The Evolution of Culture in Heterogeneous Social Networks: A Comparative Approach

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A thesis submitted for the degree of Doctor of Philosophy

December 2024

Cover photo: A juvenile male baboon engaging in touchscreen activities, recorded by Simon Paul Kenworthy in Tsaobis (Namibia). Photo credit: Amelia Ramage

DECLARATION OF ORIGINALITY

I, Simon Paul Kenworthy, confirm that the work presented in my thesis is my own. Where information has been derived from other sources, I confirm that this has been indicated in the thesis. Author contributions for each research chapter are provided in a dedicated section at the end of the thesis. The pictures shown in this thesis are my own unless otherwise stated.

London, 02/12/2024

Simon Paul Kenworthy

ABSTRACT

The evolution of culture is reliant upon the social transmission of novel behaviours. The transmission of social behaviours via social learning is not always guaranteed, as individual heterogeneity impacts how animals use social information. This in turn influences how cultural behaviours do or do not spread (chapter 1). In this thesis, I addressed the representation of taxonomic groups in social learning literature, as well as tasks presented and in what setting, to compare social learning use and evaluate commonalities and disparities (chapter 2). I identified significant biases in taxonomic spread, task presented and experimental setting across comparative studies. I then addressed the possible constraints on the evolution of culture in chacma baboons (*Papio ursinus*) by presenting the first multi-touchscreen, multi-task (easy and difficult task) experiment to wild primates. I assessed whether age, sex or rank impacted: the participation in novel touchscreen tasks (chapter 3), their success in completing novel tasks (chapter 4), and whether they acquired task behaviours via asocial or social learning (chapter 5). The easier task showed greatest participation and performance measures across all baboons, evidencing greater task success on simpler tasks (chapter 3). However, task success occurred mainly via asocial learning. There were three main barriers to information flow. Firstly, those who were most likely to observe others (young individuals) did not access the tasks to apply social information. Secondly producers of social information of high quantity (older individuals and males) and high quality (older and dominant individuals) were only observed by other touchscreen users, trapping social information. Thirdly, the presence of high-ranking individuals prevented the effective application of social information by

low-ranking individuals. Overall, I argue that barriers relating to the varying use of social information by use heterogeneous actors limits the emergence and persistence of group-level culture in baboons.

IMPACT STATEMENT

This thesis increased our understanding of which factors may constrain the transmission of social information and therefore culture in baboons and other species. This research has relevant impacts both inside and outside of academia.

Inside academia, this research contributes to addressing key gaps in our understanding of cultural evolution, particularly regarding the conditions that influence the emergence and persistence of social learning. Across the comparative social learning literature, representation is uneven, yet the evidence from baboons in this thesis highlights that individual heterogeneity – differences in traits such as motivation, cognitive ability, attention and social connectivity that may be shaped by age, sex or rank – can strongly influences the spread or stagnation of social information. This variation at the individual level may help explain why some behaviours fail to propagate, even when opportunities for social learning are present.

However, this perspective must be considered alongside group-level dynamics, especially in socially complex species like baboons, which live in large, cohesive groups. In such settings, the costs of social living can constrain cultural transmission. In other words, behaviours may not be widely adopted unless they are assessable and beneficial to a majority of individuals at the same time. This contrasts with species like chimpanzees, where smaller, more fluid fission-fusion groupings may allow for more flexible or individualised learning opportunities.

Therefore, this thesis places each stage of social learning into a broader context, examining not only individual differences but also how these interact with social structure and group organisation (although only within one species and so wider questions regarding species differences in group dynamics are beyond the scope of this thesis). This thesis therefore discusses the role that individual heterogeneity plays in the spread (or lack thereof) of social information. This thesis puts each stage of social learning into perspective within the wider fields of cultural evolution and adaptation via social learning.

In terms of academic output, this thesis is structured as a series of academic manuscripts in preparation for submission to a journal/s. Importantly, the findings in this thesis have important ramifications for the fields of social learning (when addressing knowledge gaps and academic practices) as well as cultural evolution via identifying barriers to social information flow. The barriers to social information flow can be used across disciplines to evaluate why species show or do not show cultural behaviours.

This research is also heavily applicable to non-academic interest, mainly informing conservation. Animal culture is of recent conservation interest due to the importance of maintaining behavioural diversity to ensure adaptive potential in response to rapid change. By identifying knowledge gaps in current social learning and cultural research, conservationists can better target efforts towards identifying cultural behaviours in poorly studied taxa. Furthermore, the impact of individual heterogeneity on the flow of potentially adaptive social information within baboons, highlights the need to integrate individual heterogeneity into the conservation of adaptive behaviours. Through comparative metrics outlined in

this thesis and accompanying appendices, the use of social learning across taxa and contexts can be evaluated and conservation practices prioritised.

ACKNOWLEDGMENTS

I would first like to thank my supervisory team of Alecia Carter and Guy Cowlishaw who accompanied me throughout the ups and downs of my PhD journey. They gave me valuable advice on every aspect of my research, demonstrating kindness and showing encouragement towards my research pursuits. I would also like to thank Elise Hutchard for her invaluable support and feedback during my PhD upgrade that helped shaped this thesis. All three have given me much needed support and guidance during testing conditions conducting remote fieldwork and throughout my research in the UK.

I would also like to thank the Natural Environment Research Council (NERC) for funding my research through the London NERC DTP (cohort 7). The studentship covered university fees, my stipend for living in London, and research expenses.

I also thank the Ministry of Environment and Tourism for research permission in Namibia, the Gobabeb Research and Training Centre for affiliation, the Tsaobis beneficiaries for permission to work at Tsaobis, the Snyman and Wittreich families, Gerald Roux, and Johan Venter for permission to work on their land; and the staff of the Tsaobis Restcamp for their assistance at the campsite. Thanks also to Herman and Lizzet Strydom for hosting us and providing storage for our equipment in Windhoek, and for being always helpful on anything related to life in Namibia.

I owe a huge debt of gratitude to many of the people who contributed, directly or indirectly, to fieldwork in Namibia. First, I would like to thank my team co-leaders, particularly Axelle Delaunay (2021) and Vittoria Roatti (2021 and 2022) for showing me the ropes and sharing the joys and troubles of managing a field team in the desert. I also want to thank the field assistants at the Tsaobis Baboon Project for their invaluable help in data collection throughout the 2021 and 2022 field seasons. A special mention must go to those who aided in the complex logistics and data collection regarding the touchscreen experiments: Punaete Kandjii (pilot study), Rachel Thomson, Winona Meek, Maria Kahungu, Helvi Amanyanga, Meriam Shinima and Petoorua Mberirua. Also, thanks go to the field assistants whose data collection of the day to day lives of the Tsaobis baboons informed so much of this thesis: Julianne Joswiak, Alanna Brownell, Joe Jacobs, Rose Ellis and Sandra Njubei. Also, I can never repay the solace shown to me in Namibia by Amelia and Rachel, they never desert-ed me.

I also want to thank all of my collaborators at ZSL, who wholeheartedly have supported my comparative social learning project (Appendix 2) and shown great enthusiasm for my vision: Lewis Rowden, Jim Mackie, Teague Stubbington, Shannon Farringdon and the small mammals team, Tony Cholerton and the primates and predators team and Amanda Robinson and the Whipsnade primate team. Of course, my research assistants demand infinite gratitude for their die-hard commitment, they have grown so much over the past 2 years, and I could not be prouder of them as colleagues: Julianne Joswiak, Kassandra Giragosian, Maurita Bates and Zoe Cobb.

Thank you also to my friends and family for their endless support and comfort (thanks Mum!). I must give a special thank you to my partner Amelia for her unwavering support and love, I owe you the world. It has truly been an honour to have started my science journey with you more than 10 years ago. Thinking back on our time in Foundation year at the University of Manchester, freshers in Richmond Park – you must have thought me a little odd for obsessing over animals. I would not be the scientists that I am without you and the science adventures we've shared – Greece, Platt Fields, Brecon Beacons, Ecuador, Lolldaiga, Borneo, Thailand, Mpala, Tsaobis, Skomer, USA, Brussels, Paris. You have helped to support me through my worst times, guide me through my blatant stupidity and empowered and enlightened me to succeed through foundation year, BSc, MSc and now PhD. I hope our science adventure never stops and someday, we can bring new life into this world in the shape of a co-authored and peer-reviewed paper.

I also have to mention the friends old and new who have supported me throughout my studies and social science life. To everyone at IoZ, you have no idea how amazing it has been to have such a supportive, kind, driven and hilarious community. I have enjoyed every minute of doing my PhD at IoZ and I look forward to keeping those everlasting relationships going. Also thank you of course to IoZ staff as well as students, I have felt at times as though I have a dozen supervisors who I can lean on for advice, guidance or to complain about the struggles of academia to.

Finally, but very importantly, I would like to thank the Tsaobis baboons. Their camaraderie and drama filled a Coronation Street-sized hole in my life during

fieldwork. They provided me with such wonderful spectacles and inspired my curiosity, making me the scientist I am today as I sought to understand their fascinating lives. I consider myself privileged to have shared their daily experiences and honoured to investigate what makes them tick.

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CHAPTER 1: GENERAL INTRODUCTION

1.1 INTRODUCTION

Culture is a fundamental characteristic of humanity, and is increasingly being identified in other social animals (Brakes et al., 2021, 2025; Whiten, 2021, 2019). Social learning – learning that is facilitated by the observation of, or interaction with, another individual or the products of another's behaviour (Hoppitt and Laland, 2013) – is a critical requirement for the development of culture and is widespread in the animal kingdom. However, confirmed instances of cultural behaviours are still rare (Laland, 2004; Schuppli and Schaik, 2019; Tennie et al., 2020, 2009). Variation in how individuals socially learn behaviours has been indicated as an explanatory component in the emergence and persistence of group-specific behaviours or cultures (Boyd and Richerson, 1985). This variation can present in an animal's ability to acquire, apply and exploit social information (Carter et al., 2016). Socially learned behaviours are transmissible within (horizontal) and between (vertical) generations, forming non-genetically transmitted, heritable traits. Behaviours inherited through social learning can allow animals to exploit novel resources with increasing efficiency without gathering costly personal information (Laland, 2004). Social learning therefore can allow the rapid dissemination of novel information between individuals. This means social learning is integral for the conservation of species for whom learning cultural behaviours can aid in adaptation to rapidly changing environments (Brakes et al., 2019). In this Introduction, I will explore the factors that may enhance or constrain the transmission of social information (§1.2 – 1.5), and the potential consequences this may have for the evolution of

culture (§1.6). This will lead onto an overview of the aims of this thesis and the study system in which this research was undertaken (§1.7). My Introduction ends with a summary of my thesis structure (§1.7.4).

1.2 Social learning and culture

1.2.1 Social learning: an overview

Behavioural traits acquired through social learning can improve the fitness of the learner, for example by allowing the learner to access a new food source through tool-use (Casanova et al., 2008; Lefebvre et al., 2004; Reader and Laland, 2003), access mates through learned courtship behaviour (Rosa et al., 2012), increase movement efficiency through learning more efficient travel routes (Lindeyer and Reader, 2010; Rose et al., 2016) or avoid predators through learning the acoustic cues of other species (Keen et al., 2020). Social learning therefore forms a secondary inheritance mechanism that allows animals to make potentially adaptive decisions and to learn about their environment efficiently (Feldman and Laland, 1996; Laland et al., 2010; Lefebvre and Giraldeau, 1996).

Social learning may not always be adaptive to individuals or spread to others. For instance, if conforming to the behaviour of others is more beneficial than adopting an alternative socially learned behaviour, novel behaviours may not spread through a group (Bikhchandani et al., 1992; Giraldeau et al., 2002). Evolutionarily neutral socially-learned behaviours have no clear impact on fitness, such as “fashion” in chimpanzees (van Leeuwen et al., 2014). Social

learning can also have negative fitness consequences for animals, such as the learning of maladaptive behaviours as seen through the adoption of less efficient tools by female chimpanzees when immigrating into a group (Luncz et al., 2018). Furthermore, social inhibition, the act of not acquiring a behaviour, for example due to disinterest or preference for another behaviour, can reduce the spread of such socially-learned maladaptive behaviours (Brown and Laland, 2002). As a result, animals often balance social and individual (asocial) learning, shifting learning strategies based on the context (Kendal et al., 2005; Mesoudi et al., 2016).

Social learning takes place in three steps (Carter et al., 2016): first, individuals must gather social information e.g. by observing others (acquisition; §Chapter 5); second, individuals require the opportunity to use gathered information (application; §Chapter 3); and finally, individuals need to reap the rewards (or face the consequences) from performing a learned behaviour (exploitation; §Chapter 4). In order to investigate how different factors impact the acquisition, application and exploitation of social information, observational, experimental and mathematical modelling approaches have been applied (Agee and Monfils, 2018; Barrett and Perry, 2020; Camacho-Alpízar and Guillette, 2023). Within experimental studies of social learning (§Chapter 2), two approaches are common: firstly, to compare the performance of a novel behaviour by subjects exposed to a successful demonstration of that behaviour by a demonstrator (experimental group) with that of a control group who are denied such social learning opportunities (Hoppitt and Laland, 2013; Whiten, 2024). Secondly, to track the diffusion of social information – the patterns of transmission of behaviours between individuals – through groups. An experimental method for

seeding a behaviour into a group is through a controlled diffusion, whereby researchers train (an) individual/s to perform a specific behaviour (the demonstrator). By assessing how this behaviour spreads in controlled conditions such as laboratories (Hoppitt and Laland, 2013), researchers can pinpoint facilitators and barriers to social learning through a reduction of confounding variables. Similar studies may also be conducted in more naturalistic populations, such as free-ranging, or wild groups (§Chapter 5). If behaviours are seeded into these groups, the diffusion of behaviours can be tracked and allow researchers to investigate natural facilitators and barriers to social information diffusion that may not emerge in controlled conditions (Pritchard et al., 2016; van de Waal et al., 2013). In some cases, seeding behaviours into groups may not be necessary, as a novel behaviour may emerge in a group through natural innovation (Allen et al., 2013; Kendal et al., 2010). The learning of this behaviour can then be tracked as a natural diffusion (§6.3.1). Perhaps the most famous example of such cases is the spread of sweet potato-washing in Japanese macaques (*Macaca fuscata*; Imanishi, 1953; Schofield et al., 2018), that kickstarted the field of social learning and culture (Hoppitt and Laland, 2013).

While diffusion experiments have become increasingly prevalent in social learning studies, their methodologies are not without their flaws. One particular concern is that novel behaviours seeded into groups may not always be representative of natural behaviours, such as those that use man-made objects, or if individuals are trained by humans. As a result, the ecological validity of the findings may be compromised (Fischer, 2022). Although the issue of artificiality may make it challenging to apply some conclusions to evolutionary questions,

such a degree of human interference may be necessary to observe social learning pathways given the rarity of natural innovations, which also must have the capacity to diffuse. Even when natural innovations do occur, it is difficult to guarantee that such innovations are truly novel to the innovator without the researcher's knowledge. Therefore, natural diffusions require researchers to be in the right place at the right time, creating a low likelihood of replicability for such studies. Furthermore, using artificial experimental paradigms may make it easier for researchers to address research questions with greater accuracy and with greater flexibility – such as is offered through an integration of touchscreens into experimental designs (Egelkamp and Ross, 2019). Taken together though, a combination of experimental comparisons and natural diffusions can be an ideal compromise for researchers to investigate the facilitators of and barriers to social learning.

Social learning enables individuals to acquire behaviours rapidly by observing others, but indiscriminate copying is rarely an optimal strategy for solving novel tasks (Hoppit and Laland, 2013). For example, Randell et al. (2010) used simulations to model fitness payoffs of different social learning strategies — methods by which individuals decide how and when to learn socially — showing that social learners achieve higher fitness than asocial learners only when copying is relatively rare. This occurs because when environmental conditions change, the value of social information diminishes if too few individuals independently sample their environment. As a result, social learners employ adaptive strategies to decide when and who to copy (Boyd and Richerson, 1985; Laland, 2004). For instance, individuals may adopt a "copy when uncertain" strategy, where they copy others when their current behaviour or lack of knowledge is inefficient or unproductive (Boyd and Richerson, 1988). Social

learning is also more likely when asocial learning carries high risks or costs, such as acquiring information about a novel predator (Chivers and Smith, 1995).

The selection of whom to copy often depends on the ability to access reliable social information and is influenced by a combination of individual traits and social pressures. For example, individuals may prioritise copying high-performing or knowledgeable individuals while simultaneously being subject to pressures to conform to group norms (van Leeuwen et al., 2013; Kendal et al., 2015). This highlights the nuanced interplay between individual decision-making and group-level dynamics in social learning. Social learning is not inherently adaptive but is applied flexibly in combination with asocial learning, depending on the specific ecological and social context (Kendal et al., 2005).

In the context of animal culture, social learning strategies are fundamental in shaping the transmission of behaviours and traditions across individuals and generations. For example, biased learning strategies, such as copying kin or dominant individuals, can facilitate the spread of adaptive behaviours while limiting maladaptive ones (Laland, 2004; Kendal et al., 2009). These strategies enable animals to balance innovation with the stability needed to maintain group-level traditions, a hallmark of cultural processes in non-human animals. Thus, understanding how social learning strategies operate is critical for studying the emergence and persistence of animal cultures.

1.2.2 Animal culture: an overview

Defining cultural behaviours in non-human animals (henceforth animals) has been the topic of debate since the inception of the field, with multiple definitions proposed (Table 1.1). While no single definition has achieved consensus, most agree on three common criteria for cultural behaviours. First, the candidate behaviours must be innovated (Galef, 1990; Laland and Janik, 2006; McGrew, 1998). Secondly, the candidate behaviours much be inherited via social learning by another (transmission). Finally, the candidate behaviours must be present over multiple generations (Carter et al., 2016; Hoppitt and Laland, 2013; Krützen et al., 2005), although cross-generational transmission may be difficult to observe due to long species generation times and a low persistence of candidate behaviours (Whitehead, 2024).

The method of exclusion, although debated (Fragaszy and Perry, 2003; Langergraber et al., 2011; Schöning et al., 2008), is a method used to determine whether genetic or ecological factors influence inter-group variation in behavioural repertoires (McGrew, 1998). If all other factors are ruled out, inter-group variation in the expression of a behaviour suggests that it is a cultural phenomenon, and that social learning is the most plausible explanatory factor for that behaviour (Krützen et al., 2007; van Schaik et al., 2003; Whiten et al., 1999).

Following the identification of a cultural behaviour (innovation, social learning and excluding genetic or ecological causes) defining cultural behaviours can be categorised further into four main domains (Table 1.2). These domains aid cultural researchers to frame comparative studies (Whiten, 2024), interrogate evolutionary processes (Schillinger et al., 2015; van Schaik et al., 2003) and

better apply distinct cultural behaviours to conservation (Brakes et al., 2021). Unfortunately, the lack of consensus on how to define culture means that comparisons across animal cultural studies can be difficult and uninformative (Schuppli and Schaik, 2019).

Table 1.1: Definitions of culture cited from multiple sources within the literature.

Definition of Culture	**Reference**
"Culture is considered to be group-specific behaviour that is acquired, at least in part, from social influences. *Prima facie* evidence of culture comes from within-species but across-group variation in behaviour."	McGrew (1998), p. 305
"All group-typical behaviour patterns, shared by members of animal communities, that are to some degree reliant on socially learned and transmitted information."	Laland and Janik (2006), p. 542
"The cultural traditions of non-human primate species represent behavioural biases of different populations, all within the respective species' zone of latent solutions, generated by founder effects, individual learning, and product-oriented (rather than process-oriented) copying."	Tennie et al. (2009), p. 2413
" A behavioural trait is considered to vary culturally if it is acquired through social learning from conspecifics and transmitted repeatedly within or between generations"	Krützen et al. (2005), p. 8939

Table 1.2: Domains of cultural behaviours obtained from the literature.

Domain	**Explanation**	**Example**
Material	Use or making of physical objects	Tool-use in chimpanzees (*Pan troglodytes*; McGrew et al., 1979)
Foraging	Behaviours employed for the purpose of food acquisition, processing, and consumption	Sweet potato washing in Japanese Macaques (*Macaca fuscata;* Imanishi, 1953)
Communication	Use of vocal, olfactory or gestural cues to convey information	Gestural, olfactory and vocal population differences in Geoffory's spider monkey (*Ateles geoffroyi;* Santorelli et al., 2011)

		Vocal (sonar) population differences and ecotypes in orcas (*Orcinus orca;* Yurk, 2005)
Social	Behaviours that involve directed social interactions with another individual	Trust games of white-faced capuchins (Cebus imitator*;* Perry et al., 2003)

The first scientific description of an animal culture was when Imanishi observed a group of Japanese macaques uniquely wash sweet potatoes (Imanishi, 1953). The first cross-population study was conducted by Whiten et al. (1999) across six chimpanzee populations. Out of the 65 behaviours assessed by Whiten et al. (1999), 39 were deemed likely to have been inherited through social learning due to lack of ecological or genetic explanatory factors, and therefore likely to be cultural. van Schaik et al. (2003) reported similar results in orangutans (*Pongo pygmaeus*), identifying 24 likely cultural behaviours. Lower numbers of cultural behaviours have been identified in other great apes, namely bonobos (*Pan paniscus*) and gorillas (*Gorilla spp.*), but this may be due to the limited data available (Hohmann and Fruth, 2003; Robbins et al., 2016). A review by Izar et al., (2025) revealed that overall, in nonhuman primates (hereafter primates), cultural variation has been identified across the great apes including object manipulation and communication in *Pan* (n = 39), *Pongo* (n = 26-35), *Gorilla* (n = 23). In Catarrhines, variation has been observed in stone handling / tool use have been observed in two species of *Macaca*, dietary, sociality and communication variation between *Chlorocebus* populations and a unique transition to a peaceful social system following adult male mortality has been suggested as cultural in *Papio* (Sapolsky, 2006). Although no cultural behaviours have been identified in Lemuriformes, in Platyrrhines cultural variants have been identified in *Cebus* (n = 26). Although primates form the

majority of cultural investigations (Brakes et al., 2025, Izar et al., 2025), culture is perhaps common within the group.

Culture is theoretically possible in any species that can learn a behaviour socially, not just primates. One such group is cetaceans, where sperm whales (*Physeter macrocephalus*) show distinct vocal clans (Gero et al., 2016; Rendell and Whitehead, 2003; Whitehead, 2024). Other cetaceans also show geographically unique vocalisations, mostly likely due to the fine-tuning of their sonar frequencies used in specialist hunting strategies used to catch regional prey items (Brakes et al., 2021; Rendell and Whitehead, 2001). Akin to some cetaceans, migratory animals such as some birds learn specific and sometimes ancient migratory routes from their conspecifics over generations (Jesmer et al., 2018; Palacín et al., 2011). Cultural behaviours therefore may be widespread in the animal kingdom, key to the survival and reproduction of species that rely on the transmission of social information (Brakes et al., 2021, 2025).

The research above has demonstrated that culture is not uniquely human and may be widespread in the animal kingdom. There are a number of reasons why culture is so rarely acknowledged and described in animals; firstly researchers are unlikely to observe cultural transmission in real time as social transmission can be rapid (Whitehead et al., 2021). Secondly, some criteria for defining cultural behaviours require cross-generational transmission, this would mean that such transmission in long-lived species may be difficult to observe, with a reliance upon historical data. Finally, a lack of consensus within the culture and social learning literature means that researchers may struggle to classify a behaviour as cultural (Kendal et al., 2018).

Nevertheless, the importance of cultural behaviours has been recognised in conservation policy (§6.4), with particular focus in the Convention on the Conservation of Migratory Species (Brakes et al., 2019, 2021, 2025; CMS, 2024). Within the past five years, a population of West African chimpanzees have received special conservation measures due to their unique nut-cracking culture, as well as Eastern Pacific sperm whales due to their vocal clans (UNEP, 2020). To enable a unified approach to conservation implementation of animal culture, a broad definition of animal culture has been fortified within legislation (CMS, 2024). Within CMS, animal culture is defined as information or behaviours that are shared by a community and acquired through social learning from conspecifics (CMS, 2024). This definition bypasses limitations with other definitions of culture that require cross-generational inheritance or long-term maintenance that would slow the identification and application of required conservation actions. This thesis takes a similar applicative approach, investigating the transmission of behaviours throughout vertebrates comparatively and experimentally – and discusses implications for cultural evolution and conservation. Therefore, the definition of culture suggested by CMS will be used throughout this thesis. As animal culture gains traction within conservation discussions (Brakes et al., 2021, 2025; Izar et al., 2025), resources and research attention can only shed more light on the extent of and the evolution of culture (Schuppli and Schaik, 2019).

1.3 Constraints on the acquisition of social information

The acquisition of social information can take place across a multitude of sensory modalities, but all are constrained by an individual's access to social information generated by others (Giraldeau et al., 2002). Access to social information is driven by phenotypic factors (§Chapters 3 and 5) such as age, sex, rank, social integration and personality dictating the likelihood of obtaining close proximity to, and motivation to see information (Carter et al., 2016, 2015). In addition, group- or species-level variables may affect access to social information, such as social tolerance, group size, conformity or the group structure of a species (Mathiron et al., 2015; Momennejad, 2022; Overduin-de Vries et al., 2020). These factors can shape the social learning strategy that learners employ, and therefore greatly impact the spread of cultural behaviours (Pasquaretta et al., 2014; Sosa et al., 2021). Variation in these traits, which give rise to heterogeneous groups, are addressed in turn, focusing on how each can affect the acquisition of information from others.

