preference were stable over time. The Dyad condition followed the same procedure, using just two chimpanzees and one hour of open-access. The Asocial condition used individual chimpanzees, which were each provided with 30 minutes of open-access to the apparatus. The reward for successfully opening the box in all conditions was a single grape. A detailed description of the methods used for training and each condition can be found below.

### *Group condition*

The Group condition comprised four stages: 1. training, 2. open-access, 3. solo sessions and 4. a final open-access session, as detailed below.

### *Stage 1: Training*

In each group, a single individual was selected as the MIN-I who was trained on one method of opening the apparatus (either 'up' or 'down'). Previous work with the apparatus established that chimpanzees do not have a strong directional bias toward either option (Watson et al., 2017), but nevertheless we counterbalanced trained methods across groups (three MIN-I trained on 'up', two on 'down'). MIN-I were chosen based on the advice of care-staff who have known the animals for 5+ years, selecting in each case a female individual who was of medium-to-low social rank so that they would

be able to gain access to the task but would not monopolise it. The rationale for this was that observational accounts of wild chimpanzees exhibiting conformist behaviour involve females migrating to a new group, which they typically enter at the lower end of the hierarchy (Luncz & Boesch, 2014). All other members of the group were designated as MAJ-I. As many of these individuals as possible were trained on the alternative method to the MIN-I of their group. Four individuals in the Group condition were not willing to participate in training at all, and did not engage with the task (though they were physically present) during later sessions. This was the case for no more than one individual per group, still leaving an effective majority of individuals trained on the majority method.

The training process for method learning was facilitated by leaving the door of the puzzle-box halfway open so that the trainee could see the reward and access it easily. On subsequent trials, the puzzle-box door was left increasingly closed so that the trainee had to move it to get the grape. This continued until the trainee was able to open it from a fully closed position. Models were considered to be 'trained' once they completed a total of 30 sequential uses of the trained method without deviation. The alternative direction was not blocked in any way. This number of trials was chosen as it was thought to be sufficient to instil a strong behavioural preference in the trained individual, making deviation unlikely without potent external motivating factors (Hopper, Schapiro, Lambeth, & Brosnan, 2011; Hrubesch, Preuschoft, & van Schaik, 2009; Marshall-Pescini & Whiten, 2008). No individuals in any condition deviated from their trained method during training. With just two exceptions, all individuals in all conditions were trained while separated from the rest of their group. These two individuals were not comfortable being separated from their group and were therefore trained while in each other's company.

### *Stage 2: Open-access*

Stage 2 consisted of five hours of unrestricted access to the apparatus in a group context, during which time any individual was able to approach and manipulate the apparatus or observe others doing so. Access was divided into single hour-long testing sessions which, when possible, were carried out on consecutive days (Monday to Friday). One group received only 4 hours of open-access as it was not possible to test on the fifth day. For each trial of Stage 2, the apparatus was baited with a single grape in each reward chamber and pushed towards the mesh of an enclosure, facing forwards, and held there until an individual approached and successfully opened the door. After an individual retrieved a reward, the apparatus was withdrawn by one metre, the door was reset to the central position and the reward chambers were both re-baited. When resetting the door, the apparatus was covered with a cloth to avoid possible directional cues from the experimenter. If the door was partially opened by an individual and no further interaction occurred for 10 seconds, the apparatus was withdrawn and reset as described above. Any individuals within 3m whose heads were oriented towards the Vert and did not have their view obviously obstructed were recorded as having observed the trial.

### *Stage 3: Solo sessions*

At 3-5 days after completion of Stage 2, MIN-I were separated from their group and given 20 minutes of access to the puzzle box ('Solo Session 1'). This happened again 7-10 days following Solo Session 1 ('Solo Session 2'). The purpose of these sessions was to discover whether any behavioural changes in MIN-I were maintained in the absence of observers.

#### *Stage 4: Final open-access session*

Between four and eight days after Stage 3, the entire group was given a final open-access session with the apparatus, lasting one hour. This followed the same protocol as Stage 2. The purpose of this was to determine whether any behavioural changes in MIN-I were persistent over time.

#### *Dyad condition*

For each of the six dyads (N=12), two individuals were selected from the same group. Individuals were selected based on the advice of care staff regarding which individuals were likely to be comfortable sharing a room with each other for an hour. Once selected, each individual in the dyad was individually trained on alternative methods ('Up' and 'Down') of opening the apparatus. The procedure for training followed the same protocol as for MIN-I in the Group condition. Two individuals in the dyad condition had prior exposure to the task and so were not included for analysis (but their partner was).

The day after training had taken place for a dyad, the two individuals were separated from their group, as a pair, for one hour. During this hour, unrestricted access to the apparatus was provided. This followed the same procedure as Stage 2 of the Group condition. This open-access phase of the Dyad condition was limited to one hour, as the feasibility of getting two specific individuals alone together on five consecutive days was expected to be low. Furthermore, based on the advice of care staff, one hour was judged to be a length of time in which two individuals would be reliably motivated to participate in the task before becoming noticeably motivated to return to their group. Secondly, prior work (Watson et al., 2017) using the same puzzle-box suggested the box could be opened and rebaited at a rate of roughly two trials per minute. Given the rapid onset of conformist behaviour in previous studies (Aplin et al., 2015a; Pike & Laland,

2010; van de Waal et al., 2013) and indeed the fact that all MIN-I who switched did so within their first five trials, this was judged to be an adequate amount of exposure to the task for behavioural switching to manifest.

### *Asocial condition*

Individuals (N=10) in the asocial condition received the same training as those in the dyad condition. The next day, subjects received 30 minutes of unrestricted access to the apparatus while alone, having never observed another individual interact with it. The purpose of this condition was to determine how frequently chimpanzees would explore the non-trained method when not provided with social information about it to determine whether this is sufficient to explain switching patterns in the Group and Dyad conditions. Sessions were limited to 30 minutes primarily to minimise the amount of time that individuals spent alone and separated from group-mates. Furthermore, 30 minutes allowed for a potential of ~60 trials per individual, which was judged to be sufficient access to the task for motivated individuals to explore an alternative method.

### *Statistical analyses*

We used Generalised Linear Mixed Models (GLMMs), using R packages 'lme4' and 'MuMin' (Bates et al., 2016; MuMIn, 2016) with a binomial error structure and a logit link function to determine whether 'Condition' (MIN-I vs. MAJ-I, MIN-I vs. Dyad and Dyad vs. Asocial) had a significant effect upon our response variable: a binary indicator of whether an individual used their trained or un-trained method on any given trial. When comparing MIN-I with MAJ-I and MIN-I with Dyad conditions, we also fit as a fixed effect the number of demonstrations an individual had observed of their non-trained method on each trial.

In each case we fitted a 'full' model containing all fixed effects. Any non-significant effects were dropped from the model to create a 'final' model, which we then compared



with the 'null' model (no fixed effects) using a likelihood-ratio test to determine whether either was a significantly better fit for the data. Because each individual contributed multiple data points, we fitted Individual as a random factor in all models. In the first analysis, comparing MIN-I and MAJ-I responses, test session (from one to five) was also fitted as a random effect. For each final model we also calculate a marginal  $R^2$  value, which describes the proportion of variance explained by the fixed effects (Nakagawa & Schielzeth, 2013). We used the R package 'rptR' (Schielzeth & Nakagawa, 2011) to estimate whether there was a significant effect of repeatability (where  $H_0$  is  $R = 0$ ) between the proportion of trials in which MIN-I used their non-trained method firstly in stages 2 and 3, then in stages 2 and 4. All analyses were conducted in R v.3.2.3 (R Development Core Team, 2016) with R Studio v.0.99.491 (R Studio Team, 2015).

Inter-observer reliability was carried out with an independent observer on the method ('up' or 'down') used in 30, 30 second video clips of individuals opening the apparatus, as well as which individuals observed those demonstrations, with 100% agreement. The datasets analysed during the current study are available in the Open Science Framework repository and can be accessed at: <https://osf.io/seq8b/>

## **RESULTS**

### *Analysis 1: Group condition*

In the Group condition, four out of five MIN-I learned the unanimous majority method, all of whom did so after observing at least one MAJ-I but before observing the majority of their group (Table 3.1). Three of these individuals used it on the majority of trials in each test session (Figure 3.2). All individuals in both MIN-I and MAJ-I had multiple observations of their non-trained method by the end of the fifth hour of testing (Table 3.2). The full model found a significant effect of Condition but not frequency of observations of non-trained method on switching behaviour, so we dropped this variable from the final model (Table 3.3). This final model was found to be a significantly better fit

for the data than the null model (likelihood ratio test:  $X^2 = 8.333$ ,  $df = 1$ ,  $p < 0.003$ , Table 3.3). The final model estimated that the probability that MIN-I would switch to their non-trained method on any given trial was 0.54 (95% CI: 0.262, 0.791), whereas the probability of MAJ-I switching methods was less than 0.001 (95% CI: 0.000, 0.002). The proportion of variance explained by the fixed effects in the final model was  $R^2 = 0.515$ .

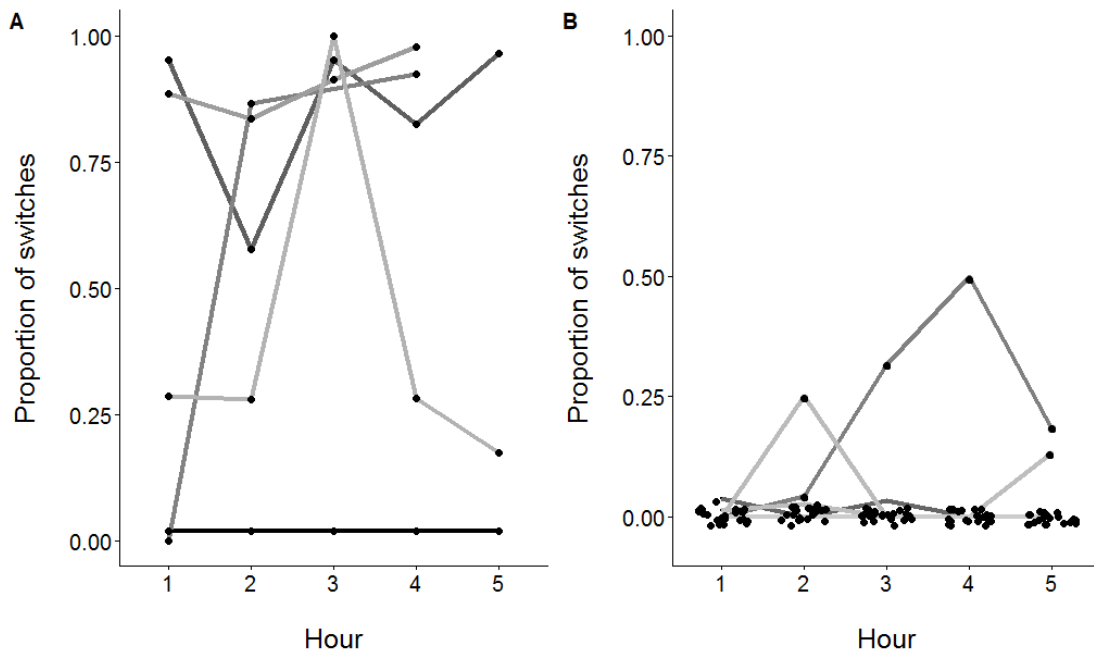


Figure 3.2. Proportion of trials in which an individual used their non-trained method in each hour. A = MIN-I ( $n = 5$ ), B = MAJ-I ( $n = 23$ ). Each line represents an individual. Points in B are jittered to avoid overlapping. Not all individuals participated in all sessions.

ID	Trials before switch	Number MAJ-I seen at time of switch	No. group-mates that participated	Total group size
JOS	No switch	No switch (6 seen)	6	8
HAN	2	1	4	4
DAH	4	3	6	7
IDA	4	2	6	7
AHN	2	2	6	<u>6</u>

Table 3.1. Trial number on which MIN-I first switched to non-trained method, number of individuals they had observed using this method by that point, and total number of group-mates (minus MIN-I).

#### Observations

Condition	Median	Minimum	Maximum
MAJ-I	31	2	109
MIN-I	104	72	117

#### Trials

Condition	Median	Minimum	Maximum
MAJ-I	80	1	289
MIN-I	124	37	339

Table 3.2. Summary of observations and trials carried out by MIN-I and MAJ-I in Group condition across all test sessions.

Analysis	Model	Log likelihood	Fixed effect	Beta	Standard Error	Lower 95% CI	Upper 95% CI	Z	p
MIN-I VS. MAJ-I	Null	-358.2	Intercept	-12.899	2.371	-17.545	-8.252	-5.441	
			Full	352.7	Intercept	-10.635	2.243	-15.032	-6.238
	Final	-354.0	Condition	11.691	2.955	5.899	17.484	3.956	<0.001
			Observations	-0.014	0.009	-0.032	0.003	-1.529	0.126
			Intercept	-10.778	2.215	-15.120	-6.436	-4.866	
			Condition	10.926	2.820	5.399	16.452	3.875	<0.001
Group vs. Dyad	Null	-132.6	Intercept	-10.954	2.307	-15.476	-6.431	-4.748	
			Full	-127.3	Intercept	-10.289	3.444	-17.039	-3.538
	Interaction	-127.7	Condition	0.098	0.127	3.785	16.939	0.773	0.913
			Observation	10.362	3.355	-0.151	0.348	3.088	0.002
			Intercept	-9.150	2.801	-14.641	-3.661	-3.267	
			Condition	0.027	0.135	2.656	14.810	0.201	0.004
			Observation	8.733	3.101	-0.237	0.292	2.817	0.840
			Observation *						
	Final	-126.8	Condition	0.247	0.256	-0.255	0.749	0.963	0.336
			Intercept	-8.562	1.897	12.279	4.844	-4.514	
Group vs. Control	Null	-18.0	Condition	8.948	2.242	4.554	13.342	3.991	<0.001
			Intercept	-11.298	3.184	-17.537	-5.057	-3.549	
			Final	-18.0	Intercept	11.457	3.632	-18.475	-4.338
			Condition	0.377	3.469	-6.422	7.176	0.109	0.913

Table 3.3. Summary outputs for each model tested

It was found that there was only weak repeatability between Stages 2 and 3 ( $R = 0.309$ , 95% CI: 0, 0.852,  $p = 0.322$ ), suggesting that MIN-I behaved differently depending on whether they were in a group context or by themselves (Figure 3.3). There was also a significant effect of repeatability between Stages 2 and 4 ( $R = 0.862$ , 95% CI: 0.183, 0.981,  $p = 0.007$ ), demonstrating that switching behaviour was persistent over time. The confidence intervals for these estimates are very wide due to the small sample size used to calculate them, so should be interpreted with caution (Zou, 2012).

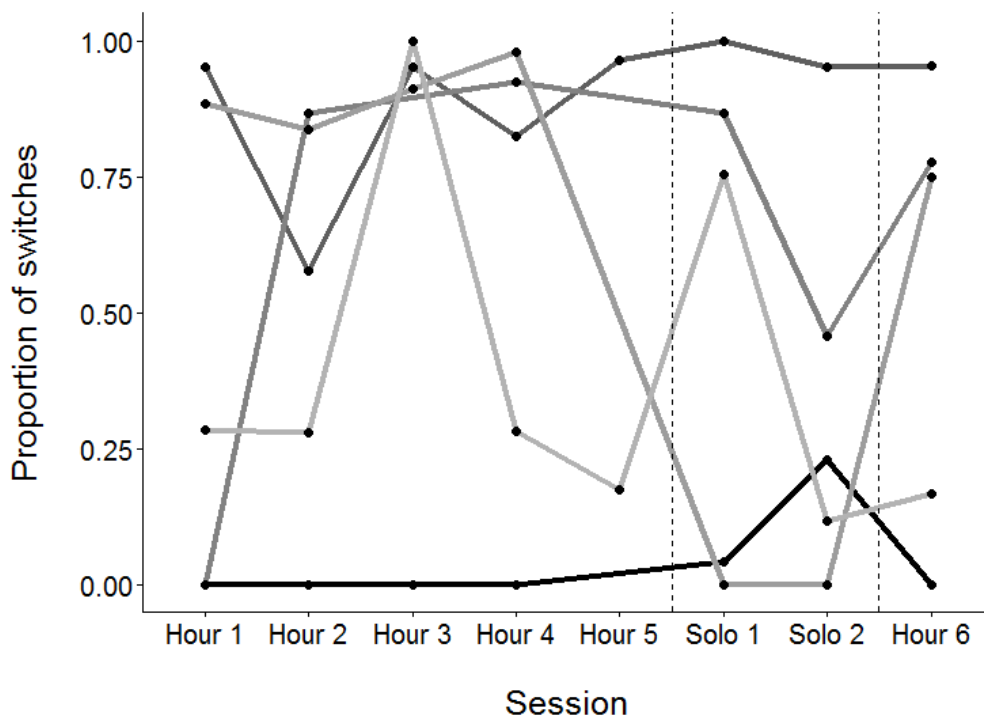


Figure 3.3. Proportion of trials in which MIN-I used their non-trained method in each hour of testing, including solo and final group sessions. Each line represents an individual. Dashed vertical lines serve as a visual aid for contrasting solo and group sessions. Not all individuals participated in all sessions.

### Analysis 2: Dyad and Control conditions

Of all individuals in the Dyad condition (N = 12), only one explored the method demonstrated by their partner (2/65 trials). Only one individual in the Asocial condition (N = 10) discovered the non-trained method, and used it on only a single trial out of 10 (Figure 3.4). Individuals in the Asocial condition had a median of 55 trials (range: 10-80) trials, while individuals in the Dyad condition had a median of 64 trials (range = 6-100). In the full model comparing Dyad and Control individuals, there was no significant effect of Condition (Table 3.3). Consequently, we dropped this fixed effect and use the Null model as our final model, from which the full model did not significantly differ (log-likelihood ratio test:  $X^2 = 0.012$ ,  $df = 1$ ,  $p = 0.913$ ). From this final model we calculated that the probability with which any individual would switch to their non-trained method on any given trial was less than 0.001 (95% CI: 0.000, 0.003).

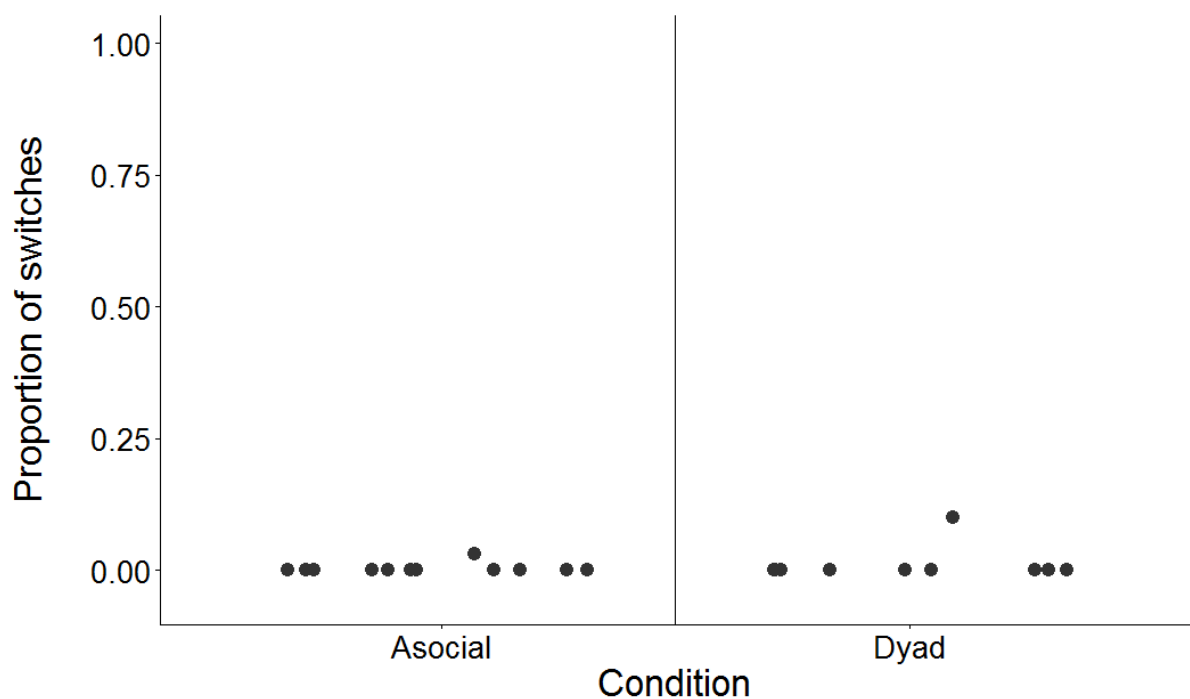


Figure 3.4. Proportion of trials in which an individual used their non-trained method in the Asocial (N = 10) and Dyad (N = 10) conditions. Each point represents an individual. Points are jittered.

### *Analysis 3: Group and Dyad conditions*

The median number of observations in Dyad and MIN-I conditions was 18 (range:2-34) and 29 (range: 5-46) respectively, and the two groups did not differ significantly ( $n_{\text{dyad}} = 10$ ,  $n_{\text{minority}} = 5$ ,  $U = 18$ ,  $p = 0.439$ , two-tailed) in their number of observations at time of switching nor their total number of observations ( $n_{\text{dyad}} = 10$ ,  $n_{\text{minority}} = 5$ ,  $U = 14$ ,  $p = 0.206$ , two-tailed, Figure 3.5).

Our full model included both Condition (MIN-I vs. Dyad) and frequency of observations as fixed effects (Table 3.3). In this model, frequency of observations refers to the number of observations an individual had made prior to the trial when they first used their non-trained method. Where an individual never used their non-trained method, we used the number of observations made at the time of their final trial in their first hour of testing. In the full model, Condition was found to have a significant effect but number of observations was not. To explore whether frequency of observations might influence MIN-I differently to those in the Dyad condition, we also fitted a model with an interaction between number of observations and Condition. In this interaction model, neither the interaction of frequency of observations with Condition, nor frequency of observations itself was found to have a significant effect on switching behaviour (Table 3.3). Consequently, we dropped both the interaction and fixed effect of number of observations from the final model. In the final model, Condition was found to have a significant effect on whether individuals switched to their non-trained method on a given trial (Table 3.3), with an estimated probability that MIN-I would switch on a given trial of 0.518 (95% CI: 0.447, 1) and a probability that individuals in the Dyad condition would switch of less than 0.001 (95% CI: 0.000, 0.003). The proportion of variance explained by the fixed effects in the full model was  $R^2 = 0.572$ .