1.3.1 Age

The age of individuals influences their environmental experience, which can shape their roles as users of personal information (innovators) or social information (learners). Both innovators and learners can produce social information by enacting learned behaviours in the presence of others, and thus become demonstrators. Older individuals, with their likely greater experience, are often more inclined to produce information, as experience can foster innovation (Reader and Laland, 2001). Indeed, adult primates exhibit higher innovation rates compared to immatures (Amici and Widdig, 2019). Conversely,

less experienced immature individuals may rely more on learning from others, aligning with a strategy of copying when uncertain or when the current behaviour (such as exploratory behaviour) is ineffective (Grueter et al., 2010; Grüter et al., 2013; Kendal et al., 2009; Laland, 2004). Studies consistently show that younger individuals pay greater attention to social information than adults (Whiten and van de Waal, 2018). For instance, young chimpanzees rather than adults show greatest observation toward knowledgeable individuals such as successful tool-users (Biro et al., 2006; Wobber and Warneken, 2013) and juvenile chacma baboons (*Papio* ursinus) observe others solving novel food tasks more than older age groups (Carter et al., 2014; Martina et al., 2020).

Although younger age groups generally depend more on social information, they may also produce information under conditions where inexperience is less restrictive. Their natural curiosity about the environment can drive such information-generating behaviour (Amici and Widdig, 2019; Biro et al., 2003). For example, juvenile chacma baboons were more likely to discover experimental food patches using personal information when all group members were equally naïve about the patch locations (Cambefort, 1981; Carter et al., 2016). However, most of the juveniles in these studies were males, and their inclination for individual learning might also relate to their sex and associated social integration.

1.3.2 Sex

Sexual dimorphism significantly influences individuals' roles as demonstrators or learners. The larger and more socially dominant sex often explore high-payoff foraging opportunities, relying on their ability to scrounge information and

resources from lower-ranking individuals if unsuccessful (Carter et al., 2016; Harrison et al., 2023; Reader and Laland, 2001). In chacma baboons, the need to sustain a larger body often drives males to seek resources more frequently than females, leading to personal experience of novel information and eventual information production. Supporting this, studies have shown higher innovation rates in males (Carter et al., 2016). These findings are also supplemented within other sexually dimorphic taxa, such as findings from a long-term observational study on white-faced capuchins (Perry et al., 2017).

In contrast, the smaller sex tends to exhibit a greater tendency to learn from others. For example, female vervet monkeys (*Chlorocebus pygerythrus*) in adult-dominated groups learned twice as fast as males to open a baited box (Canteloup et al., 2020), and captive female chimpanzees used social information more effectively to solve experimental tasks than their male counterparts (Watson et al., 2018). However, this pattern is less consistent among immature individuals, as studies have reported mixed results regarding sex differences in tool-use learning, most likely reflecting adult proficiency with tools (Falótico and Ottoni, 2014; Gruber et al., 2010).

Additionally, females' reproductive states can influence their reliance on information. Pregnant and lactating chacma baboons are more likely than females in other reproductive states to use social information when foraging, i.e., to scrounge food by joining patches occupied by males (King et al., 2009). This behaviour may stem from higher energetic demands during pregnancy and lactation (Barrett et al., 2006), reducing the costs of independent foraging (inefficiency and risk of harm) or reflecting a preference for staying near the father of their offspring (Baniel et al., 2016).

1.3.3 Social rank

Dominance rank plays a critical role in dictating an individual's ability to access resources (King et al., 2008). Subordinate individuals often derive greater benefits from innovations that improve access, as their access to resources is constrained by agonistic interactions with dominant conspecifics (Reader and Laland, 2001). This is reflected in studies showing that low- and middle-ranking primates are more likely to innovate than their higher-ranking counterparts (Perry et al., 2017). In contrast, dominant individuals are more likely to scrounge, leveraging their hierarchical advantage to monopolise resources identified by subordinates (King et al., 2008). For instance, dominant chacma baboons frequently use the presence of conspecifics at a patch to locate food and prefer foraging near subordinates to exploit their discoveries (King et al., 2009; Marshall et al., 2012).

While dominance generally increases reliance on social learning, evidence suggests rank-related trends can vary. For example, dominance rank was positively correlated with obtaining social information regarding experimental food patches in chacma baboons (Carter et al., 2016), yet lower-ranking captive chimpanzees demonstrated a greater propensity to use social information when learning to open a baited box (Kendal et al., 2015).

1.2.4 Social integration

Social integration, assessed through social networks, plays a vital role in shaping information transmission at both individual and group levels. Social networks map the relationships within a group, which are often quantified through spatial proximity or social interactions, such as affiliative or dominance

behaviours (Carrington et al., 2005; Croft et al., 2009). Social networks therefore reflect the opportunities for information acquisition, with individuals more likely to gather information from those with whom they frequently interact or are in close proximity (Atton et al., 2012; Claidière et al., 2013; Coussi-Korbel and Fragaszy, 1995). However, care must be taken when comparing social networks made with differing techniques (Castles et al., 2014), and social integration does not always guarantee information acquisition.

Social networks can be analysed at both the individual and group level. At the individual level, social connections impact the ability to acquire information in several ways. Firstly, individuals cannot learn from others they do not associate with, as seen in fission-fusion societies (Sueur et al., 2011). Secondly, social network metrics such as centrality can be correlated with the likelihood that an individual acquires social information, with central individuals having more opportunities to access social information through their frequent and diverse social ties (Claidière et al., 2013; Sosa et al., 2021). Social centrality enhances information acquisition, as demonstrated by socially central ring-tailed lemurs and squirrel monkeys learning to open a baited box faster than less central individuals (Claidière et al., 2013; Kulahci et al., 2018), possibly due to the acquisition of novel behaviours attracting conspecifics to gather social information (Kendal et al., 2015; Kulahci and Quinn, 2019). Thirdly, an individual's learning preferences often favour nearby individuals or those with strong affiliative bonds, such as grooming partners (Coelho et al., 2015; Grampp et al., 2019).

At the group level, phenotype-driven associations, such as homophily by age or sex, may influence information flow. Immatures often associate with same-sex

peers, which, combined with their higher reliance on social learning, could potentially limit information spread (Carter et al., 2015). This is because immatures can play a key role in social information transmission, but if immatures primarily associate with each other there is less opportunity for social information to 'escape' this social clique and spread to other group members. This separation is particularly pronounced in female-philopatric species, where females' greater social centrality and males' peripheral positions further constrain group-level information transmission (Lehmann and Ross, 2011; Sosa et al., 2021).

1.2.5 Personality

Personality traits are behavioural patterns that are consistent over time and across contexts (Carter et al., 2012). Personality traits can also predict individual differences in information acquisition. Traits like boldness (measured through tendency to explore novelty) and anxiety (measured through response to threats) have been linked to information dynamics in chacma baboons, where bold individuals are more likely to use personal information rather than social information, while anxious individuals are more likely to show the reverse pattern (Carter et al., 2013). Sociability, or the tendency to initiate social interactions, often correlates with centrality in social networks, enhancing opportunities for learning (Krause et al., 2010).

1.2.6 Group size and structure

Group size and structure influence social learning by altering interaction opportunities. Larger groups provide more chances for social learning, as suggested by the correlation between group size, relative brain size, and

cognitive abilities (Dunbar, 2008). Some evidence relating group size to cognitive abilities comes from rhesus macaques, where individuals that incorporate more group members tend to have greater synaptic density in social areas of the brain (Sallet et al., 2011). Associations between relative brain size, as well as group size have therefore been drawn with higher levels of social learning (Street et al., 2017; van Schaik and Burkart, 2011). Through a greater understanding of their social environment, social intelligence (Reader and Laland, 2002), individuals in larger groups have a wide variety of opportunities to acquire social information and are able to adjust their social relationships accordingly (Pasquaretta et al., 2014). This means that larger groups often have more efficient social networks, enabling faster information transmission through fewer connections (Momennejad, 2022; Pasquaretta et al., 2014).

Cohesion and dominance structure also impact learning. Cohesive groups, such as those of chacma baboons, facilitate faster information spread compared to less cohesive groups like vervet monkeys (Cambefort, 1981). Dominance hierarchies, common in despotic groups, may enhance vigilance and social cue monitoring (King et al., 2008), benefiting information flow through direct or indirect observation of information production. However, this contrasts with the hypothesis that social tolerance, rather than dominance, better facilitates information spread by allowing closer observation of behaviours (Ottoni and Izar, 2008).

1.2.7 Social tolerance

Social tolerance, characterised by relaxed social relationships, facilitates closer proximity and interaction (Ottoni and Izar, 2008). Within species, tolerance towards immatures and social affiliates promotes learning from those same

individuals, irrespective of kinship (King et al., 2011). Social tolerance can therefore facilitate the acquisition of social information that is limited by distance between demonstrators and learners, such as observable behaviours (Ottoni and Izar, 2008). Social tolerance has a varying degree of importance depending on the complexity of information acquired, with complex information requiring longer periods of proximity to acquire, such as tool use (van Schaik et al., 1999), and simpler information such as the location of a food patch requiring little temporal proximity (Laidre, 2013). Primates tend to exhibit greater tolerance for the proximity of young immatures compared to older individuals, a pattern observed in both despotic (Tarnaud and Yamagiwa, 2008) and more egalitarian species (Ottoni et al., 2005). This tolerance, combined with the inexperience of younger individuals, likely explains their greater tendency to learn from others (Rapaport and Brown, 2008). Additionally, social affiliates are often more tolerant of each other's proximity, making them preferred learning partners, especially in despotic societies (Tan et al., 2018). These social affiliates may include both kin and non-kin. For example, Japanese macaques frequently forage alongside close kin (Belisle and Chapais, 2001), while chacma baboons are known to acquire information from close grooming partners, regardless of genetic relatedness (King et al., 2011).

Between species, tolerant societies often have flatter social hierarchies and more interconnected networks, enabling faster information spread (Pasquaretta et al., 2014). In contrast, despotic societies with stronger kin-based subgroups can limit group-wide information transmission (Pasquaretta et al., 2014), unless clusters are well-connected (Momennejad, 2022).

1.4 Constraints on the application of social information

The application of social information involves performing actions directly influenced by the acquired information (§Chapters 4 and 5). For instance, when an individual observes a conspecific feeding and subsequently moves to the same patch, it demonstrates the application of acquired knowledge about food location (Carter et al., 2016). Observational studies often rely on evidence of subsequent behaviour, such as practice following observation, to infer that information was acquired, even if the acquisition itself cannot be directly measured (Ottoni and Izar, 2008; Schuppli and Schaik, 2019). However, it is often difficult to disentangle the application of acquired information with the exploitation of information (when resources are successfully obtained), as both are inherently linked and so commonalities between constraints on the application and exploitation of social information are likely.

Since application follows acquisition, the factors enhancing or constraining acquisition often similarly affect application. For example, juvenile chacma baboons, who pay more attention to novel food tasks and hidden food challenges, also exhibit the greatest improvement in applying the acquired information (Carter et al., 2014). However, the time spent in applying information is not always proportional to the time spent acquiring it, suggesting that opportunities to apply an acquired behaviour can be impacted by social and demographic factors.

1.4.1 Age

As with information acquisition, younger individuals tend to apply social information more than older ones, although this pattern was not found in chacma baboons (Carter et al., 2016). For example, infant and juvenile

orangutans spend more time than older juveniles manipulating their nest-building materials, reflecting the a greater time spent watching demonstrators (Schuppli et al., 2016). In addition, after observing conspecifics, younger common marmosets pay closer attention to demonstrators than older individuals and forage near them (Schiel and Huber, 2006).

1.4.2 Sex

The sex differences observed in social information acquisition extend to its application. In immature individuals, opposite tendencies are often reported for males and females. For example, eastern chimpanzee daughters observe their mothers termite-fishing more than sons (Lonsdorf et al., 2004), while juvenile male bearded capuchins (*Sapajus libidinosus*) watch adult males using tools to displace hidden prey more than female peers (Falótico et al., 2021). This may be why female chimpanzees spend more time attempting to fish near termite mounds, whereas male capuchins more frequently manipulate probes (Falótico et al., 2021; Lonsdorf et al., 2004).

Female reproductive states can also influence information application, particularly under conditions of high intragroup competition. Female chacma baboons, for example, are less likely to join experimental food patches than males, possibly due to a preference for more reliable natural foraging options to meet their increased energetic demands, or a tendency to be more risk averse (Carter et al., 2016).

1.4.3 Social rank

Access to opportunities can be dictated by an individual's position in the dominance hierarchy, due to rank-related exclusions from such resources. For

example, high-ranking chacma baboons monopolise food resources (King et al., 2008), preventing low-ranking individuals from potentially applying social information. Similarly, in rhesus macaques, low-ranking individuals are only able to apply socially learned information when high-ranking individuals are absent (Drea and Wallen, 1999). Rank can therefore impact individual's ability to apply social information in novel challenges, such as cognitive experiments (Fagot and Paleressompoulle, 2009; Harrison et al., 2023). By limiting the access of low-ranking individuals to novel challenges, this reduces their likelihood of information application and consequently increases their likelihood to seek social information.

1.4.4 Social tolerance

Social tolerance facilitates the application of social information. This is particularly relevant for behaviours requiring close observation and practice, such as tool use and social customs (Bonnie and de Waal, 2006; van Schaik et al., 1999). For instance, immature western chimpanzees (Biro et al., 2003) and tufted capuchins (Sapajus apella) are allowed to handle tools used by adults for nut-cracking, explore gathered nuts, and feed on scraps left behind (Ottoni et al., 2005). Similarly, in captive chimpanzees, the degree of affiliation between individuals predicts the acquisition of hand-clasp grooming behaviours, with some learning these social customs from experienced group mates over a 12-year period (Bonnie and de Waal, 2006). In addition, the centrality of individuals within a social network, an indicator of social tolerance, predicted when individuals would first open an artificial fruit (Claidière et al., 2013). Furthermore, stronger social bonds between individuals (social network strength) can allow

access to resources and facilitate the application of behaviours (Fruteau et al., 2009; Henzi and Barrett, 2002).

1.4.5 Cognition

Assuming individuals can acquire social information and access a situation where they can potentially apply it, they may still lack the physical or mental capacity to do so successfully. This is most true for younger individuals who lack the experience and cognitive ability to process and apply information as successfully as older individuals (van de Waal et al., 2013). Furthermore, experience may not come with age, but simply exposure to cognitively demanding tasks. This means that those individuals who have been challenged most frequently, may outperform those who lack the exposure or motivation to participate in cognitively challenging tasks. This is most evident through the captivity effect, whereby captive animals frequently outperform their wild counterparts, due to a greater application of socially learned behaviours (Fischer, 2022; Hopper, 2017; Kendal et al., 2010; Pritchard et al., 2016).

1.5 Constraints on exploitation of social information

The exploitation of social information refers to successfully utilising acquired knowledge to obtain a resource (§Chapters 4 and 5). For instance, when an individual observes another foraging in a specific patch, moves to the location, and begins to forage there successfully, gaining food items, then they are exploiting the information about the food's location (Carter et al., 2016). While exploitation builds upon acquisition and application, additional factors, such as physical limitations or social dynamics, can influence an individual’s ability to fully exploit social information (Carter et al., 2016; Visalberghi et al., 2016).

1.5.1 Age

Although younger individuals may acquire and apply social information effectively, physical limitations like lower manual dexterity or strength can restrict their ability to exploit resources. In tool-using species, juveniles often require years of practice to match adults' efficiency in extracting embedded foods (Fragaszy et al., 2004; Visalberghi et al., 2016). In bearded capuchins, older age and higher body mass predict nut-cracking efficiency. While body mass correlates with success in cracking tough fresh nuts, experience shortens processing times for both fresh and dry nuts (Visalberghi et al., 2016).

1.5.2 Sex

Sex differences in social information exploitation often parallel differences in application. For instance, juvenile female eastern chimpanzees learn to fish for termites about two years earlier than males and obtain more termites per attempt (Lonsdorf et al., 2004). These early advantages extend into adulthood, where females are generally more proficient tool users than males (Gruber et al., 2010). In contrast, adult male bearded capuchins primarily practice probe tool use, a behaviour linked to males observing this technique during development more frequently than females (Falótico et al., 2021; Falótico and Ottoni, 2014).

1.5.3 Social rank

Dominance rank significantly influences the ability to exploit social information. Dominant animals have priority-of-access to monopolisable resources, while subordinate individuals may avoid applying and thus exploiting information to avoid conflict with dominants. For instance, shyer and calmer chacma baboons,

despite acquiring information, were less likely to apply or exploit it compared to bolder, more anxious individuals, possibly due to concerns over resource monopolisation by dominants (Carter et al., 2016, 2014). Experiments with rhesus macaques support this idea: subordinates were less successful at exploiting information in mixed-rank (joint) conditions but matched dominants' success when tested separately (split condition) (Drea and Wallen, 1999; Lonsdorf et al., 2016).

Any rewards gained may be scrounged by others, which may decrease the motivation of scrounging victims (such as low-ranking individuals) to apply behaviours whilst also making the same victims targets of social information gathering from scroungers (King et al., 2009). High-ranking individuals possess the greatest choice with how to gain rewards after the application of social information, either via scrounging or being able to monopolise resources, and are therefore highly experienced in exploiting social information. Together, this may mean that individuals who are inexperienced or unable to exploit resources could observe knowledgeable individuals (such as high-ranking monopolisers) to gain high-quality social information that will allow them to quickly exploit resources when a short window of opportunity is presented.

1.5.4 Social tolerance

While dominance interactions may inhibit exploitation for subordinate animals, social tolerance can enhance it. Central chacma baboons within a grooming network were better at exploiting information about food patches than peripheral individuals, as social bonds reduced aggression during foraging (Carter et al., 2016; Marshall et al., 2015). Grooming dominants early in the day further

enhanced tolerance during foraging activities (Sick et al., 2014). Experiments on vervet monkeys illustrate the strategic use of social behaviours: individuals allocated grooming effort in proportion to the food rewards they could gain from group mates (Borgeaud and Bshary, 2015; Fruteau et al., 2009).

1.5.5 Cognition

Similar to constraints to applying social information, if individuals are theoretically able to apply social information, this does not guarantee that they have the cognitive capacity to exploit it (§Chapter 4). For example, individuals may be able to acquire and successfully apply key behaviours required to complete a cognitive task, but if those behaviours are combined into a sequence, exploitation is hindered. This is evidenced through a series of cognitive experiments given to great tits (*Parus major*), whereby a single step cognitive action was easily performed by the subjects (Aplin et al., 2015), but when two variations of those actions were combined into a sequence, individual success was lower (Aplin, 2019).

1.6 Evolution of culture

Individuals differ in their ability to use social information at the point of acquisition, application an exploitation. This means that group composition may influences the efficiency with which social information spreads through groups. This is a fundamental building block of the emergence of culture (Whiten, 2019).

As discussed previously (§1.2.2), there is wavering consensus on how culture is defined and measured. This creates significant barriers to assessing the evolutionary mechanisms of culture, and also applying conclusions to present

and future directions such as conservation (Brakes et al., 2021; Kendal et al., 2018). A common indication used for the presence of cultural behaviours is inter-group differences in behavioural repertoires (Fragaszy and Perry, 2003; Langergraber et al., 2011; Whiten et al., 1999). Within this method of exclusion, it is vital to the current definitions of animal culture to understand how groups can differ in the behavioural repertoires they inherit from one another and the previous generation. Therefore, heterogeneity in group composition or dynamics must be the most influential factor in shaping the emergence and maintenance of cultural behaviours.

Group-level heterogeneity is impacted by the connectedness between heterogeneous actors in groups (Christensen et al., 2010; Griffin and Nunn, 2012; Pastor-Satorras and Vespignani, 2001; Salathé and Jones, 2010). Connectedness, mediated through grooming, for example (Carter et al., 2015), can predict the spread of information through a network better than individual traits such as rank. Group-level topology can also greatly impact the spread of social information around the group (Allan et al., 2025), for example clustering within groups, and increased proportion of bridged connections aiding in the spread of innovations compared to single stable groups (Derex and Boyd, 2016; Momennejad, 2022). This means that well-connected but clustered groups create more efficient networks for information diffusion. However, when heterogeneity in the inter-node distance and number and strength of social bonds increases, speed and robustness of information diffusion decreases (Voelkl and Noë, 2010). This demonstrates that individual interactions and heterogeneities within groups can drastically impact the efficiency of social information flow at a group level, creating heterogeneity between groups with

different social actors within them. Inter-group differences in the flow of social information (and therefore the emergence of different behaviours due to the disproportionate spread of innovations) is a key indicator for the emergence of cultural behaviours, with heterogeneity of actors impacting the maintenance of cultural behaviours (Hoppitt and Laland, 2013; Rendell and Whitehead, 2003; Whiten et al., 1999).

What is not fully understood is how the position of heterogeneous actors within a social network impacts the flow of social information (Allan et al., 2025). Models of social information transmission through social networks commonly underestimate learner and demonstrator heterogeneity, or only alter the structure of networks but not the traits of actors between simulations (Ilany and Akçay, 2016; Smolla et al., 2016; Smolla and Akçay, 2019; Vital and Martins, 2009; Voelkl and Noë, 2010, 2008). Positionality of actors within a group is an important factor to consider when integrating node/actor heterogeneity into social networks as changing the positions of actors may impact their connections to conspecifics and thus their ability to exchange social information. As discussed above, connectivity and topology of social networks can greatly impact the flow of information around them, with the most influential actors located centrally or bridged between clusters groups (Derex and Boyd, 2016; Momennejad, 2022; Snijders et al., 2014). This means that if the position of these influential actors is altered, the flow of social information through the social network may differ. This has real-world implications within animal social systems in natural conditions and for conservation when actors are removed. In natural conditions, particularly within hierarchical societies, social network position is dictated by rank and social bonds (Carter et al., 2015; Lusseau and

Newman, 2004; Pasquaretta et al., 2014). This means that if high-ranking individuals are more likely to play demonstrator roles within social learning (Canteloup et al., 2020; Reader and Laland, 2001), their centrality within social networks is key to the diffusion of social information that they produce. The identity of high-ranking individuals towards the centre of social networks is in constant flux in some hierarchical animal groups, such as baboons, due to intra-sexual competition for dominance leading to high rates of turnover (King et al., 2008). Therefore, when central individuals change position within social networks, social information flow through the network could potentially change if the 'replacement' individual differs in traits which impact social learning, such as age, personality or cognitive ability, even if they are similar to their predecessor in terms of competitive abilities. Additionally, altering the position of any individual within a social network could change with whom that individual can gain social information in their new position, and who can pay attention to them. Positions of every individual are likely to change over time due to changes to age, rank, personality, experience and social bonds (including with individuals which leave and enter the social network) over an individual's lifetime (Wrzus et al., 2013). Within dynamic social groups, this means that the flow of social information is greatly tied to the position of learners and demonstrators within a social network, which can be in constant albeit low-level flux. This is a factor within social learning and social network studies which is poorly understood but has clear applications to dynamic social systems of animal groups reliant upon social learning for their survival. In turn, a greater understanding of how heterogeneous actors impact the flow of social information through their social networks could shed light on the emergence and persistence of cultural behaviours stemming from this variation.

Group-specific behaviours may arise due to a between group variation in factors that impact the likelihood or ability of individuals to acquire, apply and exploit socially learned behaviours. Such variation that can impact the spread of socially learned behaviours through a group can include the traits of individuals (both naïve and knowledgeable to the behaviour), the strength of social connections in the group (Coelho et al., 2015) and social learning strategies specifying when an individual should copy a behaviour and who from (Boyd and Richerson, 1985; Laland, 2004).

If a group contains fewer individuals which are able acquire, apply, or exploit social information, the group as a whole is less likely to demonstrate that behaviour (Becker et al., 2017). The composition of individual traits within groups can vary substantially in age, sex, rank, personality, cognitive abilities and social network position. The diffusion of social information through a group has been well studied within social learning literature (Allen et al., 2013; Claidière et al., 2013; Coelho et al., 2024), with heterogeneity of actors (leaners or demonstrators) within networks subjected to scrutiny as explanatory variables for group-level observations (Watson et al., 2017). However, there has been little empirical evidence linking heterogeneous traits such as age (Perry et al., 2021), sex, rank/stress (Mesoudi et al., 2016) or cognition to the effectiveness of social information spread at the group level within animals (Fogarty et al., 2015).

1.7 This study

1.7.1 Aims

Social learning has been studied in a multitude of species, including substantial research incorporating non-human primates (Brakes et al., 2021; Izar et al., 2025; Whiten, 2024), but fundamental gaps in our knowledge remain (Brakes et al., 2025; Whiten and van de Waal, 2017). In order to understand the evolution of culture, useful insights can be gained by taking a comparative approach across species (Mesoudi, 2016). The shared mechanism of inheritance of cultural behaviour is social learning, and it is variations within the acquisition, application and exploitation of social information that dictate the spread of potentially cultural behaviours (Carter et al., 2016). Indeed, factors that impact the acquisition, application and exploitation of social information have been extensively researched, but only one study to date has investigated social learning at each stage simultaneously (Carter et al. 2016). In addition, despite a wide taxonomic reach within the social learning literature, cultural research has largely ignored non-tool-using primates, that make up the vast majority of primate species (Whiten and van de Waal, 2018).

Furthermore, there has been a recent surge in cross-species research within social learning and culture, to firstly shed light on the evolution of culture via social learning (Kendal et al., 2018), but also to inform conservation (Brakes et al., 2025, 2021, 2019). However, comparative approaches are hindered by an absence of consistency in experimental designs (Perry et al., 2021; Schuppli and Schaik, 2019) and technical terminologies (Hoppitt and Laland, 2013; Kendal et al., 2018).

The main objective of the research in this thesis was to frame social learning and cultural research into a comparative paradigm. I first assessed the development of the field of social learning by investigating variation in researched taxa, social learning task and experimental setting within studies whose data can be analytically compared. Leading from this, I investigated how social learning is impacted by taxa, task type and experimental setting (§Chapter 2), and suggest a standardised comparative social learning paradigm (§Appendix 2). Secondly, I simultaneously investigated the acquisition, application and exploitation of social information within two troops of chacma baboons. To achieve this, I presented the first ever multi-touchscreen experiment to wild primates, using an easy and difficult task. Here I assessed baboons' acquisition, application and exploitation of social information, as well as the use of asocial learning regarding the touchscreen tasks. Firstly, I investigated individuals' access to the task (potential application of task information) via their participation in the experiment (§Chapter 3). Next, I evaluated their task performance in touchscreen tasks (potential exploitation of task information) of varying difficulty (§Chapter 4). Finally, I investigated how individuals acquired task information, either via social or asocial learning, marrying this with opportunities for social information acquisition (§Chapter 5). I then discussed my general findings, highlighting factors that are facilitators and barriers to social learning in baboons and across taxa, whilst discussing applications to the evolution of culture and conservation (§Chapter 6).

1.7.2 Tsaobis Baboon Project

The Tsaobis Baboon Project (TBP) is a collaborative initiative led by Dr. Guy Cowlishaw (Institute of Zoology, Zoological Society of London), Dr. Alecia

Carter (University College London), and Dr. Elise Huchard (University of Montpellier). Since 2000, TBP has conducted a long-term, individual-based study focusing on the behaviour, ecology, genetics, and health of a chacma baboon population. The field site is situated at Tsaobis Nature Park (22°23'S, 15°45'E), a semi-desertic landscape on the edge of the Namib Desert in central Namibia, covering approximately 45 ha / 200 km² and surrounding farmland (Figure 1.1).

Tsaobis' landscape features a combination of sandy riverbeds from ephemeral rivers, rocky hills, and open plains, with altitudes ranging from 683–1445 m. The Swakop River, which crosses the baboons' ranges, runs from east to west and is the primary watercourse in the area. Woodland patches dominate the riverbeds, characterised by tall trees and large shrubs. Predominant tree species include *Faidherbia albida*, *Prosopis glandulosa*, and *Salvadora persica*. In contrast, the hills and plains are sparsely vegetated with herbs, small shrubs, and dwarf trees like *Monechma cleomoides*, *Sesamum capense*, and *Commiphora virgata* (Cowlishaw and Davies, 1997; Figure 1.2).

Figure 1.1: Location of Tsaobis Nature Park



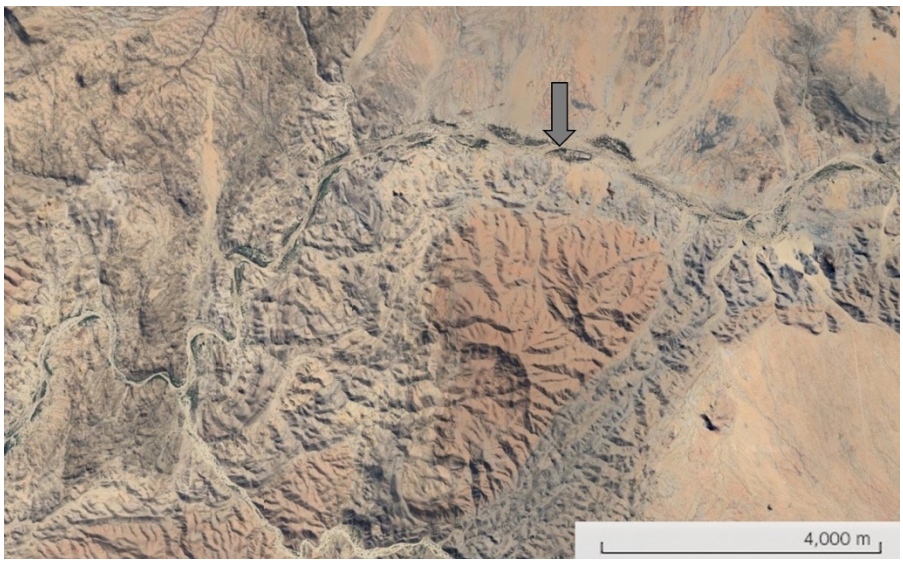


Figure 1.1: Location of Tsaobis Nature Park from a map of Namibia (above) and a closer satellite view of the area (below). The red arrow points to the location of the Tsaobis Nature Park, the grey arrow points to the location of the Swakop river that runs east to west (right to left) through Tsaobis Nature Park. Images taken from Google Earth, (2024).

Figure 1.2: Tsaobis ecology



Figure 1.2: A photograph of the landscape at Tsaobis Nature park, showing the Swakop river running from right to left, with dense riparian woodland (food-producing all year round) either side of the river and patchy vegetation (seasonally food-producing) in the surrounding hills and plains.

The climate at Tsaobis is seasonal, with a long dry season during the austral winter (April to September) and sporadic rainfall during the shorter austral summer (October to March) resulting in low food availability from April until October. Annual rainfall is low, averaging 85 mm/year (N = 5 years), and typically occurs between January and March. As is characteristic of desert environments, temperatures fluctuate significantly between day and night and across seasons, with summer temperatures reaching up to 40°C in the shade (with upwards of 45°C in direct sunlight) and winter lows dropping to 0°C (Cowlishaw and Davies, 1997).

TBP currently studies two baboon troops, designated as “J” and “L.” These troops have been habituated to the presence of human observers, enabling detailed behavioural data collection. Most individuals can be identified by unique ear marks (Figure 1.3; Appendix 3) The troops have overlapping ranges, with J troop occupying the southwestern side of the primary Tsaobis study area and L troop favouring the north-eastern side. Both troops experience the same ecology and conflict with predators and humans. The semi-arid vegetation and sparse cover ensure excellent visibility for both individual and group observations.

Figure 1.3: Chacma baboons at Tsaobis





Figure 1.3: Photographs of chacma baboons at Tsaobis Nature Park on a sleeping cliff (above) and foraging around the Swakop river (below).

While foraging, baboons maintain group cohesion but can spread across areas up to 1 km² (King and Cowlishaw 2009). Foraging behaviours differ between habitats: woodland food patches can support multiple foraging individuals, whereas open desert patches rarely accommodate more than one (Cowlishaw 1999). In the austral winter, the baboons' diet mainly consists of berries, flowers, pods, and immature leaves from five primary plant species: *Faidherbia albida*, *Prosopis glandulosa*, *Salvadora persica*, *Acacia erioloba*, and *Tapinanthus oleifolius* (Cowlishaw, 1997a). At night, troops sleep on cliffs as a strategy to deter predators, though predation risk at Tsaobis is low due to the rarity of leopards, their primary predator (Cowlishaw, 1997a, 1997b, 1994). Baboon mortality has been recorded anecdotally and in long-term data collection as part of TBP as caused by other baboons during fighting, snake bites, disease, non-intentional injury (for instance from a fall), or human-caused injury (human-wildlife conflict) including from gunshot or snare.

This environment offers an ideal natural laboratory for observing the baboons' social, ecological, and foraging behaviours. The habitat's combination of extreme environmental conditions, sparse resources, and diverse landscapes provides insights into the adaptive strategies employed by this population. As sleeping cliffs and movement of baboons are recorded daily, it is possible to integrate predictive movements into experimental designs. This means that if data require collection that is location specific, e.g., baboons interacting with novel but static items, it is possible to estimate when baboons will encounter that area based upon previous sleeping cliff, available water sources, location of the other troop, recent stressors (e.g., human-wildlife conflict) and 'typical' movement patterns during the field season.

1.7.3 Baboons as a model species

Chacma baboons live in cohesive groups (troops) of varying sizes, from a few individuals up to 100 (Strier, 2021; DeVore and Washburn, 1963; Washburn amd DeVore, 1961). Social organisation within troops is founded on a linear dominance hierarchy. Female dominance is inherited matrilineally, with male dominance in frequent flux a result of fighting and social interactions (King et al., 2008). Social bonds are mainly mediated through grooming networks (Carter et al., 2016; Cheney and Seyfarth, 2008), ritualised greetings (Dal Pesco and Fischer, 2018), signals such as oestrous swellings (Huchard et al., 2009), vocalisations (Hammerschmidt and Fischer, 2019) and gestures (Molesti et al., 2020). Although kinship plays an important role in social bond strength, social bonds are not necessarily reflective of this (Smith et al., 2003). Instead, chacma baboons often form close ‘friendships’ within or between sexes (Moscovice et al., 2010). Such friendships have been suggested to serve protective purposes against infanticide, and directly impact the reproductive success of females (Silk et al., 2003) and centrality within social networks (Cheney et al., 2016).

As opportunistic omnivorous primates, foraging forms a primary role within chacma baboon daily activities and movement. After sheltering on sleeping cliffs away from predators such as leopards, troops disperse in the early morning to begin foraging. Group foraging decisions and consequent group movement are likely resultant of the foraging decisions of dominant individuals (King et al., 2008; Strandburg-Peshkin et al., 2015). Foraging tolerance is mediated in part through grooming networks, with individuals that have more grooming partners and more frequently reciprocated grooming, receiving less aggression from conspecifics (Marshall et al., 2015). Chacma baboons can thrive in human-

modified habitats, and modify their behaviour accordingly – becoming less neophobic but more aggressive and less social in anthropomorphic landscapes (Chowdhury et al., 2020). To adapt to anthropomorphic environments, chacma baboons have demonstrated innovative behaviours such as raiding crops from monocultural environments whilst avoiding direct human and guarding conflict (Walton et al., 2021) as well as opening bins that are varied in the methods required to open them at human waste sites (Mazué et al., 2023). Baboons therefore show cognitive flexibility when faced with diverse or changing landscapes.

Due to the significance of social interactions within chacma baboon troops, individuals show a large degree of social awareness (Cheney and Seyfarth, 2008). Individual baboons respond differentially to vocalisations of troop members of differing ranks (Wittig et al., 2007), demonstrating knowledge of individual rank and kinship of the group. This means that chacma baboons' awareness of heterogeneity (age, sex, rank) within the group could mediate social information transmission if individuals choose not to give or receive information based on known heterogeneity.

When investigating social learning and consequent cultural behaviours, it is useful to understand the cognitive abilities of the species and subjects involved (Matsuzawa, 1996). This is important, as when examining cultural behaviours such as tool-use, only some taxa may be capable of performing such actions within dedicated experimental settings or wild populations, and so study species and populations must be chosen with care (Visalberghi and Tomasello, 1998). Within wild populations, baboons have only rarely been observed performing

behaviours as cognitively complex as tool-use – using stones to wipe their mouths following feeding (Lawick-Goodall et al., 1973). A number of studies have presented touchscreens to free-ranging but captive baboons, utilising a series of dots that appear and disappear when touched in increasingly complex tasks (Claidière et al., 2018, 2014). Within these touchscreen studies, Guinea baboons (*Papio* papio) showed cumulative cultural evolution, improving on the success of predecessors. Furthermore, cognitive studies have previously taken place at Tsaobis, with baboons presented with puzzle boxes, paper bags, coloured tiles and toys (Carter et al., 2015, 2014; Carter and Cowlishaw, 2021; Martina et al., 2021, 2020; Reiderman et al., 2024). Baboons at Tsaobis therefore make ideal candidates in cognitive experiments in natural conditions due to their diverse landscape, visibility, flexibility and TBP's knowledge of their social system, lineage and ecology.

Chacma baboons have a complex social system that contains a wide aspect of heterogeneity within age, sex, social rank, social network connectivity and position, and cognitive abilities (DeVore and Washburn, 1963; Washburn amd DeVore, 1961). This heterogeneity can impact the ability of individuals to acquire, apply and exploit social information successfully in order for cultural behaviours to become established in groups. Integrating known individual heterogeneity within a group into experimental social learning studies such as diffusion experiments can shed light on how heterogeneity affects the spread of information through a network and ultimately impact the evolution of culture.

1.7.4 Thesis outline

All chapters contained within this thesis are written as standalone manuscripts. Consequently, I recognise that there may be some overlap in methodologies between chapters that employed the same physical experiment. However, I have made every effort to make clear theoretical, methodological and analytical differences where appropriate. All data are to be deposited in publicly available repositories in partnership with journals to which manuscripts will be submitted.

In chapter 2, I examine the current landscape of research methodologies within the fields of social learning and culture. Specifically, I gather and refine previous literature whose data can be extracted and comparatively analysed through standardised metrics. Within this literature sample, I identify variations in the taxonomic representation that have been subjected to social learning investigations. Furthermore, I assess variations in social learning task presented (such as the complexity of task) to subjects, and also in what setting these presentations took place (such as in captivity or in the wild). Using the comparative metric outlined above, I then compare task success following social learning opportunities across taxa, task type and experimental setting. This allows me to evaluate if comparative social learning can be informative to the evolution of culture and be applicable to the conservation of culture.

In chapters 3 to 5, I presented a touchscreen experiment that is both the first multi-touchscreen experiment and first multi-task touchscreen experiment to wild primates. Within this experiment, four simultaneously presented touchscreens displayed an easy and a difficult task to two troops of chacma baboons.

In chapter 3, I investigate how individual heterogeneity (age, sex and rank) within baboon groups, as well as task difficulty, impact an individual's likelihood and ability to participate in cognitively challenging tasks. I firstly assess if age, sex or rank predicts whether an individual used the touchscreen during the experiment. Secondly, I investigate how age, sex and rank impacted the duration of touchscreen use (both for short durations and long durations). Thirdly, I assess if age, sex or rank predicts a preference for either the easy or difficult task.

In chapter 4, I scrutinise individual performance in completing touchscreen tasks successfully (gaining a food reward). Firstly, I assess whether overall task performance differed depending upon the difficulty of the touchscreen task a participant attempted. Secondly, I investigate cognitive predictors (such as the number of incorrect choices made during touchscreen tasks) of seeking alternative solutions to obtaining food rewards from touchscreens. Thirdly, I assess whether age, sex, rank or time attempting tasks predicted whether individuals learned touchscreen tasks. Fourthly, from individuals that completed touchscreen tasks successfully, I investigate whether age, sex, rank and other cognitive factors such as memory impacted task success of individuals. Finally, to better understand how hierarchical dynamics impact cognitive performance, I investigate how the presence of another individual at a neighbouring touchscreen impacted the task success of an individual, specifically how a difference in rank between the two neighbours impacted performance.

In chapter 5, I question whether individuals learned to complete touchscreen tasks or use the touchscreens via social learning or asocial learning. In order to achieve this, I installed opaque panels on half of the touchscreens to restrict opportunities for social learning on some touchscreens but not others. The success of restricting social learning opportunity with these panels was evaluated by analysing the duration of observations, and task success at touchscreens with and without panels. To investigate whether the observation of others played a major role in task success, I firstly question whether age, sex or rank impacted the duration that both an individual gathered social information from others, and the duration that others gathered social information from them. Using these observation data, I then assess whether the observation of task success in others impacted the task success of the observer (indicating acquisition, application and exploitation of social information). Secondly, I use network-based diffusion analysis to interrogate the order in which individuals learned touchscreen tasks and assess whether this order was best explained by social learning or asocial learning.

1.7.5 Key definitions in the thesis

Table 1.3. Table of key definitions used in this thesis and the chapters in which they are prominently used within.

Chapters Used	**Term**	**Definition**
Throughout	Social learning	Learning that is facilitated by the observation of, or interaction with, another individual or the products of another's behaviour (Hoppitt and Laland, 2013)
	Culture	Definition taken from Convention on the Protection of Migratory Species (2024): Information or behaviours that are shared by a community and acquired through social learning from conspecifics.
	Heterogeneity	Diversity in behavioural traits among individuals within a population (e.g., rank, personality, cognitive capacity).
	Cognition	An individual's capacity to gather information from its environment, process and interpret it, store it for future use and ultimately apply it to guide behaviour and decision-making.
	Innovation	The invention of a novel behaviour or strategy.
	Task success / Performance	The positive or negative gains obtained from engaging in a behaviour or solution. Often used in relation to cognitive puzzle-solving whereby an individual may perform well or be successful at solving the task if a greater percentage of their actions are correct or the puzzle is solved quickly.
Chapter 2	Simple task	A cognitive task requiring one step or a choice to complete it (e.g., opening a lid on a box or choosing one of two routes to travel).
	Complex task	A cognitive task requiring multiple steps to complete it, perhaps in a specific sequence or context (e.g., tool-use)
Chapter 3	Participation	The degree at which an individual engages with a cognitive task or experiment.
	Social network	A representation of the social relationships and interactions among individuals within a group, modelled as nodes (individuals) connected by edges (social ties such as grooming, proximity, communication, or observation).
Chapter 4	Neighbour effect	How the behaviour or, presence or traits of a nearby individual influences the behaviour of a focal individual.
Chapter 5	Social learning strategy	A rule or bias that an individual uses to decide when, from whom and what to learn by for instance observing others, rather than learning through individual trial-and-error (asocial learning).

CHAPTER 2: THE SCOPE OF SOCIAL LEARNING IN VERTEBRATES

2.1 ABSTRACT

Social learning, the learning of behaviour from another, has been widely studied, with significant interest dedicated to understanding the evolution of social learning. Evolutionary studies, and consequentially conservation prioritisation, are facilitated by cross-taxonomic comparative research to understand how potentially adaptive behaviours emerge and are maintained. In this meta-analysis, our aim was to identify and quantify previous social learning studies to better understand how this research field is developing with respect to the range of taxa involved, the tasks used to test those taxa, and experimental settings whose data can be analysed comparatively. We then aimed to compare task success following social learning opportunities and assess how this was impacted by these three axes. We found that mammals (primates) and birds (Passeriformes) formed most of our sample, with mainly simple tasks presented in captive settings. Of our sample, bony fish showed the greatest task improvement following social learning opportunities. We also found that task success following social learning showed the greatest increase in simple tasks compared to complex tasks. Furthermore, we showed that wild-born individuals showed greatest task improvement following social learning. Together, we show that social learning can be compared using a standardised metric, but we highlight that there are large knowledge gaps in the current literature that could facilitate informative comparative research.

2.2 INTRODUCTION

Social learning can generally be defined as learning that is facilitated by the observation of, or interaction with, another individual or the products of its behaviours (§1.2.1; Hoppitt and Laland, 2013). This differs from personal (asocial) learning because, in social learning, information is gained from others, avoiding the potential costs learning via trial and error (Laland, 2004). Social learning can occur via two routes: vertical transmission (from parents) or horizontal transmission (from a conspecific or heterospecific; Schofield et al., 2018). Behavioural traits acquired through social learning can improve the fitness of the learner, for example by allowing the learner to access a new food source (Casanova et al., 2008; Lefebvre et al., 2004; Reader and Laland, 2003). However, social learning can lead behaviours that are less efficient than known behaviours (Luncz et al., 2018) or that have no clear fitness benefits spreading through a group (van Leeuwen et al., 2014), for instance due to conformity (Hopper et al., 2011). Nonetheless, social learning can form a secondary inheritance mechanism that allows animals to learn potentially adaptive behaviours efficiently (§Chapter 5; Feldman and Laland, 1996; Laland et al., 2010; Lefebvre and Giraldeau, 1996).

Understanding how social learning and evolution intertwine can give insights into how animals can learn to adapt to rapid change. Socially learned behaviours that persist over generations, are group-specific or show geographical variation are generally acknowledged as cultural behaviours (§1.2.2; Laland and Galef, 2009; Laland and Janik, 2006; McGrew, 1998; Tennie et al., 2009; Whiten et al., 1999). The conservation of animal culture is a

topic of recent interest (Brakes et al., 2025, 2021, 2019). As animal populations decline, such as due to anthropogenic change, opportunities for social learning decrease (van Schaik, 2002). This means that individuals may be unable to make adaptive decisions and learn about their rapidly changing environments efficiently. For instance, proximity to disturbance due anthropogenic activity has led to a loss of cultural behaviours in chimpanzees (Kühl et al., 2019), and this pattern is likely to exist across taxa reliant on social learning (Brakes et al., 2025, 2021, 2019; Izaz et al., 2025). Consequentially, animal culture has been designated as a specific area of interest within the Convention on the Conservation of Migratory Species (CMS), with populations exhibiting unique cultures, such as nut-cracking chimpanzees and uniquely vocalising sperm whales, awarded special conservation status (UNEP, 2020). When addressing the conservation of threatened species displaying cultural behaviours, it is inevitable that within and between species comparisons will be drawn to facilitate conservation prioritisation discussions (§6.4). Therefore, the ability to assess the innovation and spread of cultural behaviours across groups and species is paramount to facilitate cultural conservation. The root of animal culture – social learning – is a candidate for an appropriate comparative measure that could be used to inform cultural conservation assessments (§Appendix 2; CMS, 2024). Cultural behaviours may arise due to between-group variation in factors that impact the likelihood or ability of individuals to acquire, apply, and exploit socially learned behaviours (Carter et al., 2016). Sources of variation that can affect the spread of socially learned behaviours through a group can include: the traits of individuals (both naïve and knowledgeable of the behaviour), the strength of social connections in the group (Coelho et al., 2015), and social learning strategies about when an individual

should copy a behaviour and from whom (§6.3.4; Boyd and Richerson, 1985; Laland, 2004). The evolution and spread of cultural behaviours can therefore be understood through investigating these factors (Hoppitt and Laland, 2013), and potentially applied to conservation goals (§6.4).

To investigate how socially learned behaviours can be acquired, applied and then exploited, observational and experimental research approaches have been conducted in both captive and wild animal groups. These studies frequently compare the performance of subjects exposed to a successful demonstration of a behaviour or task (the experimental group) and naïve individuals (the control group) that are denied such exposure (Hoppitt and Laland, 2013; Whiten, 2024). The performance of the experimental group/s can then be compared to the observed task performance of control group/s to assess the extent social learning played a role in the performance of the experimental groups. Furthermore, the impact of social learning can be inferred by comparing task actions or behaviours to control groups that could only learn asocially. Alternatively, it may be challenging to create distinct experimental or control groups where demonstrators can be intentionally pre-selected (for instance in wild populations). Instead, diffusion experiments (§Chapters 3 – 5) can be used to track how a behaviour spreads through a group, allowing researchers to investigate factors that promote or inhibit the social transmission of behaviours (Coelho et al., 2024; Hasenjager et al., 2021). Diffusion experiments do not require trained demonstrators (although such a design is often used) as simply the first individual to learn a novel action or behaviour becomes the demonstrator, and the order in which conspecifics also learn the task or behaviour is tracked (Allen et al., 2013).

Social learning experiments encompass a wide variety of taxa. As previously mentioned, the ability of individuals to acquire, apply and exploit social information is greatly influenced by heterogeneities of both learners and demonstrators (Camacho-Alpízar and Guillette, 2023), as well as their social structure (Allan et al., 2025; Carter et al., 2016, 2015; Hoppitt, 2017). For instance, the likelihood of individuals observing others or being observed is not uniform across the animal kingdom (§Chapter 5), with variation found across age (Amici and Widdig, 2019; Carter et al., 2014; Tan et al., 2018), sex (Amici and Widdig, 2019; Reader and Laland, 2001; Watson et al., 2018) and social rank (Carter et al., 2016; Kendal et al., 2015). Consequently, any variation between taxa in how these factors impact social learning means that the ability of individuals to socially learn may differ dependent upon the species involved. This is evident from previous literature where similar individual heterogeneities (such as sex) has opposing impacts on who used social information in different taxa. In vervet monkeys (Chlorocebus *pygerythrus*) adult females are most likely to produce social information due to their dominance in the despotic society (Harrison et al., 2023; van de Waal et al., 2013), whereas adult females are most likely to gather social information in chacma baboons (*Papio ursinus*; Martina et al., 2021, 2020) due to their subordinance to males (King et al., 2008). This means that the spread social information in vervet monkeys and baboon groups may differ as individual actors differ functionally in how they produce and gather information. By undertaking a cross-taxa approach to assess who animals learned from, Camacho-Alpízar and Guillette, (2023) showed that the characteristics of demonstrators greatly influences social learning, with demonstrator knowledge, age and rank impacting the use of

social information by learners. This shows that although taxa differ in how individuals socially learn, general trends underlying effective social learning can be unearthed with cross-taxonomic comparisons.

The tasks presented to subjects, or the behaviours tracked within groups can vary widely across species studied in social learning investigations. Some behaviours of interest to researchers are universally performed across multiple species, such as the reaction of naïve individuals to a novel predator following social learning opportunities (Manassa et al., 2014; Mathiron et al., 2015; Vilhunen et al., 2005). Equally, a socially learned behaviour may be taxonomically or contextually specific, such as tool-use (Biro et al., 2003; Coelho et al., 2024; Tan et al., 2018), limiting the generalisation of conclusions outside of such contexts and taxa that may also be culturally unique (Whiten et al., 1999). When similar tasks are presented to different taxa within the same study, taxonomic differences in the spread of social information can be identified (Bebko and Russon, 2015; Bergman and Kitchen, 2009; Gruber et al., 2010). For instance, in a study by Ladds et al., (2017), there was strong evidence for social transmission of cognitive task solutions in smooth-coated otters (*Lutrogale perspicillata*) but not Asian short-clawed otters (*Aonyx cinereus*). Furthermore, if different tasks are presented to the same taxonomic group (Renner et al., 2019; Rodriguez Escalada et al., 2014), the strategies that animals use to efficiently learn tasks either asocially or by social learning can be investigated (Kendal et al., 2005; Laland, 2004). Overall, it is clear that the type of task presented to animals can greatly impact their use of social learning.