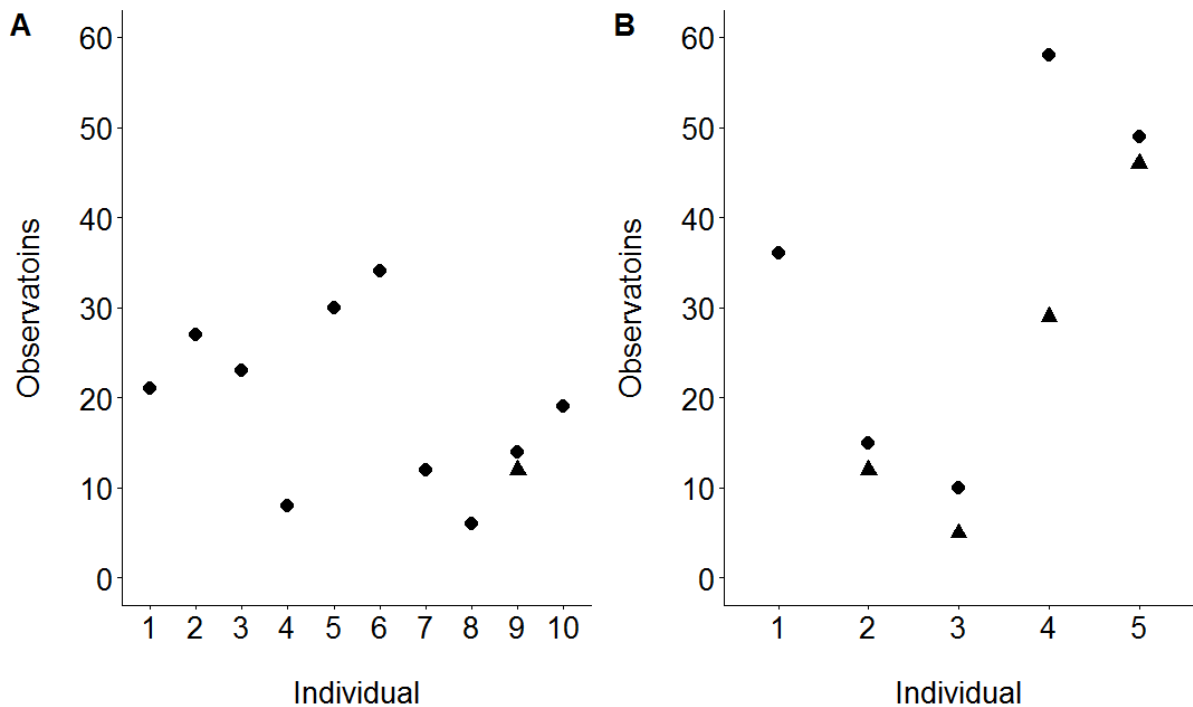


Figure 3.5. Number of times individuals in the Dyad condition (A) and MIN-I (B) observed individuals using their non-trained method. Circles represent total number of observations in first hour of testing. Triangles represent number of observations by time of an individual's first switching event.

## DISCUSSION

Results showed that minority individuals (MIN-I) were, relative to majority individuals (MAJ-I), highly likely to prioritise social information over pre-existing methods when in a group context, even though neither method was more efficient or productive. Moreover, switching to the novel method generally occurs rapidly (within first 5 trials, Table 3.1), then remains stable over time (Figure 3.2a). Conversely, there was no suggestion that MAJ-I faced with demonstrations of an alternative, equally rewarding behaviour from a lone minority were motivated to switch method (Figure 3.2b). Individuals did not deviate from a pre-existing method when exposed to the alternative method of a single conspecific, nor did individuals who received no social information



independently discover the alternative method (Figure 3.4). Crucially, the evidence does not support the possibility that switching was influenced by the frequency of observations (Figure 3.5b), nor the number of individuals observed using the alternative method (Table 3.1). Indeed, one MIN-I ('HAN') switched after observing just a handful of trials of a single individual. Because MIN-I were not aware that the observed method was preferred by a unanimous majority at the time of switching, this outcome does not easily align with conventional definitions of conformity, particularly conformity to a unanimous majority. Due to the open-diffusion paradigm used, we were unable to systematically test each MIN-I after each additional group member was observed. Consequently, it is not possible from the Group condition alone to determine whether all MIN-I who switched methods would, like 'HAN', have done so after observing just a single individual.

These results suggest that knowledgeable chimpanzees behave in a largely conservative manner unless they find themselves in a group context. Within in a group context, we recorded a strong motivation for most individuals to switch to a consistently demonstrated behaviour. This outcome contrasts with prior work where individuals' non-trained behaviour had acquired a negative valence from previous experience (Haun et al., 2014; Vale et al., 2017) or had potentially been socially reinforced by observing it used by others (Van Leeuwen et al., 2013). Moreover, changes in behavioural preference elicited in this context had a rapid onset (Table 3.1) and were stable over time, as MIN-I demonstrated behaviour consistent with their performance in the initial experimental period in an additional group session carried out three weeks afterwards (see Figure 3.5). The importance of a group context in motivating social information use is further reflected in the fact that there was no statistically significant repeatability in switching behaviour between the open-diffusion social context of Stage 2 and the solo context of Stage 3. This trend then reversed when individuals were put back into a group context for Stage 4, which had high repeatability with Stage 2.

In sum, our results suggest that being in a group context motivated the prioritisation of very limited amounts of social information over well-established, pre-existing behaviours. This is somewhat surprising given that some previous research has suggested that chimpanzees are conservative with regards to adopting novel behaviours (Hopper, Schapiro, Lambeth, & Brosnan, 2011; Hrubesch, Preuschoft, & van Schaik, 2009; Marshall-Pescini & Whiten, 2008). We suggest that social context is therefore a largely unexplored but potentially potent influence on behavioural flexibility and social learning that is worthy of further attention.

One way in which the group context may have motivated changes in behavioural preference is the possibility that MIN-I made inferences about the rest of the present group's behavioural preferences based on their observations of a subset of individuals, and acted in a conformist fashion in accordance with this prediction. Such a motivation to converge on perceived social norms, estimated from limited personal experience, has been established in humans (Rimal & Real, 2005; Terry, Hogg, & White, 1999) and this capacity to generalise from small samples to a wider population is present in human infants as young as 8 months old (Denison & Xu, 2010; Téglás, Giretto, Gonzalez, & Bonatti, 2007; Xu & Garcia, 2008). While we are not aware of systematic evidence addressing whether chimpanzees make such statistical inferences from a sample to a population, all four great ape species have been shown to generalise from populations to samples (Rakoczy et al., 2014).

Due to our study sharing similar behavioural outcomes to conformity, alternative explanations levelled at studies reporting this phenomenon (Acerbi et al., 2016; Van Leeuwen & Haun, 2013, 2014; Van Leeuwen et al., 2015) should also be considered in relation to our results. For example, that individuals may 'copy when uncertain', such as when moving to a novel environment, is one alternative explanation offered (Van Leeuwen et al., 2015) for behavioural convergence in great tits (Aplin et al., 2015a) and vervet monkeys (van de Waal et al., 2013). In the case of our study, there were no such

environmental changes and therefore no obvious reason for uncertainty-triggered copying. If through some mistake of design, some unintentional uncertainty was introduced by the paradigm, we would expect to see individuals in the Dyad condition also prioritise social information over their pre-existing method, but this was not the case. It has also been suggested that randomly copying a single individual could create an illusion of conformity to the options demonstrated by a majority in a group (Acerbi et al., 2016; Van Leeuwen et al., 2015). However, much previous research in chimpanzees has reported conservatism rather any evidence of random copying of observed methods (Davis, Vale, Schapiro, Lambeth, & Whiten, 2016; Haun et al., 2014; Hrubesch et al., 2009; Van Leeuwen et al., 2013). More importantly, random copying is not consistent with the outcome of our Dyad condition, where there was only a single individual to choose from, yet all individuals remained faithful to their trained method.

One thing which may explain the difference found between group and dyad or control conditions is that individuals may feel more comfortable in a group context due to having their allies around them, leading them to be more relaxed and consequently more likely to explore alternative methods of opening the puzzle-box. This may account for the fact that although very few MAJ-I used their non-trained method, those that did used it on a greater number of trials than those in the dyad condition. However, it is not necessarily true that it is more relaxing to be in a group condition, where the resource is less easily monopolised and subordinate individuals must be vigilant towards aggression from others. Research in capuchin monkeys found that subordinate individuals were less motivated to demonstrate an acquired token-exchange behaviour when in a group context (Addessi, Paglieri, & Focaroli, 2011) or in the presence of a dominant individual (Lonsdorf et al., 2016), suggesting that the presence of others can, in some species, inhibit behaviour in an experimental task.

A bias towards copying dominant individuals ('rank-bias') is thought to influence from whom naïve chimpanzees choose to learn (Horner, Proctor, Bonnie, Whiten, & de

Waal, 2010; Kendal et al., 2015), and therefore could also conceivably influence the social learning decisions of knowledgeable individuals. This would fit the pattern of results observed in the Group condition, as MIN-I were all judged as being medium-to-low in social rank by care staff, and were therefore exposed to higher ranking demonstrators than themselves. While we cannot rule this out entirely, it would be inconsistent with the results of the Dyad condition. Linear rank assessments for the Dyad condition were not practical, but rank disparities were inevitable due to the linear hierarchy of chimpanzee social structure. However, no individuals in the Dyad condition adopted their partner's method. Moreover, studies in which a proportion of individuals with pre-existing behaviours were faced with more prestigious or more dominant demonstrators of the alternative method did not find evidence of behavioural switching (Haun et al., 2014; Van Leeuwen et al., 2013). This suggests that while *naïve* chimpanzees may selectively copy dominant models (Horner et al., 2010; Kendal et al., 2015; but see Watson et al., 2017), chimpanzees with an established method are not motivated to forego this in order to converge on the behaviour of these individuals.

We would emphasise, however, that while various social learning biases are often treated as competing explanations for the emergence of traditions, it is possible that they act in complementary ways, and that different individuals make use of different learning strategies depending on their own life-history. For example, while all children preferentially copy competent models, some prefer to copy a majority when given the choice (Burdett et al., 2016). It seems likely that similar variation could exist within the social learning habits of non-human species, and the individual differences that may contribute towards such variation will continue to confound studies of unitary biases until research on combinatorial effects is pursued. Indeed, our results are suggestive of notable individual differences in behavioural social information use. Some chimpanzees are apparently motivated to rapidly converge on behaviours observed in a group context, while others are not, even after extensive exposure to demonstrations of the alternative

method from a large number of individuals. This outcome is broadly comparable with human conformity studies where, while *many* individuals conform to unanimous majorities, *most* do not (Asch, 1951). Given the fission-fusion social structure that typifies wild chimpanzees, in the wild individuals will often have information on the preferences of only a small sample of the larger community to which they belong, so being prepared to make inferences from a small sample to a larger group may be an adaptive strategy for them. They may also need to be somewhat flexible in terms of who they are motivated to socially learn from. Accordingly, we suggest that in future work additional attention be placed on the individual characteristics of the learners, as well as the models, and the contextual factors that may promote or inhibit 'risky' behaviour, such as exploring new methods (Davis et al., 2016). The use of methodologies that discriminate between multiple social learning biases (e.g. Kendal et al., 2015) operating at once in a single group, or a single individual, may be crucial.

Amongst the factors influencing social learning to be investigated in the future, based on our findings we strongly encourage the examination of how the presence and size of a group may influence copying decisions of animals. Our finding that chimpanzees are motivated by the presence of an audience to relinquish existing behaviours and converge on an equally rewarding, socially demonstrated alternative suggests a potential commonality between humans and chimpanzees in the potency of social influence, with important implications for the study of cultural diffusion.

## REFERENCES

- Acerbi, A., Van Leeuwen, E. J., Haun, D. B., & Tennie, C. (2016). Conformity cannot be identified based on population-level signatures. *Scientific Reports*, 6, 36068.
- Addessi, E., Paglieri, F., & Focaroli, V. (2011). The ecological rationality of delay tolerance: insights from capuchin monkeys. *Cognition*, 119(1), 142-147.
- Aplin, L. M., Farine, D. R., Morand-Ferron, J., Cockburn, A., Thornton, A., & Sheldon, B. C. (2015a). Counting conformity: evaluating the units of information in frequency-dependent social learning. *Animal Behaviour*, 110, e5-e8.
- Aplin, L. M., Farine, D. R., Morand-Ferron, J., Cockburn, A., Thornton, A., & Sheldon, B. C. (2015b). Experimentally induced innovations lead to persistent culture via conformity in wild birds. *Nature*, 518(7540), 538-541.
- Asch, S. E. (1951). Effects of group pressure upon the modification and distortion of judgments. In H. Guetzkow (Ed.), *Groups, Leadership, and Men* (pp. 177-190): Pittsburgh: PA Carnegie Press.
- Bates, D., Maechler, M., Bolker, B., Walker, S., Christensen, R. H. B., Singmann, H., . . . Bolker, M. B. (2016). Package 'lme4'.
- Bond, R., & Smith, P. B. (1996). Culture and conformity: A meta-analysis of studies using Asch's (1952b, 1956) line judgment task. *Psychological Bulletin*, 119(1), 111-137.
- Boyd, R., & Richerson, P. J. (1988). *Culture and the evolutionary process*: University of Chicago Press.
- Burdett, E. R., Lucas, A. J., Buchsbaum, D., McGuigan, N., Wood, L. A., & Whiten, A. (2016). Do children copy an expert or a majority? Examining selective learning in instrumental and normative contexts. *PLoS One*, 11(10), e0164698.
- Claidière, N., & Whiten, A. (2012). Integrating the study of conformity and culture in humans and nonhuman animals. *Psychological Bulletin*, 138(1), 126.
- Davis, S. J., Vale, G. L., Schapiro, S. J., Lambeth, S. P., & Whiten, A. (2016). Foundations of cumulative culture in apes: improved foraging efficiency through

- relinquishing and combining witnessed behaviours in chimpanzees (Pan troglodytes). *Scientific Reports*, 6, 35953.
- Denison, S., & Xu, F. (2010). Integrating Physical Constraints in Statistical Inference by 11-Month-Old Infants. *Cognitive Science*, 34(5), 885-908.
- Haun, D. B., Rekers, Y., & Tomasello, M. (2014). Great apes stick with what they know; children conform to others. *Psychological Science*, 25(12), 2160-2167.
- Haun, D. B., & Tomasello, M. (2011). Conformity to peer pressure in preschool children. *Child Development*, 82(6), 1759-1767.
- Haun, D. B., Van Leeuwen, E. J., & Edelson, M. G. (2013). Majority influence in children and other animals. *Developmental Cognitive Neuroscience*, 3, 61-71.
- Hopper, L. M., Lambeth, S. P., Schapiro, S. J., & Whiten, A. (2008). Observational learning in chimpanzees and children studied through 'ghost' conditions. *Proceedings of the Royal Society of London B: Biological Sciences*, 275(1636), 835-840.
- Hopper, L. M., Schapiro, S. J., Lambeth, S. P., & Brosnan, S. F. (2011). Chimpanzees' socially maintained food preferences indicate both conservatism and conformity. *Animal Behaviour*, 81(6), 1195-1202.
- Horner, V., Proctor, D., Bonnie, K. E., Whiten, A., & de Waal, F. B. (2010). Prestige affects cultural learning in chimpanzees. *PloS One*, 5(5).
- Hrubesch, C., Preuschoft, S., & van Schaik, C. (2009). Skill mastery inhibits adoption of observed alternative solutions among chimpanzees (Pan troglodytes). *Animal Cognition*, 12(2), 209-216.
- Kendal, R. L., Hopper, L. M., Whiten, A., Brosnan, S. F., Lambeth, S. P., Schapiro, S. J., & Hoppitt, W. (2015). Chimpanzees copy dominant and knowledgeable individuals: implications for cultural diversity. *Evolution and Human Behavior*, 36(1), 65-72.

- Lonsdorf, E., Bonnie, K., Grim, M., Krupnick, A., Prestipino, M., & Whyte, J. (2016). Seeding an arbitrary convention in capuchin monkeys: The effect of social context. *Behaviour*, *153*(5), 633-654.
- Luncz, L. V., & Boesch, C. (2014). Tradition over trend: Neighboring chimpanzee communities maintain differences in cultural behavior despite frequent immigration of adult females. *American Journal of Primatology*, *76*(7), 649-657.
- Marshall-Pescini, S., & Whiten, A. (2008). Chimpanzees (*Pan troglodytes*) and the question of cumulative culture: an experimental approach. *Animal Cognition*, *11*(3), 449-456.
- MuMIn, B. K. (2016). Multi-model inference. R package version 1.10.0. 2014.
- Nakagawa, S., & Schielzeth, H. (2013). A general and simple method for obtaining R<sup>2</sup> from generalized linear mixed-effects models. *Methods in Ecology and Evolution*, *4*(2), 133-142.
- Pike, T. W., & Laland, K. N. (2010). Conformist learning in nine-spined sticklebacks' foraging decisions. *Biology Letters*, *6*(4), 466-468.
- R Development Core Team. (2016). R: A language and environment for statistical computing. Vienna, Austria: R Foundation for Statistical Computing. Retrieved from <https://www.R-project.org>
- R Studio Team. (2015). RStudio: Integrated Development for R. Boston, MA: R Studio, Inc. Retrieved from [www.rstudio.com](http://www.rstudio.com)
- Rakoczy, H., Clüver, A., Saucke, L., Stoffregen, N., Gräbener, A., Migura, J., & Call, J. (2014). Apes are intuitive statisticians. *Cognition*, *131*(1), 60-68.
- Rimal, R. N., & Real, K. (2005). How behaviors are influenced by perceived norms: a test of the theory of normative social behavior. *Communication Research*, *32*(3), 389-414.
- Schielzeth, H., & Nakagawa, S. (2011). rptR: Repeatability for Gaussian and non-Gaussian data. *R package*.



- Smaldino, P. E., Aplin, L. M., & Farine, D. R. (2017). Do Sigmoidal Acquisition Curves Indicate Conformity? *bioRxiv*, 159038.
- Téglás, E., Giroto, V., Gonzalez, M., & Bonatti, L. L. (2007). Intuitions of probabilities shape expectations about the future at 12 months and beyond. *Proceedings of the National Academy of Sciences*, *104*(48), 19156-19159.
- Terry, D. J., Hogg, M. A., & White, K. M. (1999). The theory of planned behaviour: self-identity, social identity and group norms. *British Journal of Social Psychology*, *38*(3), 225-244.
- Thornton, A., Samson, J., & Clutton-Brock, T. (2010). Multi-generational persistence of traditions in neighbouring meerkat groups. *Proceedings of the Royal Society of London B: Biological Sciences*, *277*(1700), 3623-3629.
- Vale, G. L., Davis, S. J., van de Waal, E., Schapiro, S. J., Lambeth, S. P., & Whiten, A. (2017). Lack of conformity to new local dietary preferences in migrating captive chimpanzees. *Animal Behaviour*, *124*, 135-144.
- van de Waal, E., Borgeaud, C., & Whiten, A. (2013). Potent social learning and conformity shape a wild primate's foraging decisions. *Science*, *340*(6131), 483-485.
- Van Leeuwen, E. J., Cronin, K. A., Schütte, S., Call, J., & Haun, D. B. (2013). Chimpanzees (*Pan troglodytes*) flexibly adjust their behaviour in order to maximize payoffs, not to conform to majorities. *PLoS One*, *8*(11), e80945.
- Van Leeuwen, E. J., & Haun, D. B. (2013). Conformity in nonhuman primates: fad or fact? *Evolution and Human Behavior*, *34*(1), 1-7.
- Van Leeuwen, E. J., & Haun, D. B. (2014). Conformity without majority? The case for demarcating social from majority influences. *Animal Behaviour*, *96*, 187-194.
- Van Leeuwen, E. J., Kendal, R. L., Tennie, C., & Haun, D. B. (2015). Conformity and its look-a-likes. *Animal Behaviour*, *110*, e1-e4.

- Watson, S. K., Reamer, L. A., Mareno, M. C., Vale, G. L., Harrison, R. A., Lambeth, S. P., . . . Whiten, A. (2017). Socially transmitted diffusion of a novel behaviour from subordinate chimpanzees. *American Journal of Primatology*, 9999; e22642.
- Whiten, A., Horner, V., & De Waal, F. B. (2005). Conformity to cultural norms of tool use in chimpanzees. *Nature*, 437(7059), 737-740.
- Whiten, A., & Van Schaik, C. P. (2007). The evolution of animal 'cultures' and social intelligence. *Philosophical Transactions of the Royal Society of London B: Biological Sciences*, 362(1480), 603-620.
- Xu, F., & Garcia, V. (2008). Intuitive statistics by 8-month-old infants. *Proceedings of the National Academy of Sciences*, 105(13), 5012-5015.
- Zou, G. (2012). Sample size formulas for estimating intraclass correlation coefficients with precision and assurance. *Statistics in medicine*, 31(29), 3972-3981.

# CHAPTER 4

## CHIMPANZEES DEMONSTRATE PERSISTENT INDIVIDUAL DIFFERENCES IN SOCIAL INFORMATION USE

This chapter has been submitted for peer review at *Animal Cognition* with the authorship listed below.

### *Authors*

Stuart K Watson<sup>1</sup>, Gillian L Vale<sup>2</sup>, Lydia M Hopper<sup>3</sup>, Lewis G Dean<sup>1</sup>, Rachel L Kendal<sup>4</sup>, Elizabeth E Price<sup>5</sup>, Lara AN Wood<sup>6</sup>, Sarah J Davis<sup>1</sup>, Steven J Schapiro<sup>2, 7</sup>, Susan P Lambeth<sup>2</sup> & Andrew Whiten<sup>1</sup>.

### *Affiliations*

<sup>1</sup>Centre for Social Learning and Cognitive Evolution, and Scottish Primate Research Group, School of Psychology & Neuroscience, University of St Andrews, UK

<sup>2</sup>National Center for Chimpanzee Care, Department of Veterinary Sciences, Michale E. Keeling Center for Comparative Medicine and Research, UT MD Anderson Cancer Center, Bastrop, TX USA

<sup>3</sup>Lester E. Fisher Center for the Study and Conservation of Apes, Lincoln Park Zoo, Chicago, IL 60614, USA

<sup>4</sup>Centre for the Coevolution of Biology and Culture, Department of Anthropology, Durham University, U.K.

<sup>5</sup>Centre for Behaviour and Evolution, Institute of Neuroscience, Newcastle University, Newcastle upon Tyne, NE2 4HH

<sup>6</sup>Division of Psychology, Abertay University, Bell Street, Dundee, DD1 1HG

<sup>7</sup>Department of Experimental Medicine, University of Copenhagen, Denmark

## **ABSTRACT**

Studies of social learning biases have greatly informed our understanding of how behaviour patterns may diffuse through animal populations, yet within-species inter-individual variation in social information use has received little attention and remains poorly understood. We have now been able to address this question by examining individual performances across multiple experiments with the same population of primates. We have compiled a data set spanning 16 social learning studies carried out at the same study site over a 12-year period, incorporating a total of 167 chimpanzees. We applied a binary scoring system code to each participant's performance in each study according to whether they demonstrated evidence of social information use or not. Bayesian binomial mixed effects models were then used to estimate consistency of individuals' dependence on social learning, together with any effects of sex, rearing history, age, research experience and task type on social information use. It was found that individuals demonstrated moderate repeatability in reliance on social learning across studies, demonstrating that individual differences play an important role in social learning. Females were more likely to use social information than males, but no other predictors were found to have an important effect, and pedigree records showed that social information use was not a strongly heritable trait. Our study offers a novel, transferable method for the study of individual differences in social learning.