The experimental setting that cognitive or social learning experiments take place in can impact the success that individuals have in completing presented tasks. This is evidenced through the ‘captivity effect’ whereby captive individuals outperform their wild counterparts due to a higher exposure to cognitive tests and a greater likelihood of task participation (Fischer, 2022; Harrison et al., 2023). The experimental setting in which social learning studies can take place is dependent upon the taxa investigated, the task presented, and the research questions addressed. For instance when investigating the spread of tool-using behaviours, the experimental setting is limited by what taxa can display tool-using behaviours of interest (Tennie et al., 2020; Whiten, 2024), where tool-using animals and associated tasks are located (Biro et al., 2006), and also where researchers can accurately measure social transmission (Fischer, 2022; Kendal et al., 2010; Pritchard et al., 2016). To maximise the ecological validity of studies investigating the facilitators and barriers to social information transmission in natural populations, researchers are often constrained to experimental settings that include animals that are both accessible and accustomed to human presence, ensuring they are not significantly impacted by the researchers’ activities (Fischer, 2022). Collectively, the experimental setting of social learning studies has consequences for the pattern of social learning observed, and consequentially evolutionary conclusions drawn regarding the evolution of culture and social learning use.

Although social learning is now recognised as a fundamental process, we only have a very limited understanding of how social learning strategies have evolved across species and populations. In order to give us a deeper understanding of social learning strategies and the influence of individual traits

on the spread of social information, a comparative approach investigating social learning patterns across species, task type and experimental setting could provide valuable insights on the evolutionary history of social learning (Kendal et al., 2010). However, inter-species and even inter-group comparisons of social learning experiments can be problematic due to inconsistencies in experimental design, including the type of task presented and the experimental setting (Hoppitt et al., 2008; Perry et al., 2021; Schuppli and Schaik, 2019). A further complication with comparing social learning experiments lies in the terminology used across the literature to describe social learning mechanisms (Table 2.1). The field of social learning is multi-disciplinary, encompassing fields such as evolutionary biology, behavioural ecology, anthropology, psychology and neuroscience (Kendal et al., 2018). However, the broad use of social leaning terms to classify and explain the mechanisms by which social learning operates have reached only a partial consensus across disciplines over the terminology (Hoppitt and Laland, 2013). It is often also difficult to determine which social learning mechanisms are operating in published studies (Hoppitt and Laland, 2008), for instance due to multiple mechanisms operating simultaneously or to a failure to use any social learning terms (e.g., if social learning is beyond the scope of the study). This further hinders cohesion across social learning literature, and limits comparisons between groups and species when studies are unlikely to agree on the social learning mechanisms observed and the terminology used to describe them. Taken together, there are barriers to employing comparative approaches using multiple studies. While a comparative approach would be beneficial, it requires a standard approach to measuring social learning and the factors that may impact its efficiency. Such

standardisation within the field of social learning is necessary for comparative approaches to render insightful results (§6.4; Appendix 2).

This study aimed to identify and quantify previous social learning studies in the vertebrate literature to better understand how this research field is developing with respect to (1) the range of taxa involved, the tasks used to test those taxa, and experimental settings, and (2) how the observed patterns of social learning vary across these three axes. Bearing this in mind, we first aimed to assess patterns of representation across (Aim 1a) taxonomic groups, (Aim 1b) social learning tasks, and (Aim 1c) experimental settings. We then aimed to compare task success (or the adoption of a behaviour) following social learning opportunities and assess how this was impacted by (Aim 2a) taxon, (Aim 2b) social learning task, and (Aim 2c) experimental settings. To achieve these aims, we adopted a meta-analysis approach. We used vertebrates as the taxonomic model due to their overrepresentation within the animal behaviour literature and their highly social nature compared to rare invertebrate examples (such as Hymenoptera in invertebrates (Alem et al., 2016; Rosenthal et al., 2017), maximising the comparative sample size. By focusing exclusively on vertebrates, we also avoided complications associated with comparing social learning across taxa that possess fundamentally different sensory modalities and neural architectures. The differences between vertebrates and invertebrates in how they perceive, capture, and process social information would likely introduce variability that would make cross-taxa comparisons problematic and potentially misleading.

Table 2.1: A summary of the terminology used to describe social learning mechanisms, based on Hoppitt and Laland (2013)

Social learning classification	**Description of social learning classification**	**Examples of Social Learning**
Social facilitation	Presence of a demonstrator affects the observer's behaviour (Zajonc, 1965)	Observer is more likely to follow a demonstrator escape route than one chosen at random.
Opportunity providing	Products of the behaviour of the demonstrator provide the observer with an opportunity to engage in operant learning that would otherwise be unlikely to arise (Caro and Hauser, 1992; Hoppitt et al., 2008)	Rat pups (*Rattus* sp.) 'steal' partially unopened pinecones from their mothers, providing them with the opportunity to learn how to open them backwards (Terkel, 1996).
Inadvertent coaching	Response of the demonstrator to the behaviour of the observer inadvertently acts to encourage or discourage the behaviour (Caro and Hauser, 1992; Hoppitt et al., 2008).	Mother fowl (*Gallus* gallus) move towards and peck areas of palatable food and move away from, and do not peck, areas of unpalatable food (Nicol and Pope, 1996).
Stimulus enhancement	Observation of a demonstrator (or its products) exposes the observer to a single stimulus at time *t*1, and a single stimulus exposure effects a change in the observer detected in any behaviour at *t*2 (Heyes, 1994). Can only occur when local enhancement ruled out (i.e., the location of the stimulus randomised).	Great tits were more likely to interact with a particular 'type' of place for food (Krebs et al., 1972).
Local enhancement	A subset of stimulus enhancement where after observing a demonstrator's presence, or interaction with objects in a particular location, an observer is more likely to visit or interact with objects in that location (Thorpe, 1963)	Bumblebees (*Bombus sp.*) offered a choice of two coloured flowers, one of which was visited by a demonstrator (Leadbeater and Chittka, 2007).
Observational conditioning	The observation of a demonstrator exposes the observer to a relationship between stimuli at *t*1, and exposure to this relationship effects a change in the observer at *t*2 (Heyes, 1994). Local and stimulus enhancement can fall into this category if the demonstrator is rewarded, and so an S-S association is formed.	Rhesus macaque with no previous experience of snakes observes another who has such experience. The observer's behaviour towards a snake is then measured (Cook et al., 1985).

Observational R-S learning	The observation of a demonstrator exposes the observer to a relationship between a response and a reinforcer at *t*1, and exposure to this relationship effects a change in the observer at *t*2 (Heyes, 1994)	An observer watched a demonstrator step on a treadle to receive a grain reward lit by a red light or pecking at the treadle to receive a reward lit by a green light. One action was then devalued so no reward was given, observers then preferentially chose the rewarded action (Saggerson et al., 2005).
Response facilitation	Presence of a demonstrator performing an act (often resulting in a reward) increases the probability of an observer that sees it doing the same (Byrne, 1994). There must be no other external cue other than the demonstrator that impacts the behaviour of the observer.	Rates of domestic fowl drinking from a bowl increased if the was a demonstrator already drinking from an adjacent bowl (Hoppitt and Laland, 2008).
Production imitation	After observing a demonstrator perform a novel action, or novel sequence or combination of actions, none of which are in its own repertoire, an observer then becomes more likely to perform that same action or sequence of actions (Byrne, 2002).	An observer sees a demonstrator open a box by sliding a lock in one direction and then lifting a lid to obtain a reward in sequence. The observer then attempts the same task alone.
Contextual imitation	Directly through observing a demonstrator perform an action in a specific context, an observer becomes more likely to perform that action in the same context (Byrne, 2002).	Observer pigeons (*Columba sp.*) watched a demonstrator depress a treadle for a reward by stepping or pecking (Akins and Zentall, 1996).
Emulation	After observing a demonstrator interacting with objects in its environment, an observer becomes more likely to perform any actions that have a similar effect on those objects (Tomasello, 1990).	Rat observers saw a pendulum swing in one direction and food was revealed, whereas no food was revealed when the pendulum swung in the other direction. Observers then pushed the pendulum in the rewarded direction (Denny et al., 1983).
Social enhancement of food preferences	After being exposed to a demonstrator carrying cues associated with a particular diet, the observer becomes more likely to consume that diet (Hoppitt and Laland, 2013).	An observer sees a demonstrator eating a particular food item, the observer is then alone given the choice of this same food item or another.

2.2 Methods

2.2.1 Literature gathering

This meta-analysis took a systematic approach to searching the literature within the field of social learning within vertebrates (Chordata). As recommended in the PRISMA guidelines (Page et al., 2021), multiple academic search tools were used to gather the relevant literature (Appendix Table A1.1). Only studies published up to and including April 2021 were extracted for refinement because this was the date at which the literature search began. Furthermore, only primary research articles were included in our literature gathering. General search terms such as “Social Learning” were initially used, but this yielded close to 1 million studies. Therefore, more specific search terms were utilised, and studies were consequently refined towards zoological, ecological, and behavioural focuses (Appendix Table A1.1). In total, the initial literature search yielded 2,214 studies for screening and refinement for the specific aims of this meta-analysis (Figure 2.1).

2.2.2 Literature refinement

To address the aims of this study, literature refinement was conducted to include only studies that reported data in such a way that allowed comparison between studies. Firstly, to ensure social learning rather than asocial learning was measured, we only selected social learning tasks that were likely to be novel to the observers, as this eliminates prior personal information impacting the observers’ subsequent behaviour. Every effort was made to trace the history

of subjects and research groups within the literature to unearth prior experience of similar tasks. Only studies that did not yield any indication of prior task experience after historical interrogation were selected. Secondly, we only selected studies that focused on intra-species social learning, where the learner and demonstrator are conspecifics. This is the standard approach across social learning studies as inter-species or heterospecific social learning would compromise the cross-taxa comparative aims of this study. This refinement process culminated in a final total of 185 studies to be used in the analyses (the full list is provided in Appendix Table A1.2).

Figure 2.1: Stages of systematic literature refinement

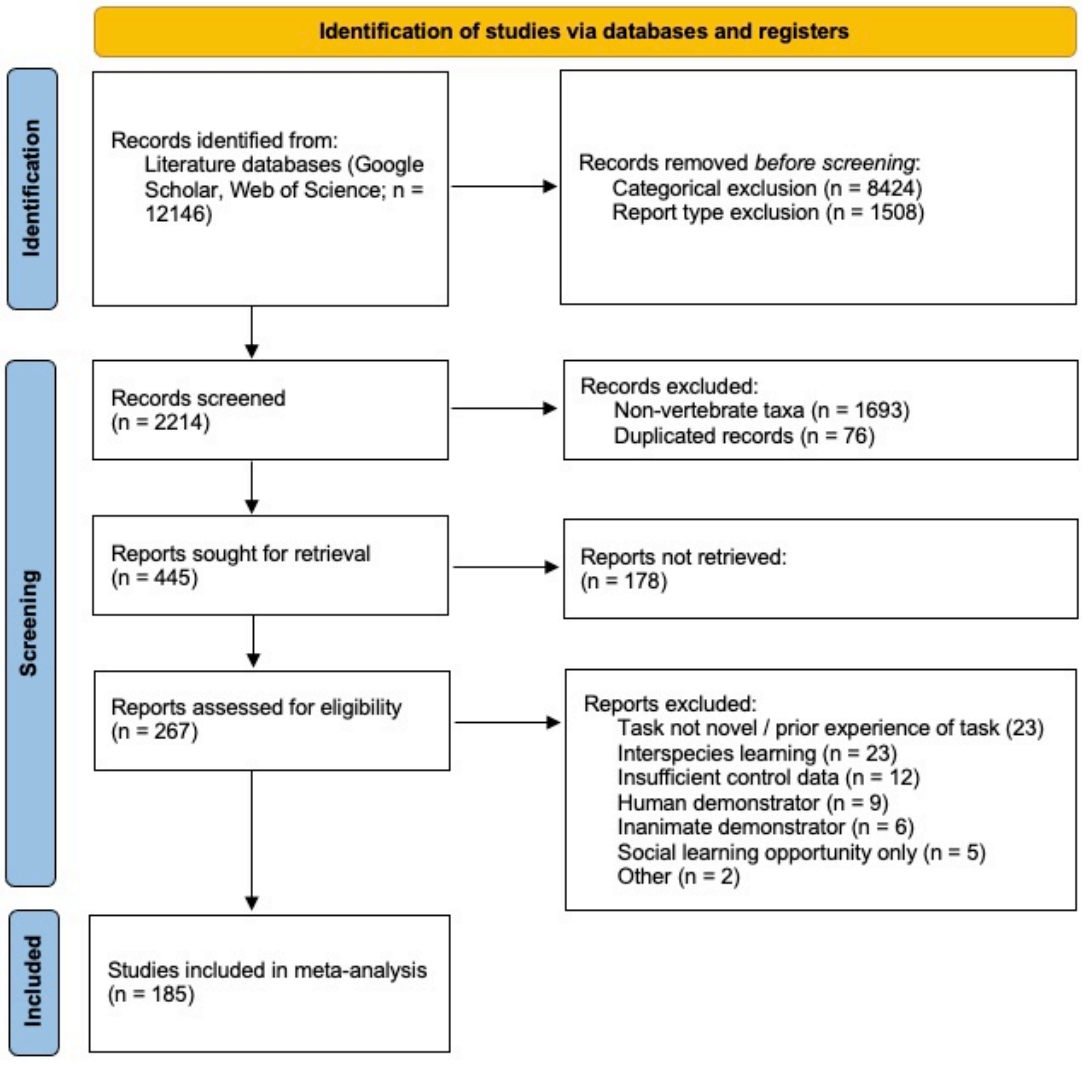


Figure 2.1: A flow diagram adapted from (Page et al., 2021) depicting the phases of the systematic literature refinement for studies included in analyses. Reports not retrieved refers to studies that were not accessible, such as removal from journal archives or authors were not contactable.

From the gathered literature, we classified tasks (Table 2.2) and experimental settings (Table 2.3) in a standardised way to allow comparison across my variables of interest. In addition, we extracted the taxonomic classification of subjects within studies. These taxonomic classifications were standardised and expanded to include species, genus, family and order according to the catalogue of life (Bánki et al., 2024) to account for changes in taxonomic classification over time. While the tasks used to test social learning could be easily classified across studies, the mechanisms of social learning reported by the authors was less amenable to assignment because of the lack of consensus of social learning terms across different fields. Consequently, the mechanism of social learning was not analysed in this study. Furthermore, due to data under-reporting, the characteristics of learners and demonstrators were not included in the analyses.

Generally, the extent to which a task is completed can be measured in two ways. Firstly, researchers can measure the proportion of attempts or proportion of individuals that were successful at completing tasks. Assuming social learning increases the efficiency with which tasks are completed, this measure should increase following social learning opportunities and be higher in experimental groups than control groups. Secondly, researchers can measure the time taken to achieve task completion (often called latency). If social learning increases task efficiency, the time taken to complete tasks following social learning opportunities should decrease and be lower than control groups.

Within the gathered literature, social learning performance was therefore standardised as two main measures: firstly, as a frequency or proportion of individuals that learned a behaviour socially, and secondly, as the time taken to learn a behaviour socially (Figure 2.2). All data were extracted from the main published paper, open-source data and supplementary material. When data were only available in figures, data were extracted using Webplot Digitizer (version 4.4) when they could not be reliably read directly from the figures.

Table 2.2: Experimental task type standardised classification.

Task classification	Description of task classification	Example of task	Sample size of studies
One-step	Task that has only one step to solve, inclusive of alternative actions (such as slide left or slide right).	Open a box by lifting lid	24
Two-step	Task that requires two separate steps to solve. Steps can be completed in any order.	Open a box by sliding a bolt right and lifting a lid	25
Three-step	Task that requires three separate steps to solve. Steps can be completed in any order.	Open a box by sliding a bolt right and unscrewing a screw and lifting a lid	5
Two-sequence	Task that requires two steps to be completed in order. The order of these steps must be completed in the correct order.	Open a box by unscrewing a bolt to unlock the lid, which then must be lifted	3
Four-sequence	Task that requires four steps to be completed in order. The order of these steps must be completed in the correct order.	Open box by pulling out a pin which blocks the bolt cover, then sliding the bolt cover to the right, which exposes the screw, then unscrewing the bolt which unlocks the lid, which then must be lifted	2
Anti-predator behaviour	A learner observes a demonstrator being exposed to a novel predator or predator cue and the response of the learner is measured upon the same exposure.	A learner sees a demonstrator evade a novel predator.	19
Matching stimuli	A learner must produce the same sequence of behaviours as a demonstrator. This differs from other tasks as it utilises non-natural actions such as use of a touchscreen	Demonstrator touches 4 dots in sequence on a touchscreen to gain a reward	1
Mate choice	A learner is exposed to demonstrator choice of mating partner and the response of the learner is measured upon the same exposure.	A learner observes a demonstrator choosing a mating partner	5

Migration	A learner is exposed to migratory behaviour or sequence of routes with a time component	A naïve learner is translocated into a population that has established migratory routes; the learner can then travel the same route	1
Novel food capture	A learner observes a demonstrator capture food in a novel way	A learner bat observes a demonstrator glean an insect from a tree trunk	4
Novel food choice	A learner observes demonstrator make a choice of which novel food type to eat and is then offered the same choice	A learner observes a demonstrator exposed to novel foods, one is blue and the other is red. The demonstrator chooses blue. The learner is then offered the same choice.	37
Novel food manipulation	A learner observes demonstrator manipulate or open a known food in a novel way	A young orangutan observes their mother open a fruit by squeezing rather than peeling	2
Novel natural behaviour	A learner observes demonstrator perform a novel behaviour which is an extension of a used natural behaviour.	A lemur dips their tail into water and then drinks from it, individuals who didn't previously do this can then perform this novel behaviour	7
Novel object choice	A learner observes demonstrator make a choice of which novel object to interact with and is then offered the same choice	A learner observes demonstrator exposed to 2 novel objects, one is blue and the other is red. The demonstrator chooses blue. The learner is then offered the same choice.	1
Patch choice	A learner observes demonstrator choose or interact with an area; they are then offered a choice between this location and another novel area	A demonstrator is offered a choice between moving towards locations 1 or 2, a learner observes this choice and is then offered the same choice following this	36
Route choice	A learner observes demonstrator move through or along a route, the learner is then offered a choice to move along the same route or an undemonstrated route	The demonstrator is presented with 2 holes and chooses to move through one of them which the learner observes. The learner is then offered the same choice.	13
Tool use	A leaner observes a demonstrator use a tool and then can attempt to use the tool alone. This differs to 'action' tasks as tool use requires numerous physical and cognitive processes which are difficult to quantify.	A demonstrator chimp fishes for termites using a tool they fashioned; a learner can then attempt to do the same.	4

Transitive inference	A learner observes an interaction between 2 demonstrators, based off information gathered from this observation, the learner's response to one of the demonstrators is measured.	Demonstrator A defeats demonstrator B. Demonstrator B then defeats the learner. The response of the learner to demonstrator A is then measured.	1

Table 2.3: Classification of experimental setting described by included studies.

Experimental setting	Description of experimental setting	Sample Size
Captive	Subjects were obtained from and housed in captive settings such as zoological collections or laboratories and the experiment was conducted in controlled conditions in an enclosure or laboratory.	104
Captured	Subjects were obtained from wild or semi-wild populations and brought into controlled conditions in an enclosure or laboratory for the duration of the experiment.	45
Semi-wild	Subjects lived within an enclosed or managed population that were only partially reliant upon humans for survival (such as a sanctuary or soft release enclosure). The experiment also took place in this area.	2
Wild	Subjects were in their natural habitat and were able to participate in the social learning task free of human interference.	33
Unlisted	Study did not specify the origin of subjects or where the experiment took place.	1

2.3 Statistical analysis

All statistical analyses were conducted on R v2023.06.02 build 561. To address our first aims (1a-c) about the representation of taxonomy and variation in task type and experimental setting, Chi-squared tests with Fischer's exact test and Monte Carlo simulations (to account for low sample size) were conducted. This was followed by pairwise comparisons with Bonferroni correction applied to account for multiple comparisons, to assess biases in the literature. Specifically, we conducted four Chi-squared tests to assess taxonomic bias (Aim 1a) within the class, order and family taxonomic levels. We did not conduct any statistical analyses regarding genus or species as a deviation from expected taxonomic frequencies at lower taxonomic levels is unavoidable (Rosenthal et al., 2017). Expected taxonomic frequencies were generated from the recorded number of species within each taxon as a proportion of total number of species in Chordata in the Catalogue of Life (Roskov et al., 2023). Furthermore, we conducted two further Chi-squared tests, one to assess variation in task presentation (Aim 1b) and one test to assess variation in experimental setting (Aim 1c). When experimental setting was unlisted, these data were removed from the Chi-squared analysis.

To address the second set of research aims (2a-c), task performance following the opportunity for social learning was standardised across all studies. To determine whether tested individuals successfully learnt socially, we generated two measures of task success by comparing learners' behaviour before and after demonstrator exposure (Figure 2.2). Firstly, for studies that measured task performance following social learning opportunities as a frequency or

proportion, these data were standardised into the change in percentage of task success following social learning. Secondly, for studies that measured task performance following social learning opportunities through latency or time taken to complete a task, these data were standardised into the change in the latency to complete a task following social learning.

Figure 2.2: Standardised comparative social Learning metric

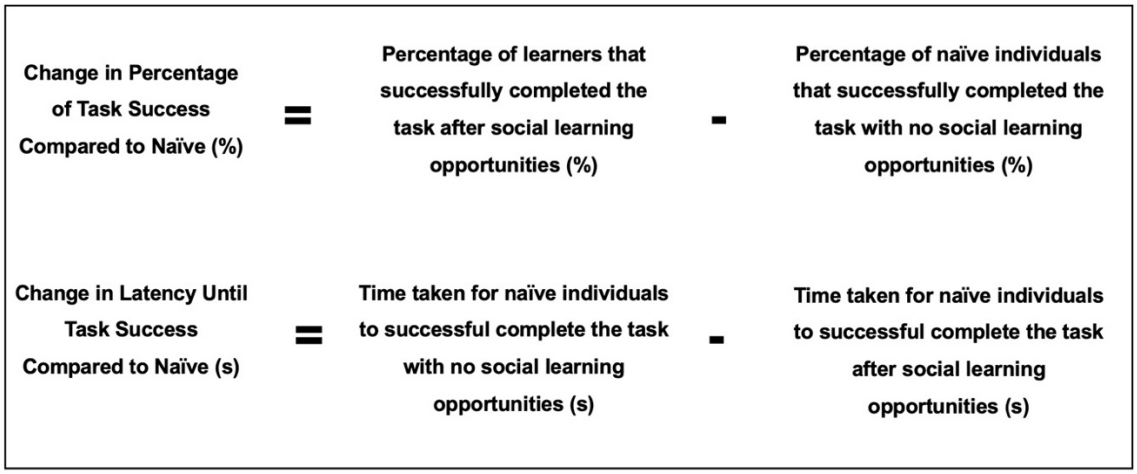


Figure 2.2: Equations used in the meta-analysis to standardise and compare task success following social learning opportunities across studies.

Comparisons of task performance following social learning (Aims 2a-c) were conducted across taxonomy, task type and experimental setting, and used the metrics of either the change in percentage of task success following social learning or the change in the latency to complete a task following social learning (summarised in table 2.4). If a data category was represented by fewer than four studies, it was not included in the analyses to improve model performance. In the first case, to address aims (2a-c) for the percentage of task success response, we conducted six ANOVAs and post hoc Tukey tests. Due to the bound proportionality of the standardised data (of values between -100 and 100) the data were transformed to range between $0 < 1$ ($(x + 100) / 200$ with e added to 0 values and taken away from values equal to 1). In the second case, to address Aims 2a-c for data measured by the change in the latency to complete a task following social learning, a further six ANOVAs and post hoc Tukey tests were run. To fit the assumptions of ANOVA, the standardised latency data were transformed to above zero values ($(x + \text{minimum value}) + 1$) and then log transformed to correct for positive skew. To ensure the model assumptions of ANOVA were met, residual normality was assured visually using Q-Q plots and statistically using a Shapiro-Wilk test (with all models showing no deviation from normality; $p > 0.05$).

Table 2.4: Table summarising statistical models 2a-c.

Research questions	Aims	Model	Total number of studies included	Number of categories in model
Taxonomic representation	1a. Assess patterns of representation across taxonomic groups	Models 1a. Chi-Sq, pairwise comparisons; Class, Order, Family	185	Class - 6 Order - 29 Family - 53
Task type variation	1b. Assess patterns of representation across social learning tasks presented in studies	Model 1b. Chi-Sq, pairwise comparisons	185	18
Experimental setting variation	1c. Assess patterns of representation across experimental settings	Model 1c. Chi-Sq, pairwise comparisons	185	5
Differences between taxa	2a. Compare task success following social learning across taxa	Models 2a. ANOVA, post-hoc Tukey; Change in percentage; Class, Order, Family _____ Change in latency; Class	Class - 149 Order - 132 Family - 102 _____ Class - 26	Class - 4 Order - 11 Family – 14 _____ Class - 3

Differences between task type	2b. Compare task success following social learning across task type	Models 2b. ANOVA, post-hoc Tukey; Change in percentage _____ Change in latency	139 _____ 21	9 _____ 3
Differences between experimental settings	2c. Compare task success following social learning across experimental setting	Models 2c. ANOVA, Post-hoc Tukey; Change in percentage _____ Change in latency	148 _____ 28	3 _____ 2

2.3 Results

2.3.1 Patterns in the literature

2.3.1.1 Taxonomic representation

Data from 153 of the 185 collated studies (83%) contributed to the comparison of change in the percentage of task success, and 32 of the 185 collated studies (17%) contributed to the comparison of change in the latency to complete a task. There were 22 studies that included both measures of task performance. In total, 103 species and 90 genera were represented (with one subspecies, and one defined only to genus). To address taxonomic bias (Aim 1a), we applied a chi-squared test to assess whether the observed frequencies of taxonomic classes (Mammalia, Aves, Actinopterygii, Reptilia, Chondrichthyes, and Amphibia) differed significantly from their expected frequencies, only jawless fish (Agnatha), coelacanths (Actinistia) and lungfish (Dipnomorpha) were not represented by at least one species in the analyses. The analysis revealed a highly significant result ($\chi 2(5) = 335.16$, $p < 0.001$), indicating substantial deviations between observed and expected proportions. Post hoc pairwise comparisons highlighted that mammals (forming 43% of all studies) exhibited significantly higher observed frequencies compared to bony fish ($Z = 5.80$, $p < 0.001$), reptiles ($Z = 10.88$, $p < 0.001$), cartilaginous fish ($Z = 11.43$, $p < 0.001$), and amphibians ($Z = 9.41$, $p < 0.001$). Similarly, birds (representing 34% of all studies) showed significantly higher frequencies compared to bony fish ($Z = 3.85$, $p < 0.01$), reptiles ($Z = 8.00$, $p < 0.001$), cartilaginous fish ($Z = 11.43$, $p < 0.001$), and amphibians ($Z = 9.41$, $p < 0.001$). In contrast, no

significant differences were observed among the remaining classes that represented 25% of studies; bony fish (17%), reptiles (4%), cartilaginous fish (2%) and amphibians (1%).

The chi-squared test conducted to evaluate whether the observed frequencies of taxonomic orders differed significantly from their expected frequencies did not yield a significant result (Figure 2,3). However, post hoc pairwise comparisons showed that studies including primates (22% of all studies) exhibited significantly higher observed frequencies compared to other orders, including Rodentia ($Z = 4.30$, $p < 0.01$), Carnivora ($Z = 5.13$, $p < 0.001$), Artiodactyla ($Z = 5.35$, $p < 0.001$), Chiroptera ($Z = 5.82$, $p < 0.001$), and Perissodactyl ($Z = 6.59$, $p < 0.001$). Similar trends were observed when comparing primates to orders with smaller observed frequencies such as Diprotodontia, Proboscidea, and Testudines, with consistently significant differences ($Z > 6.5$, $p < 0.001$). The order Passeriformes (22% of all studies) also showed significantly higher frequencies compared to other orders, including Carnivora ($Z = 4.91$, $p < 0.001$), Chiroptera ($Z = 5.82$, $p < 0.001$), and Perissodactyl ($Z = 6.59$, $p < 0.001$). Analyses of the observed frequencies of taxonomic families did not yield any significant results, nor did pairwise comparisons. Within the two most common orders, there were 23 perching bird species (Passeriformes) and 16 primate species (with one primate subspecies and one described to genus). The most common mammal species was chimpanzees (*Pan troglodytes*; N = 9 studies, 12 % of mammals, 5% of all species) followed by common marmosets (*Callithrix jacchus*; N = 8 studies, 10% of mammals, 4% of all species), while the most common bird species was zebra finches (*Taeniopygia guttata*; N = 8 studies, 13% of birds, 4% of all species) followed by domestic chickens (*Gallus* gallus; N = 7 studies, 11% of birds, 4% of all species).

Figure 2.3: Taxonomic representation in social learning studies

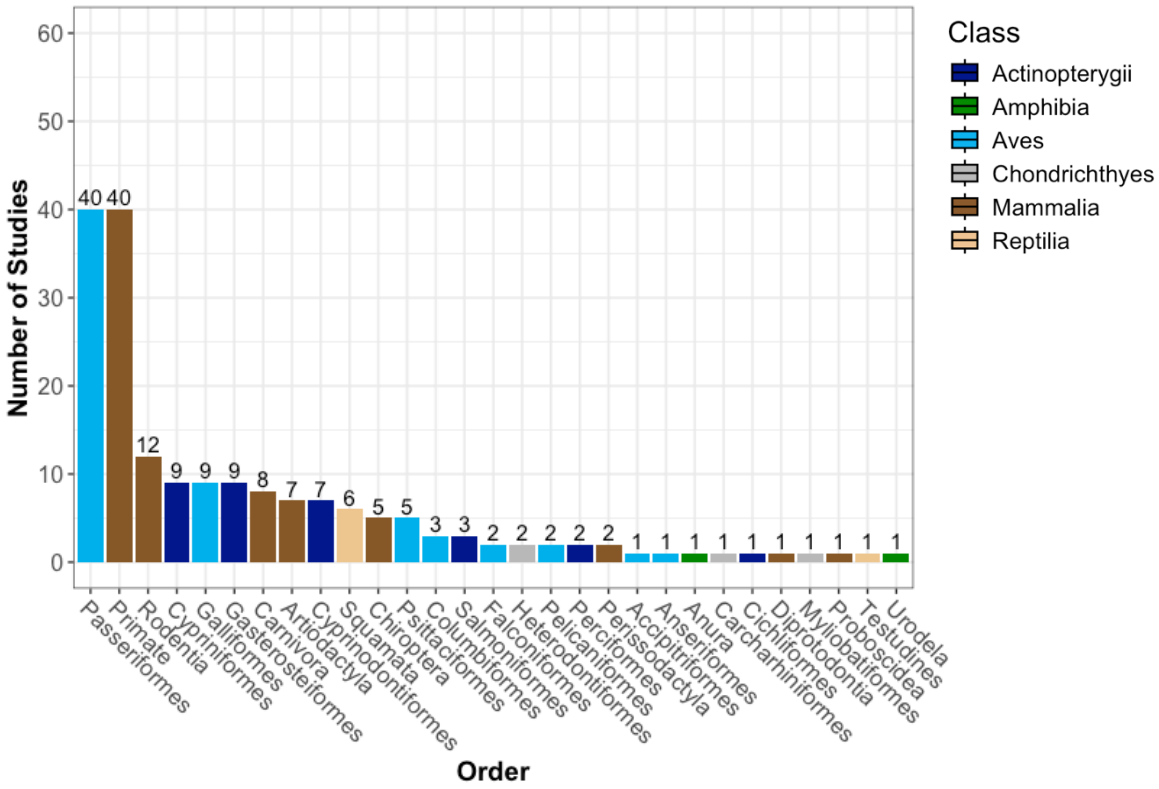


Figure 2.3: Bar plot of the number of studies per taxonomic order (coloured by taxonomic class) that met our eligibility criteria for comparative analyses. The number of studies within each taxonomic order are represented above the relevant bar.

2.3.1.2 Variation in task type presented

In total, 190 social learning tasks were conducted across the 185 studies (Figure 2.4), with 178 studies presenting a single task, four studies presenting two tasks and one study presenting three tasks to its subjects (of multiple species). To assess variation in the frequency that task types were presented (Aim 1b), we applied a Chi-squared test to task type. We found task types were not represented equally in the sample ($\chi^2(2) = 57.691$, $p < 0.001$). Post hoc analyses identified that the novel food choice task was significantly more

frequent that anti-predator behaviour tasks ($Z = 4.03$, $p < 0.01$), route choice tasks ($Z = 5.37$, $p < 0.001$), novel natural behaviour tasks ($Z = 7.72$, $p < 0.001$) and tasks such as tool use, two-sequence and four-sequence ($Z > 7.00$, $p < 0.001$). Similarly, patch choice tasks exhibited significantly higher frequencies than anti-predator behaviour tasks ($Z = 3.81$, $p < 0.05$), route choice tasks ($Z = 5.15$, $p < 0.001$), and novel natural behaviour tasks ($Z = 6.49$, $p < 0.001$). Tasks such as one-step and two-step also had significantly higher frequencies compared to rarer tasks like novel food capture and tool use ($Z > 8.00$, $p < 0.001$). These differences were also pronounced between highly observed tasks such as novel food choice and underrepresented tasks such as migration or novel object choice ($Z > 8.00$, $p < 0.001$).

Half of the tasks presented (48%) gave learners a single choice of behaviours to perform such as a novel food choice (20%), patch choice (20%), route choice (7%), mate choice (6%) or novel object choice (1%). Tasks requiring multiple steps, a sequence of steps or use of a tool to complete the task represented 21% of presented tasks (multiple actions; 16.4%, sequence of actions; 3%, tool use; 2%). Tasks that involved learning a new, naturally occurring behaviour represented 18% of studies including anti-predator behaviour (13%), novel natural behaviours (4%), novel food capture (2%), novel food manipulation (1%) and migration (1%). With respect to how task types varied between taxa, the most common task for the two most common mammal species (chimpanzees and common marmosets) was a two-step task (N = 5 tasks, 26% of studies involving these two species) followed by a one-step task (N = 4 tasks, 21% of studies involving these two species). In comparison, the most common task for the two most common bird species (zebra finches and domestic chickens) was

a novel food choice task (N = 5 tasks, 31 % of studies involving these two species) followed by a mate choice task (N = 3 tasks, 19 % of studies involving these two species).

Figure 2.4: Task representation in social learning studies

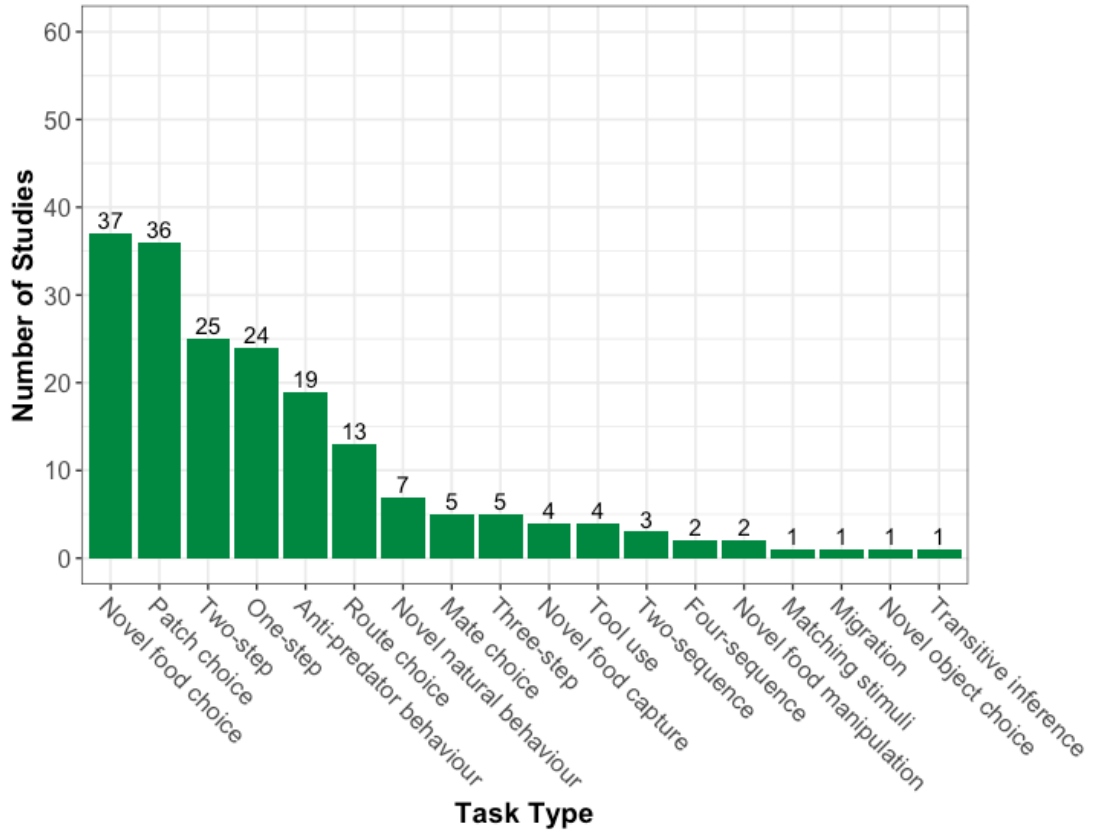


Figure 2.4: Bar plot of the number of studies that presented similar task types (Table 2.2) that met our eligibility criteria for comparative analyses. The number of studies within task type are represented above the relevant bar.

2.3.1.3 Variation in experimental setting

Within 185 studies, 183 presented social learning tasks within a single experimental setting, one study presented tasks to captive and captured learners and another study to captured and semi-wild learners (Appendix Table A1.2). To assess variation in the experimental setting and source population of

subjects in my sample, we applied a Chi-squared test to experimental setting categorisation (Figure 2.5). Experimental settings were not represented equally in this sample ($\chi^2(3) = 118.91$, $p < 0.001$). Post hoc analyses revealed that studies taking place in captive settings were observed at significantly higher frequencies in the sample than captured settings ($Z = 7.10$, $p < 0.001$), wild settings ($Z = 8.55$, $p < 0.001$), and semi-wild settings ($Z = 12.28$, $p < 0.001$). Additionally, experiments taking place with captured subjects were observed at higher frequencies than semi-wild ($Z = 5.18$, $p < 0.001$), whilst wild settings were also more frequent than semi-wild settings ($Z = 3.73$, $p < 0.01$).

The most common experimental setting in the analyses was in laboratory conditions or in zoological collections (81%), with subjects obtained from captive populations (57%) overrepresented in my sample and captured from wild populations representing close to expected representation (25%). Social learning tasks presented to wild subjects in wild conditions were underrepresented in the sample (18%). With respect to how experimental setting varied between taxa, the most common setting for the two most common mammal species (chimpanzees and common marmosets) was in captivity (N = 12 settings, 70% of studies involving these two species) followed by a wild setting (N = 3, 18% of studies involving these two species). In comparison, the two most common bird species (zebra finches) both took place entirely within captive settings (N = 15 settings, 100% of studies involving these two species). With respect to how experimental setting varied between task, the most common setting for the two most common tasks (novel food choice and patch choice) was in captive settings (N = 38 settings, 20% of studies involving these two tasks) followed by a setting whereby individuals were captured from wild

populations and housed in captivity (N = 23, 12% of studies involving these two tasks).

Figure 2.5: Experimental setting representation in social learning studies

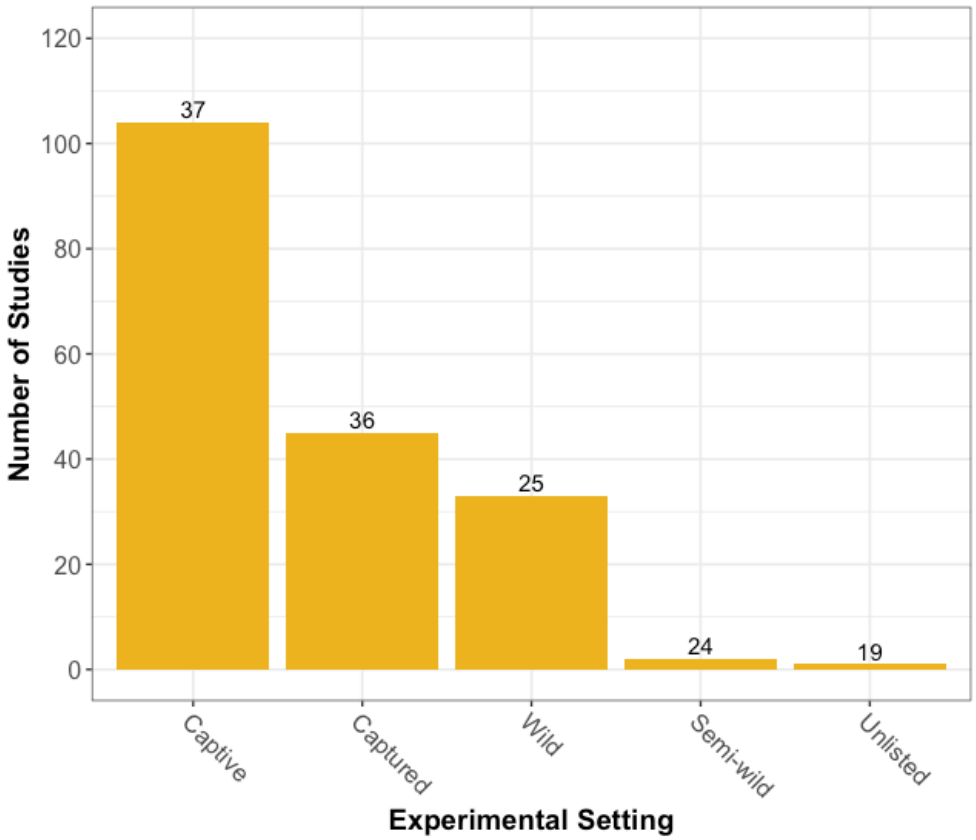


Figure 2.5: Bar plot of the number of studies that took place in different experimental settings (Table 2.3) that met our eligibility criteria for comparative analyses. The number of studies within each experimental setting are represented above the relevant bar.

2.3.2 Comparative social learning

2.3.2.1 Social learning across taxa

We compared difference in performance for social learners compared to asocial learners through both the change in percentage of task success and the change in the latency to complete a task following opportunities for social learning. To begin with Aim 2a, we specifically addressed the influence of taxonomic levels

(class, order, family and species) on task performance. To allow comparisons within taxonomic levels, we ran three analysis of variance (ANOVA) and three post-hoc Tukey tests to assess the percentage change in task performance. However, due to a low sample size of available studies (< 4 studies per taxonomic category) we were only able to assess the latency change in task performance in the class level (Table 2.4.).

An analysis of percentage change (Table 2.5.) in task success in learners compared to naïve individuals, revealed significant differences at the class ($F(3,1078) = 13.48$, $p < 0.001$), order ($F(10,962) = 11.44$, $p < 0.001$; Figure 2.5) and family levels ($F(13,809) = 10.85$, $p < 0.001$). At the class level, post hoc comparisons (Table 2.6.) revealed that birds exhibited lower proportional changes compared to bony fish ($\Delta = -0.092$, $p < 0.001$) and mammals ($\Delta = 0.035$, $p < 0.01$). Furthermore, mammals had lower proportional change than bony fish ($\Delta = -0.057$, $p < 0.001$). At the order level, post hoc comparisons highlighted that Cyprinodontiformes exhibited greater proportional changes compared to Artiodactyla ($\Delta = 0.237$, $p < 0.001$), Carnivora ($\Delta = 0.213$, $p < 0.001$), and Chiroptera ($\Delta = 0.239$, $p < 0.001$). Conversely, Galliformes, Gasterosteiformes and Passeriformes showed significantly lower proportional changes compared to Cyprinodontiformes ($\Delta = -0.190$, $\Delta = -0.210$, and $\Delta = -0.204$, respectively, all $p < 0.001$). Notably, Primate orders demonstrated higher proportional changes than Gasterosteiformes ($\Delta = 0.076$, $p < 0.05$) and Passeriformes ($\Delta = 0.069$, $p < 0.001$). At the family level, Poeciliidae showed significantly higher proportional changes compared to families like Cebidae ($\Delta = 0.115$, $p < 0.05$), Cercopithecidae ($\Delta = 0.144$, $p < 0.001$), and Estrildidae ($\Delta = 0.210$, $p < 0.001$). In contracts, families such as Strunidae exhibited lower

proportional changes compared to Poeciliidae (Δ = -0.265, $p < 0.001$). An analysis of latency change in time taken until task success in learners compared to naïve individuals, revealed no significant differences at the class level (Table 2.5; Figure 2.6), nor between classes in a post hoc test (Table 2.6.).

Table 2.5: Results of ANOVA tests comparing task success following opportunities for social learning in percentage change and change in latency across different taxonomic levels. Due to small sample sizes, ANOVA could not be conducted on taxonomic levels below class regarding latency.

Measure	Taxonomic level	Df	Sum Sq	F	P
Percentage change from naïve	**Class**	**3, 1078**	**1.087**	**13.48**	**< 0.001**
	Order	**10, 962**	**2.917**	**11.44**	**< 0.001**
	Family	**13, 809**	**3.258**	**10.85**	**< 0.001**
Change in latency from naïve	Class	2, 244	0.001	2	0.138
	Order	-	-	-	-
	Family	-	-	-	-

Table 2.6: Results of post hoc Tukey tests comparing task success following opportunities for social learning in percentage change and change in latency across different taxonomic levels within ANOVA models. Due to small samples sizes, post hoc tests could not be conducted regarding latency.

Measure	Taxonomic level	Comparison	Difference	Lower bound	Upper bound	P
Percentage change from naïve	Class	Aves - Actinopterygii	-0.092	-0.131	-0.053	< 0.001
		Mammalia - Actinopterygii	-0.057	-0.096	-0.018	< 0.001

		Mammalia - Aves	0.035	0.007	0.063	< 0.01
	Order	Cyprinodontiformes - Artiodactyla	0.237	0.097	0.377	< 0.001
		Cyprinodontiformes - Carnivora	0.213	0.109	0.317	< 0.001
		Cyprinodontiformes - Chiroptera	0.239	0.128	0.350	< 0.001
		Primate - Chiroptera	0.104	0.011	0.196	< 0.05
		Galliformes - Cyprinodontiformes	-0.190	-0.280	-0.100	< 0.001
		Gasterosteiformes - Cyprinodontiformes	-0.210	-0.307	-0.113	< 0.001
		Passeriformes - Cyprinodontiformes	-0.204	-0.279	-0.129	< 0.001
		Primate - Cyprinodontiformes	-0.135	-0.211	-0.059	< 0.001
		Rodentia - Cyprinodontiformes	-0.199	-0.293	-0.106	< 0.001
		Primate - Gasterosteiformes	0.076	0.001	0.151	< 0.05
		Primate - Passeriformes	0.069	0.026	0.112	< 0.001
	Family	Estrildidae - Callitrichidae	-0.104	-0.204	-4.731	< 0.05
		Paridae - Callitrichidae	-0.143	-0.256	-3.016	< 0.01
		Phyllostomidae - Callitrichidae	-0.140	-0.268	-1.241	< 0.05
		Sturnidae - Callitrichidae	-0.157	-0.315	-2.285	< 0.05
		Estrildidae - Cebidae	-0.097	-0.188	-7.040	< 0.05
		Paridae - Cebidae	-0.136	-0.242	-3.128	< 0.01
		Phyllostomidae - Cebidae	-0.133	-0.254	-1.255	< 0.05
		Poeceiliidae - Cebidae	0.115	0.008	2.214	< 0.05
		Estrildidae - Cercopithecidae	-0.068	-0.130	-6.936	< 0.05
		Paridae - Cercopithecidae	-0.108	-0.189	-2.577	< 0.001
		Phyllostomidae - Cercopithecidae	-0.105	-0.206	-3.338	< 0.05
		Poeciliidae - Cercopithecidae	0.144	0.060	2.274	< 0.001
		Poeciliidae - Corvidae	0.172	0.041	3.024	< 0.001

		Pyllostomidae - Corvidae	-0.139	-0.269	-9.692	< 0.05
		Paridae - Cyprinidae	0.212	0.134	2.904	< 0.05
		Poeciliidae - Estrildidae	0.210	0.114	3.066	< 0.001
		Paridae - Hominidae	-0.106	-0.194	-1.738	< 0.001
		Peociliidae - Hominidae	0.146	0.056	2.356	< 0.01
		Peociliidae - Muridae	0.194	0.090	2.986	< 0.001
		Peociliidae - Paridae	0.251	0.156	3.463	< 0.001
		Peociliidae - Phasianidae	0.190	0.100	2.790	< 0.001
		Peociliidae - Phyllostomidae	0.248	0.136	3.605	< 0.001
		Sturnidae - Poeciliidae	-0.265	-0.410	-1.204	< 0.001
Change in latency from naïve	Class	-	-	-	-	-
	Order	-	-	-	-	-
	Family	-	-	-	-	-

Figure 2.6: Percentage change in task completion from naïve according to taxonomic order

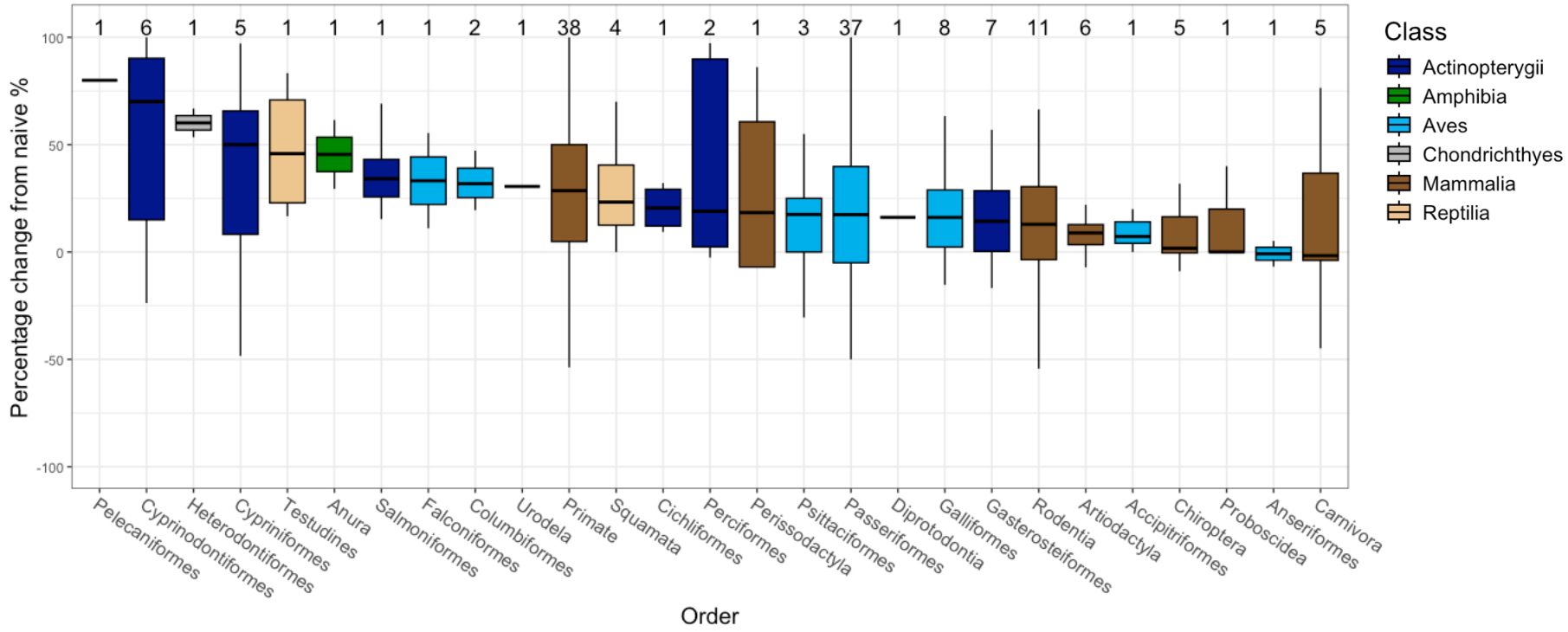


Figure 2.6: Box and whisker plot depicting the percentage change of learners to solve social learning tasks according to taxonomic order following social learning opportunities compared to naïve individuals (calculated through figure 2.2) across all task types and experimental settings. Colours represent the taxonomic class (key) that taxonomic orders sit within. Numbers above each box represent the number of studies within the meta-analysis, only taxonomic orders represented by four or more studies were included in the analyses.