## INTRODUCTION

Overzealous copying of one's peers may lead to the adoption of sub-optimal (e.g. a poor foraging method) or irrelevant behaviours (such as a male copying a female courtship gesture) (Giraldeau, Valone, & Templeton, 2002; Kendal, Coolen, van Bergen, & Laland, 2005). It has therefore been proposed that in order for social learning to be adaptive, individuals' copying behaviour is to be guided by biases that direct them as to when social information is best utilised and from whom it is best sourced (Laland, 2004). To date, research on social learning biases has primarily focussed on model-biases (e.g. 'copy dominant individuals') or contextual biases (e.g. 'copy when uncertain') (Price, Wood, & Whiten, 2017; Watson & Whiten, in press). However, recently there has been an increasing interest in stable aspects of individual differences in social information use that may complement contextual variation (Mesoudi, Chang, Dall, & Thornton, 2016). Optimal learning strategies are likely to vary between individuals depending on their circumstances (e.g. rapidly changing versus stable habitat), and even within individuals across their own lifetime (e.g. from infancy to adulthood - Wood, Kendal & Flynn, 2013). Consequently, social learning may be predicted to be somewhat plastic to accommodate such different needs. For example: Farine, Spencer, and Boogert (2015) experimentally elevated stress hormones in some zebra finch nestlings, but not their siblings. Individuals whose hormones had not been elevated followed the developmentally typical strategy of copying parental behaviour, whereas stressed individuals exclusively copied unrelated adults. This demonstrates how even genetically similar individuals may adopt very different social learning strategies based on the developmental context they find themselves in.

Mesoudi et al. (2016) eschew broad claims about species-typical social learning habits ('species X displays imitation') and instead advocate greater attention to inter-individual variation in social learning. However, implementing this concept empirically presents new methodological challenges in attaining large enough sample sizes to

explore such variation with adequate statistical power. This is particularly true in the study of chimpanzees, which have been the focal species in a large proportion of studies on primate social learning, due to small and aging populations.

In the current study we present a novel meta-analytical method of examining individual differences in behaviour'. Just as many accumulated years of observational research at field sites have eventually allowed detailed longitudinal analyses of cultural behaviour in wild populations of animals, such as apes, monkeys, marine mammals and meerkats (Santorelli et al., 2011; Allen, Weinrich, Hoppitt, & Rendell, 2013; Perry et al., 2003; Robbins et al., 2016; Thornton, Samson, & Clutton-Brock, 2010; Whitehead & Rendell, 2014; Whiten et al., 1999), a similar accumulation of experimental data has now accrued at some captive research sites. This presents an unprecedented opportunity to examine individual performance of the same individuals across many experiments. The National Center for Chimpanzee Care in Texas is one such site, where 16 experimental studies (three unpublished) have investigated social learning carried out over a 12-year period (Davis, Vale, Schapiro, Lambeth, & Whiten, 2016; Dean, Kendal, Schapiro, Thierry & Laland, 2012; Hopper, Lambeth, & Schapiro, 2012; Hopper, Lambeth, Schapiro, & Whiten, 2008, 2015; Hopper et al., 2007; Kendal et al., 2015; Price, Lambeth, Schapiro, & Whiten, 2009; Vale et al., 2017a; Vale, Davis, Lambeth, Schapiro & Whiten, 2017b; Vale, Flynn, Lambeth, Schapiro, & Kendal, 2014; Watson et al., 2017; Whiten et al., 2007). We collated these data to investigate whether chimpanzees demonstrate stable individual differences in their propensity for social information use, and if so, which, if any, characteristics these individuals share with one another. We have directed this investigation in accordance with findings of prior research, introduced below, which are suggestive of effects of rearing history, age and sex on social learning.

As noted in reference to Farine et al. (2015) mentioned above, early-life environmental differences can have a profound influence on the social learning behaviour of some animal species. Chimpanzees that have been raised by humans (so-

called 'enculturated' chimpanzees) have been found to be more likely to imitate behaviours demonstrated by humans than conspecific-reared individuals (Bering, Bjorklund, & Ragan, 2000; Bjorklund & Bering, 2003; Buttelmann, Carpenter, Call, & Tomasello, 2007), although it should be noted that non-enculturated individuals also have imitative capabilities (Whiten & Custance, 1996). However, it has not been established whether this extends to a greater reliance on social information *in general*, or just that the preferred *processes* (e.g. imitation vs. emulation) of social learning is different in enculturated individuals. These influences of early life-history events on social learning behaviour suggest that chimpanzees may undergo a highly plastic period in early-life with regards to social information use. This is supported by some evidence that chimpanzees have a 'critical period' (between three and five years of age) during which to socially learn the challenging skill of nut-cracking behaviour. If this does not occur, then such individuals are extremely unlikely to master the skill later in life (Biro et al., 2003). Whether wild chimpanzees acquire the bulk of their cultural repertoire during this early juvenile period, or if it only affects the acquisition of highly technical skills, such as nut-cracking (just as humans 'grow out of' being able to learn a language with ease), remains unclear.

As well as the developmental effects described above, there is limited evidence for sex differences in chimpanzee social learning. Lonsdorf (2005) found that wild female juvenile chimpanzees (from 1 to 11 years old) spend more time watching their mother termite-fishing than do their male counterparts and consequently, the females fished both more often and more successfully. This may indicate an important sex difference in social information use of chimpanzees. However, Lonsdorf's (2005) study had a very limited sample size (three chimpanzees of each sex) and it does not necessarily follow that any observed differences will persist into adulthood.

Also of note are several studies that have applied batteries of cognitive tests to large numbers of humans and apes in order to investigate between- and within-species

differences in physical and social cognition (Herrmann, Call, Hernández-Lloreda, Hare, & Tomasello, 2007; Herrmann, Hare, Call, & Tomasello, 2010; Lacreuse, Russell, Hopkins, & Herndon, 2014). While these studies detected intra-specific influences of age and sex on performance in some domains including social cognition, there was limited focus on social learning specifically and social information was always provided by a human experimenter rather than a conspecific.

As described, previous research has suggested that sex, rearing history and age are three factors that already have some support from the literature as influencing social information use in specific paradigms. Moreover, Thornton and Lukas (2012) found that these same factors were important in explaining individual variation in performance in physical cognition-based tasks across a number of species. We have therefore focussed on these variables to determine whether they may also explain individual variation in social information use. While the rank of an individual chimpanzee has been found to influence their use of social information (Kendal et al., 2015), we do not have longitudinal hierarchy data, so were unable to include this in our analysis. With regards to rearing history, we drew comparisons between individuals who were born in captivity or the wild, and individuals who were raised by their mother or in a nursery setting. Matrilineal relationships seem to be critical for cultural transmission in several species; for example, communicative signals in chimpanzees (Tagliatela et al., 2013), vocalisations in hump-back whales (Yurk et al., 2002) and food-cleaning techniques in vervet monkeys (van de Waal et al., 2012). Since the parentage of most individuals within the population studied was known and multiple individuals from the same family units were present in the population, we also investigated heritability in propensity for social information use. Genetic inheritance of proclivity for social learning has been identified in fruit flies (Foucaud, Philippe, Moreno, & Mery, 2013) but is otherwise underexplored. Finally, an important consideration for many scientists choosing their sample is that individuals with a long history of participating in research may behave differently to less experienced



peers (e.g. by being more proficient at experimental tasks). Consequently, we also explored whether the number of social learning studies in which individuals had participated influenced the likelihood that they would use social information in the next study.

## **METHODS**

### *Study site*

Participants were 167 (76 male) chimpanzees housed at the National Center for Chimpanzee Care located at the Michale E. Keeling Center for Comparative Medicine and Research of The University of Texas MD Anderson Cancer Center in Bastrop, Texas, USA. In 2005, when the earliest data included here were collected, the median age was 20 years old (range: 3 to 43). In 2016, when the final data were collected, the median age was 31 (range: 14 to 51). An important distinction in this analysis was between mother-reared and nursery-reared individuals (Table 4.1). Nursery-reared individuals were chimpanzees who had been separated from their mother at birth due to abandonment, incompetency or health complications that put their lives at risk. While nursery-reared individuals were housed together when they were old enough to move, they also generally received large amounts of human contact (up to several hours per day) for the first few years of life.

	<b>Mother</b>	<b>Nursery</b>	<b>Unknown</b>	<b>Total</b>
<b>Wild</b>	42	0	0	42
<b>Captive</b>	97	23	4	124
<b>Unknown</b>	0	0	1	1
<b>Total</b>	139	23	5	167

Table 4.1. Summary table of rearing history and birthplace of subjects

### *Data collation*

We contacted all researchers who had carried out studies related to social learning at the study site between the years of 2005 and 2016. In each case we requested:

- A summary of the methods used in the study
- A list of all participants used in all conditions
- Detailed response measures for each participant
- The dates data were collected

This resulted in a data-set comprised of 16 studies, 13 of which are currently published (Davis et al., 2016; Dean et al., 2012; Hopper et al., 2007, 2008, 2012, 2015; Kendal et al., 2015; Price et al., 2009; Vale et al., 2017a; Vale et al., 2017b; Vale et al., 2014; Watson et al., 2017; Whiten et al., 2007). This included data from a total of 167 individuals who had participated in at least 1 (mode = 2, median = 4) experimental condition (Table 4.2). Only conditions in which individuals were exposed to either a live model or video demonstration of a conspecific were included (i.e. no asocial controls, no human demonstrations, or 'ghost' conditions).

<b>Number of experiments</b>	<b>N participated</b>
1	13
2	25
3	31
4	24
5	25
6	30
7	11
8	3
9	4
10	1

Table 4.2. Breakdown of the number of chimpanzees who participated in a given number of experiments. Greatest number of experimental participations by any individual was 10. Total = 167.

In order to make meaningful comparisons between studies with a disparate array of methodologies, it was necessary to standardise the outcomes as far as possible. In a 'classic' meta-analysis this would be done by drawing effect sizes from each of many studies, each using a different sample, to identify an overall effect of a given variable. For example, investigating the influence of sex across a range of measures of impulsivity (Cross, Copping & Campbell, 2011). However, this was not possible in the present study where our data points were repeated-measures of individual performance in multiple studies. Consequently, we created a binary scale applied to the results of each study, which assigned a Social Information Score (SIS) to each individual. A SIS of 0 indicated that an individual showed no evidence or ambiguous evidence of social learning. A SIS of 1 indicated that the individual demonstrated convincing evidence for social learning. For example, Watson et al. (2017) employed a simple two-action puzzle-box paradigm in an open-diffusion context. Groups were seeded with a method of opening the box from either a high- or low-ranking model. A score of 0 would indicate that an individual either a) never successfully opened the box, or b) first learned to open the box using a method they had not observed, suggesting that they learned the solution asocially. A score of 1 was given to individuals who had observed the seeded behaviour and used it as their first choice of method. The scale used for each study can be found in Table 4.3. This binary measure of social learning unfortunately meant losing granularity in the data associated with each study. However, this was preferable to the degree of subjective assessment that would be required for a more nuanced scale.

Study	Data collection	SIS	Score criteria
Hopper et al. (2015)	01/09/2005	1	Used the seeded method on their first trial
		0	Either never opened the puzzle-box or did not use seeded method on first trial
Hopper et al. (2007)	01/02/2006	1	Used the seeded method on their first trial
		0	Either never opened the puzzle-box or did not use seeded method on first trial
Hopper et al. (2008)	01/04/2006	1	Used the seeded method on their first trial
		0	Either never opened the puzzle-box or did not use seeded method on first trial
Hopper et al. (2012)	01/05/2006	1	Used the seeded method on their first trial
		0	Either never opened the puzzle-box or did not use seeded method on first trial
Whiten et al. (2007)	01/06/2006	1	Learned seeded method
		0	Did not learn seeded method
Dean et al. (2012)	06/06/2007	1	Reached level 1
		0	Did not reach level 1
Kendal et al. (2015)	01/10/2007	1	Used the seeded method on their first trial
		0	Either never opened the puzzle-box or did not use seeded method on first trial
Price et al. (2009)	01/04/2008	1	Scored => 11 on the 'combine' score
		0	Scored < 11 on the 'combine' score
Vale et al. (2013)	01/03/2010	1	Ate at resource-rich location >75% of the time.
		0	Ate at resource-rich location <75% of the time.
Wood et al. (unpublished)	01/05/2011	1	Solved problem after observation
		0	Never solved
Vale et al. (unpublished)	01/04/2012	1	More than 75% of alternative tokens exchanged
		0	Less than 75% of alternative tokens exchanged
Vale et al. (2017a)	01/03/2015	1	Ate previously unpalatable food more than 25% of the time
		0	Ate previously unpalatable food less than 25% of the time
Davis et al. (2016)	03/04/2015	1	Switched to observed alternative method in Experiment 1
		0	Did not switch to observed alternative method in experiment 1
Watson et al. (2017)	01/06/2015	1	Used the seeded method on their first trial
		0	Either never opened the puzzle-box or did not use seeded method on first trial
Vale et al. (2017b)	01/06/2015	1	Learned in phase 1 or 2
		0	Never learned or learned in phase 3
Watson et al. (unpublished - Chapter 3)	01/06/2016	1	Switched to observed alternative method
		0	Never switched to observed alternative method

Table 4.3. List of studies used, date of data collection began and SIS criteria. SIS = 1:

Individual shows convincing evidence of social information use. SIS = 0: Individual shows no evidence or ambiguous evidence of social information use. The same criteria applied to all experimental conditions within a study.

Conditions within studies often differed considerably in the methods used, and so each condition was treated as a separate 'experiment' for the purposes of the random effect 'Experiment'. Ages of individuals at the time of study were calculated by deducting their date of birth from the approximate date at which data collection for a study began. Pedigree data were also collated for each chimpanzee to determine relatedness between individuals. This allowed us to measure the effect of genetic relatedness on our outcome measures.

### *Analysis*

In order to determine which factors were likely to be common to individuals with high social learning scores, we fitted a series of binomial (probit link function) generalised linear mixed-models using a Bayesian framework. This was carried out using 'RStudio' (R Studio Team, 2015) and 'R' (R Development Core Team, 2016) with the package 'MCMCglmm' (Hadfield, 2010). This package allows the use of pedigree data to estimate the genetic heritability ( $h^2$ ) of a given trait, a type of analysis known as an 'animal model' (Wilson et al., 2010). Values of  $h^2$  that are close to 0 indicate that there is a negligible effect of pedigree, whereas values close to one indicate a strong effect. For example, if closely-related individuals perform more similarly than distantly related or unrelated individuals then we would predict a high value of  $h^2$ . MCMC chains were run for 2,000,000 iterations, with a burn-in period of 100,000 iterations and a thinning interval of 500 iterations to reduce autocorrelation. All models were fit with uninformative priors ( $V=1$ ,  $n=0.002$ ) and the residual variance was fixed to 1 because this cannot be estimated when using a binary response variable. Convergence was assessed visually using trace plots of posterior distributions and acceptably low levels of autocorrelation were ensured by determining that all estimated parameters had an effective sample size of over 1000.

We ran two full models, Full Model A (FMA) and Full Model B (FMB). These two models were identical except in how we classified individuals' early-life history. In FMA we examined whether nursery- (i.e. human) reared chimpanzees performed differently from conspecific-reared individuals (Fixed effect = Rearing), and in FMB we examined whether captive-born chimpanzees behaved differently than wild-born individuals (Fixed effect = Born). Table 4.4 details the fixed and random effects present in each model. Repeatability, the proportion of variance explained by individual identity, was calculated by dividing the variance explained by individual identity by the total variance in SIS (Nakagawa & Schielzeth, 2010). These two fixed effects could not be included in the same model as they were somewhat linearly dependant (e.g. all nursery-reared individuals were necessarily captive-born). Fixed effects were determined as having an important influence according to whether the 95% credibility intervals of their posterior distribution crossed zero. If a variable has a negligible effect, we expect its posterior distribution to be centred close to zero. An influential variable is expected to be shifted away from and not substantially overlapping zero.

<b>Fixed Effects</b>	
Age	Age (years) of the individual at the time of a given experimental condition.
Sex	Sex of the individual.
Rearing (FMA only)	Whether individual was raised by their mother or in a nursery.
Born (FMB only)	Whether individual was born in captivity or the wild.
Experience	The number of experimental conditions which the individual had participated in at that time.
<b>Random effects</b>	
ID	Controlling for multiple observations per individual.
Pedigree	An individual's parentage, if known. Used to estimate heritability of SIS.
Condition	The experimental condition (N = 27) the data point was taken from.
<b>Outcome</b>	
SIS	A binary measure of social learning for a given experimental condition.

Table 4.4. Fixed effects, random effects and outcome variable used in our models.

## RESULTS

FMA and FMB were found to fit the data substantially better than the null model according to their Delta Information Criterion (Table 4.5), accounting for 98% of the total DIC weight between them. In both FMA and FMB, individuals demonstrated moderate repeatability in SIS (FMA:  $R = 0.526$ , 95% CI: 0.170, 0.745, FMB:  $R = 0.545$ , 95% CI: 0.141, 0.727. Maximum possible  $R$  is 1).

FMA and FMB did not differ greatly in how well they fit the data and their outputs were very similar for shared fixed effects (Figure 4.1, Table 4.6), indicating that neither of the differences in rearing regime had a substantial effect on SIS. However in both FMA and FMB, females were found to be more likely to use social information than males (Figure Figure 4.1, Figure 4.2). We used the inverse logit of the coefficients to obtain the estimated posterior probability that individuals would use social information based on their sex, according to each model (Table 4.7). No other fixed effects in either model had 95% CIs which did not cross zero, indicating that SIS had no relationship with the other variables we tested. There was also no evidence for an effect of heritability, with the posterior estimate of  $h^2$  being less than 0.01 in all models.

<b>Model</b>	<b>DIC</b>	<b>Total DIC Weight</b>
Null	613.54	0.02
FMA	606.43	0.69
FMB	608.53	0.29

Table 4.5. Information criterion statistics for each model.

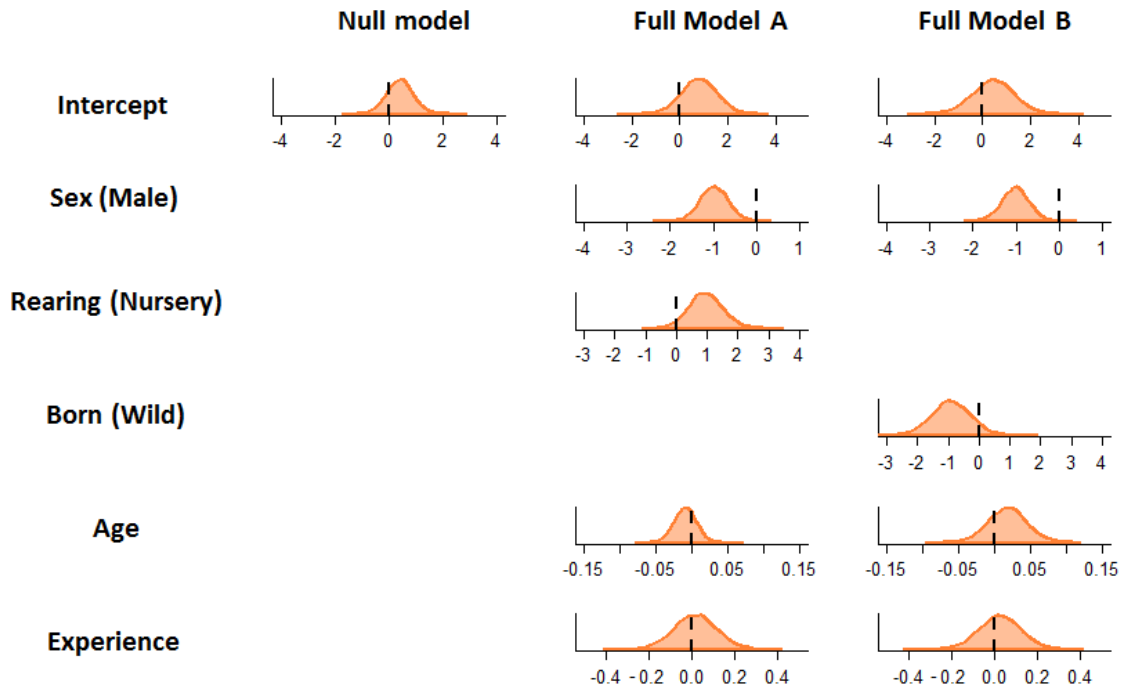


Figure 4.1. Posterior density distribution plots for each parameter in each model tested. FMA contrasted nursery- with mother-reared chimpanzees. FMB contrasted wild- with captive-born chimpanzees.

Model	Fixed effect	Posterior mean	Lower 95% CI	Upper 95% CI	Effective sample size
Null	Intercept	0.409	-0.569	1.400	4900
FMA	Intercept	0.815	-0.646	2.264	4764
	Sex (Male)	-0.986	-1.609	-0.347	4900
	Rearing (nursery)	0.963	-0.111	2.019	4900
	Age	-0.008	-0.038	0.022	4464
	Current Experience	0.016	-0.191	0.204	5303
FMB	Intercept	0.446	-263.000	2.150	4900
	Sex (Male)	-1.011	-1.645	-0.390	5672
	Born (Wild)	-0.912	-2.201	0.336	4900
	Age	0.018	-0.036	0.744	4900
	Current Experience	0.025	-0.172	0.215	4900

Table 4.6. Full summary outputs for each model.



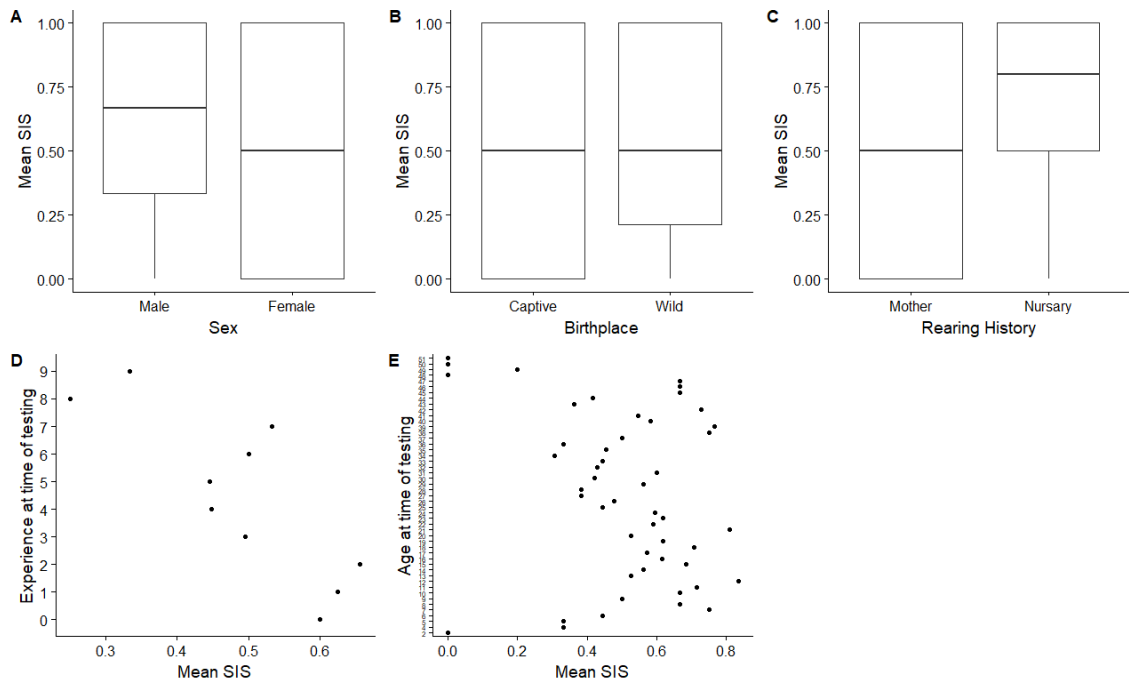


Figure 4.1. Summary plots showing mean SIS for each of the variables used in our statistical analysis based on the raw data. For plots A, B and C, data points are mean SIS for each individual belonging to each level of each factor. For plots D and E, data points are the mean SIS for the level of each factor across all individuals.