Figure 2.7: Change in latency until task completion from naïve according to taxonomic order

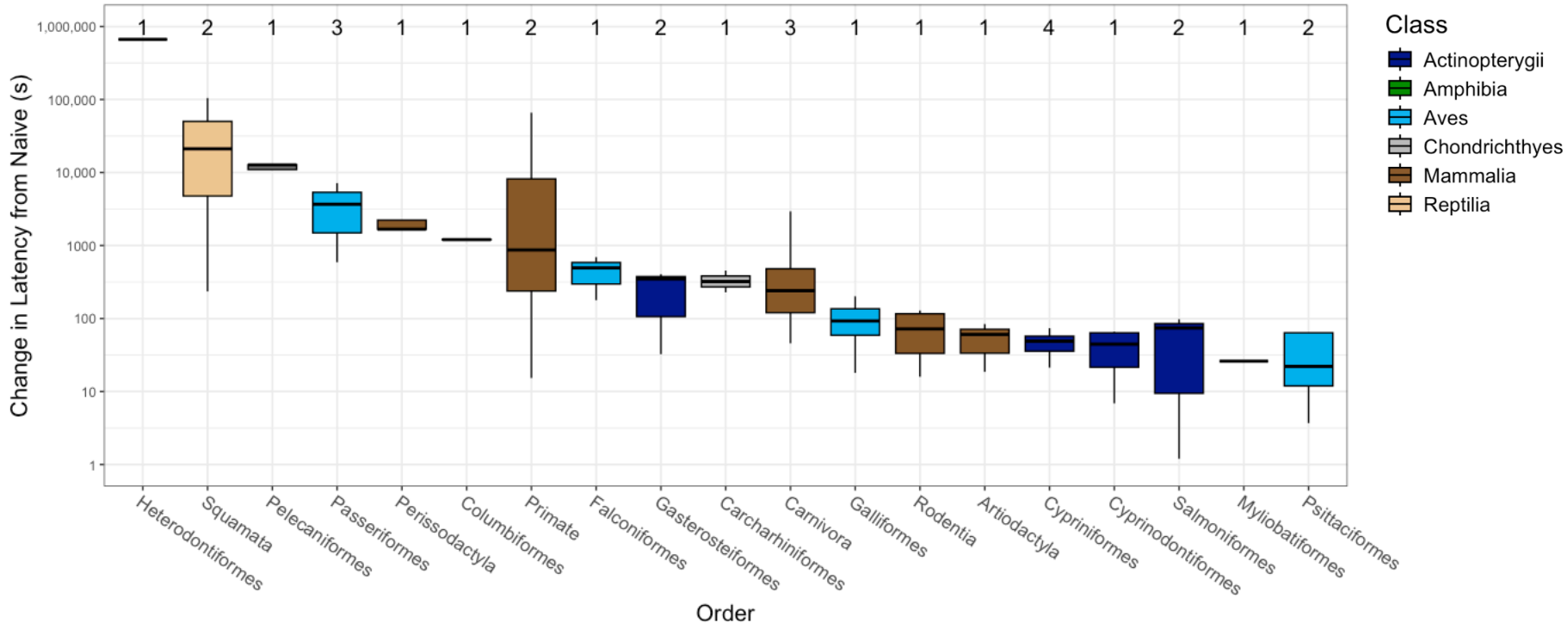


Figure 2.7: Box and whisker plot depicting the improvement in latency (s) of learners to solve social learning tasks according to taxonomic order following social learning opportunities compared to naïve individuals (calculated through figure 2.2) across all task types and experimental settings. Colours represent the taxonomic class (key) that taxonomic orders sit within. Numbers above each box represent the number of studies within the meta-analysis, only taxonomic orders represented by four or more studies were included in the analyses.

2.3.2.2 Impact of task type on task success following social learning

In order to address Aim 2b, we assessed the impact of social learning task type on task performance. The analysis revealed a significant effect of task type on the change in percentage success of learners compared to naïve individuals ($F(8,960) = 8.014$, $p < 0.001$; Table 2.7; Figure 2.7). Post hoc comparisons (Table 2.8) indicated that one-step tasks exhibited greater proportional changes compared to anti-predator behaviour ($\Delta = 0.088$, $p < 0.05$) and novel food choice tasks ($\Delta = 0.128$, $p < 0.001$). Similarly, patch choice tasks had significantly higher proportional changes compared to novel food choice tasks ($\Delta = 0.068$, $p < 0.001$). In contract, three-step tasks exhibited significantly lower proportional changes compared to one-step tasks ($\Delta = -0.174$, $p < 0.001$), patch choice ($\Delta = -0.114$, $p < 0.001$), and route choice tasks ($\Delta = -0.116$, $p < 0.05$). Two-step tasks also showed significantly lower proportional changes than one-step tasks ($\Delta = -0.084$, $p < 0.05$) but higher proportional changes than three-step tasks ($\Delta = 0.089$, $p < 0.05$). The analysis of latency changes across tasks revealed a marginally non-significant overall effect ($F(2,136) = 3.048$, $p = 0.051$; Table 2.7; Figure 2.8). However, post hoc comparisons indicated that route choice tasks were completed significantly faster than one-step tasks ($\Delta = -0.670$, $p < 0.05$; Table 2.8).

Table 2.7: Results of ANOVA tests comparing task success following opportunities for social learning in percentage change and change in latency according to task type.

Measure	Df	Sum Sq	F	P
Percentage change from naïve	**8, 960**	**1.630**	**8.014**	**< 0.001**
Change in latency from naïve	2, 136	7.660	3.048	0.051

Table 2.8: Results of post hoc Tukey tests comparing task success following opportunities for social learning in percentage change and change in latency across different task types within ANOVA models.

Measure	Comparison	Difference	Lower bound	Upper bound	P
Percentage change from naïve	One step – Anti-predator behaviour	0.088	0.006	0.170	< 0.05
	Three step – Anti-predator behaviour	-0.086	-0.170	-0.001	< 0.05
	One step – Novel food choice	0.128	0.060	0.197	< 0.001
	Patch choice – Novel food choice	0.068	0.025	0.111	< 0.001
	Three step – One step	-0.174	-0.265	-0.082	< 0.001
	Two step – One step	-0.084	-0.162	-0.007	< 0.05
	Three step – Patch choice	-0.114	-0.188	-0.039	< 0.001

	Three step – Route choice	-0.116	-0.231	-0.001	< 0.05
	Two step – Three step	0.089	0.009	0.170	< 0.05
Change in latency from naïve	Route choice – One step	-0.670	-1.319	-0.022	< 0.05

Figure 2.8 Percentage change in task completion from naïve according to task type presented

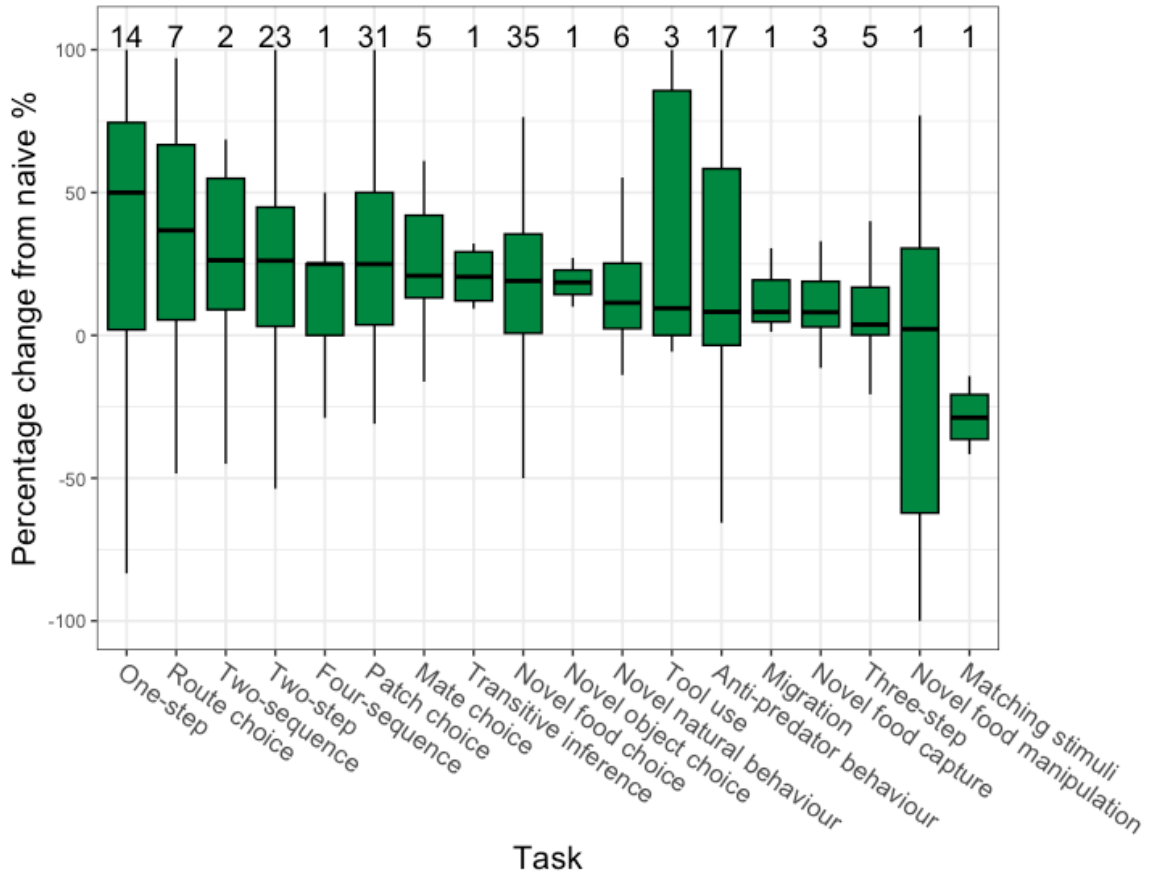


Figure 2.8: Box and whisker plot depicting the percentage change of learners to solve social learning tasks according to the task type presented following social learning opportunities compared to naïve individuals (calculated through figure 2.2) across all taxa and experimental settings. Numbers above each box represent the number of studies within the meta-analysis, only task types represented by four or more studies were included in the analyses.

Figure 2.9: Change in latency until task completion from naïve according to task type presented

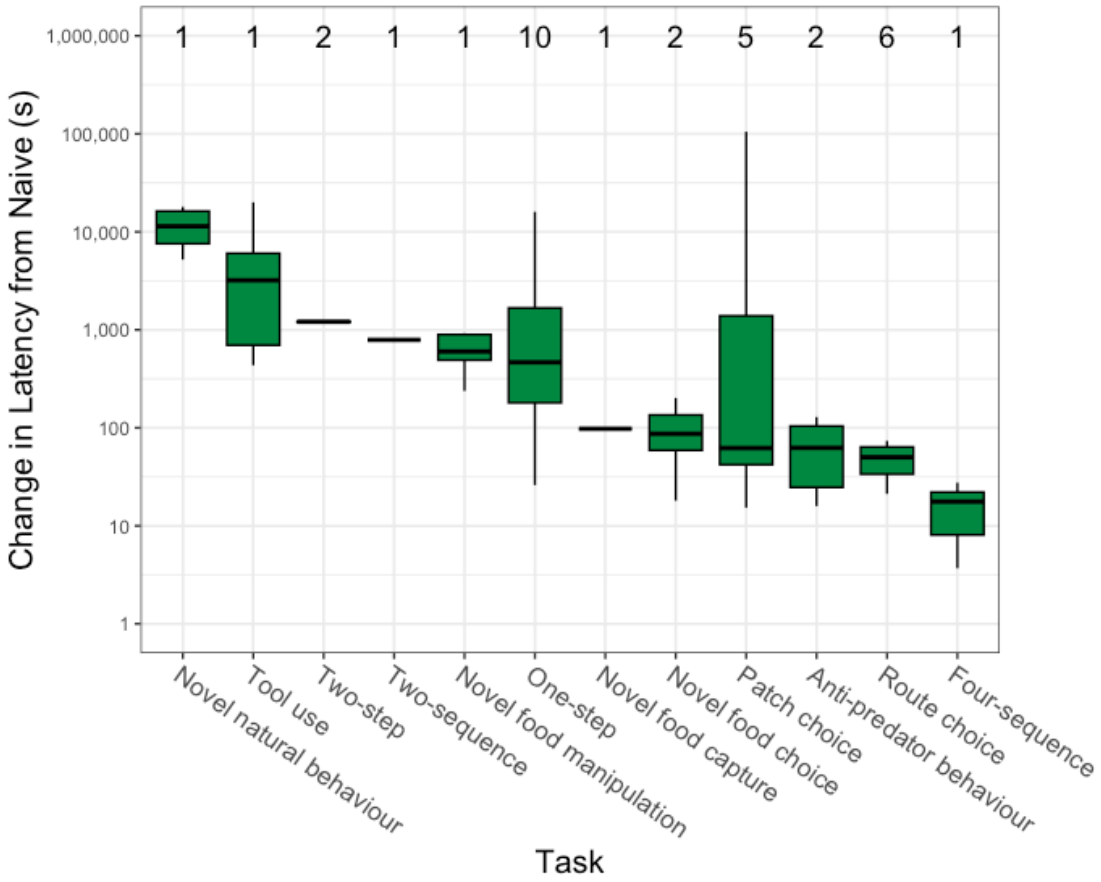


Figure 2.9: Box and whisker plot depicting the improvement in latency of learners to solve social learning tasks according to task type presented following social learning opportunities compared to naïve individuals (calculated through figure 2.2) across all taxa and experimental settings. Numbers above each box represent the number of studies within the meta-analysis, only task types represented by four or more studies were included in the analyses.

2.3.2.3 Impact of experimental setting on task performance

In order to address Aim 2c, we assessed the impact of the experimental setting and the origin of experimental subjects on task performance. The analysis on the change in percentage of task success of learners compared to naïve individuals revealed a significant effect across experimental settings ($F(2,1065) = 3.455$, $p < 0.05$; Table 2.9; Figure 2.9). Post hoc comparisons (Table 2.10) indicated that individuals from wild populations exhibited significantly greater proportional changes compared to captured individuals ($\Delta = 0.042$, $p < 0.05$). However, no other significant differences were observed among experimental settings. The analysis of latency changes revealed a significant effect of experimental setting ($F(1,225) = 6.701$, $p < 0.05$; Table 2.9; Figure 2.10). Post hoc comparisons (Table 2.9) showed that captured individuals exhibited significantly shorter latencies compared to captive individuals ($\Delta = -0.005$, $p < 0.05$).

Table 2.9: Results of ANOVA tests comparing task success following opportunities for social learning in percentage change and change in latency according to experimental setting.

Measure	Df	Sum Sq	F	P
Prop	**2, 1065**	**0.191**	**3.455**	**< 0.05**
Latency	**1, 225**	**0.001**	**6.701**	**< 0.05**

Table 2.10: Results of post hoc Tukey tests comparing task success following opportunities for social learning in percentage change and change in latency across different experimental settings within ANOVA models.

Measure	Comparison	Difference	Lower bound	Upper bound	p
Prop	Wild - Captured	0.042	0.003	0.080	< 0.05
Latency	Captured - Captive	-0.005	-0.009	-0.001	< 0.05

Figure 2.10: Percentage change in task completion from naïve according to experimental setting

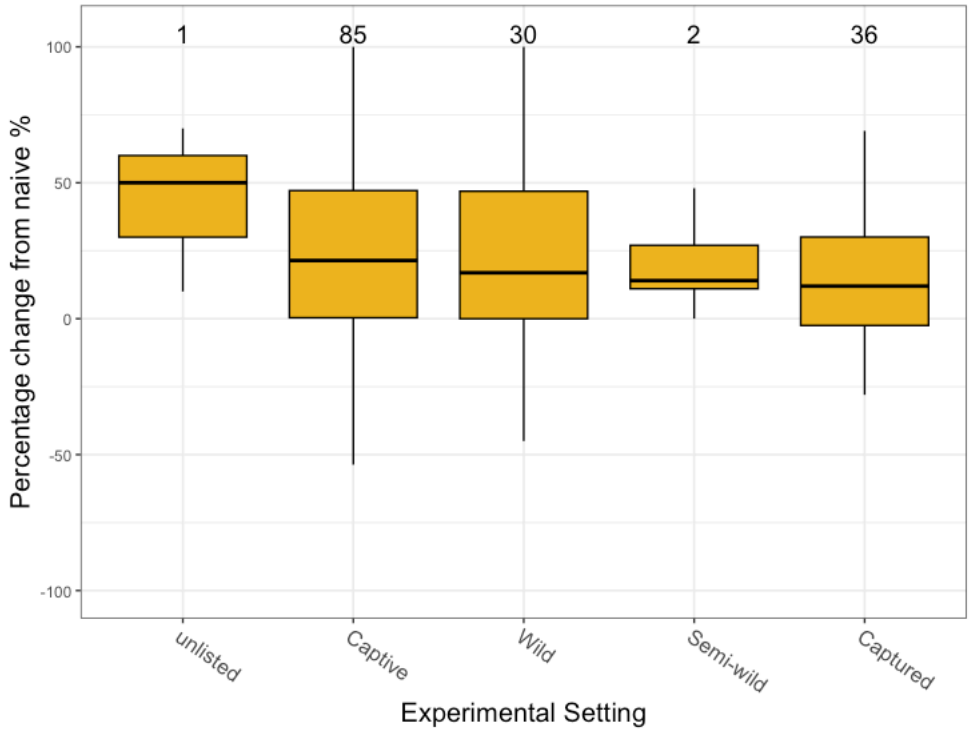


Figure 2.10: Box and whisker plot depicting the percentage change of learners to solve social learning tasks according to the experimental setting that tasks were presented following social learning opportunities compared to naïve individuals (calculated through figure 2.2) across all taxa and tasks presented. Numbers above each box represent the number of studies within the meta-analysis, only experimental settings represented by four or more studies were included in the analyses, unlisted experimental settings were removed prior to analysis.

Figure 2.11: Change in latency until task completion from naïve according to experimental setting

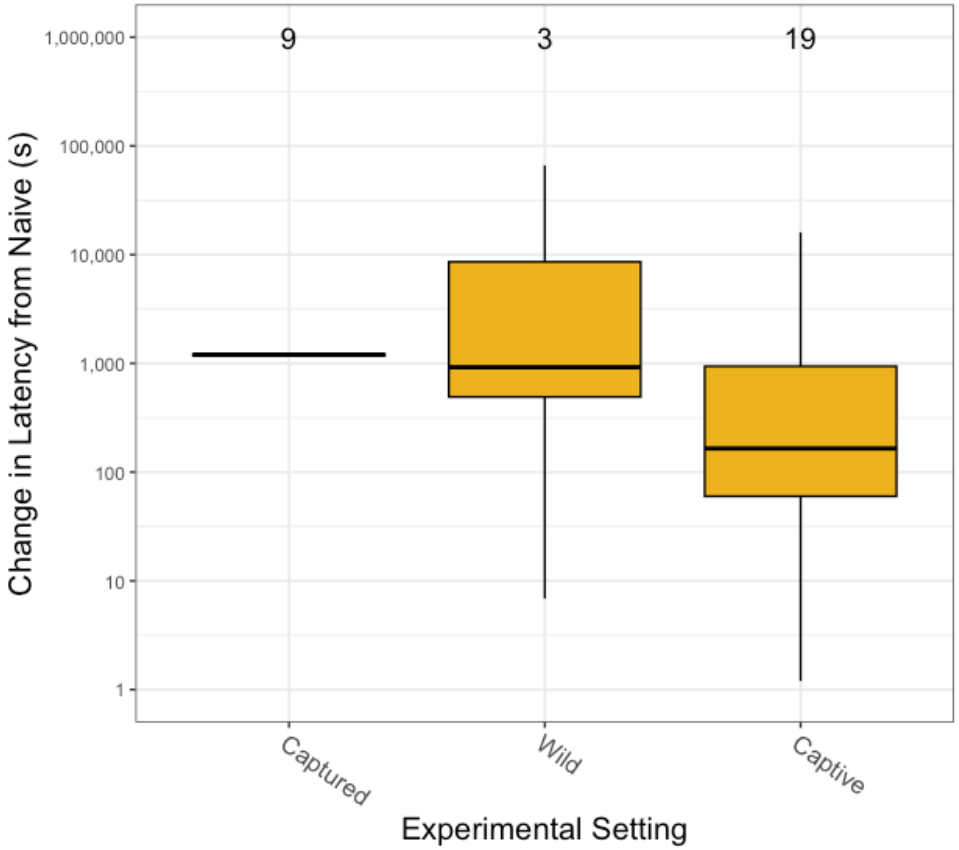


Figure 2.11: Box and whisker plot depicting the improvement in latency of learners to solve social learning tasks according to the experimental setting tasks were presented following social learning opportunities compared to naïve individuals (calculated through figure 2.2) across all taxa and task types presented. Numbers above each box represent the number of studies within the meta-analysis, only experimental settings represented by four or more studies were included in the analyses.

2.4 Discussion

The purpose of this study was to assess representation and variation in the social learning literature whose measures of social learning could be used comparatively. We found significant variation in taxonomic representation, task type presented and experimental setting across studies that met the eligibility criteria for comparative analyses. Birds and mammals (particularly Passeriformes and primates) were heavily over-represented, with over 75% of comparable studies including these taxonomic classes, despite them accounting for less than 25% of all vertebrate species. When assessing the social learning task presented to subjects within our study sample, we found that half of the tasks presented (48%) gave learners a single choice of behaviours to perform (such as novel food choice) whereas tasks requiring multiple steps represented 21% of presented tasks (such as multi-step tasks). Furthermore, the experimental setting that tasks were presented in were frequently located in laboratory conditions or in zoological collections (81% of all studies), with subjects bred in captivity or captured from wild populations representing 57% and 25% of all studies respectively. When comparing task success following opportunities for social learning across taxa, the guppy family (Poecilia), and bony fish in general showed the greatest improvement in task completion percentage change. Out of the two most represented taxonomic orders in this sample, primates demonstrated a greater overall improvement in task success than perching birds (Passeriformes). Through assessing the impact of task type presented on task success, we also found that task success following social learning opportunities was highest when tasks required fewer steps to solve (§1.7.5: simple tasks). Out of the two most common tasks

presented, improvement in task success was greater for patch choice tasks than novel food choice tasks. Finally, we found that wild individuals showed a higher proportional change in task success than captured individuals, and that captured individuals solved tasks faster than captively bred individuals. Below we will discuss how the discipline of comparative social learning is developing, the implications of our comparative results and future directions for comparative social learning.

The taxonomic biases found in this study are likely present for multiple reasons, including tractability and the personal preferences of researchers. Such a taxonomic bias is reflective of a wider mammalian and avian bias in animal behaviour, biodiversity and conservation research (Donaldson et al., 2017; dos Santos et al., 2020; Rosenthal et al., 2017; Troudet et al., 2017). A great degree of mammals and birds are social (Aplin, 2019; Clutton-Brock, 2021), and are known to be reliant upon social learning for the inheritance of charismatic behaviours such as tool-use (Coelho et al., 2024; Holzhaider et al., 2010; Whiten, 2024). Cognition and social learning in primates in particular (over-represented within my sample) has been studied since the 1880s (Schwartz and Beran, 2022), due to the candidacy of primates for helping to understand how social learning evolved in humans (Byrne, 2007; Castro and Toro, 2004; Whiten and van de Waal, 2017). Mammals and birds therefore make excellent study subjects when investigating how social information is acquired, applied and exploited, and ultimately how social learning is used and evolved (van der Post et al., 2017). This study highlights that the use of a comparable metric of social learning (change in percentage in task success following opportunities for social learning), can be used to infer macroevolutionary patterns of social

learning. However, this study is limited in its statistical power due to the sample size of studies that met the criteria for comparative analyses. Nevertheless, this study found that out of the two most common taxonomic families (primates and perching birds), task success following social learning opportunities was significantly higher in primates than their avian counterparts. These findings are surprising considering that primates were mostly subjected to social learning experiments requiring specific (and often multiple) steps, whereas birds were mostly subjected to simpler choice tasks. One explanation for this pattern is that naïve primates are incapable of performing the complex tasks (§1.7.5) presented without social learning, and therefore their improvement following social learning opportunities is greater than choosing between two food items or locations that can be completed asocially. Alternatively, primates are among the most cognitively enriched animals in zoological settings (Hopper, 2017), due to legislated welfare requirements (Cronin et al., 2017), research output (Egelkamp and Ross, 2019) and visitor experience. Consequently, primates are greatly experienced in solving novel tasks due to continued exposure to forms of enrichment that could mimic novel tasks to some degree. This may explain why primates showed greater task improvement following social learning opportunities – simply due to their exposure to cognitive tasks. Together, this could indicate (although greater statistical power should be sought) that primates may be more reliant on social learning to learn potentially adaptive behaviours than birds, making social learning and therefore culture a key conservation target for primates (UNEP, 2020; CMS, 2024). Following future integration of social learning research in comparative paradigms, of which social learning research is likely to continue growing (Schuppli and Schaik, 2019), hypotheses around the comparative evolution of social learning and

phylogenetic signals in social learning ability could be investigated with greater statistical power (Kamilar and Cooper, 2013; Lycett, 2010; Ord and Martins, 2006).

The two most commonly presented tasks across studies included, tested universal behaviours regarding the location of resources (patch choice) and learning what food item to consume (novel food choice). The over-representation of these task types likely reflects the amenability of these experiments to a wide range of taxa and experimental settings, as well as serving as a proxy to more complex behaviours (Mörchen et al., 2023). In addition, studies investigating how animals learn what food items to consume or where they are located are grounded by established theoretical frameworks such as optimal-foraging theory and producer-scrounger dynamics (Charnov, 1976; King et al., 2009; King and Cowlishaw, 2009). This allows such experimental approaches to delve deeper into factors impacting social learning than studies that investigate the social transmission of behaviours where fitness benefits of acquiring such behaviours are unknown (Huebner et al., 2018; Kendal et al., 2010). By presenting multiple social learning tasks to the same subjects (or taxa), the impact of task difficulty can be linked with social learning strategies used (Laland, 2004) and most interestingly when animals switch between asocial and social learning (Kendal et al., 2005). Within this sample however, only five studies presented multiple tasks to study subjects, likely reflecting an experimental design that is easier to implement than a multi-task paradigm (Ladds et al., 2017). This comparative study highlights the usefulness of comparing social learning across multiple studies in order to include multiple taxa and task types. Despite an over-representation of

universally applicable social learning tasks in this sample, comparative analyses regarding tasks success highlighted a link between task difficulty and improvement following social learning opportunities. Specifically, task success following social learning opportunities in one-step tasks was higher than in two-step and three-step tasks (one-step > two-step > three-step). These results give further weight to previous studies that demonstrated that simpler tasks are more easily learnt from others than complex tasks (Ivanova et al., 2018; Ladds et al., 2017). However, they oppose findings from Kendal et al. (2009) whereby individuals focused the gathering of social information to facilitate learning a more complex task, and instead utilised asocial learning for simple tasks. One surprising result from these analyses was that anti-predator behaviour task improvement was not greater than tasks not linked to the immediate survival of the learner. Selection pressure for learning anti-predator behaviours rapidly and accurately is strong, as any impediment or mistake in acquiring such behaviours can result in death (Hoppitt and Laland, 2013). The severity of such mistakes means that a social learning strategy to copy behaviours when asocial learning is costly is often employed when acquiring anti-predator behaviours (Boyd and Richerson, 1985). It is therefore puzzling that across the taxonomic range in this study, individuals less effectively applied anti-predator behaviour acquired from conspecifics than one-step tasks. One explanation for this pattern could be that captive individuals (where most anti-predator behaviour experiments took place) may be habituated to captive conditions and therefore of low risk aversion to predatory behaviours. Collectively, comparing task success across task types can give insights into optimal social learning strategies and link these to specific challenges and contexts faced by learners.

Within comparable studies in this sample, social learning tasks presented to learners were mainly presented within laboratories or zoological collections. This is not surprising considering the practical and conceptual challenges of observing or seeding novel behaviours in wild animals (Morand-Ferron et al., 2016). By undertaking social learning research in controlled conditions such as these, researchers can tailor experimental designs to address specific research questions that may involve manipulating group composition to investigate how demographic factors impact social learning (Fischer, 2022; Hopper, 2017). Furthermore, an underlying issue in conducting social learning research is motivating subjects to participate in the experiment, of which it is easier to achieve in captivity where food deprivation and physical isolation of subjects is possible (Fischer, 2022). However, captive studies must account for the captivity effect when drawing species-wide conclusions, whereby captive animals often outperform their wild counterparts (Benson-Amram et al., 2013; Harrison et al., 2023). Through comparative analyses in this study, individuals in wild settings showed a greater improvement in task success following social learning opportunities than captured individuals (%), who in turn solved tasks faster than captive individuals. A possible explanation for why wild individuals would outperform captured individuals could involve a level of stress felt by individuals when captured (Dickens et al., 2010; Trondrud et al., 2022) that may impede cognitive function and therefore learning (Blackburn et al., 2022; Soravia et al., 2021). Wild individuals also face a wide variety of problem-solving situations in order to adapt to their shifting social and physical environments (Pritchard et al., 2016). Within humans, the anatomical impacts on the brain and subsequent cognitive benefits of interacting with natural environments are well documented (Baena-Extremera et al., 2024). Similarly,

although less understood, it has been suggested that the brains (and cognition) of wild animals – the wild brain – has a great deal of cogntivie flexibility due to environmental enhancements compared to ‘reduced’ anatomical and cognitive features associated with a captive brain (Clark et al., 2023). This means that captured individuals are likely more experienced at tackling novel tasks of greater complexity and/or are more flexible in applying novel approaches than captive individuals such as simple novel patch or food choices and monotonous cognitive enrichment (Clark, 2017), but this opposes the captivity effect (Forss et al., 2022). However, due to the low statistical power within the analyses, it is not possible to isolate factors that may have contributed to this pattern and more research could be conducted across social learning studies to distinguish how experimental setting impacts social learning.

Our study contributes to a recent flurry of activity in the comparative analysis of social learning (Camacho-Alpízar and Guillette, 2023; Whiten, 2024), by proposing a comparative metric of task success following social learning that can be used across taxa, task types and experimental settings. However, there are limitations to applying a standardised metric. Firstly. although every effort was made to ensure study subjects were naïve to tasks in our sample, prior experience individuals could not be accurately accounted for. Consequently, some individuals (and subsequently species) may have had a cognitive advantage when solving novel tasks or may have been differentially familiar with their learning environments (Clark et al., 2023). Furthermore, the varied life history across vertebrates included in this study is palpable and must be acknowledged. Whilst this study successfully grouped tasks into generalised categories (e.g., one-step, two-step paradigms), these tasks were originally

designed with species-specific considerations in mind. It is important to recognise that species differ in their predispositions to perform certain tasks, not due to cognitive limitations per se, but often because they have not faced the relevant selection pressures in their evolutionary histories. As such, this study strongly recommends that the interpretation of results reflect the same level of caution applied during experimental design. Specifically, the life history and ecological context of each species should be considered before drawing broad or comparative conclusions – a principle that has been emphasised throughout these analyses. Despite the above limitations to applying a standardised metric, comparative analyses suggested in this study become more robust and generalisable as a greater variety of individuals and species are incorporated (Farrar et al., 2021). In addition, greater sample sizes improve the detectability and interpretability of outliers / consistencies within the data by establishing clearer norms.

Although we compare task performance following social learning across taxa, task type and experimental setting, it was not possible to incorporate all key variables in my comparative analyses. Information related to the number, and trait characteristics, of asocial learners, social learners and demonstrators would have been very informative. Currently these data are poorly reported, as shown by Camacho-Alpízar and Guillette's (2023) comparative study of the effects of demonstrator characteristics on social learning, in which the authors were only able to use a fifth of eligible studies. It is a recommendation of this study that data that could impact social learning are clearly reported to facilitate comparative research. By conducting such research, bridges can be built between fields of cognitive psychology, neuroscience, evolutionary biology and

behavioural ecology (Kendal et al., 2018) with a goal of informing wider biological questions more achievable. In addition, as social learning and culture are discussed ever increasingly in conservation policy and practices (Brakes et al., 2025, 2021, 2019; CMS, 2024; Izaz et al., 2025; Schuppli and Schaik, 2019; UNEP, 2020), it has never been more important to understand how animals acquire, apply and exploit potentially adaptive behaviours from one another.

In conclusion, our study highlights large variation within social learning studies that passed the criteria for comparative analyses. Although we demonstrate that task performance following social learning opportunities can be compared through standardising measures, meaningful comparisons are nonetheless impacted by small sample sizes in lower taxonomic categories, complex tasks presented, and studies conducted in wild settings. We therefore recommend that future social learning studies more clearly communicate variables contained within experimental designs that could impact social learning (such as demonstrator characteristics), as well as align performance measures with previous studies (or the metrics presented in this chapter or Appendix 2) to allow comparative research. Through such standardisation and by addressing highlighted biases, wider biological questions of the mechanism, function and use of social learning can be addressed. By encouraging researchers across disciplines to adopt consistent definitions and practices, the field of social learning can better support comparative research to obtain greater insight into when and why animals use social learning.

3.0 Predictors of Participation in a Choice and Sequence Task using Multiple Touchscreens in Wild Chacma Baboons

3.1 Abstract

Participation of individuals in cognitive tests can vary due to neophobia, motivation, environment, and social factors. Inconsistent participation in cognitive experiments can lead to misleading conclusions. To better understand what might drive such inconsistencies, we explored individual patterns of participation and how these related to personal traits in a wild chacma baboon population through the first multi-touchscreen experiment conducted with wild primates. We tested 142 individuals of varying age, sex and rank across two study groups using two touchscreen tasks of differing complexity. Participation in this study was of similar recruitment level to captive studies. Using a mixed models approach, we found participation varied between individuals, with young individuals most likely to participate at least once. However, older individuals participated for the longest periods. Furthermore, no sex difference was found in the likelihood of participation, but males showed longer daily participation than females. We found that rank had no impact on participation, likely facilitated by the multi-touchscreen setup allowing low-ranking individuals to participate elsewhere if displaced by high-ranking individuals. A preference for participating in the easier task was ubiquitous across age, sex, and rank. These results suggest that predictors of individual participation can be identified, raising the possibility that future researchers might be able to design their experiments to widen participation or otherwise statistically control for the potential biases arising.

3.2 Introduction

Cognition refers to an animal's ability to acquire, process, store, and act upon information from their environment. Historically, cognitive testing on non-human animals has been conducted in controlled laboratory conditions or on captive populations housed in zoological collections and sanctuaries (§2.3.1.3; Cronin et al., 2017; Hopper, 2017a; Martin et al., 2022; Pritchard et al., 2016). Whilst captive studies have demonstrated important cognitive capacities such as tool use and understanding of fairness and cooperation, animals' use of these capacities may be restricted in the wild, leaving questions about the adaptive form of these capacities and how they evolved (Engelmann et al., 2019; Engelmann and Herrmann, 2016; Morand-Ferron et al., 2016; Rowe and Healy, 2014; Szabo et al., 2022). In captivity, multiple factors can be controlled that could affect cognitive experiments conducted in wild settings, such as food availability and predation threat. Further to this, participation in cognitive studies in captivity is often high (Fischer, 2022) through forced isolation or due to participants having more 'free-time' in captivity than in the wild, driving voluntary participation (Kummer and Goodall, 1985; Reader and Laland, 2003).

To understand what natural behaviours can influence performance in cognitive tests and their adaptive value, there has been a recent surge in wild cognitive studies (see Martina et al., 2020 for a summary). However, while these studies can increase the ecological relevance of the conclusions drawn from cognitive experiments, cognitive testing in the wild suffers its own drawbacks, due in large part to variation in individuals' participation. Confounding factors that exist in wild populations include environmental variability, intergroup competition and

predation risk that may affect the willingness of group members to participate in cognitive tasks, but also individual trait variation may exacerbate participation differences within groups. Participation could be categorised at two levels: initial interaction with a cognitive task (short-lived explorative actions towards an object) and as continued engagement with the task (longer, more sustained, problem-solving actions towards an object). Individual variation in the performance of shorter or longer engagements might reflect multiple factors. Foremost among these, and the primary focus of this chapter, is that individuals perform longer bouts when individuals gain experience of success in solving cognitive tasks (van Horik et al., 2017). An example of such influence is seen in Laidre, (2008), where the number of olive baboons (*Papio* anubis) and time spent participating in different cognitive tasks decreased when none solved the task, and increased as more baboons were successful. However, it is also possible that shorter bouts occur as the result of the presence of dominant individuals (Drea and Wallen, 1999), we consider all these possibilities in our analysis below.

The decision of wild individuals to voluntarily participate in cognitive tasks may be influenced by their current energetic and social needs. Individual variation in participation through interaction and engagement can stem from at least three sources. In the first case, individuals' participation in cognitive tasks in the wild may be variable due to differential interactions of individuals with the environment and conspecifics (Morton et al., 2013). For instance, unlike cognitive experiments undertaken in captivity, wild participants cannot be systematically food-deprived before experiments or influenced by animal handlers to interact with cognitive tasks (Fischer, 2022; Pritchard et al., 2016; Ross et al., 2022). Motivation to obtain food rewards from cognitive tasks may also be balanced against the

potential of intraspecific conflict, which impacts individual decisions to participate (Moran et al., 2021). In the second case, variation in task neophobia can contribute to variation in participation (Almeling et al., 2016; Biondi et al., 2010), and is problematic in the wild where animals are less familiar with human-made objects. However, steps can be taken to reduce the effects of neophobia on participation through familiarising wild individuals with experimental apparatuses, such as by exposing participants to objects before the experiment or by measuring the latency to approach novel objects to account for individual variation in neophobia (§2.3). In the third case, if individuals are initially unsuccessful at obtaining food rewards from cognitive tasks upon their first interactions, they may not be motivated to continue engagement. In captive studies, researchers can restrict food availability outside of the cognitive tasks, but in wild studies, initially unsuccessful participants are able to seek food or other stimulation elsewhere. Collectively, these sources of individual variation can contribute to what can be highly variable participation of wild individuals in cognitive studies. For example, across species, only 17% of individuals participated in 13 cognitive tasks in the wild, compared to a mean of 77% of individuals participating in 19 tasks in captivity (Martina *et al*. 2020). Understanding why task participation in wild populations varies is vital to ensure sampling biases can be accounted for when exploring the fitness consequences of variation in cognitive abilities (Fischer, 2022; Rowe and Healy, 2014).

Performance in cognitive tests is likely to be partially dependent on individual motivation to interact and engage with tests, as well as an individual's cognitive ability. Consequently, care must be taken to allow for such differences in motivation when drawing inferences from variation in animals' behaviour in

cognitive experiments (Fischer, 2022). Such motivational differences may arise from demographic, social and health factors (Pritchard et al., 2016). Although captive studies can control for such factors, e.g., by manipulating test group composition, this is not possible in the wild and has led to findings of differential participation in previous cognitive studies in wild populations. Firstly, younger individuals are often the most explorative of cognitive tasks due to higher levels of neophilia than other age groups (Bergman and Kitchen, 2009; Biondi et al., 2010; Carter et al., 2014). However, thus far, juveniles and infants have been poorly incorporated in field cognitive studies (Fischer, 2022). In addition to age, within despotic animal societies, high-ranking individuals monopolise cognitive tasks as high-value resources (Harrison et al., 2023; van Horik et al., 2017). Conversely, high-ranking individuals may be less motivated to engage in cognitive tasks as they are better able to exploit resources elsewhere (Lee et al., 2016; Rathke and Fischer, 2020; Reader and Laland, 2001). Finally, an individual's physical condition can impact their ability to participate in a cognitive test. For example, captive pheasants in good body condition (*Phasianus colchicus*) were more likely to participate in a task (van Horik et al., 2017). Such age-, rank-, and condition-related variation may create differing motivation to participate in cognitive tasks between individuals in wild populations.

A key innovation in cognitive testing in recent decades is the use of computerised touchscreen devices (Egelkamp and Ross, 2019; Inoue and Matsuzawa, 2007; Perdue et al., 2017). Programmable apparatuses allow researchers to manipulate and change experimental tasks presented to participants (Martin et al., 2022). This allows new research questions to be asked without changing the testing apparatus, and thus avoids the problem of neophobia that could arise with

the introduction of a new apparatus. While touchscreens do not represent natural behaviours, their flexibility in presenting novel information to participants can offer insights into cognitive and learning mechanisms (Joly et al., 2014). By ensuring learned information is novel, any differences in learning ability found between populations or individuals can be captured more reliably by using touchscreens than by using tasks that are less novel. Touchscreen studies have mainly been confined to captive conditions due to electrical and internet connection requirements (Kendal et al., 2010). Within captive touchscreen studies, voluntary participation has been encouraged as this reduces stress in participants compared to presenting touchscreens to individuals that are forcibly isolated. Such voluntary participation is also argued to be representative of voluntary foraging decisions in wild populations (Calapai et al., 2017; Cronin et al., 2017; Fagot et al., 2014; Gazes et al., 2013; Ross et al., 2022). Within zoological collections, the majority of touchscreen studies have involved primates (Egelkamp and Ross, 2019), with further taxa represented in other captive settings (e.g., domestic dogs, *Canis lupus familiaris*: Wallis et al., 2017; wolves, *Canis lupus*: Dale et al., 2019; sheep, *Ovis aries*: McBride et al., 2016; red-footed tortoises, *Chelonoidis carbonaria*: Mueller-Paul et al., 2014). If restrictions to deploying touchscreens in wild populations can be overcome, the strong foundation of cognitive research conducted in captivity (§2.3.2.3) can be built upon in wild populations, and ecological and evolutionary theories can be tested with more natural representation of participants in free-living groups.

To the best of our knowledge, only one study has used touchscreen technology in wild primate populations (Harrison et al., 2023). This study presented simple associative learning tasks to eight groups of vervet monkeys (*Chlorocebus*

phygerythrus), four in the wild and four in captivity. A portable touchscreen (Schmitt, 2018) was attached to a tree (in the wild) or an enclosure fence (in captivity), with researchers controlling tasks using a laptop whilst maintaining a 5 m distance. Individual participation was voluntary but restricted to 30 attempts (food-rewarded if correct) before the touchscreen was turned off. The wild groups in the study were less likely to interact with the touchscreen at least once. Due to dissimilarities in age and sex classes between wild and captive groups, the impact of age and sex on participation was only investigated in the wild groups. Here, juvenile males and adult females were more likely to interact with the touchscreen at least once. However, no statistically significant impact of age or sex on the number of attempts made through sustained engagement was found. This study also found inter-group differences in participation, but not performance, in a simple task. Although the wild vervets voluntarily participated in touchscreen tasks, the authors presented a single portable touchscreen. As a high-value and defendable resource, the touchscreen was monopolised by dominant females. Commonly in captivity, multiple cognitive tasks are presented simultaneously to subjects to minimise such competition and monopolisation (Clark, 2017, 2022; Egelkamp and Ross, 2019; Hopper, 2017). However, no study to date has presented multiple touchscreens to wild primates simultaneously, with only a few presenting multiple touchscreens to captive primates (see Egelkamp and Ross, 2019 for review).

In this study, we explore individual variation in participation in two equally rewarded cognitive tasks spread across four simultaneously-presented touchscreens in a wild primate population. We build upon previous studies utilising touchscreen technology but expand this to a voluntary simultaneous

multi-touchscreen layout deployed in a wild setting to two troops of chacma baboons (*Papio ursinus*). We expand on previous work on cognitive task participation in this population by Martina et al. (2021) by presenting more complex and automated tasks. We did not target specific individuals, permitting all individuals to interact freely with the tasks. We aimed to assess individual factors that affected task participation by measuring whether baboons' age, sex, and rank predicted: (1) the likelihood of engaging with the touchscreen; (2) whether they interacted with the touchscreens for a short period of time (short engagement); or (3) for a longer period of time (long engagement); and (4) their preference for attempting a relatively easy or difficult task presented simultaneously with the same reward. Previous studies have shown that juveniles are more likely than adults to participate in cognitive tasks in spotted hyenas (*Crocuta Crocuta*; Benson-Amram and Holekamp, 2012), chimangos (*Milvago chimango*; Biondi et al., 2010) and chacma baboons (Martina et al., 2021). This is hypothesised to be because juveniles are highly neophilic (Harrison et al., 2023; Martina et al., 2021; Reader and Laland, 2001). Hunger has also been proposed to explain higher participation in cognitive tasks of both male meerkats (Thornton and Samson, 2012) and low-ranking vervet monkeys (Harrison et al., 2023). Furthermore, male baboons (*Papio papio;* Fagot and Bonté, 2010) were more likely than females to interact with touchscreen tasks in a captive setting, likely because females are more risk averse (King et al., 2008; Wittig et al., 2008). We therefore predicted that younger (P1a), male (P1b), and low-ranking (P1c) baboons would be most likely to interact with the touchscreens at least once. An individual's previous experience of cognitively demanding tasks (such as exploiting a novel food source) would mean they are more likely to succeed in gaining food rewards from the touchscreen tasks (van Horik et al., 2017). This

would sustain their motivation for participating in the experiment to maximise resource exploitation (King et al., 2008). Therefore, we predicted that younger (P2a), female (P2b) and low-ranking (P2c) individuals would only be more likely to participate for short periods of time due to their inexperience, and older (P3a), male (P3b) and high-ranking (P3c) individuals would participate for longer periods of time (Biro et al., 2006; Laland, 2004; Tan et al., 2018; van Horik et al., 2017; Wobber and Warneken, 2013). If touchscreens with the easier (choice) task are preferentially used by experienced individuals (older individuals, males or high-ranking individuals), then we might expect to see younger, female, or low-ranking baboons being more likely to engage with the touchscreens offering the more difficult (sequence) task in order to receive the same reward (Predictions P4a-c, respectively). However, as both tasks were rewarded, we expected baboons to be motivated to participate to some degree in both tasks as the potential reward was of a high value.

3.3 Methods

3.3.1 Study site, species and subjects

This study took place at Tsaobis Nature Park, Namibia (22°23'S, 15°45'E) between 21st July and 3rd October 2022, with a pilot study taking place in 2021. Two habituated troops (J and L) of wild chacma baboons were the subjects, comprising a total of 64 and 78 individuals in J and L respectively, that could potentially participate in the study. Age of baboons (in years) was calculated as a continuous variable from the known or estimated date of birth to the beginning of the experimental phase of this study, using methods from Dezeure et al., (2021).

Tsaobis is a highly seasonal environment, characterised by dry and wet seasons. Food availability varies across these seasons and is particularly low in the dry season, indicated by normalised difference vegetation indices (NDVI) - see Dezeure et al., (2021). Throughout the duration of this study, food availability was generally low across the Tsaobis landscape expect within the riparian woodlands along the dry Swakop river (Fig 1.2). These flora, including *Faidherbia albida*, *Prosopis glandulosa*, *Salvadora persica*, *Acacia erioloba*, and *Tapinanthus oleifolius* (Cowlishaw, 1997a), provide baboons in Tsaobis with a reliable food source all year round and support continuous breeding within the population (Dezeure et al., 2021). Consequently, although this study took place in the dry season, there were foraging opportunities outside of the experimental area.

3.3.2 Ethical statement

All research regarding the presentation of touchscreens to chacma baboons as part of the Tsaobis Baboon Project was conducted under ZSL Ethical Review 412-PCE-0120.

3.3.3 Experimental area

Touchscreens used in this study were 15-inch open-frame LCD Elo 1950L. These capacitive touchscreens were integrated with a bespoke automatic feeding mechanism and housed within a durable black plastic carrying case (Pelican case). The touchscreens were powered by internal 12 V batteries that provided around two hours of power to touchscreens when touchscreens were being used.