Sex	Model	Probability	Lower 95% CI	Upper 95% CI
Female	FMA	0.675	0.315	0.939
Male	FMA	0.478	0.144	0.832
Female	FMB	0.597	0.208	0.930
Male	FMB	0.398	0.398	0.830

Table 4.7. Estimated posterior probability of using social information by sex and rearing history according to the best fitting model (FMA).

## DISCUSSION

This study utilised data collated across 27 experimental conditions from 16 different studies on social learning, carried out at the same study site, in order to explore the individual-level factors that influence social information use in chimpanzees. We found that chimpanzees demonstrated a moderate level of repeatability across experiments with regard to whether or not they used social information. In other words, individuals who demonstrated social learning in a given study were likely to do so in other studies, and vice versa for those who did not.

We also found that female chimpanzees were more likely to use social information than males. However, perhaps surprisingly, there were no important differences between captive- and wild-born individuals, nor nursery- and mother-reared individuals. Neither age nor the number of social learning studies an individual had participated in were found to have an important effect on SIS. Finally, there was not good evidence to suggest that proclivity for social learning is a heritable trait, unlike performance in paradigms designed to test 'general' intelligence (Hopkins, Russell, & Schaeffer, 2014).

The moderate level of individual repeatability identified by our analysis suggests that motivation for social information use is a stable trait in chimpanzees and that individual differences play an important role in the transmission of social information. In the future it would be worthwhile to incorporate measures of personality into similar analyses, as it is also stable over long periods of time in chimpanzees (King, Weiss, & Sisco, 2008). There is some precedent for this, as a relationship between 'exploratory' personalities and social information use has been found to be positive in some avian and piscine species (Marchetti & Drent, 2000; Nomakuchi, Park, & Bell, 2009). Furthermore, wild baboons that were scored most highly on 'boldness' or 'anxious' traits were found to show a greater improvement on a foraging task after observing a demonstrator (Carter et al., 2014).

The fact that nursery-reared individuals were not more likely to use social information than mother-reared ones is somewhat unexpected, given that prior literature found human-raised chimpanzees more readily engaged in imitative behaviour (Bering et al., 2000; Bjorklund & Bering, 2003; Buttelmann et al., 2007; Tomasello, Savage-Rumbaugh, & Kruger, 1993). This may be because even mother-reared chimpanzees were exposed to sufficient human contact to become somewhat 'enculturated', causing a ceiling effect. Alternatively, it may be that enculturation influences the process of social learning that individuals preferentially deploy (i.e. imitation), but not general proclivity for social information use, the broad granularity of effect measured here. A third possibility is that although nursery-reared individuals were exposed to large amounts of human contact, they were not raised within a human family, as with the studies cited above, and consequently the degree of enculturation may not have been not as extreme.

Our finding that females were more likely to use social information than males is consistent with the findings of Lonsdorf (2005) regarding infant tool-use behaviour in the wild, where it was found that young females observed their mothers more and acquired related competence earlier. A greater motivation for female chimpanzees to use social information than males may also be reflected by Reader and Laland's (2001) finding that a disproportionate number of innovations (i.e. asocial learning) originate in male chimpanzees. However, in chimpanzees, males are typically socially dominant relative to females, so it is possible that in our analysis, sex served as a proxy variable for social dominance. Because the data set used for this analysis spanned 12 years, during which hierarchies are likely to have shifted over time (particularly for individuals who moved between social groups), and were not systematically recorded, it was not possible to dissociate dominance and sex (or to include an accurate measure of rank in our models). Although these two factors are inexorably tied together, an example of why a distinction might matter comes from Kendal et al. (2015, included in our data set) who introduced a puzzle-box to 42 chimpanzees living in four social groups (two groups with solutions

seeded by trained demonstrators, two without) and observed the diffusion of solutions to this novel foraging problem. It was found that there was a general tendency for individuals to attend to demonstrations from individuals more dominant than themselves. Furthermore, whether or not individuals chose to use social information at all varied greatly according to their own knowledge states and position in the social hierarchy, with more dominant individuals being less likely to attend to the demonstrations of others. One explanation for this might be that, as dominant individuals typically have priority access to food resources, they are not accustomed to 'waiting their turn' while others demonstrate how to exploit it, whereas a subordinate individual would observe many others before gaining access to the resource.

There are certain limitations to bear in mind when drawing inferences from the present results. Firstly, although we attempted to standardise the measures used in this analysis across studies, there was no way to objectively control for task difficulty. As a result, individuals who may have participated in five cognitively 'easy' tasks (e.g. choosing whether to slide a door left or right as in Kendal et al., 2015) were judged by the same criteria as those who participated in five 'difficult' tasks (e.g. combining tools as in Price et al., 2009). It is therefore possible that participants in these latter tasks utilised social information, but were still unsuccessful. Another limitation was that none of the studies included in the data set investigated social learning under totally 'natural' conditions (c.f. Hobaiter et al., 2014) and involved human experimenters (i.e. were conducted by familiar humans, although all used conspecifics as models, in contrast to others, such as Tomasello et al., 1993). We cannot therefore necessarily dissociate motivation to participate in experiments (rewarding due to interaction with humans and food prizes) from social information use *in general*. Less human-oriented individuals who avoid experiments may nevertheless commonly use social information in more everyday contexts. As an example of how human-chimpanzee relationships can confound experiments, Brosnan et al. (2015) found that human-oriented chimpanzees were found

to be more reactive to inequity in food payoffs compared to other individuals. The authors argue that this may have been because the food was distributed by a human, leaving the human-oriented individuals antagonised not only by the reduced payoff but also by the apparent slight from the researcher (see also Engelman, Clift, Hermann & Tomasello, 2017).

Despite these limitations, our findings have important implications for how experimenters conducting studies of chimpanzee behaviour choose their sample. For example, when attempting to determine the existence of a hotly contested behaviour such as conformity (Van Leeuwen & Haun, 2013; Van Leeuwen, Kendal, Tennie, & Haun, 2015), it may be beneficial to sample individuals who are typically most reliant on social learning. This way, the likelihood of identifying an extant, but elusive, behaviour is amplified. In contrast, using a sample consisting of individuals who rarely use social information is likely to yield false negatives. Either way, we must then, of course, be extremely cautious about generalising such samples to wider populations.

This study applied a novel method of using a 'meta-data' set at a chimpanzee research site, incorporating 16 studies carried out over the last 12 years, to examine consistent inter-individual differences in performance across a spread of social learning experiments. It was found that individuals showed significant consistency in their motivation to use social information and that this propensity was somewhat mediated by sex. Our methods could, in principle, be applied to any population with a similar scale of data to draw upon.

## REFERENCES

- Allen, J., Weinrich, M., Hoppitt, W., & Rendell, L. (2013). Network-based diffusion analysis reveals cultural transmission of lobtail feeding in humpback whales. *Science*, *340*(6131), 485-488.
- Bering, J. M., Bjorklund, D. F., & Ragan, P. (2000). Deferred imitation of object-related actions in human-reared juvenile chimpanzees and orangutans. *Developmental Psychobiology*, *36*(3), 218.
- Biro, D., Inoue-Nakamura, N., Tonooka, R., Yamakoshi, G., Sousa, C., & Matsuzawa, T. (2003). Cultural innovation and transmission of tool use in wild chimpanzees: evidence from field experiments. *Animal Cognition*, *6*(4), 213-223.
- Bjorklund, D. F., & Bering, J. M. (2003). A note on the development of deferred imitation in enculturated juvenile chimpanzees (*Pan troglodytes*). *Developmental Review*, *23*(3), 389-412.
- Brosnan, S. F., Hopper, L. M., Richey, S., Freeman, H. D., Talbot, C. F., Gosling, S. D., ... & Schapiro, S. J. (2015). Personality influences responses to inequity and contrast in chimpanzees. *Animal behaviour*, *101*, 75-87.
- Buttelmann, D., Carpenter, M., Call, J., & Tomasello, M. (2007). Enculturated chimpanzees imitate rationally. *Developmental Science*, *10*(4), 31-38.
- Carter, A. J., Marshall, H. H., Heinsohn, R., & Cowlshaw, G. (2014). Personality predicts the propensity for social learning in a wild primate. *PeerJ*, *2*, e283.
- Cross, C. P., Copping, L. T., & Campbell, A. (2011). Sex differences in impulsivity: a meta-analysis. *Psychological bulletin*, *137*(1), 97.
- Davis, S. J., Vale, G. L., Schapiro, S. J., Lambeth, S. P., & Whiten, A. (2016). Foundations of cumulative culture in apes: improved foraging efficiency through relinquishing and combining witnessed behaviours in chimpanzees (*Pan troglodytes*). *Scientific reports*, *6*, 35953.

- Dean, L. G., Kendal, R. L., Schapiro, S. J., Thierry, B., & Laland, K. N. (2012). Identification of the social and cognitive processes underlying human cumulative culture. *Science*, *335*(6072), 1114-1118.
- Engelmann, J. M., Clift, J., Hermann, E., & Tomasello, M. (2017). Social disappointment explains chimpanzees' behavior in the inequity aversion task. *Proceedings of the Royal Society B: Biological Sciences*, *284*(1861), 20171502.
- Farine, D. R., Spencer, K. A., & Boogert, N. J. (2015). Early-life stress triggers juvenile zebra finches to switch social learning strategies. *Current Biology*, *25*(16), 2184-2188.
- Foucaud, J., Philippe, A.-S., Moreno, C., & Mery, F. (2013). A genetic polymorphism affecting reliance on personal versus public information in a spatial learning task in *Drosophila melanogaster*. *Proceedings of the Royal Society of London B: Biological Sciences*, *280*(1760), 20130588.
- Giraldeau, L. A., Valone, T. J., & Templeton, J. J. (2002). Potential disadvantages of using socially acquired information. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *357*(1427), 1559-1566.
- Hadfield, J. D. (2010). MCMC methods for multi-response generalized linear mixed models: the MCMCglmm R package. *Journal of Statistical Software*, *33*(2), 1-22.
- Herrmann, E., Call, J., Hernández-Lloreda, M. V., Hare, B., & Tomasello, M. (2007). Humans have evolved specialized skills of social cognition: The cultural intelligence hypothesis. *Science*, *317*(5843), 1360-1366.
- Herrmann, E., Hare, B., Call, J., & Tomasello, M. (2010). Differences in the cognitive skills of bonobos and chimpanzees. *PLoS One*, *5*(8), e12438.
- Hobaiter, C., Poisot, T., Zuberbühler, K., Hoppitt, W., & Gruber, T. (2014). Social network analysis shows direct evidence for social transmission of tool use in wild chimpanzees. *PLoS biology*, *12*(9), e1001960.
- Hopkins, W. D., Russell, J. L., & Schaeffer, J. (2014). Chimpanzee intelligence is heritable. *Current Biology*, *24*(14), 1649-1652.

- Hopper, L. M., Lambeth, S. P., & Schapiro, S. J. (2012). An evaluation of the efficacy of video displays for use with chimpanzees (*Pan troglodytes*). *American Journal of Primatology*, *74*(5), 442-449.
- Hopper, L. M., Lambeth, S. P., Schapiro, S. J., & Whiten, A. (2008). Observational learning in chimpanzees and children studied through 'ghost' conditions. *Proceedings of the Royal Society of London B: Biological Sciences*, *275*(1636), 835-840.
- Hopper, L. M., Lambeth, S. P., Schapiro, S. J., & Whiten, A. (2015). The importance of witnessed agency in chimpanzee social learning of tool use. *Behavioural Processes*, *112*, 120-129.
- Hopper, L. M., Spiteri, A., Lambeth, S. P., Schapiro, S. J., Horner, V., & Whiten, A. (2007). Experimental studies of traditions and underlying transmission processes in chimpanzees. *Animal Behaviour*, *73*(6), 1021-1032.
- Kendal, R. L., Coolen, I., van Bergen, Y., & Laland, K. N. (2005). Trade-offs in the adaptive use of social and asocial learning. *Advances in the Study of Behavior*, *35*, 333-379.
- Kendal, R. L., Hopper, L. M., Whiten, A., Brosnan, S. F., Lambeth, S. P., Schapiro, S. J., & Hoppitt, W. (2015). Chimpanzees copy dominant and knowledgeable individuals: implications for cultural diversity. *Evolution and Human Behavior*, *36*(1), 65-72.
- King, J. E., Weiss, A., & Sisco, M. M. (2008). Aping humans: age and sex effects in chimpanzee (*Pan troglodytes*) and human (*Homo sapiens*) personality. *Journal of Comparative Psychology*, *122*(4), 418.
- Lacreuse, A., Russell, J. L., Hopkins, W. D., & Herndon, J. G. (2014). Cognitive and motor aging in female chimpanzees. *Neurobiology of aging*, *35*(3), 623-632.
- Laland, K. N. (2004). Social learning strategies. *Animal Learning & Behavior*, *32*(1), 4-14.



- Lonsdorf, E. V. (2005). Sex differences in the development of termite-fishing skills in the wild chimpanzees, *Pan troglodytes schweinfurthii*, of Gombe National Park, Tanzania. *Animal Behaviour*, *70*(3), 673-683.
- Marchetti, C., & Drent, P. J. (2000). Individual differences in the use of social information in foraging by captive great tits. *Animal Behaviour*, *60*(1), 131-140.
- Mesoudi, A., Chang, L., Dall, S. R., & Thornton, A. (2016). The evolution of individual and cultural variation in social learning. *Trends in Ecology & Evolution*, *31*(3), 215-225.
- Nakagawa, S., & Schielzeth, H. (2010). Repeatability for Gaussian and non-Gaussian data: a practical guide for biologists. *Biological Reviews*, *85*(4), 935-956.
- Nomakuchi, S., Park, P. J., & Bell, M. A. (2009). Correlation between exploration activity and use of social information in three-spined sticklebacks. *Behavioral Ecology*, *20*(2), 340-345.
- Perry, S., Baker, M., Fedigan, L., Gros-Louis, J., Jack, K., MacKinnon, K. C., . . . Rose, L. (2003). Social conventions in wild white-faced capuchin monkeys. *Current Anthropology*, *44*(2), 241-268.
- Price, E. E., Lambeth, S. P., Schapiro, S. J., & Whiten, A. (2009). A potent effect of observational learning on chimpanzee tool construction. *Proceedings of the Royal Society of London B: Biological Sciences*, *276*(1671), 3377-3383.
- Price, E. E., Wood, L. A., & Whiten, A. (2017). Adaptive cultural transmission biases in children and nonhuman primates. *Infant Behavior and Development*, *48*, 45-53.
- R Development Core Team. (2016). R: A language and environment for statistical computing. Vienna, Austria: R Foundation for Statistical Computing. Retrieved from <https://www.R-project.org>
- R Studio Team. (2015). RStudio: Integrated Development for R. Boston, MA: R Studio, Inc. Retrieved from [www.rstudio.com](http://www.rstudio.com)
- Reader, S. M., & Laland, K. N. (2001). Primate innovation: sex, age and social rank differences. *International Journal of Primatology*, *22*(5), 787-805.

- Robbins, M. M., Ando, C., Fawcett, K. A., Grueter, C. C., Hedwig, D., Iwata, Y., . . .  
Stoinski, T. S. (2016). Behavioral Variation in Gorillas: Evidence of Potential  
Cultural Traits. *PLoS One*, *11*(9), e0160483.
- Santorelli, C. J., Schaffner, C. M., Campbell, C. J., Notman, H., Pavelka, M. S.,  
Weghorst, J. A., & Aureli, F. (2011). Traditions in spider monkeys are biased  
towards the social domain. *PLoS One*, *6*(2), e16863.
- Russell, J. L., McIntyre, J. M., Hopkins, W. D., & Taglialatela, J. P. (2013). Vocal learning  
of a communicative signal in captive chimpanzees, *Pan troglodytes*. *Brain and  
Language*, *127*(3), 520-525.
- Thornton, A., & Lukas, D. (2012). Individual variation in cognitive performance:  
developmental and evolutionary perspectives. *Philosophical Transactions of the  
Royal Society of London B: Biological Sciences*, *367*(1603), 2773-2783.
- Thornton, A., Samson, J., & Clutton-Brock, T. (2010). Multi-generational persistence of  
traditions in neighbouring meerkat groups. *Proceedings of the Royal Society of  
London B: Biological Sciences*, *277*(1700), 3623-3629.
- Tomasello, M., Savage-Rumbaugh, S., & Kruger, A. C. (1993). Imitative learning of  
actions on objects by children, chimpanzees, and enculturated chimpanzees.  
*Child Development*, *64*(6), 1688-1705.
- Vale, G. L., Davis, S. J., van de Waal, E., Schapiro, S. J., Lambeth, S. P., & Whiten, A.  
(2017a). Lack of conformity to new local dietary preferences in migrating captive  
chimpanzees. *Animal Behaviour*, *124*, 135-144.
- Vale, G. L., Davis, S. J., Lambeth, S. P., Schapiro, S. J., & Whiten, A. (2017b).  
Acquisition of a socially learned tool use sequence in chimpanzees: Implications  
for cumulative culture. *Evolution and Human Behavior*, 635-644.
- Vale, G. L., Flynn, E. G., Lambeth, S. P., Schapiro, S. J., & Kendal, R. L. (2014). Public  
information use in chimpanzees (*Pan troglodytes*) and children (*Homo sapiens*).  
*Journal of Comparative Psychology*, *128*(2), 215-223.

- Van Leeuwen, E. J., & Haun, D. B. (2013). Conformity in nonhuman primates: fad or fact? *Evolution and Human Behavior*, *34*(1), 1-7.
- Van Leeuwen, E. J., Kendal, R. L., Tennie, C., & Haun, D. B. (2015). Conformity and its look-a-likes. *Animal Behaviour*, *110*, e1-e4.
- van de Waal, E., Krützen, M., Hula, J., Goudet, J., & Bshary, R. (2012). Similarity in food cleaning techniques within matrilineal groups in wild vervet monkeys. *PLoS One*, *7*(4), e35694.
- Watson, S. K., Reamer, L. A., Mareno, M. C., Vale, G. L., Harrison, R. A., Lambeth, S. P., . . . Whiten, A. (2017). Socially transmitted diffusion of a novel behaviour from subordinate chimpanzees. *American Journal of Primatology*, *9999*; e22642.
- Watson, S. K., & Whiten, A. (in press). Culture in non-human animals. In Z. Clay (Ed.), *Encyclopaedia of Animal Cognition and Behaviour*. Springer.
- Whitehead, H., & Rendell, L. (2014). *The cultural lives of whales and dolphins*: University of Chicago Press.
- Whiten, A. & Custance, D. (1996). Studies of imitation in chimpanzees and children. In C. M. Hayes & B. G. Galef (Eds.), *Social learning in animals: the roots of culture*, pp. 291–318. Academic Press.
- Whiten, A., Goodall, J., McGrew, W. C., Nishida, T., Reynolds, V., Sugiyama, Y., . . . Boesch, C. (1999). Cultures in chimpanzees. *Nature*, *399*(6737), 682-685.
- Whiten, A., Spiteri, A., Horner, V., Bonnie, K. E., Lambeth, S. P., Schapiro, S. J., & De Waal, F. B. (2007). Transmission of multiple traditions within and between chimpanzee groups. *Current Biology*, *17*(12), 1038-1043.
- Wilson, A. J., Reale, D., Clements, M. N., Morrissey, M. M., Postma, E., Walling, C. A., . . . Nussey, D. H. (2010). An ecologist's guide to the animal model. *Journal of Animal Ecology*, *79*(1), 13-26.
- Wood, L. A., Kendal, R. L., & Flynn, E. G. (2013). Whom do children copy? Model-based biases in social learning. *Developmental Review*, *33*(4), 341-356.

Yurk, H., Barrett-Lennard, L., Ford, J. K. B., & Matkin, C. O. (2002). Cultural transmission within maternal lineages: vocal clans in resident killer whales in southern Alaska. *Animal Behaviour*, 63(6), 1103-1119.

# CHAPTER 5

## GENERAL DISCUSSION

In the series of studies reported in this thesis I investigated various factors that influence social information use in chimpanzees. First, I investigated whether subordinate chimpanzees are capable of seeding novel traditions in their community. In the second, I set out to examine whether chimpanzees demonstrate conformity, but ended up examining the influence of social context upon social learning decisions. Finally, I determined the extent to which individual differences influence social information use in chimpanzees. I will now discuss these studies with regards to their implications for future research and the field at large.

### **SUBORDINATE CHIMPANZEES CAN EFFECTIVELY SEED FORAGING INNOVATIONS**

Chimpanzees are a highly innovative species. Any chimpanzee researcher or caretaker is likely to have a suite of often-shared stories about individuals with novel and surprising ways chimpanzees have found of getting attention, reaching food or subverting an experimental paradigm. However, chimpanzees also have a reputation for being behaviourally conservative, as they are either unable or unwilling to switch from pre-existing behaviours to novel alternatives, even if these are more efficient or productive (Hopper, Schapiro, Lambeth, & Brosnan, 2011; Hrubesch, Preuschoft, & van Schaik, 2009; Marshall-Pescini & Whiten, 2008). Nishida, Matsusaka, and McGrew (2009) spent several decades observing the Mahale community of chimpanzees in Tanzania, recording innovations and their subsequent use by other individuals. Neatly highlighting both the creativity and conservatism of chimpanzees, these authors

identified 32 novel behavioural patterns but as many as 21 of these innovations never spread beyond one or a few individuals and six of them extinguished completely over time. There is an open question, therefore, as to what factors govern whether a novel behaviour will spread, and in some cases diffuse throughout a community of chimpanzees to become the kind of tradition recorded in the wild (Whiten et al., 1999). It has been proposed that a bias towards copying dominant individuals might account for this, since Reader and Laland (2003) found that many innovations originate in subordinate individuals, who might be intrinsically less likely to be copied. Since dominant individuals typically have the most access to food resources and mating privileges (Cowlshaw & Dunbar, 1991), it makes some intuitive sense that naïve individuals might take their cues on how best to behave from them. Kendal et al. (2015) lend some support to this 'rank bias hypothesis', finding that individuals preferentially attended to dominant individuals during the open-diffusion of opening a puzzle-box task. However, this attentional bias does not necessarily preclude the transmission of behaviours from subordinate chimpanzees. On simple tasks, such as a sliding-door puzzle box or equivalents in the wild, it may take only a single observation to learn a behaviour. Horner, Proctor, Bonnie, Whiten, and de Waal (2010) also report evidence that chimpanzees preferentially copy 'prestigious' individuals – the authors' own compound variable of age, rank and experience. In this study, observing chimpanzees were found to be more likely to copy a behaviour demonstrated by an individual of high rather than low prestige. However, contrary to Kendal et al. (2015) individuals were not found to preferentially attend to demonstrations from the 'prestigious' model.

The only two studies to investigate the existence of rank-bias in non-chimpanzee species of primate did not find evidence for it. Dindo, Leimgruber, Ahmed, Whiten, and de Waal (2011) found that tufted capuchin monkeys did not preferentially copy dominant models over less dominant individuals in a puzzle-box task. Although it is important to note that testing occurred in private, therefore eliminating any potential social influence

on the subject's choice. However, in field experiment Botting et al. (under review) found that vervet monkeys also did not demonstrate a rank bias when choosing to copy either a dominant or subordinate individual's demonstrations of opening a puzzle-box. Very little research has been carried out as to whether rank-bias might exist more widely in the animal kingdom, but it has been found that domestic hens preferentially copy the pecking behaviour of dominant individuals (Nicol & Pope, 1999). Interestingly, they did so regardless of whether these individuals were effective foragers. This may be interpreted in two ways. On the one hand, it may be that rank-bias is such a potent heuristic for social learning that it supersedes information on likely payoffs. Alternatively, it may be that individuals do not adopt the behaviour of dominant individuals solely to improve their foraging success, but also for social reasons such as facilitating social bonding with the dominant individual. For example, there is evidence that humans behave more pro-socially towards individuals who imitate them (Carpenter, Uebel, & Tomasello, 2013; Van Baaren, Holland, Kawakami, & Van Knippenberg, 2004). However, the social payoffs of such behaviour in animals are completely unexamined. Finally, there is also some evidence that humans are subject to rank- and/or prestige-bias. Flynn and Whiten (2012) found that children were more likely to attend to the actions of more dominant and prestigious peers in a tool-use task. Furthermore, McGuigan (2013) found that children were more likely to over-imitate (copy causally irrelevant actions) the higher ranking of two adult models.

The two studies of rank-bias in chimpanzees described above (Horner et al., 2010; Kendal et al., 2015) examined whether they generally prefer to copy a novel behaviour from, or attend to, dominant/high-prestige than subordinate/low-prestige individuals. However, no study has determined whether subordinate or non-prestigious individuals would be copied in the absence of a better option. An absence of copying in this context is what would be necessary in order to constrain the diffusion of subordinate innovations. In **Chapter 2** I set out to systematically examine whether the group-mates

of subordinate individuals were motivated to copy the subordinate's demonstration of a novel method of extracting food from a puzzle-box. It was found that they readily did so, thus problematizing the 'rank-bias hypothesis' with regards to chimpanzee cultural transmission.

In fact, not only did subordinate individuals successfully seed novel behaviours within their group, but there was more evidence of their method being copied than in groups which had dominant males as demonstrators. One explanation for this finding may be that the motivation towards using social information provided by dominant and subordinate models may not have differed greatly. Rather, the social learning *process* at work may have been different. In the groups with low-ranking models, observers almost unanimously copied the directionality of movement seeded by the model. In groups with high ranking individuals, several individuals did not copy the direction of movement but did nevertheless successfully open the box (using the opposite direction of opening the door from the model). It may therefore have been that subordinate individuals were imitated, or the results of their actions replicated through emulation. Conversely, dominant individuals may have been emulated in the broader sense that the action of sliding the door on the foraging device was replicated, but learners did so in the opposite direction.

**Chapter 4**, which found that female chimpanzees were more likely than males to use social information across a range of social learning experiments, may shed light on why female (subordinate) models were more likely than (dominant) males to be copied by other individuals in **Chapter 2**. If a particular category of individual (such as females) typically make more use of social information, others may be biased towards copying these individuals since they are likely to have a broad repertoire of useful, socially learned behaviours. For example, there is evidence that human children preferentially copy individuals that they have observed being taught a behaviour over individuals who acquire the same behaviour asocially (Burdett et al. unpublished). If a chimpanzee has



not personally observed the manner in which a behaviour was learned, they may gravitate towards copying individuals who they know are more likely to learn socially. This is one way in which individual differences in social learning may influence not just the individual in question, but also most adaptive learning strategies for conspecifics. Whether or not chimpanzees are indeed more likely to learn from individuals that have a high proclivity for social learning has not yet been investigated. One way to explore this would be to revisit observation records from the individual studies which comprised the meta-data set analysed in **Chapter 4**, such as **Chapters 2 and 3**, to determine whether attendance is biased towards individuals, or categories of individuals, with a high average social learning score.

I speculated in **Chapter 2** that although individuals may be highly attentive towards dominant individuals (Kendal et al., 2015), the primary purpose for this attention may primarily be vigilance towards these often powerful and relatively dangerous individuals rather than learning new skills. If imitation, or at least some form of copying by matching, is a more sophisticated form of social learning (Whiten, McGuigan, Marshall-Pescini, & Hopper, 2009) than emulation (thereby having greater cognitive demands) then it may be more readily used in observations of subordinate models where attention can be entirely dedicated to the actions of the demonstrator rather than having to also be wary of signs of aggression in the case of dominant males. A more straightforward alternative explanation is simply that the method used by a demonstrator may often have been obscured by their body, meaning that observers had to get in close proximity in order to determine which direction they were moving the puzzle-box door. Consequently, it may be that subordinate individuals were easier to copy accurately because they were more socially tolerant (Van Schaik, Fragaszy, & Perry, 2003). The importance of social tolerance in social learning has been speculated about but there is little empirical work to support it either way. Lonsdorf, Ross, Linick, Milstein, and Melber (2009) argue that differences in tool-use behaviour between captive chimpanzees and

gorillas can be partially explained by differences in social tolerance and social structure. Similarly, Boose, White, and Meinelt (2013) found that chimpanzee tool-users typically had more individuals in close proximity to them than bonobos and therefore argue that tolerance may be key to transmission of these complex behaviours. However, other studies have found that bonobos are typically much more socially tolerant than chimpanzees in a feeding context, leading to greater success on cooperation tasks (Hare, Melis, Woods, Hastings, & Wrangham, 2007). It may therefore be that the differences in audience size identified by Lonsdorf et al. (2016) and Boose et al. (2013) can be more readily explained by interest in the task. Species who are less prone to tool use relative to chimpanzees are perhaps simply less likely to show an interest in this type of behaviour.

A further explanatory hypothesis for the lesser degree of social learning directed towards dominant models in **Chapter 2** might be that individuals purposefully avoid overlapping with the method demonstrated by a dominant individual, perhaps so as to avoid appearing to encroach on ‘their’ resource. Lonsdorf et al. (2016) found that capuchin monkeys who would demonstrate a behaviour in private which they had previously copied from a dominant individual, but were not willing to do so in a group context. This suggests that some primates may diverge from the behaviour of dominant individuals in certain contexts, perhaps to avoid aggression. However, in chimpanzees, Kaminski, Call, and Tomasello (2008) found that subordinate individuals did not avoid food that a more dominant individual had already seen in favour of eating a food that the dominant individual was unaware of. Indeed, **Chapter 3** of this thesis found that individuals were more likely to copy behaviours they had observed demonstrated by more dominant individuals within a group context. This suggests that an aversion to public demonstration of behaviours copied from dominant individuals, as identified in capuchins by Lonsdorf et al. (2016), does not explain the findings of **Chapter 2**.

Although **Chapter 2** demonstrated that captive chimpanzees readily copy subordinate individuals on a novel task, this may not be the scenario typically faced in wild contexts. Given a relatively stable environment, it is unlikely that an average wild chimpanzee will come across many novel ecological problems to solve. Any innovations are, therefore, likely to be different (possibly, but not necessarily, improved) methods of achieving goals for which there are already existing solutions. Several studies have argued that chimpanzees demonstrate a high degree of behavioural conservatism (Hopper et al., 2011; Hrubesch et al., 2009; Marshall-Pescini & Whiten, 2008), meaning that they are resistant to relinquishing their first-learned solution to a problem even after observing a better alternative. Davis, Vale, Schapiro, Lambeth, and Whiten (2016) found that some individuals were willing to relinquish a first-learned method to copy another but only when the efficiency of their original method became dramatically reduced. Similarly, Yamamoto, Humle, and Tanaka (2013) found that all of their (five) chimpanzee subjects were motivated to switch from their first-learned method of obtaining a juice reward to a more efficient technique.

In a turn of events unanticipated by our experimental design, **Chapter 2** offered further insight on chimpanzee behavioural flexibility. Two subordinate individuals (in different groups) innovated a method of opening the puzzle-box, so increasing their reward (two grapes instead of one). Subsequently, individuals who had already mastered one method of opening the box copied this improved method. This demonstrates that chimpanzees are not so conservative that variants on existing traditions that have an improved payoff will not spread. Contrary to the findings of Davis et al. (2016), it was not necessary for the pre-existing behaviour to become less efficient for an alternative to be copied. In this case, it was sufficient that the alternative behaviour had a greater payoff. In an even more extreme example, **Chapter 3** of this thesis found that individuals would even switch to *equally* efficient and rewarding behaviours after simply observing them in a group context. Taken together, these findings suggest that chimpanzees can be more

willing to relinquish pre-existing behaviour patterns than has previously been claimed. Unpacking the factors that promote or constrain this flexibility is likely to be a fruitful avenue of research. The type of task and therefore difficulty of learning a behaviour may be important here, as the studies of Hrubesch et al. (2009) and Marshall-Pescini and Whiten (2008), in which chimpanzees behaved conservatively, both utilised a tool-use paradigm. Conversely, the studies of **Chapter 2** (Watson et al., 2017), **Chapter 3** and Davis et al. (2016), in all of which individuals behaved somewhat flexibly, used puzzle-box paradigms that required only manual manipulation.

## **CHIMPANZEE SOCIAL LEARNING IS INFLUENCED BY SOCIAL CONTEXT**

In the research reported in **Chapter 2** I discovered that some chimpanzees are motivated to switch from a pre-existing behaviour to a more rewarding alternative. However some traditions recorded in wild populations, such as the ‘grass in ear’ behaviour described by Van Leeuwen, Cronin, and Haun (2014) do not have direct food-related payoff, so these behaviours are presumably rewarded on some other level. One possibility is that sharing behavioural repertoires serves as a way of facilitating social bonds by acting as an ‘in-group identifier’. As mentioned in my discussion of **Chapter 1**, there is evidence of such normatively motivated copying in humans (Carpenter et al., 2013; Van Baaren et al., 2004), but it is unknown whether it extends to other species. Curious about these possible social influences on chimpanzee social learning decisions, in **Chapter 3** I set out to determine whether chimpanzees were motivated to relinquish a pre-existing method of opening a puzzle-box in order to adopt an equally efficient, equally rewarding behaviour demonstrated by the majority of their group-mates. I refer to this as conformist behaviour (Haun & Tomasello, 2011; Whiten & Van Schaik, 2007), but it is worth noting that this term is used differently in some literature to describe the process of naïve individuals disproportionately copying the behaviour of a majority (Boyd & Richerson, 1988).

I investigated conformist behaviour in chimpanzees by training one individual in each of five groups on a method of opening a puzzle-box and all other individuals in the group on an alternative method, before bringing them together for five hours of open-diffusion, thereby creating a unanimous majority with an alternative behavioural preference to the minority individual. This was the 'Group' condition. Recent evidence for majority influence in animals has been critiqued for insufficiently ruling out the possibility that so-called 'conformist' individuals were simply copying individuals at random (Acerbi, Van Leeuwen, Haun, & Tennie, 2016; Van Leeuwen, Kendal, Tennie, & Haun, 2015). Therefore, I wanted to be able to control for random-copying as an explanation for any switching behaviour identified in the Group condition. Consequently, I ran a 'Dyad condition' in which a single individual was trained on both methods and then given access to the task with just one other individual. The idea behind this was that if chimpanzees sample and copy behaviours at random and there is only one individual present, then they would copy this individual. The Dyad condition also allowed me to explore whether observing a high frequency of demonstrations of an alternative behaviour was sufficient to motivate switching, since this has also been offered as a confounding explanation for conformity (Van Leeuwen & Haun, 2014; Van Leeuwen et al., 2015).

It was found that individuals in the Group condition were highly likely to switch to the behavioural preference of the majority. By contrast, only one out of ten individuals in the Dyad condition explored the alternative method. Moreover, this individual used the alternative method on just three trials before switching back to their first-learned method, making it a highly transient change in behaviour. However, complicating any inference regarding conformity was the fact that minority individuals in the group condition switched behaviour *before* sampling the behaviour of enough individuals to know what the majority behaviour was. Three individuals switched to the new method after observing two individuals demonstrate, and another switched after observing just one. Furthermore, the

number of observations individuals in the group condition made of the majority method were not significantly different from the number observed by individuals in the Dyad condition in their full hour of testing, therefore ruling out frequency bias as a simple explanation. However, three of the dyads were male-female pairs (all others were female-female). The finding of **Chapter 4** that, on average, male chimpanzees are less likely than females to use social learning means that these individuals may not make an appropriate comparison with the entirely female MIN-I. A refinement of the paradigm used in **Chapter 3** would be to use the same individuals in both Group and Dyad conditions – using different, but similar, puzzle boxes for each condition. This repeated measures design would help minimise the confound of individual differences and isolate the effect of interest.

I believe my finding in **Chapter 3**, that minority individuals switched behaviour before knowing the majority method, is best explained by the social context in which their observations took place since this is the only major remaining difference between the Group and Dyad conditions. The influence of social context is likely to be important in species with a fission-fusion social structure like chimpanzees, where individuals spend extended periods of time away from many members of their core group. When group composition is flexible, learning biases need to accommodate for this. This finding that individuals are more likely to use social information in a group context emphasises the value of open-diffusion paradigms in social learning studies. A further interesting example of context influencing the expression of socially learned behaviours is described by van de Waal, van Schaik, and Whiten (2017) which followed small groups of low-ranking female vervet monkeys after they permanently splintered from their larger natal groups. The original groups had been part of van de Waal et al.'s (2013) study in which groups were instilled with a preference for a particular colour of dyed corn by making one of two colours highly unpalatable through use of an additional ingredient. Eventually, the unpalatable ingredient was no longer added, but groups retained their original

preference. The subordinate individuals of van de Waal, van Schaik and Whiten (2017) had very limited access to the group-preferred colour and so often sampled the alternative (and similarly palatable) colour while part of that group. However, after a permanent fission event separated the subordinates from their natal group, they were offered both colours of corn again and demonstrated a 100% preference for the colour they themselves had previously eaten least, but was most preferred by their group. A further example of context having a powerful influence on the expression of socially learned behaviours is reported by Lonsdorf et al. (2016), who found that capuchin monkeys who would demonstrate a behaviour copied from a dominant individual in private, were not willing to do so in a group context. While four out of five minority individuals in **Chapter 3** were motivated to use the majority method while in the Group context, one never did. However, this individual did explore the alternative method during the two twenty-minute 'solo' sessions carried out after open-diffusion had finished, where no other individuals were present. This perhaps hints at individual differences in sensitivity to social context.

**Chapter 3** suggests that although it is not necessary to observe many individuals in a group context to motivate a change in behavioural preference, it is important that the behaviours observed are consistently of the same form. This is demonstrated by the fact that the majority individuals in **Chapter 3** almost never used the minority method, despite most of them having observed it a number of times. This draws something of a parallel with the findings of Van Leeuwen, Cronin, Schütte, Call, and Haun (2013). This study examined majority-influence on chimpanzee social learning in an open-diffusion paradigm similar to that of **Chapter 3**, except it used a token-exchange paradigm and minority *sub-groups* rather than individuals. It was found that neither majority nor minority sub-groups were motivated to switch to the alternative method until one of them was made to have a greater payoff than the other. I suspect that the lack of behavioural switching in the majority subjects from my own study and the minority sub-groups from

van Leeuwen et al (2013) can be partially explained by the fact that their first-learned behaviour was reinforced by observations of that same method.

Perhaps it should not be surprising that minority individuals in **Chapter 3** switched behaviours before observing the behaviour of the majority of individuals in their group. To do so would mean an extended period of foregoing access to the task and its rewards in order to acquire reliable information about the most prevalent behaviour. In a species where conformist behaviour is commonplace, an individual may draw accurate inferences about group behaviour patterns from sampling the behaviour of just a few individuals. In this case, the criterion to determine the best option to adopt is that all the behaviour sampled displays choice of one option, and not the other. In other words, that it is unanimous within the individuals sampled. Humans have been found to converge on perceived rather than properly sampled social norms (Rimal & Real, 2005; Terry, Hogg, & White, 1999), so the extent to which animals are capable or motivated to predict the behaviour of unseen individuals would be an interesting question for future study. Apes have already been found to be 'intuitive statisticians' able to generalise from populations to samples (Rakoczy et al., 2014), so exploring whether they and other animals can make inferences in the opposite direction would be a worthwhile endeavour. This issue of how animals draw inferences about group behaviour patterns is important for our understanding of how majority-influences on social learning are processed. Several critiques (Acerbi et al., 2016; Van Leeuwen & Haun, 2013, 2014; Van Leeuwen et al., 2015) of studies which argued to have demonstrated conformity in animals have emphasised the importance of recording observations during experiments to determine how much of their group each individual has actually sampled at any given time. The argument being that in order to demonstrate conformity one must prove that individuals have an understanding of what the majority behavioural preference is. For example, Aplin et al. (2015b) report that birds with pre-existing methods of opening a puzzle-box adopted the most frequently observed variant upon migrating to a new area. This



inference was criticised because the most frequently observed behaviour does not necessarily translate to being the majority preference in a community if, for example, three individuals demonstrate Method A once but a single individual demonstrates Method B seven times (Van Leeuwen et al., 2015). However, in a response to this critique, the original authors demonstrated that the 'conformist' birds had indeed also sampled an effective majority of demonstrators (Aplin et al., 2015b) and argued that that in most ecological contexts the two measures are likely to be functionally equivalent.

In the future it would be worthwhile to examine how the effect of social context identified in **Chapter 3** interacts with other learning biases. For example, it would be interesting to test whether the motivation to switch to a behaviour consistently observed in a group context (as in **Chapter 3**) is inhibited if this behaviour is less efficient or productive than the existing method. Van Leeuwen et al. (2013) found that chimpanzees adjust their behaviour to match observed behaviours with greater payoffs than pre-existing behaviours, so it would be interesting to find whether reduced payoffs can also inhibit behavioural flexibility. If a reduced payoff of the majority method were not found to inhibit copying behaviour in minority individuals, this would suggest that there is some payoff above and beyond the immediate food reward that motivates this switching. For example, social rewards such as increased prosocial behaviour, or decreased aggression, from those who share the behaviour. Vale, Davis, van de Waal, et al. (2017) found that chimpanzees who were trained to prefer one colour of food (by making the alternative colour taste unpalatable) and then introduced to a new group of chimpanzees who unanimously preferred the alternative colour did not consistently switch to the majority method (though it was explored more often than by control individuals). This is potentially explained by the negative valence that the majority-preferred food had during training (Vale, Davis, van de Waal, et al., 2017). In **Chapter 3**, none of the majority individuals persistently switched to the minority method (though a handful explored it). By contrast, great tits much more readily eschew behaviours adopted via conformity

(Aplin et al., 2015b) when switching to a more rewarding alternative (Aplin, Sheldon, & McElreath, 2017).

## **INDIVIDUAL DIFFERENCES IN CHIMPANZEE PROPENSITY FOR SOCIAL LEARNING**

While three out of five individuals in the minority condition in **Chapter 3** did consistently switch behaviours, one never did and another switched only temporarily. Within just these five individuals there was therefore a wide spectrum of individual variation. Such individual differences in social learning have been largely overlooked in favour of making broad, species-wide claims about learning processes (Mesoudi, Chang, Dall, & Thornton, 2016). Often, this may be due to practical constraints. Studies of great apes both in captivity and the wild are often limited in their sample size, so although individual variation may be common it is not easy to analyse statistically. In **Chapter 4** I collated data from 168 chimpanzees across 11 years of social learning experiments carried out at MD Anderson Cancer Research Center, Texas. I applied a binary scale to assess whether each individual in each study used social information or not. This allowed me to determine whether individuals demonstrated consistent individual differences in performance across multiple studies. I was also interested in which individual factors covaried with individuals being particularly likely or unlikely to use social information. I found that consistency in social information use was high across studies, showing that chimpanzees demonstrate individual differences in social learning that show a degree of consistency. The likelihood that an individual would have a high proclivity for social learning was predicted by the sex of the individual, with females being more likely to use social information. Somewhat unexpectedly, neither the age nor rearing history of an individual had an important effect on their social information use.

Theoretical analyses have found that social learners have higher fitness than asocial learners, but only if there are enough asocial learners to facilitate a good flow of

productive, reliable behaviours (Boyd & Richerson, 1988; Giraldeau, Valone, & Templeton, 2002; Rogers, 1988). The population is therefore expected to reach an equilibrium in levels of social and asocial learning (Barnard & Sibly, 1981; Rogers, 1988). There are a number of ways this equilibrium might be met. For example, individuals may be flexible in their use of social or asocial information – relying on the relatively ‘cheap’ process of social learning until it becomes less adaptive and then attempting to learn asocially instead. **Chapter 4** suggests that individual differences are another factor that might mediate this equilibrium. While sex was found to be a useful variable for predicting these differences, it is not clear why these sex differences would exist or what other life-history factors might contribute towards an individual’s propensity for social learning.

Sex differences in asocial learning, or innovation, have been identified in a range of species such as meerkats (Thornton & Samson, 2012), ruffed lemurs (Dean, Hoppitt, Laland, & Kendal, 2011) guppy fish (Laland & Reader, 1999) and primates (Reader & Laland, 2001). However, whether males or females are more prone to social learning is inconsistent across species and the factors influencing this are poorly understood. Sex differences in social learning have only so far been reported in a limited number of other animal species; chimpanzees (Lonsdorf, 2005) and tool-use behaviour in bottlenose dolphins (Mann & Sargeant, 2003) and human children (Flynn & Whiten, 2008). I make the point in **Chapter 4** that sex may simply be a proxy variable for other, unknown factors which may covary with sex (Maney, 2016) such as personality traits like neophilia, which have been linked to asocial learning (Day, Coe, Kendal, & Laland, 2003), dominance or hormonal differences. Personality data can be relatively fast and cheap to obtain and may provide further correlates of these cognitive abilities, so would be worthwhile including in future similar analyses. Brosnan et al. (2015) found that chimpanzees who scored highly on the ‘human-oriented’ personality trait were more likely to be reactive to inequity in rewards between themselves and another individual for performing the same behaviour. They suggest that this is because they were more responsive to being

'deceived' by the human experimenter. The relationships that captive animals develop with experimenters may have an important influence on social learning studies also. An individual who finds interactions with humans especially rewarding is likely to spend relatively more time in proximity to experiments, thereby increasing their opportunities for social and asocial learning on the task. All of the experiments collated in the data set used in **Chapter 4** used foraging behaviour as their focus, which is reflective of empirical studies of social learning more widely. Foraging-based paradigms have the advantage of being relatively straight-forward in design. However, foraging is just one of many domains of behaviour that are influenced through social learning. This is readily apparent in the fact that so many observational studies of social learning focus on non-foraging behaviours such as hand-clasp grooming in chimpanzees (Wrangham et al., 2016), or vocalisations such as highly complex, culturally transmitted whale song (Noad, Cato, Bryden, Jenner, & Jenner, 2000).

Making generalisations based on foraging behaviour and applying them to other domains is problematic. I therefore agree with Watson and Caldwell (2009) that it is important to begin broadening the range of methodologies employed in cultural transmission studies. This is challenging because introducing a novel behaviour to a group typically involves training at least one individual to repeat it, and most animal training paradigms are food-focussed. Moreover, foraging behaviours are easily identifiable (e.g. opening a puzzle box) and differentiated from one another (different methods of using a tool) relative to more subjective distinctions between, for example, two styles of grooming behaviour. Watson and Caldwell (2010) present one example of how this can be achieved. In this study, recordings of affiliative and agonistic vocalisations were played back to marmosets as though coming from a neighbouring group. It was found that the marmosets experienced social contagion in response to these vocalisations, displaying more aggressive or affiliative behaviours after each

corresponding playback. It would be interesting to examine whether prolonged exposure to the positive stimuli could cause a persistent cultural change in pro-sociality.

**Chapter 3** demonstrated that the social context in which experiments take place can be an important factor in determining whether individuals use social information. Consequently, not only would it be prudent to control for this in future analyses similar to that of **Chapter 4** (e.g. by using social context as a random effect in models), but it would also be interesting to examine whether there is individual variation in how chimpanzees respond to these context effects. For example, if Individual A has participated in many experiments then this may result in them habituating more quickly to unusual social contexts (such as the Dyad condition from **Chapter 3**) compared to Individual B, who has relatively little research experience. This could result in Individual A being more relaxed than Individual B and, consequently, be more willing to explore alternative behaviours in these contexts, even if they behave similarly to Individual B in a group setting.

Sapolsky and Share (2004) also reported cultural changes in levels of aggression after tuberculosis resulted in the deaths of many dominant males in a group of baboons, leaving behind only less aggressive males. This resulted in a change towards a more 'pacific' culture which persisted for at least a decade and was even transmitted to new males who migrated to the group. These sort of cultural changes are interesting because they do not meet the appearance of the types of traditions typically examined in social learning studies (the spread of a novel behaviour through a group). Instead, they are the result of changes in the occurrence of a large package of pre-existing behaviour patterns (grooming, tolerance, food-sharing to name a few) which contribute towards an overall 'zeitgeist' for the group. Examining factors that can result in cultural changes in cooperation, pro-sociality and tolerance would be extremely interesting as it may shed light on similar processes that are proposed to have occurred in the human lineage (Henrich, 2015)

It was not possible to determine whether the individuals who consistently achieved a high social information score in **Chapter 4** demonstrated a greater *motivation* or *capability* for social learning than their peers. For example, in experiments with tasks that involved complex tool-use (Price, Lambeth, Schapiro, & Whiten, 2009; Vale, Davis, Lambeth, Schapiro, & Whiten, 2017), individuals who were motivated to socially learn may not have been able to successfully complete the task due to either not understanding which of the demonstrator's actions were causally relevant, or by lacking the necessary manual dexterity to recreate them. Consequently, it would be interesting to see if individuals who consistently scored highly on our measure of social information use would also do so on other cognitive tests, such as the Primate Cognitive Test Battery (Hopkins, Russell, & Schaeffer, 2014). Alternatively, studies examining asocial learning carried out at our study site could be developed into a dataset similar to the one used here. This could then be used firstly to examine individual differences in asocial learning, but also to investigate whether there is a correlation between individuals' social and asocial learning abilities. If social learning and general intelligence or asocial learning were to covary, this may support claims that social learning depends largely on domain-general cognitive processes (Heyes, 2016).

## **CONCLUDING REMARKS**

Throughout more of the animal kingdom than was suspected a few decades ago, cultural transmission has provided a 'second inheritance system' (Whiten, Ayala, Feldman, & Laland, 2017) which works both in tandem with, in addition to or in interaction with genetic inheritance, the latter a process known as 'gene-culture coevolution'. As one of the most culturally varied species (Whiten et al., 1999, 2001), chimpanzees have provided a logical focal point for much research into the processes and mechanisms that underpin social learning. This thesis has attempted to shed further light on these processes. I found that chimpanzees will readily learn novel behaviours seeded in their

group by subordinate females, suggesting that rank-bias in social learning does not constrain the diffusion of novel foraging behaviours. Second, while investigating conformist behaviour I found that chimpanzees were highly motivated to give up a pre-existing method of opening a puzzle-box in order to adopt an equally rewarding method observed in a group context. However, adoption of novel methods occurred after observing only one or two individuals demonstrate the behaviour. This finding is suggestive of either a potent audience effect on the social learning decisions of individuals, or that chimpanzees are able to make inferences about the distribution of a behaviour based on a limited sample, thereby eliciting a pre-emptively conformist response. Finally, through a form of 'meta-analysis' of a data set incorporating 16 studies carried out at the same study site, I found that chimpanzees demonstrated strong and significantly consistent individual differences in their motivation to use social information. Individuals who socially learned in one study were likely to do so in others, and vice versa. Sex was a predictor of whether an individual was likely to have a high proclivity for social learning, with females using social information more often than males. Age, rearing history and research experience were not found to have an important effect – suggesting that this proclivity for social information use is a trait that may be fixed quite early in life and remains stable. In summary, model biases, contextual influence and individual differences all interact and play critical roles in the transmission of social information in chimpanzees and the complex cultural lives they lead.

## REFERENCES

- Acerbi, A., Van Leeuwen, E. J., Haun, D. B., & Tennie, C. (2016). Conformity cannot be identified based on population-level signatures. *Scientific Reports*, 6.
- Aplin, L. M., Farine, D. R., Morand-Ferron, J., Cockburn, A., Thornton, A., & Sheldon, B. C. (2015a). Counting conformity: evaluating the units of information in frequency-dependent social learning. *Animal Behaviour*, 110, e5-e8.
- Aplin, L. M., Farine, D. R., Morand-Ferron, J., Cockburn, A., Thornton, A., & Sheldon, B. C. (2015b). Experimentally induced innovations lead to persistent culture via conformity in wild birds. *Nature*, 518(7540), 538-541.
- Aplin, L. M., Sheldon, B. C., & McElreath, R. (2017). Conformity does not perpetuate suboptimal traditions in a wild population of songbirds. *Proceedings of the National Academy of Sciences*, 114(30), 7830-7837.
- Barnard, C. J., & Sibly, R. M. (1981). Producers and scroungers: a general model and its application to captive flocks of house sparrows. *Animal Behaviour*, 29(2), 543-550.
- Boose, K. J., White, F. J., & Meinelt, A. (2013). Sex differences in tool use acquisition in bonobos (*Pan paniscus*). *American Journal of Primatology*, 75(9), 917-926.
- Boyd, R., & Richerson, P. J. (1988). *Culture and the evolutionary process*: University of Chicago Press.
- Brosnan, S. F., Hopper, L. M., Richey, S., Freeman, H. D., Talbot, C. F., Gosling, S. D., . . . Schapiro, S. J. (2015). Personality influences responses to inequity and contrast in chimpanzees. *Animal Behaviour*, 101, 75-87.
- Burdett, E. R. R., McGuigan, N., Harrison R., Whiten, A. (unpublished). The interaction of social and perceivable causal factors in shaping 'over-imitation'.
- Carpenter, M., Uebel, J., & Tomasello, M. (2013). Being mimicked increases prosocial behavior in 18-month-old infants. *Child Development*, 84(5), 1511-1518.



- Cowlshaw, G., & Dunbar, R. I. (1991). Dominance rank and mating success in male primates. *Animal Behaviour*, 41(6), 1045-1056.
- Davis, S. J., Vale, G. L., Schapiro, S. J., Lambeth, S. P., & Whiten, A. (2016). Foundations of cumulative culture in apes: improved foraging efficiency through relinquishing and combining witnessed behaviours in chimpanzees (*Pan troglodytes*). *Scientific Reports*, 6.
- Day, R. L., Coe, R. L., Kendal, J. R., & Laland, K. N. (2003). Neophilia, innovation and social learning: a study of intergeneric differences in callitrichid monkeys. *Animal Behaviour*, 65(3), 559-571.
- Dean, L. G., Hoppitt, W., Laland, K. N., & Kendal, R. L. (2011). Sex ratio affects sex-specific innovation and learning in captive ruffed lemurs (*Varecia variegata* and *Varecia rubra*). *American Journal of Primatology*, 73(12), 1210-1221.
- Dindo, M., Leimgruber, K., Ahmed, R., Whiten, A., & de Waal, F. (2011). Observer choices during experimental foraging tasks in brown capuchin monkeys (*Cebus apella*). *American Journal of Primatology*, 73(9), 920-927.
- Flynn, E., & Whiten, A. (2008). Cultural transmission of tool use in young children: A diffusion chain study. *Social Development*, 17(3), 699-718.
- Flynn, E., & Whiten, A. (2012). Experimental "microcultures" in young children: Identifying biographic, cognitive, and social predictors of information transmission. *Child Development*, 83(3), 911-925.
- Giraldeau, L. A., Valone, T. J., & Templeton, J. J. (2002). Potential disadvantages of using socially acquired information. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 357(1427), 1559-1566.
- Hare, B., Melis, A. P., Woods, V., Hastings, S., & Wrangham, R. (2007). Tolerance allows bonobos to outperform chimpanzees on a cooperative task. *Current Biology*, 17(7), 619-623.
- Haun, D. B., & Tomasello, M. (2011). Conformity to peer pressure in preschool children. *Child Development*, 82(6), 1759-1767.

- Henrich, J. (2015). *The secret of our success: how culture is driving human evolution, domesticating our species, and making us smarter*. Princeton University Press.
- Heyes, C. (2016). Blackboxing: social learning strategies and cultural evolution. *Phil. Trans. R. Soc. B*, 371(1693), 20150369.
- Hopkins, W. D., Russell, J. L., & Schaeffer, J. (2014). Chimpanzee intelligence is heritable. *Current Biology*, 24(14), 1649-1652.
- Hopper, L. M., Schapiro, S. J., Lambeth, S. P., & Brosnan, S. F. (2011). Chimpanzees' socially maintained food preferences indicate both conservatism and conformity. *Animal Behaviour*, 81(6), 1195-1202.
- Horner, V., Proctor, D., Bonnie, K. E., Whiten, A., & de Waal, F. B. (2010). Prestige affects cultural learning in chimpanzees. *PloS One*, 5(5).
- Hrubesch, C., Preuschoft, S., & van Schaik, C. (2009). Skill mastery inhibits adoption of observed alternative solutions among chimpanzees (*Pan troglodytes*). *Animal Cognition*, 12(2), 209-216.
- Kaminski, J., Call, J., & Tomasello, M. (2008). Chimpanzees know what others know, but not what they believe. *Cognition*, 109(2), 224-234.
- Kendal, R. L., Hopper, L. M., Whiten, A., Brosnan, S. F., Lambeth, S. P., Schapiro, S. J., & Hoppitt, W. (2015). Chimpanzees copy dominant and knowledgeable individuals: implications for cultural diversity. *Evolution and Human Behavior*, 36(1), 65-72.
- Laland, K. N., & Reader, S. M. (1999). Foraging innovation in the guppy. *Animal Behaviour*, 57(2), 331-340.
- Lonsdorf, E. V. (2005). Sex differences in the development of termite-fishing skills in the wild chimpanzees, *Pan troglodytes schweinfurthii*, of Gombe National Park, Tanzania. *Animal Behaviour*, 70(3), 673-683.
- Lonsdorf, E. V., Bonnie, K., Grim, M., Krupnick, A., Prestipino, M., & Whyte, J. (2016). Seeding an arbitrary convention in capuchin monkeys: The effect of social context. *Behaviour*, 153(5), 633-654.

- Lonsdorf, E. V., Ross, S., Linick, S., Milstein, M., & Melber, T. (2009). An experimental, comparative investigation of tool use in chimpanzees and gorillas. *Animal Behaviour*, *77*(5), 1119-1126.
- Maney, D. L. (2016). Perils and pitfalls of reporting sex differences. *Phil. Trans. R. Soc. B*, *371*(1688), 20150119.
- Mann, J., & Sargeant, B. (2003). Like mother, like calf: the ontogeny of foraging traditions in wild Indian Ocean bottlenose dolphins (*Tursiops* sp.). *The biology of traditions: Models and evidence*, 236-266.
- Marshall-Pescini, S., & Whiten, A. (2008). Chimpanzees (*Pan troglodytes*) and the question of cumulative culture: an experimental approach. *Animal Cognition*, *11*(3), 449-456.
- McGuigan, N. (2013). The influence of model status on the tendency of young children to over-imitate. *Journal of Experimental Child Psychology*, *116*(4), 962-969.
- Mesoudi, A., Chang, L., Dall, S. R., & Thornton, A. (2016). The evolution of individual and cultural variation in social learning. *Trends in Ecology & Evolution*, *31*(3), 215-225.
- Nicol, C., & Pope, S. (1999). The effects of demonstrator social status and prior foraging success on social learning in laying hens. *Animal Behaviour*, *57*(1), 163-171.
- Nishida, T., Matsusaka, T., & McGrew, W. C. (2009). Emergence, propagation or disappearance of novel behavioral patterns in the habituated chimpanzees of Mahale: a review. *Primates*, *50*(1), 23-36.
- Noad, M. J., Cato, D. H., Bryden, M., Jenner, M.-N., & Jenner, K. C. S. (2000). Cultural revolution in whale songs. *Nature*, *408*(6812), 537-537.
- Price, E. E., Lambeth, S. P., Schapiro, S. J., & Whiten, A. (2009). A potent effect of observational learning on chimpanzee tool construction. *Proceedings of the Royal Society of London B: Biological Sciences*, *276*(1671), 3377-3383.
- Rakoczy, H., Clüver, A., Saucke, L., Stoffregen, N., Gräbener, A., Migura, J., & Call, J. (2014). Apes are intuitive statisticians. *Cognition*, *131*(1), 60-68.

- Reader, S. M., & Laland, K. N. (2001). Primate innovation: sex, age and social rank differences. *International Journal of Primatology*, 22(5), 787-805.
- Reader, S. M., & Laland, K. N. (2003). *Animal innovation* (Vol. 10): Oxford University Press Oxford.
- Rimal, R. N., & Real, K. (2005). How behaviors are influenced by perceived norms a test of the theory of normative social behavior. *Communication Research*, 32(3), 389-414.
- Rogers, A. R. (1988). Does biology constrain culture? *American Anthropologist*, 90(4), 819-831.
- Sapolsky, R. M., & Share, L. J. (2004). A pacific culture among wild baboons: its emergence and transmission. *PLoS Biology*, 2(4), e106.
- Terry, D. J., Hogg, M. A., & White, K. M. (1999). The theory of planned behaviour: self-identity, social identity and group norms. *British Journal of Social Psychology*, 38(3), 225-244.
- Thornton, A., & Samson, J. (2012). Innovative problem solving in wild meerkats. *Animal Behaviour*, 83(6), 1459-1468.
- Vale, G. L., Davis, S. J., Lambeth, S. P., Schapiro, S. J., & Whiten, A. (2017). Acquisition of a socially learned tool use sequence in chimpanzees: Implications for cumulative culture. *Evolution and Human Behavior*, 38(5), 635-644.
- Vale, G. L., Davis, S. J., van de Waal, E., Schapiro, S. J., Lambeth, S. P., & Whiten, A. (2017). Lack of conformity to new local dietary preferences in migrating captive chimpanzees. *Animal Behaviour*, 124, 135-144.
- Van Baaren, R. B., Holland, R. W., Kawakami, K., & Van Knippenberg, A. (2004). Mimicry and prosocial behavior. *Psychological Science*, 15(1), 71-74.
- van de Waal, E., Borgeaud, C., & Whiten, A. (2013). Potent social learning and conformity shape a wild primate's foraging decisions. *Science*, 340(6131), 483-485.

- van de Waal, E., van Schaik, C. P., & Whiten, A. (2017). Resilience of experimentally seeded dietary traditions in wild vervets: Evidence from group fissions. *American Journal of Primatology*.
- Van Leeuwen, E. J., Cronin, K. A., & Haun, D. B. (2014). A group-specific arbitrary tradition in chimpanzees (*Pan troglodytes*). *Animal Cognition*, 17(6), 1421-1425.
- Van Leeuwen, E. J., Cronin, K. A., Schütte, S., Call, J., & Haun, D. B. (2013). Chimpanzees (*Pan troglodytes*) flexibly adjust their behaviour in order to maximize payoffs, not to conform to majorities. *PLoS One*, 8(11), e80945.
- Van Leeuwen, E. J., & Haun, D. B. (2013). Conformity in nonhuman primates: fad or fact? *Evolution and Human Behavior*, 34(1), 1-7.
- Van Leeuwen, E. J., & Haun, D. B. (2014). Conformity without majority? The case for demarcating social from majority influences. *Animal Behaviour*, 96, 187-194.
- Van Leeuwen, E. J., Kendal, R. L., Tennie, C., & Haun, D. B. (2015). Conformity and its look-a-likes. *Animal Behaviour*, 110, e1-e4.
- Van Schaik, C. P., Fragaszy, D., & Perry, S. (2003). Local traditions in orangutans and chimpanzees: social learning and social tolerance. *The biology of traditions: Models and evidence*, 297-328.
- Watson, C. F., & Caldwell, C. A. (2009). Understanding behavioral traditions in primates: Are current experimental approaches too focused on food? *International Journal of Primatology*, 30(1), 143-167.
- Watson, C. F., & Caldwell, C. A. (2010). Neighbor effects in marmosets: social contagion of agonism and affiliation in captive *Callithrix jacchus*. *American Journal of Primatology*, 72(6), 549-558.
- Watson, S. K., Reamer, L. A., Mareno, M. C., Vale, G. L., Harrison, R. A., Lambeth, S. P., . . . Whiten, A. (2017). Socially transmitted diffusion of a novel behaviour from subordinate chimpanzees. *American Journal of Primatology*, 9999; e22642.

- Whiten, A., Ayala, F. J., Feldman, M. W., & Laland, K. N. (2017). The extension of biology through culture. *Proceedings of the National Academy of Sciences*, 114(30), 7775-7781.
- Whiten, A., Goodall, J., McGrew, W. C., Nishida, T., Reynolds, V., Sugiyama, Y., . . . Boesch, C. (1999). Cultures in chimpanzees. *Nature*, 399(6737), 682-685.
- Whiten, A., Goodall, J., McGrew, W. C., Nishida, T., Reynolds, V., Sugiyama, Y., . . . Boesch, C. (2001). Charting cultural variation in chimpanzees. *Behaviour*, 138(11), 1481-1516.
- Whiten, A., McGuigan, N., Marshall-Pescini, S., & Hopper, L. M. (2009). Emulation, imitation, over-imitation and the scope of culture for child and chimpanzee. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 364(1528), 2417-2428.
- Whiten, A., & Van Schaik, C. P. (2007). The evolution of animal 'cultures' and social intelligence. *Philosophical Transactions of the Royal Society of London B: Biological Sciences*, 362(1480), 603-620.
- Wrangham, R. W., Koops, K., Machanda, Z. P., Worthington, S., Bernard, A. B., Brazeau, N. F., . . . Otali, E. (2016). Distribution of a Chimpanzee Social Custom Is Explained by Matrilineal Relationship Rather Than Conformity. *Current Biology*, 26(22), 3033-3037.
- Yamamoto, S., Humle, T., & Tanaka, M. (2013). Basis for cumulative cultural evolution in chimpanzees: social learning of a more efficient tool-use technique. *PLoS One*, 8(1), e55768.

## APPENDIX A – ETHICAL APPROVAL



University of St Andrews

School of Psychology & Neuroscience Ethics Committee

23 December 2014

<b>Project Title:</b>	Social learning biases in chimpanzees
<b>Researcher's Name:</b>	Stuart Watson
<b>Supervisor:</b>	Professor Andrew Whiten

Thank you for submitting your application for amendment which was considered at the Psychology & Neuroscience School Ethics Committee meeting on 16<sup>th</sup> December 2014. The following documents were reviewed:

1. Application for change(s) to a School Ethics Committee Form 16/12/2014
2. Amended Animal Ethics Form 16/12/2014

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

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

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

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

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

Yours sincerely

fp

Convenor of the School Ethics Committee

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

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

# APPENDIX B – PUBLISHED WATSON ET AL. (2017)

Received: 9 September 2016 | Revised: 14 December 2016 | Accepted: 17 January 2017

DOI 10.1002/ajp.22642

## RESEARCH ARTICLE

WILEY AMERICAN JOURNAL OF PRIMATOLOGY

## Socially transmitted diffusion of a novel behavior from subordinate chimpanzees

Stuart K. Watson<sup>1</sup> | Lisa A. Reamer<sup>2</sup> | Mary Catherine Marenò<sup>2</sup> | Gillian Vale<sup>1,2</sup> | Rachel A. Harrison<sup>1</sup> | Susan P. Lambeth<sup>2</sup> | Steven J. Schapiro<sup>2,3</sup> | Andrew Whiten<sup>1</sup>

<sup>1</sup>Centre for Social Learning and Cognitive Evolution, and Scottish Primate Research Group, School of Psychology and Neuroscience, University of St Andrews, St Andrews, UK

<sup>2</sup>National Centre for Chimpanzee Care, Michale E. Keeling Centre for Comparative Medicine and Research, Department of Veterinary Sciences, UT MD Anderson Cancer Center, Bastrop, Texas

<sup>3</sup>Department of Experimental Medicine, University of Copenhagen, Denmark

### Correspondence

Prof. Andrew Whiten, Centre for Social Learning and Cognitive Evolution, and Scottish Primate Research Group, School of Psychology and Neuroscience, University of St Andrews, St Mary's Quad, South Street, St Andrews, KY16 9JP, UK.

Email: aw2@st-andrews.ac.uk

### Funding information

The John Templeton Foundation, Grant number: ID40128; NIH Cooperative Agreement, Grant number: U42 OD-011197

Chimpanzees (*Pan troglodytes*) demonstrate much cultural diversity in the wild, yet a majority of novel behaviors do not become group-wide traditions. Since many such novel behaviors are introduced by low-ranking individuals, a bias toward copying dominant individuals ("rank-bias") has been proposed as an explanation for their limited diffusion. Previous experimental work showed that chimpanzees (*Pan troglodytes*) preferentially copy dominant over low-rank models. We investigated whether low ranking individuals may nevertheless successfully seed a beneficial behavior as a tradition if there are no "competing" models. In each of four captive groups, either a single high-rank (HR,  $n = 2$ ) or a low-rank (LR,  $n = 2$ ) chimpanzee model was trained on one method of opening a two-action puzzle-box, before demonstrating the trained method in a group context. This was followed by 8 hr of group-wide, open-access to the puzzle-box. Successful manipulations and observers of each manipulation were recorded. Barnard's exact tests showed that individuals in the LR groups used the seeded method as their first-choice option at significantly above chance levels, whereas those in the HR groups did not. Furthermore, individuals in the LR condition used the seeded method on their first attempt significantly more often than those in the HR condition. A network-based diffusion analysis (NBDA) revealed that the best supported statistical models were those in which social transmission occurred *only* in groups with subordinate models. Finally, we report an innovation by a subordinate individual that built cumulatively on existing methods of opening the puzzle-box and was subsequently copied by a dominant observer. These findings illustrate that chimpanzees are motivated to copy rewarding novel behaviors that are demonstrated by subordinate individuals and that, in some cases, social transmission may be constrained by high-rank demonstrators.

### KEYWORDS

chimpanzee, culture, dominance, rank, social learning

## 1 | INTRODUCTION

It is now generally accepted that social learning is widespread in the animal kingdom and that socially transmitted traditions ("cultures") are found in a wide range of vertebrates (Laland & Galef, 2009; Laland & Janik, 2006; Whiten, 2005). However, the processes by which a novel behavior propagates to become a group-wide tradition remain unclear (Rendell et al., 2011). Indiscriminately copying the behaviors of

conspecifics is often not an optimal strategy, as the learner runs the risk of copying costly behaviors or wasting energy on those that are not productive (Kendal, Coolen, Van Bergen, & Laland, 2005; Rendell et al., 2010). Accordingly, a number of adaptive "biases" in social learning have been proposed as possible influences on whether individuals choose to utilize social information and who they get it from, for example "when uncertain, copy the majority" (Claidière & Whiten, 2012; Henrich & McElreath, 2003; Laland, 2004;



Van Leeuwen & Haun, 2014). Due to their cultural diversity (Whiten et al., 1999) and propensity for social learning, chimpanzees have been a favored model species for studying these social learning biases. Chimpanzees also present an interesting paradox in that although innovations are not an uncommon occurrence, at one field site where researchers made an attempt to quantify their fate, it was found that a majority of innovations failed to become group-wide traditions (Nishida, Matsusaka, & McGrew, 2009). The factors that determine whether a novel behavior diffuses throughout a group or remains limited to one or a minority of individuals are largely unknown. The direct pay-off of a behavior does not seem sufficient to explain this, given reported instances of the spread of "arbitrary" traditions with no apparent functional benefits. A striking example of this is described by Van Leeuwen, Cronin, and Haun (2014), who report a single chimpanzee placing a piece of grass in its ear to no discernible benefit—a "fashion" which was soon adopted by the rest of the group. Conversely, Hopper, Schapiro, Lambeth, and Brosnan (2011) found in a token-exchange task that most chimpanzees chose the same tokens as those selected by a trained model, even when the alternative token choice resulted in a more preferred food reward, presenting an interesting example of copying a behavior which is visibly less beneficial than alternatives.

Many novel behaviors enter both wild and captive chimpanzee communities through the lower end of the dominance hierarchy—whether this be from subordinate innovators (Reader & Laland, 2001) or migrant females importing their native behavioral repertoire to their host group (Nakamura & Uehara, 2004; O'Malley, Wallauer, Murray, & Goodall, 2012). A bias toward copying dominant over subordinate individuals has been shown and proposed to explain the relative rarity of these novel behaviors becoming traditions (Kendal et al., 2015). One might suppose that this would occur for strategic reasons (dominant individuals are successful, so copying them might be an adaptive option), due to normative effects (copying the dominant individual facilitates social cohesion), or simply as a result of an attentional bias towards these individuals (e.g., dominant individuals are central in the social network). In capuchin monkeys, it has been found that subordinate individuals tend not to demonstrate acquired token-exchange behaviors in a group context (Addessi, Mancini, Crescimbene, & Visalberghi, 2011) or in the presence of a dominant individual (Lonsdorf et al., 2016), which means there is an inherent rank-bias in the source of social information available to observers. Although it has also been found that capuchins preferentially observe older, more dominant, and more proficient nut-crackers in the wild, suggesting a more active learning bias (Coelho et al., 2015). One or all of these may play a part in restricting the flow of social information from subordinate individuals and cause a group-wide convergence on the behavior of dominant individuals. To date, two studies have offered evidence for a rank-bias in chimpanzees. Kendal et al. (2015) seeded a method of opening a two-action puzzle box into two groups of chimpanzees using mid-ranking female models (and allowed two other groups to explore the task without trained models), and through complex analysis of attention states during demonstrations found evidence that individuals preferentially attend to dominant and/or knowledgeable demonstrators. Horner, Proctor, Bonnie, Whiten, and

de Waal (2010) also concluded that, when presented with demonstrations from both a "high prestige" (high rank and track record as a model) and "low prestige" (low rank) individual on a token-exchange task, chimpanzees preferentially copied the method demonstrated by the high prestige individual (Horner et al., 2010). However, there remains the question of whether or not low-ranking individuals, who demonstrate a productive novel behavior, will be copied if there are no more dominant models available. This question is important for our understanding of how innovations become traditions, and how traditions proliferate across communities.

Accordingly, we compared the diffusion of alternative methods of opening a two-action puzzle-box seeded by either a low- (female) or high-ranking (male) individual in four different groups of chimpanzees. In this context, based on prior work indicating a rank-bias in chimpanzee social learning, we predicted that either (a) social transmission of the seeded method will *only* occur in the groups with high-ranking models (we shall call this the "*hard* rank-bias hypothesis"); or (b) behavior will be socially transmitted in *both* conditions, but the effect will be stronger in groups with high-ranking models ("*soft* rank-bias hypothesis").

## 2 | METHODS

### 2.1 | Study site

This study was carried out at the National Center for Chimpanzee Care (NCCC) located at the Michale E. Keeling Center for Comparative Medicine and Research of The University of Texas MD Anderson Cancer Center in Bastrop (UTMDACC), Texas. Data were collected between April and August, 2015. A total of 38 chimpanzees (21 female) participated in the study, aged from 13 to 53 years of age. Most individuals were captive-born, but some ( $n = 5$ ) were wild-born. All individuals have participated in a wide range of previous behavioral research studies, some of which included puzzle-box tasks, but we have designed our apparatus to require different manipulations to those of earlier studies, as noted below. The participants include both nursery-reared and mother-reared individuals. Following previous studies (Hopper, Kurtycz, Ross, & Bonnie, 2015; Horner et al., 2010; Kendal et al., 2015), the social rank of each individual was determined by surveying the judgments of five staff members (behavioral researchers, trainers, and management) who had been working with these animals for at least 5 years each. Freeman et al. (2013) found that human assessment of dominance in chimpanzees has good predictive validity for relevant behavioral measures of dominance such as aggression and displacement. Each staff member was asked to rank the individuals in the group linearly from "1" (highest rank) to N (lowest rank) without discussing their rankings with other staff. Agreement between observers was high (>80%), but where disagreements occurred the mode rank for each individual was used. From these rankings, we determined the "alpha" male for each group in the HR condition and chose a subordinate (averaging in the lower third of the hierarchy) female to act as the model for each group in the LR condition. All groups have access to two or more den areas

(14 m<sup>2</sup> each) and either an outdoor habitat or dome (dome: 90 m<sup>2</sup>, habitat: 400 m<sup>2</sup>) with a range of enrichment devices and activities, and a variety of climbing and swinging structures to promote species-typical behaviors. Testing generally occurred indoors, but access to outdoor enclosures was not restricted. The full demographic and housing information for each participating individual can be found in Table 1. Ethical approval for this study was granted by the School of Psychology and Neuroscience at the University of St. Andrews and the IACUC of UTM DACC, adhering to all the legal requirements of US law and the American Society of Primatologists' principles for the ethical treatment of non-human primates. All subjects voluntarily participated in the testing procedures.

## 2.2 | Apparatus

This study employed a two-action, sliding-door puzzle-box (the "Vert," see Figure 1), a vertical variation we designed to require different actions to those common to earlier social learning studies (Aplin et al., 2015; Hopper, Lambeth, Schapiro, & Whiten, 2008; Kendal et al., 2015).

Sessions were recorded using a Panasonic HC-X920 video camera. All videos were coded using BORIS (Friard & Gamba, 2016), Version 2.05 ([www.http://penelope.unibo.it/boris](http://penelope.unibo.it/boris)). All analyses were carried out using R Statistical Package Version 3.2.3 (R Core Team, 2015) with R Studio Version 0.99.491 (RStudio Team, 2015).

## 2.3 | Procedure

For Condition LR (low-rank), in two groups ( $n = 6, 7$ ), a low-ranking female individual was voluntarily separated and trained to open the door by either sliding the door up or down. Likewise in the HR (high-rank) condition, the dominant male of each of two groups ( $n = 5, 5$ ) was trained on a method of opening the Vert. Females were used for Condition LR and males for Condition HR to maximize the rank disparity between these individuals. Since males are almost always of higher social rank than females in chimpanzee communities, in some groups it would not have been possible to select a high-ranking female to act as a model. However, Kendal et al. (2015) found no bias in whether male or female chimpanzees were preferentially attended to during their experiments, so we would not anticipate sex acting as a confound here. Nevertheless, below we include an analysis of audience sizes during demonstrations of the present study in order to explore whether males and females may differently tolerate observers. LR and HR conditions differed only in the choice of model.

Training began by presenting the baited Vert to the test subject with one of the slide-directions locked so it could not be used. Once a reward had been retrieved successfully 10 times in a row, the alternative method was unlocked and baited for all further trials. Models were considered to be "trained" once they completed a total of 30 sequential uses of the trained method without deviation.

After being trained, the model was reintroduced to the group and given access to the Vert in a group context. Two 20-min demonstration sessions were carried out on subsequent days, during which only the model had access to the box. The Vert was gently pulled out of reach if another individual displaced the model. This was to ensure a

roughly equal number of demonstrations between dominant and subordinate models and make the methods comparable with previous work on rank-bias and social learning (Hopper, Lambeth, Schapiro, & Whiten, 2015; Horner et al., 2010; Kendal et al., 2015).

The demonstration period was followed by 8 hr of open-diffusion in which unrestricted access to the Vert was provided. Open-diffusion occurred across multiple sessions, typically of 60 min but varying between 45 min (due to unforeseen interruptions), and 120 min in length (group HR2 had an unavoidably condensed test period, resulting in longer sessions to make up time).

Once any individual in the demonstration or open-diffusion phase had retrieved a reward, the Vert was withdrawn 1 m, the door was reset and the reward chamber re-baited. When re-setting the door, the Vert was covered with a cloth to avoid possible directional cues from the experimenter.

To determine whether an inherent directional bias may have influenced which method individuals from experimental groups chose to use, 15 individuals were selected from non-experimental groups to participate in an asocial control condition. Individuals were selected based on advice from care staff about their willingness to voluntarily separate from the group and engage with research procedures. Individuals separated voluntarily from their group and were then presented with the Vert for a period of 20 min, each. Both reward chambers were baited and both methods of opening the door were unlocked. If an individual completed a successful manipulation of the Vert, the Vert was reset and baited as described above.

## 2.4 | Statistical analyses

We used binomial tests to determine whether the number of individuals in the control condition to use each method on their first trial differed significantly from chance (50%), which would indicate an inherent directional bias that would have acted as a confound. We then used Barnard's exact test, an alternative to Fisher's exact test with greater power for small sample sizes (Mehta & Senchaudhuri, 2003), to test whether individuals from high- or low-rank conditions were significantly more likely to use the seeded method on their first successful trial. Binomial tests were subsequently used to determine whether the proportion of individuals in each condition who used the seeded method on their first successful trial differed significantly from chance (50%). Finally, we applied the same tests to a more conservative, truncated form of the experimental data set. In order to mitigate the possibility that individuals had learned from individuals not of direct interest to the research question, for example a dominant female who had socially learned the same method as the subordinate model, we only analyzed data (for this analysis only) from individuals in both conditions who had *only* observed their group's model demonstrating. This resulted in 11 individuals being excluded from this model, leaving  $n = 8$ . We also carried out Bayesian equivalents of the analyses described above, which can be found in the Supplemental Material by an interested reader and which were consistent with the findings reported below.

**TABLE 1** Demographic information for all participating individual

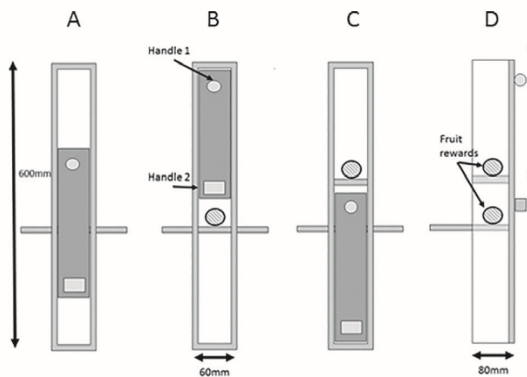
ID	Condition	Sex	Wild born?	DOB	Rearing	Housing
RAD	LR (1)	M	N	01/14/1990	Mother	Habitat
ANG*	LR (1)	F	Y	01/01/1975	Unknown	Habitat
CHE	LR (1)	F	N	12/09/1990	Nursery	Habitat
KIH	LR (1)	F	N	08/06/1988	Nursery	Habitat
MAH	LR (1)	M	N	10/26/1988	Mother	Habitat
NAH	LR (1)	F	N	07/04/1990	Nursery	Habitat
AKI	LR (2)	M	N	02/09/1980	Nursery	Dome
CEC*	LR (2)	F	N	02/24/1991	Mother	Dome
HAA	LR (2)	M	N	12/30/1991	Mother	Dome
MAR	LR (2)	F	Y	01/01/1966	Unknown	Dome
MART	LR (2)	F	Y	01/01/1965	Unknown	Dome
TAS	LR (2)	F	N	11/18/1992	Mother	Dome
ZOE	LR (2)	F	N	04/13/2002	Mother	Dome
BRI	HR (1)	F	N	08/31/1995	Mother	Dome
CHI	HR (1)	M	N	08/25/1988	Mother	Dome
MAG	HR (1)	M	N	07/24/1992	Mother	Dome
MAN	HR (1)	F	N	09/08/1984	Mother	Dome
NIC*	HR (1)	M	N	04/07/1988	Mother	Dome
BER	HR (2)	F	N	02/18/1978	Nursery	Dome
JUD*	HR (2)	M	N	08/26/1990	Nursery	Dome
KOB	HR (2)	M	Y	01/01/1972	Unknown	Dome
QUI	HR (2)	F	Y	01/01/1971	Unknown	Dome
TUL	HR (2)	F	N	05/01/1980	Mother	Dome
TOD	Control	F	Y	01/01/1971	Unknown	Dome
SAB	Control	F	Y	01/01/1968	Unknown	Dome
PEP	Control	F	Y	01/01/1967	Unknown	Dome
ALP	Control	F	N	11/08/1984	Mother	Dome
BET	Control	F	N	06/23/1994	Mother	Dome
BIL	Control	M	N	06/16/1993	Mother	Habitat
BO	Control	M	N	05/16/1993	Mother	Habitat
JOE	Control	M	Y	01/01/1972	Unknown	Dome
MAY	Control	F	Y	01/01/1965	Unknown	Dome
MOO	Control	M	Y	01/01/1971	Unknown	Dome
GRE	Control	M	Y	01/01/1970	Unknown	Dome
AJA	Control	M	N	01/01/1978	Unknown	Dome
LUL	Control	F	N	01/16/1982	Mother	Dome
TAB	Control	M	N	08/25/1991	Mother	Dome
KUD	Control	M	N	12/07/1982	Mother	Dome

Condition: HR, High rank model; LR, Low-rank model. Asterisk next to name indicates individual was the trained model for their group.

## 2.5 | Network-based diffusion analysis

NBDA is a powerful method of determining whether an observed pattern of acquisition of behaviors is consistent with the predictions of a group's social network (Allen, Weinrich, Hoppitt, & Rendell, 2013; Franz & Nunn, 2009; Hobaiter, Poisot, Zuberbuhler, Hoppitt, & Gruber, 2014; Hoppitt, Boogert, & Laland, 2010). In this case, the social network was created using the number of times Individual A

observed Individual B using the seeded method before Individual A first demonstrated this method. Because, we were able to record the exact times at which an individual first used the method, we used the Time of Acquisition Diffusion Analysis (TADA) variant of NBDA (Hoppitt et al., 2010). Times entered into the model were the number of seconds which the group had been exposed to the Vert before a given individual first opened it using the seeded method. We used an information theoretic approach (Burnham & Anderson, 2004), using



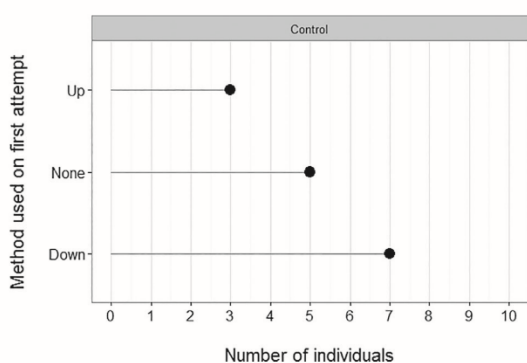
**FIGURE 1** The “vertical artificial vegetable” (the “Vert”) could be opened to reveal a food reward either by sliding the door entirely upwards (B) or entirely downwards (C). The resting position on presentation is shown in (A). The side-profile is shown in (D). Upon a completed opening, the door locked so as to restrict access to the alternative reward. The anchor platform was attached to a trolley with vice clamps

Akaike's information criterion corrected for sample size (AICc) from which total Akaike weights ( $\Sigma w_i$ ) for each model were calculated. Total Akaike Weights were then used to create model averaged estimates for the factor by which individuals' learning rates are increased per observation of the seeded method. Models were constructed based on the predictions outlined by the rank-bias hypothesis and the necessary conditions for refutation (above).

This analysis was carried out using the NBDA R Script Version 1.2.11 (available at <http://lalandlab.st-andrews.ac.uk/freeware/>).

## 2.6 | Generalized linear mixed effects models

We used two sets of generalized linear mixed effects models (GLMMs) to determine whether the sex of a demonstrator was a useful predictor in determining how many individuals were likely to be in proximity (<3 m) on any given trial. The first set of models considered audience



**FIGURE 2** Method used on first opening of the Vert by individuals in the control condition, and number of individuals who failed to open the box

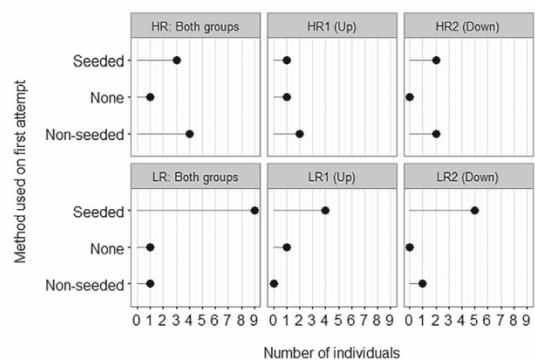
size as an absolute value, whereas the second considered it as a proportion of group size. In all models, “individual” was fit with random intercepts and random slopes to account for multiple measurements from each individual. We took an information theoretic approach to inference, using AICc to estimate model fit. From this we calculated total akaike weights and use these to compute model-averaged estimates of parameter coefficients, allowing us to estimate the effect of a parameter while taking into account model uncertainty. Due to the use of model-averaging, rather than use  $p$ -values to determine whether a parameter had an important effect on the output variable, this was established according to whether its 95% confidence intervals overlapped with 0.

## 2.7 | Video coding

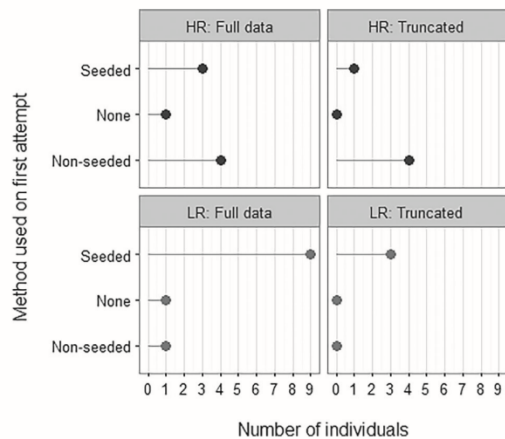
The method used by any individual who successfully opened the box was coded, as well as the identities of any individual within 3 m. Any individuals within 3 m whose heads were oriented towards the Vert and did not have their view obstructed was recorded as having observed the opening. Videos were coded by SKW. Inter-observer reliability was carried out with RAH on the method (“up” or “down”) used and who was observing each demonstration in 30 clips of individuals opening the Vert, with 100% agreement.

## 3 | RESULTS

Although the raw data from the control condition (Figure 2) are somewhat suggestive of a greater tendency for pushing down than lifting up the door, the number of individuals who chose either method did not differ significantly from chance (Up:  $n = 3$ ,  $p = 0.343$ , 95% CI = 0.07–0.65; Down:  $n = 7$ ,  $p = 0.343$ , 95% CI = 0.35–0.93). Nevertheless, the direction of the seeded method was counterbalanced across groups in the experimental condition. Furthermore, 5 out of 15 control individuals failed to open the box at all, from which we may infer that the two methods of opening the door were not so salient that



**FIGURE 3** Column 1—Methods used on first opening of the box for each condition. Columns 2 and 3—Methods used on first opening of the box in each group. Directionality of trained method indicated for each group in brackets



**FIGURE 4** Counts for methods used on first opening of the box in the original "full" data set, side-by-side with "truncated" data set

every chimpanzee was easily capable of opening it without the use of social information.

A Barnard's exact test found that individuals in the low-rank condition used the seeded method on their first successful trial significantly more often than individuals in the high-rank condition

**TABLE 2** Summary table of each individual's interactions with the puzzle box

ID	Group	First method as seeded?	Total trials	Total trials as seeded
JUD	HR1	Y	730	720
BER	HR1	N	69	0
TUL	HR1	Y	234	214
QUI	HR1	N	1	0
KOB	HR1	n/a	0	0
NIC	HR2	Y	535	463
CHI	HR2	N	109	108
MAN	HR2	N	54	48
MAG	HR2	Y	106	66
BRI	HR2	Y	9	6
CEC	LR1	Y	170	170
MAY	LR1	Y	185	184
ZOE	LR1	Y	123	121
AKI	LR1	N	171	3
TAS	LR1	Y	166	163
MAR	LR1	Y	34	34
HAA	LR1	Y	138	138
ANG	LR2	Y	146	146
CHE	LR2	Y	115	108
KIH	LR2	Y	326	133
NAH	LR2	Y	188	162
RAD	LR2	Y	13	13
MAH	LR2	n/a	0	0

**TABLE 3** AICc, delta AICc, and Total Akaike Weights ( $\Sigma w_i$ ) for each model

Model	AICc	Delta AICc	Total weighted AICc ( $\Sigma w_i$ )
S only in HR, varies between HR groups <sup>a</sup>	334.13	11.91	0.002
S in all groups	330.96	8.74	0.009
S only in HR, constant between HR groups <sup>a</sup>	330.96	8.74	0.009
S varies between all groups	328.6	6.38	0.027
No S in any group	328.27	6.05	0.036
S varies between LR and HR <sup>b</sup>	326.75	4.53	0.078
S only in LR, constant between LR groups	326.5	4.28	0.088
S only in LR, varies between LR groups	322.22	0	0.75

S, social transmission.

<sup>a</sup>Hard rank bias hypothesis.

<sup>b</sup>Soft rank-bias hypothesis candidate.

( $\chi^2 = 2.09$ ,  $N = 19$ ,  $p = 0.048$ , see Figure 3). Exact binomial tests found that individuals in the low-rank condition used the seeded method significantly more often than chance ( $n = 11$ ,  $p = 0.032$ , 95%CI = 0.53–1.0) but high-rank condition did not ( $n = 8$ ,  $p = 0.855$ , 95%CI = 0.111–1.0).

Using a truncated data set (Figure 4: procedure and rationale for exclusion detailed above), there remained a significant difference between low- and high-rank conditions in the number of individuals who used the seeded method on their first trial (Barnard's exact test:  $\chi^2 = 2.19$ ,  $n = 8$ ,  $p = 0.047$ ). However, it is worth noting that two of the four individuals in HR condition (see HR2 in Table 2) who first used the non-seeded method later switched to consistently use the seeded method. No other individuals in any group persistently switched to a method other than their first-learned, with the exception of the innovation described in detail below. Both individuals who did not solve the task were males. Neither individual tried any other method of interacting with the door (e.g., hitting, pushing, pulling, etc.), indicating that they lacked the motivation to engage with the task.

**TABLE 4** AICc, delta AICc, and Total Akaike Weights ( $\Sigma w_i$ ) for the best fitting model from Table 3 with additional individual-level variables

Asocial variable	df	AICc	Delta AICc	Total weighted AICc
Sex	4	325.73	3.51	0.07
Rearing	4	323.13	0.91	0.25
Age	4	323.08	0.86	0.26
None	3	322.22	0	0.41



**TABLE 5** Model comparison summary statistics for two sets of GLMMs

Model	K	AICc	Delta AICc	Total AICc weight
GLMM Set 1: audience = number of individuals <3 m from demonstrator				
Audience~1 ID	3	9178.19	0	0.94
Audience~Sex + Sex ID	6	9183.63	5.44	0.06
GLMM Set 2: audience = proportion of group <3 m from demonstrator				
Audience~1 ID	3	-2114.53	0	0.94
Audience~Sex + Sex ID	6	-2108.95	5.58	0.06

Sex, Sex of demonstrator; 1|ID, Random intercepts for individual; Sex|ID, random slopes and intercepts for Individual; K, number of effective parameters.

### 3.1 | Network-based diffusion analysis

There was most support for models (Table 3) in which there was an effect of social transmission (S) in the LR condition but not HR, with S varying between groups ( $\Sigma w_i = 0.75$ ). Model-averaged estimates for S indicate that each observation increased an average individual's learning rate by 3% in LR1 and 15% in LR2. Model-averaged estimates for S indicate that each observation increased an average individual's learning rate in HR1 and HR2 by 0.1% per observation. Models based on the hard rank-bias hypothesis were not well supported ( $\Sigma w_i = 0.002$  and  $\Sigma w_i = 0.009$ ). A model allowing for the soft rank-bias hypothesis had some support ( $\Sigma w_i = 0.078$ ), but contrary to the predictions of this hypothesis, the effect of S was estimated as being greater in the LR condition ( $S = 0.08$ ) than HR ( $S = 0.00$ ). Individual-level variables (sex, age, and rearing history) were added to the best fitting model, but there was little support for any of them improving the model (Table 4).

### 3.2 | GLMMs

A model-averaged estimate (Table 5) of the coefficient for the effect of demonstrator sex on audience size, when counting absolute number of individuals within 3 m was 0.14 (95%CI: -0.23, 0.51), and when considering audience size as a proportion of total group size was 0.02 (95%CI: -0.05, 0.08). We may infer that Sex did not have an important effect as the 95% confidence intervals did not overlap with zero. Furthermore, as seen in Table 5, adding Sex to the models resulted in a considerably higher AICc and therefore poorer fit.

### 3.3 | An innovation

Finally, we report an innovation which occurred in one of the high-rank condition groups. After 7 hr of open-diffusion, a subordinate individual (TUL) discovered a narrow window of motion in which the door can be opened using "Up," so that a reward can be retrieved, but the locking mechanism is not activated. This allowed her to then also use "Down" to move the door a second time and obtain a second reward. TUL had not used "Down" prior to this discovery, but had observed two other females in her group using it on multiple occasions. This suggests TUL combined her first-learned method with previously acquired social information about that used by others to generate a more productive method, although asocial learning cannot be ruled out. Despite the innovator being of low rank, after 11 observations of this improved method the dominant male (JUD) of the group, who to this point had

exclusively used the "Up" method, also began to use the combined form. A similar pattern was observed in a second group. Again, the first individual was a subordinate female (CHE) and the method was subsequently used by two higher ranking females (KIH, NAH). Due to the limited data available, it is not possible to carry out any formal analyses of these events, but we present them as "naturally" occurring examples of subordinates' innovations achieving limited diffusion through their groups.

## 4 | DISCUSSION

Rank-bias has been proposed as a way to account for the relatively rare adoption of innovations to produce traditions within chimpanzee communities (Horner et al., 2010; Kendal et al., 2015). Based on this "rank-bias hypothesis," we predicted that novel behaviors seeded by subordinates either fail to spread, or motivate a considerably lesser degree of social learning than novel behaviors seeded by dominant individuals. In our study, not only were the group-mates of low-ranking models more likely to use the seeded rather than non-seeded method on their first opening of the box, but they were also substantially more likely to do so than individuals in groups with high-rank models. Furthermore, a NBDA showed greatest support for models in which social transmission of the seeded method was present only in the low-rank condition. Finally, we reported innovations developed by two subordinate chimpanzees in separate groups which built on pre-existing methods and were subsequently used by more dominant individuals, likely as a result of social learning. While one must be cautious in interpreting isolated events, these instances are striking in their pertinence to our research question and in how they contrast with the predictions of the rank-bias hypothesis.

We conclude these findings strongly suggest that the rank-bias identified by previous studies (Kendal et al., 2015; or "prestige-bias" in Horner et al., 2010), which occurred when observers had a choice between models of various ranks, does not prohibit the successful emergence of group-wide behavior patterns from subordinate models or innovators, when no competing model is present. As well as a rank-bias, Kendal et al. (2015) identified a bias toward copying "knowledgeable" individuals, which our results suggest to be the case even when demonstrators are of low social rank. This may make adaptive sense, since if one observes an individual doing something that is rewarding, it

is counterintuitive to ignore this information simply on the basis of the demonstrator's low social status. However, this does not preclude the indirect importance of rank in more natural settings. For example, if recent immigrants tend to be spatially peripheral to the group, this would reduce the number of individuals in close enough proximity to observe (and copy) any novel behaviors being used, functionally resulting in a rank bias. By contrast, individuals in the present study could only carry out the behavior when performing it in a central, commonly used space where the researcher and experiment were set up, making them readily visible to their group. Furthermore, while we did identify comprehensive diffusion of methods seeded subordinate models, it is important to note the difference in group size between the relatively small groups studied here (between 6 and 8 individuals) and wild chimpanzee communities which can have anything from 20 to 150 members (Boesch & Boesch-Achermann, 2000; Goodall, 1986; Nishida, 1990). Communities of larger scale, as well as the presence of fission-fusion social dynamics, may present additional obstacles for behavioral diffusion.

Being raised in captivity and participating in behavioral research for so many years (e.g., Brosnan et al., 2007; Dean, Kendal, Schapiro, Thierry, & Laland, 2012; Hopper et al., 2008; Kendal et al., 2015) may also have shaped the study population to be more ready social learners (Carpenter & Tomasello, 1995), further mediating the effects of rank-bias. The influence of such developmental, cultural, environmental, and individual differences on social learning are difficult to examine in such long-lived species, but are likely to be critical in our understanding of cultural transmission (Mesoudi, Chang, Dall, & Thornton, 2016). Nevertheless, this would not explain why there was a greater effect of social transmission in the low-rank condition than in our high-rank condition.

These results contrast with prior studies (Horner et al., 2010; Kendal et al., 2015) in that the effect of social transmission was found to be stronger in our low-rank condition, and a greater proportion of individuals in the LR condition used the seeded method on their first trial than those in HR. One methodological difference between the current study and previous work that might explain this discrepancy is that our high-ranking models were dominant males rather than dominant females. This was an intentional design choice, as males are almost always dominant relative to females, and it was desirable to maximize the rank disparity between model types. However, this may have introduced additional confounds. While males were successfully used as models in Price, Lambeth, Schapiro, and Whiten (2009), the study used video demonstrations and observers were not always from the same group as the model, and were therefore unaware of their rank. Wrangham et al. (2016) found that in a community of chimpanzees where multiple grooming techniques were in use, individuals tended to converge on the method primarily used by their matriline, potentially hinting at a sex bias in chimpanzee social learning. However, the only systematically documented example of an incipient tradition diffusing through a wild chimpanzee community originated in a male chimpanzee (Hobaiter et al., 2014), indicating that males can also make effective models. Furthermore, in a series of GLMM's we examined whether the number of individuals in proximity or attending to an individual's demonstrations could be predicted by that

demonstrator's sex, and this was not found to be the case (Table 5). From this, we may infer that our use of differently sexed models did not introduce an important confound with respect to social tolerance that would explain the contrast between effects of high versus low rank models in our study. In any case, the key finding in our results is not so much the contrast between effects of high versus low ranked models, but that the low ranked female provided an adequate model whose preferred behavioral option was copied by others.

There is already good evidence for an attentional bias toward dominant individuals (Kendal et al., 2015), but it is unclear to what extent this may be vigilance rather than active social learning. Spatial tolerance between demonstrators and observers is also likely to be crucial in facilitating social learning (Van Schaik, 2003), which may be confounded when highly dominant demonstrators monopolize a resource. The difficulty associated with faithfully copying a socially intolerant individual may explain why two observers in the HR condition first discovered the non-seeded method and then switched to consistently use the seeded method for the remainder of testing. Based on previous work (Hrubesch, Preuschoft, & van Schaik, 2009) we would expect such individuals to fixate on their first-learned method, since the alternative did not provide a greater payoff (Van Leeuwen et al., 2013). It may be that, in this case, the first-used method was an "accidental" discovery on the route to learning the seeded method.

As previously discussed, capuchin monkeys inhibit demonstration of known behaviors while in the presence of dominant males (Lonsdorf et al., 2016). If the same is true of chimpanzees, then non-dominant individuals having to wait for an appropriate social context to interact with the task may have introduced additional demands on memory that would interfere with accurate copying models in the HR condition. In our experiment, the fact that we removed the Vert when models were displaced in the demonstration phase meant that the resource could not be immediately monopolized. The reason for this was to remain methodologically consistent with prior work on rank-bias (Horner et al., 2010; Kendal et al., 2015), as well as to directly examine the motivation of observers to learn from subordinate models rather than the effects of resource-monopolization on the diffusion of novel behaviors. Competition over resources remains an unexamined and potentially important influence on the diffusion of chimpanzee traditions.

While this study has shown that chimpanzees are motivated to learn novel methods of accessing a resource from subordinate individuals, it is possible this is not true of forms of imitative behavior that are thought to be normatively motivated and therefore, perhaps particularly directed toward important social partners. Examples of this include the fashion of putting grass in one's ear, invented by a high-ranking female, described by Van Leeuwen et al. (2014) or vocal convergence resulting from close social affiliation (Fedurck, Machanda, Schel, & Slocumbe, 2013; Watson et al., 2015). Further examination of context-specific qualities, such as behavioral-domain, extrinsic motivators (e.g., food or social benefits), ease of monopolization and how these inhibit or promote particular learning biases, may be a fruitful area of research.

## ACKNOWLEDGMENTS

SKW, GV, RAH, and AW are grateful for the support of the John Templeton Foundation, grant ID40128, "Exploring the evolutionary foundations of cultural complexity, creativity and trust" to AW and Kevin Laland, which funded this project. Thanks to Will Hoppitt and Charlotte Brand for statistical discussion. Thanks also to the anonymous reviewers whose suggestions greatly improved this manuscript. The National Center for Chimpanzee Care is supported by NIH Cooperative Agreement U42 OD-011197.

## REFERENCES

- Addessi, E., Mancini, A., Crescimbeni, L., & Visalberghi, E. (2011). How social context, token value, and time course affect token exchange in capuchin monkeys (*Cebus apella*). *International Journal of Primatology*, 32, 83–98.
- Allen, J., Weinrich, M., Hoppitt, W., & Rendell, L. (2013). Network-based diffusion analysis reveals cultural transmission of lobtail feeding in humpback whales. *Science*, 340, 485–488.
- Aplin, L. M., Farine, D. R., Morand-Ferron, J., Cockburn, A., Thornton, A., & Sheldon, B. C. (2015). Experimentally induced innovations lead to persistent culture via conformity in wild birds. *Nature*, 518, 538–541.
- Boesch C., & Boesch-Achermann H. (2000). *The chimpanzees of the Tai Forest: Behavioural ecology and evolution*. USA: Oxford University Press.
- Brosnan, S. F., Jones, O. D., Lambeth, S. P., Mareno, M. C., Richardson, A. S., & Schapiro, S. J. (2007). Endowment effects in chimpanzees. *Current Biology*, 17, 1704–1707.
- Burnham, K. P., & Anderson, D. R. (2004). Multimodel inference understanding AIC and BIC in model selection. *Sociological Methods & Research*, 33, 261–304.
- Carpenter, M., & Tomasello, M. (1995). Joint attention and imitative learning in children, chimpanzees, and enculturated chimpanzees. *Social Development*, 4, 217–237.
- Claidière, N., & Whiten, A. (2012). Integrating the study of conformity and culture in humans and nonhuman animals. *Psychological Bulletin*, 138, 126.
- Coelho, C. G., Falótico, T., Izar, P., Mannu, M., Resende, B. D., Siqueira, J. O., & Ottoni, E. B. (2015). Social learning strategies for nut-cracking by tufted capuchin monkeys (*Sapajus* spp.). *Animal Cognition*, 18, 911–919.
- Dean, L. G., Kendal, R. L., Schapiro, S. J., Thierry, B., & Laland, K. N. (2012). Identification of the social and cognitive processes underlying human cumulative culture. *Science*, 335, 1114–1118.
- Fedurek, P., Machanda, Z. P., Schel, A. M., & Slocumbe, K. E. (2013). Pant hoot chorusing and social bonds in male chimpanzees. *Animal Behaviour*, 86, 189–196.
- Franz, M., & Nunn, C. L. Network-based diffusion analysis: A new method for detecting social learning. *Proceedings of the Royal Society of London B: Biological Sciences*. (2009). 276, 1829–1836.
- Freeman H. D., Brosnan, S. F., Hopper, L. M., Lambeth, S. P., Schapiro, S. J., & Gosling, S. D. (2013). Developing a comprehensive and comparative questionnaire for measuring personality in chimpanzees using a simultaneous top-down/bottom-up design. *American Journal of Primatology*, 75(10), 1042–1053.
- Friard, O., & Gamba, M. (2016). BORIS: A free, versatile open-source event-logging software for video/audio coding and live observations. *Methods in Ecology and Evolution*, 7(11), 1325–1330.
- Goodall, J. (1986). *The chimpanzees of gombe: Patterns of behavior*. Cambridge, MA: Harvard University Press.
- Henrich, J., & McElreath, R. (2003). The evolution of cultural evolution. *Evolutionary Anthropology: Issues, News and Reviews*, 12, 123–135.
- Hobaiter, C., Poisot, T., Zuberbühler, K., Hoppitt, W., & Gruber, T. (2014). Social network analysis shows direct evidence for social transmission of tool use in wild chimpanzees. *PLoS Biology*, 12, e1001960.
- Hopper LM, Lambeth SP, Schapiro SJ, & Whiten A. Observational learning in chimpanzees and children studied through 'ghost' conditions. *Proceedings of the Royal Society of London B: Biological sciences*. 275 2008; 835–840.
- Hopper, L. M., Schapiro, S. J., Lambeth, S. P., & Brosnan, S. F. (2011). Chimpanzees' socially maintained food preferences indicate both conservatism and conformity. *Animal Behaviour*, 81, 1195–1202.
- Hopper, L. M., Kurtycz, L. M., Ross, S. R., & Bonnie, K. E. (2015). Captive chimpanzee foraging in a social setting: A test of problem solving, flexibility, and spatial discounting. *PeerJ*, 17(3), e833.
- Hopper, L. M., Lambeth, S. P., Schapiro, S. J., & Whiten, A. (2015). The importance of witnessed agency in chimpanzee social learning of tool use. *Behavioural Processes*, 112, 120–129.
- Hoppitt, W., Boogert, N. J., & Laland, K. N. (2010). Detecting social transmission in networks. *Journal of Theoretical Biology*, 263, 544–555.
- Horner, V., Proctor, D., Bonnie, K. E., Whiten, A., & de Waal, F. B. (2010). Prestige affects cultural learning in chimpanzees. *PLoS ONE*, 5, e10625.
- Hrubesch C., Preuschoft S., & van Schaik C., (2009). Skill mastery inhibits adoption of observed alternative solutions among chimpanzees (*Pan troglodytes*). *Animal Cognition*, 12(2), 209–216.
- Kendal, R. L., Coolen, I., van Bergen, Y., & Laland, K. N. (2005). Trade-offs in the adaptive use of social and asocial learning. *Advances in the Study of Behavior*, 35, 333–379.
- Kendal, R., Hopper, L. M., Whiten, A., Brosnan, S. F., Lambeth, S. P., Schapiro, S. J., & Hoppitt, W. (2015). Chimpanzees copy dominant and knowledgeable individuals: Implications for cultural diversity. *Evolution and Human Behavior*, 36, 65–72.
- Laland K. N., & Galef B. G. (2009). *The question of animal culture*. Cambridge, MA: Harvard University Press.
- Laland, K. N., & Janik, V. M. (2006). The animal cultures debate. *Trends in Ecology & Evolution*, 21, 542–547.
- Laland, K. N. (2004). Social learning strategies. *Animal Learning & Behavior*, 32, 4–14.
- Lonsdorf, E. V., Bonnie, K. E., Grim, M., Krupnick, A., Prestipino, M., & Whyte, J. (2016). Seeding an arbitrary convention in capuchin monkeys: The effect of social context. *Behaviour*, 153, 633–654.
- Mehta, C. R., & Senchaudhuri, P. (2003). Conditional versus unconditional exact tests for comparing two binomials. Retrieved from: <http://www.cytel.com/papers/twobinomials.pdf>
- Mesoudi, A., Chang, L., Dall, S. R., & Thornton, A. (2016). The evolution of individual and cultural variation in social learning. *Trends in Ecology & Evolution*, 31(215), 225.
- Nakamura, M., & Uehara, S. (2004). Proximate factors of different types of grooming Hand-Clasp in mahale chimpanzees: Implications for chimpanzee social customs 1. *Current Anthropology*, 45, 108–114.
- Nishida, T., Matsusaka, T., & McGrew, W. C. (2009). Emergence, propagation or disappearance of novel behavioral patterns in the habituated chimpanzees of Mahale: A review. *Primates*, 50, 23–36.
- Nishida T. (1990). *Chimpanzees of the Mahale Mountains*. Tokyo: University of Tokyo Press.
- O'Malley, R. C., Wallauer, W., Murray, C. M., & Goodall, J. (2012). The appearance and spread of ant fishing among the Kasekela chimpanzees of Gombe: A possible case of intercommunity cultural transmission. *Current Anthropology*, 53, 650.
- Price E. E., Lambeth S. P., Schapiro S. J., & Whiten A., (2009). A potent effect of observational learning on chimpanzee tool construction.



- Proceedings of the Royal Society of London B: Biological Sciences*, 276(1671), 3377–3383.
- R Core Team. 2015. A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. Available online at: <http://www.R-project.org/>
- RStudio Team. 2015. RStudio: Integrated Development for R. RStudio, Inc., Boston, MA. Available online at: <http://www.rstudio.com/>
- Reader, S. M., & Laland, K. N. (2001). Primate innovation: Sex, age and social rank differences. *International Journal of Primatology*, 22, 787–805.
- Rendell, L., Boyd, R., Cownden, D., Enquist, M., Eriksson, K., Feldman, M. W., ... Laland, K. N. (2010). Why copy others? Insights from the social learning strategies tournament. *Science*, 328, 208–213.
- Rendell, L., Fogarty, L., Hoppitt, W. J., Morgan, T. J., Webster, M. M., & Laland, K. N. (2011). Cognitive culture: Theoretical and empirical insights into social learning strategies. *Trends in Cognitive Sciences*, 15, 68–76.
- Van Leeuwen, E. J., Cronin, K. A., Schütte, S., Call, J., & Haun, D. B. (2013). Chimpanzees (*Pan troglodytes*) flexibly adjust their behaviour in order to maximize payoffs, not to conform to majorities. *PLoS ONE*, 8(11), e80945.
- Van Leeuwen, E. J., & Haun, D. B. (2014). Conformity without majority? The case for demarcating social from majority influences. *Animal Behaviour*, 96, 187–194.
- Van Leeuwen, E. J., Cronin, K. A., & Haun, D. B. (2014). A group-specific arbitrary tradition in chimpanzees (*Pan troglodytes*). *Animal Cognition*, 17, 1421–1425.
- van Schaik, C. P. (2003). Local traditions in orangutans and chimpanzees: Social learning and social tolerance. In: Fragaszy, D. M., & Perry, S. (Eds.), *The biology of traditions: Models and evidence* (pp. 297–328). Cambridge: Cambridge University Press.
- Watson, S. K., Townsend, S. W., Schel, A. M., Wilke, C., Wallace, E. K., Cheng, L., ... Slocombe, K. E. (2015). Vocal learning in the functionally referential food grunts of chimpanzees. *Current Biology*, 25, 495–499.
- Whiten, A., Goodall, J., McGrew, W. C., Nishida, T., Reynolds, V., Sugiyama, Y., ... Boesch, C. (1999). Cultures in chimpanzees. *Nature*, 399, 682–685.
- Whiten, A. (2005). The second inheritance system of chimpanzees and humans. *Nature*, 437, 52–55.
- Wrangham, R. W., Koons, K., Machanda, Z. P., Worthington, S., Bernard, A. B., Brazeau, N. F., ... Muller, M. N. (2016). Distribution of a chimpanzee social custom is explained by matrilineal relationship rather than conformity. *Current Biology*, 26(22), 3033–3037.

#### SUPPORTING INFORMATION

Additional supporting information may be found online in the supporting information tab for this article.

**How to cite this article:** Watson SK, Reamer LA, Mareno MC, et al. Socially transmitted diffusion of a novel behavior from subordinate chimpanzees. *Am J Primatol*. 2017;79: e22642. <https://doi.org/10.1002/ajp.22642>