The bespoke touchscreen software allowed multiple-coloured shapes to be displayed in a random quadrant of the screen, that would change quadrant between each task attempt. The baboons were required to touch the 'correct' shape of two shapes, or touch two shapes in the correct order, to obtain a food reward (for further details of the tasks, see below). A correct choice resulted in a green light being displayed and a food reward, 1-4 corn kernels being dispensed through one of two chutes (on either side of the touchscreen) onto the ground. An incorrect choice resulted in a red light and a reset where the shapes disappeared from the screen for one second. After a correct or incorrect choice, the shapes reappeared again in a new random configuration. A reward of corn kernels was chosen as they are a highly preferred food item in this population, used in previous field experiments regarding leadership, (King et al., 2008) foraging decisions (Marshall et al., 2013), cognition (Martina et al., 2020) and troop captures (Huchard et al., 2010; Carboni et al., 2022). The nutritional content of a single corn kernel is approximately 1.2 kCal – at 0.332 g / corn kernel and 3.65 kCal / g (Kljak et al., 2020; Siyuan et al., 2018). The delivery of 1.2 – 4.8 kCal of corn upon a correct choice therefore represented a reward of high national value (Ranum et al., 2014).

The experimental arena was located within an ~800 m^2 unenclosed area near a permanent artificial waterhole within 1 km of three commonly used sleeping cliffs of the study troops. The four touchscreens, housed in cages with grids of 10 cm width, to allow baboons to touch the screen, were placed in a semi-circle 20 m apart and angled away from one another to prevent touchscreen users from observing neighbouring touchscreens (Fig 1). The touchscreens were oriented to face south to reduce glare from the sun that could affect visibility.

Figure 3.1: Experimental touchscreen setup

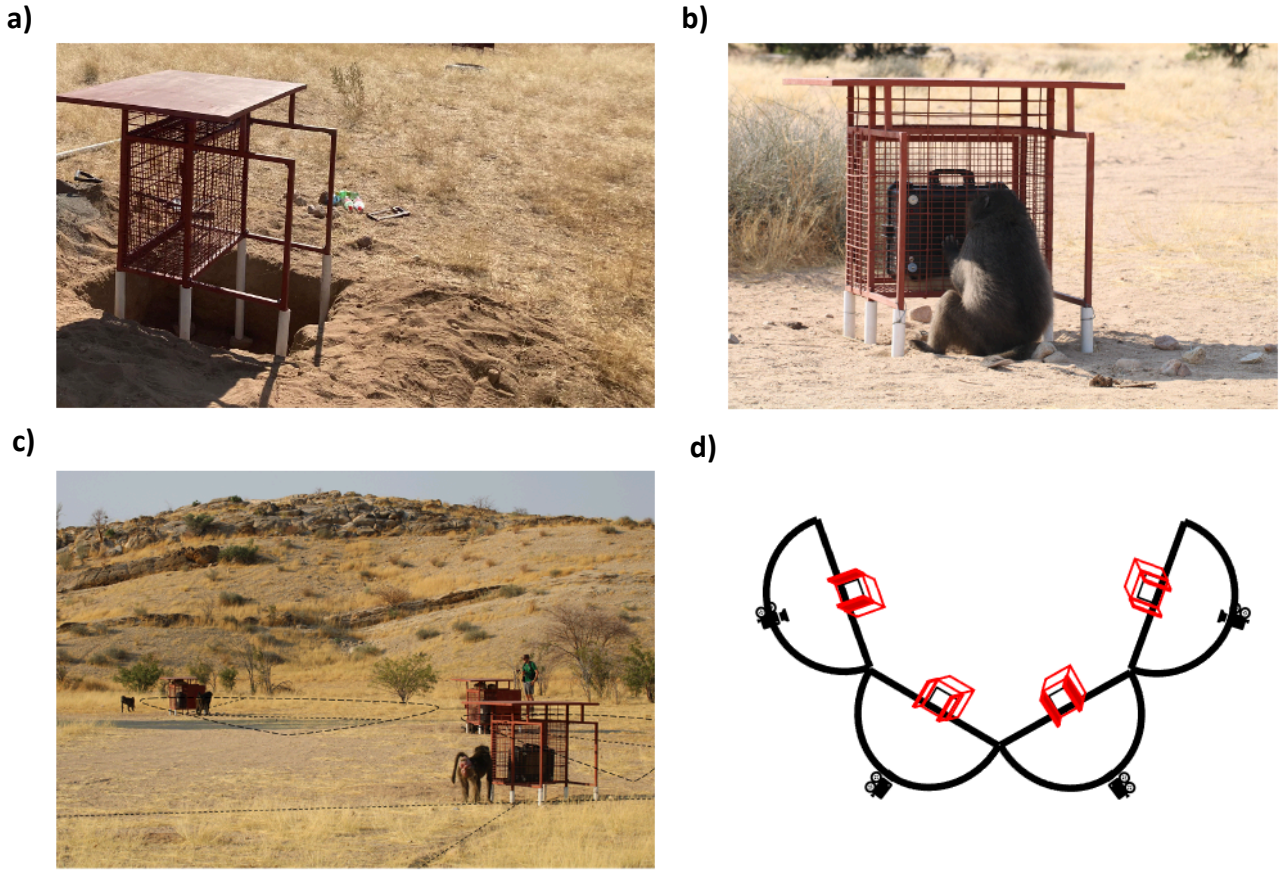


Figure 3.1: Experimental set-up. Shown are (a) a photograph of the cage in which touchscreens were housed, set into a hole ~80 cm deep with cage legs held within PVC tubes. The PVC tubes were held in place with a mix of concrete and rocks. PVC tubes were used so that the cages could be removed at the end of the experiment. (b) A photograph showing a juvenile male baboon doing screen-directed actions (SDAs) on a touchscreen. The photograph shows the touchscreen at eye height to a sitting baboon. (c) A photograph of the experimental area during the experimental phase. Dashed lines represent the area in which a baboon could see the touchscreen tasks (observer area), a 10 m radius semi-circle. (d) A schematic of the experimental area with red cages housing touchscreens; the semicircles indicating the observer area with camcorders positioned outside the area in front of the touchscreen. Touchscreen cages were static and remained in the same locations throughout the study. Touchscreens were randomly allocated to each cage on every experimental day.

3.3.4 Touchscreen set-up and general procedure

Touchscreen units were deployed when baboons were within 1 km of the experimental area but before the baboons could see the touchscreens, to avoid

the baboons making an association between the researchers and the touchscreen rewards. This occurred mostly between 12pm and 2pm as at this time, baboons often looked for water sources near to the experimental area. Touchscreens were remotely woken from sleep mode by a researcher as soon as a baboon was within 50 m of the experimental area. Each touchscreen was pre-set with either the choice or sequence task, such that each task ran continuously on the same touchscreen throughout each experiment, with each of the choice task and sequence task on two touchscreens. The position of the touchscreens with the choice and sequence tasks was randomly assigned for each experiment between four fixed positions (see Figure 3.1).

A researcher stood 15 m in front of each of the four touchscreens and dictated the identities of all baboons that came within 10 m of the touchscreen unit to a tripod-mounted camcorder (model Sony hdr-cx240e). Researchers simultaneously collected participation data using Cybertracker on handheld computers at all times (Liebenberg, 2022). Participation in the touchscreen tasks was defined as any individual that touched or inspected the screen of the touchscreen unit (within arm's reach of the screen and looking at, sniffing, or making muzzle-contact); we henceforth collectively term this as a screen-directed action (SDA), outlined in Table 3.1 and a full ethogram of touchscreen behaviours can be found in Appendix 3. The touchscreens automatically recorded presses to the screen, with the location of the touch, time, and whether the touch was successful or not depending on the pre-set task.

The tasks were presented for a maximum of two hours to a participating troop, after which point, the screens were put to sleep remotely. The touchscreens were

removed after a troop had left the experimental area, and the cages remained in place. If a technical issue arose with the touchscreens (such as the reward dispenser becoming blocked), the screens would be remotely put to sleep. Usually only one experiment was run per day with a single troop (n=18), but on a small number of occasions (n=3) we ran two experiments within a single day when both troops visited the experimental arena on two different occasions (at least two hours apart to allow touchscreen recharging).

Dominance interactions were collected *ad libitum* between May and October 2022 during full-day follows of both troops during long-term data collection, and did not include dominance interactions involving the experimental apparatus. Dominance ranks were calculated for each individual through the 'I&SI' method (De Vries, 1998; Schmid and de Vries, 2013). Ranks were standardised within troops between 0 (low-ranking) and 1 (high-ranking) using the formula 1-((1-*r*)/(1-*n*)), where *r* is the absolute rank of an individual ranging from 1 to the group size of *n* (Baniel et al., 2018). This method has been routinely applied in populations with linear dominance hierarchies, including this population (Huchard and Cowlishaw, 2011; Roatti et al., 2023).

Social networks were built using proximity data. Proximity associations were collected between May and October 2022 through recording all individuals within 10 m of a randomised focal individual (Roatti et al., 2023). Weighted social networks were then calculated, from which the strength of social connections was used in later analyses as a proxy for social learning mechanisms whereby individuals are more likely to interact with an object or location if they observe a conspecific do so (Croft et al., 2009; Hoppit and Laland, 2013).

In addition to performing rewarded SDAs, individuals could experience touchscreen success vicariously through observation of a conspecific performing rewarded SDAs. Individuals were categorised as observers when they entered the 10 m diameter semi-circle observation area surrounding a touchscreen and orientated their heads towards a baboon performing SDAs. If the touchscreen user was rewarded during this period of observation, the observing baboon would be categorised as having experienced touchscreen success. Similarly, a baboon would be categorised as experiencing touchscreen success if at least one of their SDAs were rewarded.

Table 3.1: List and explanation of touchscreen behaviours and observation measurements (ethogram in Appendix 3) used in Chapters 3, 4 and 5. Relevant measures that are used in models in the current chapter are outlined, if the measure is used in either chapters 4 or 5 and not in this chapter, the model is displayed as that chapter alone.

Behaviour / measure of interest	**Explanation**	**Model**
Observation	An individual was present within the 10 m diameter semi-circle surrounding a touchscreen and whose head was oriented toward a touchscreen participant performing SDAs. If a touchscreen contained restrictive panels, only individuals between the 60° and 120° were counted as observers.	1, 2, 3
Screen-directed action (SDA)	An action of an individual that was directed towards a touchscreen, such as touching the screen with the hand or muzzle. This measure indicated interaction with a touchscreen. The touchscreen automatically recorded SDAs and the success or failure regarding task completion. The performance of at least one SDA meant that the individual had participated in the study.	1, 2, 3, 4
SDA bout	A bout was defined as the time spent continually making SDAs, with a bout ending after at least 10 s of SDA inactivity (i.e., if an individual left the touchscreen or stopped using the touchscreen).	2, 3, 4
Time spent observing others	A measure of the total duration (s) that an individual spent observing conspecifics performing SDAs from within the observation area.	Chapter 5

Time spent being observed	A measure of the total duration (s) that an individual spent being observed by conspecifics in the observation area whilst that individual was performing SDAs.	Chapter 5
Number of correct choices observed	The cumulative number of correct SDAs that were observed by an individual at the point the individual performed SDAs themselves.	Chapter 5
Number of correct choices in the choice task	Sum of the number of stars touched within the choice task, when at least one star or cross was touched during an SDA bout. The variable was log transformed to account for positive skew.	Chapter 5
Number of correct choices in the sequence task	Sum of the number of completed sequences (red circle followed by a blue circle) within the sequence task, when at least one circle was touched during an SDA bout. This measure therefore excluded SDA bouts of participants that only selected the black background and never touched any circles. Incorrect choices included the following touches: red circle, red circle; red circle, background press; red circle, no subsequent touch; blue circle first touch. The variable was log transformed to account for positive skew.	Chapter 5
Correct choices above chance in the choice task	The participant was required to select five stars in a row to be considered to have performed the task above chance. This is due to a 50 % probability of correctly choosing a star rather than a cross by chance. Therefore, selecting five stars consecutively represented a lower than 5 % probability of doing so by chance. This measure was not restricted to single bouts on a single touchscreen but included SDAs across touchscreen transitions and across sequential bouts.	Chapters 4 and 5
Correct choices above chance in the sequence task	The participant was required to complete three sequences in a row to be considered to have performed the task above chance. This is due to a 25 % probability of correctly completing a sequence by chance. Therefore, completing three sequences consecutively represented a < 5 % probability of doing so by chance. This measure was not restricted to single bouts on a single touchscreen but included SDAs across touchscreen transitions and across sequential bouts.	Chapters 4 and 5

3.3.5 Habituation phase

Prior to beginning the experiments, it was necessary to accustom the baboons to the touchscreen units to decrease neophobia and familiarise them with the action of touching the screen to obtain a food reward (Schmitt, 2018). The habituation

phase of this study took place over 21 days between 21st July and 25th August 2022, to match the duration of the experimental study. The habituation task (Figure 3.2a) consisted of a randomly located yellow hexagon of 20 cm length on a black background that was rewarded when pressed. Two touchscreens were deployed in the second and fourth positions of the experimental arena (with position one being closet to the watering hole) simultaneously throughout the habituation phase. Both troops had the opportunity to encounter the habituation task, although equal individual exposure to the touchscreens was unlikely given the voluntary nature of participation. Unequal exposure was therefore controlled statistically in the analyses. Due to time constraints, the habituation phase lasted for 21-days, giving baboons an equal opportunity to participate in both the habituation and experimental phases.

3.3.5 Experimental phase

The experimental phase lasted for 21 days between 31st August and 3rd October 2022. In this phase, two task types (choice and sequence) were presented simultaneously to test the effect of task complexity on participation. Two units displayed one task, and two units displayed the other throughout the experimental phase. The location of each task on each day was randomised. The choice task involved choosing the correct symbol of two options, both of which were 20 cm width and were placed in random separate quadrants of the screen. The two symbols were a white star and white cross on a black background; the white star was rewarded (Figure 3.2b). The sequence task involved touching two symbols in the correct order. To be rewarded, a participant had to touch a red circle followed by a blue circle; the quadrant in which the symbols appeared was random. Both coloured circles were 20 cm in diameter and displayed at the same

time; the red circle remained on the screen even if correctly pressed first (Figure 3.2c). We presented a choice and a sequence task to baboons as previous presentations of single action tasks (such as the choice task) and multiple action tasks (such as the sequence task) to other primate taxa have shown that tasks with fewer steps were completed more quickly and more accurately (Calapai et al., 2017; van de Waal and Bshary, 2011). We were therefore interested to test if wild baboons followed a similar pattern. A video of a baboon attempting tasks in the experimental phase can be found at https://figshare.com/s/15b902b9aec4154e4d8d and data are available at https://figshare.com/s/d5274f9d48aa5717f303.

Figure 3.2: Touchscreen tasks presented

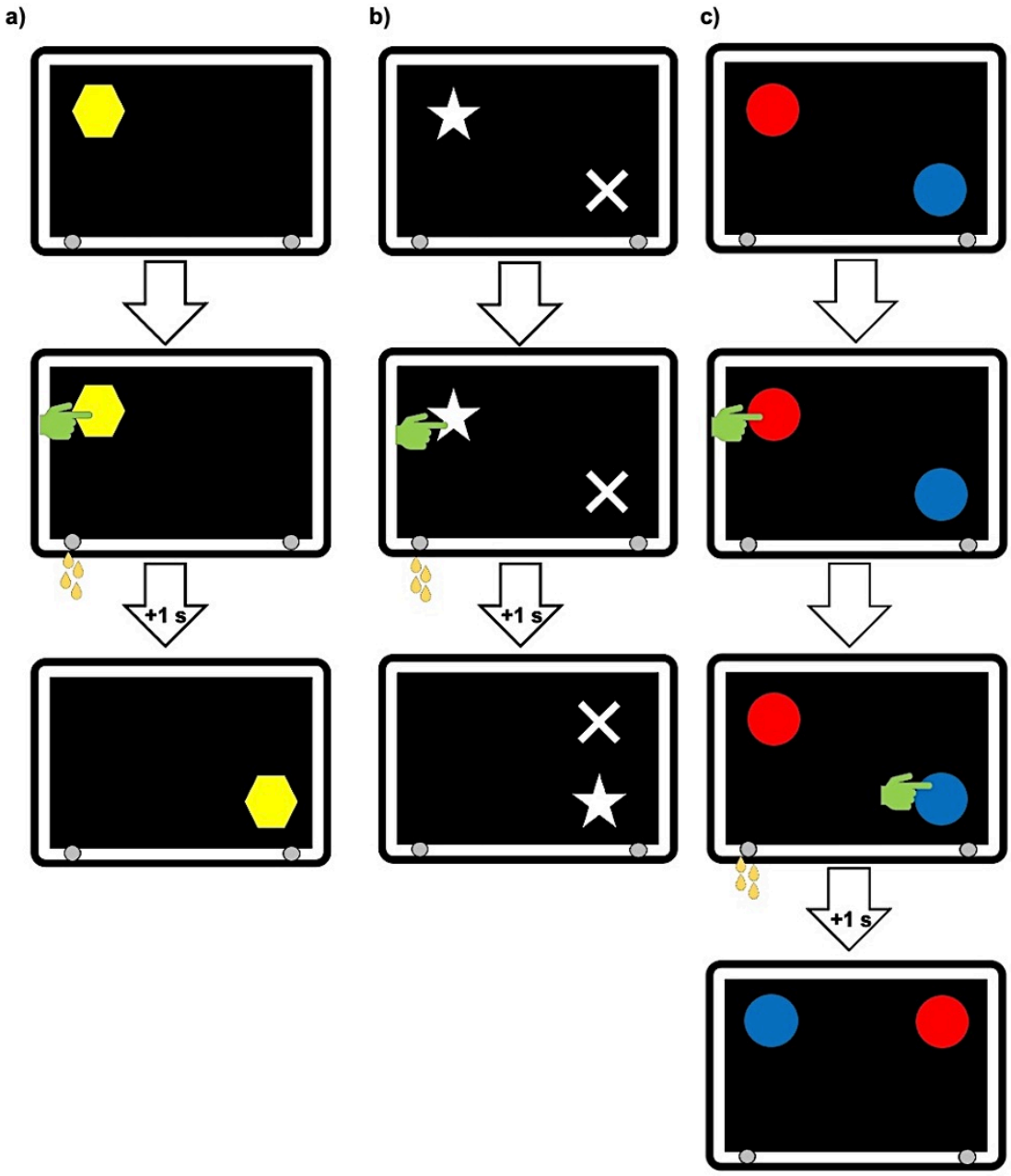


Figure 3.2: Touchscreen tasks presented. Shown are schematics of the touchscreens presented to baboons in this study. Corn reward is depicted as delivered from a random chute at the base of the touchscreen. Tasks consisted of (a) the habituation task presented on two touchscreens simultaneously. The habituation task consisted of a yellow hexagon that was rewarded when pressed. (b) The choice task presented on two of four simultaneously deployed touchscreens in the experimental phase. The choice task consisted of a white star and cross, whereby the star was rewarded when pressed and the cross was not. (c) The sequence task presented on two of four simultaneously deployed touchscreens in the experimental phase. The sequence task consisted of a red circle and a blue circle, whereby only a press to the red circle followed by a press to the blue circle would result in a reward. The red circle remained on the screen after the initial press. After a correct or an incorrect press was made to either the shapes or the background, shapes would disappear from the screen for 1 s and reappear in randomised

quadrants. The tasks would therefore be reset, and for the sequence task, any previous attempt would not carry over to the next attempt (for example if red was chosen followed by another red choice, selecting blue after a task reset would not count as a completed sequence).

3.3.6 Statistical analysis

All analyses were performed using R v2023.06.02 build 561 (see Table 3.2 for a breakdown of models used). We ran two binomial generalised linear mixed-effects models (GLMMs) and two linear mixed-effects models (LMM) using the R package “lme4” (Bates et al., 2015). To evaluate the fit of GLMMs and LMMs, we visually inspected the residuals for normality, homoscedasticity and the absence of patterns that might indicate model misspecification. Residual plots, including Q-Q plots, were used to assess whether residuals conformed to the assumptions of the model. Specifically, we checked for a lack of systematic trends in residuals versus fitted values, as well as the approximate normality of residuals (Zuur et al., 2009). We assessed multicollinearity among predictors by calculating variance inflation factors (VIFs) with the package “car” (Fox et al., 2023). These diagnostic checks ensured that the models were appropriate for the data and that parameter estimates were unbiased and reliable. The explanatory power of each variable was determined by comparing the ‘full’ model to a null model (excluding the variable of interest) through ANOVA.

All models included in the analysis used the following fixed effects: age, sex (female or male), relative rank (0 to 1), troop (J or L) and social network strength. To account for prior experience of the touchscreen and associated rewards, further fixed effects of whether individuals had observed another perform a correct SDA (Table 3.1) or performed a correct SDA themselves (0/1), and participation in the habituation phase (0/1) were included in models 1-3. In

addition, all models used a random effect of individual identification to account for repeated measures. Initially, all models were run separately for each troop because if age, sex or rank impacted participation, inter-group variation in demographic composition could lead to inter-group differences in participation. However, all combined models that included troop as a fixed effect had greater exploratory power than models separated by troop and so a combined troop model approach was taken. In addition, the reproductive state of females at the time of the experiment was included in initial models as a fixed effect, as pregnant, nursing or sexually receptive females may be risk-adverse or subjected to male attention that may impact their likelihood of approaching a concentrated resource. However, the addition of female reproductive state decreased the explanatory power of models compared to models without reproductive state and was therefore excluded.

To address our first predictions (P1a-c), a binomial GLMM with a logit link function (model 1) was used to investigate whether age, sex and rank predicted individuals' interaction with the touchscreen (Harrison et al., 2023). Participation in the experimental phase was coded as 1 if an individual performed at least one SDA across the entirety of the experimental phase and 0 if not; this was used as the response variable in the model. All potential participants (i.e., all troop members) were included in this analysis to investigate the individual predictors of likelihood of participation. This meant that individuals that were unlikely to participate, such as infants that are commonly omitted from cognitive studies (Fischer, 2022), were included in our analyses.

To address our second set of predictions (P2a-c), we investigated whether the individual characteristics of those that participated in the experiment predicted short daily SDA bouts with the touchscreen (Harrison et al., 2023). In order to guide our criteria for defining short and long SDA bouts, we scrutinised the frequency distribution of cumulative SDA bout duration and found a binomial pattern with a boundary between the peaks at approximately 60 seconds. We therefore used 60 seconds as the threshold between short and long daily SDA bouts. In order to describe the variation in the performance of short and long SDA bouts, a composite metric of the cumulative daily duration of short and long bouts for participants was used, that captured both the frequency and duration of participation. The frequency or duration of SDA bouts alone was not used, as the variation in the frequency of SDA bouts per day (1 – 66) and SDA bout duration showed a large range (1 s – 3163 s). By using a composite measure of cumulative daily duration of short and long bouts, this variation was captured and meant that differences in participation between frequent participants with short SDA bouts and rare participants with long SDA bouts (whose similar participation would not be represented by measuring frequency or duration alone) could be investigated. This composite measure was log transformed in both model 2 and 3 to account for positive skew. To address P2a-c, the cumulative daily duration performing SDAs for less than 60 s was used as the response variable in a model 2, an LMM. In addition to the random effect of the identity of participants, experiment number was included as a random effect.

In the third case (P3a-c), a LMM was used to investigate the impact of age, sex, and rank on the duration individuals spent in long cumulative daily SDA bouts with the touchscreen. The cumulative time per day spent performing SDAs over

60 s was used as the response variable for this model. In addition to the base model predictors, we included a quadratic function for age (rather than a linear function as in all other models) because visual inspection of the relationship with age suggested this, which was confirmed statistically by fitting the data more closely than a linear relationship (χ^2 = 39.82, df = 4, p < 0.01), identified *a posteriori*.

In the fourth case (P4a-c), to investigate whether age, sex and rank affected task preference, we employed a binomial GLMM with a logit link function with a measure of task preference as the response. To measure task preference, we calculated the proportion of cumulative time an individual spent performing SDAs on the choice task (s) compared to the total time the same individual spent performed SDAs on both tasks (s) as the response variable (N = 86). The resulting measure was a value between 0 and 1, where values closer to one indicated a preference for the choice task.

In addition to the above analyses used to address our predictions, we included analyses to assess whether the presence of the touchscreens as a food resource altered the foraging movements of baboons during and after the experiment. During daily follows, distances (km) that baboons travelled each day was recorded by GPS as part of long-term data collection in TBP (§1.7.2). These data included distance travelled by troops during the experimental period for days that troops did or did not encounter the experimental area, as well as distance travelled by troops on the same date for the over the next two field seasons (2023 and 2024). Mean daily distance travelled were compared via T tests (mean daily distance travelled on days that a troop encountered the experiment vs days that

a troop did not encounter the experiment during the experimental phase; mean daily distance travelled during the experimental phase vs on the same days in 2023 and 2024).

Table 3.2: Summary of binomial GLMMs and LMMs used to address P1-4. To test these predictions, the explanatory power of models was assessed by comparing full models with all biologically relevant variables to models with variables removed (ANOVA). All models presented are full models as the removal of any variable did not improve model fit without creating difficulties for biological interpretation. VIFs were checked for all models and non displayed any significant collinearity.

Research questions	Predictions	Model	Response	Fixed effects	Random effects
What predicted the likelihood of participation?	P1. Younger individuals as well as males and high-ranking individuals would be most likely to participate at least once.	Model 1. Binomial GLMM	Performed at least one SDA during the experiment (1/0)	1 Age 2 Sex 3 Rank 4 Troop 5 SN strength 6 Previous knowledge of task success (1/0) 7 Performed at least one SDA during the habituation phase (1/0)	Individual ID
Predictors of participating for short SDA bouts	P2. Individuals with little experience of cognitive challenges would participate for cumulative daily short SDA bouts.	Model 2. LMM	Cumulative daily duration of SDA bouts < 60 seconds (log transformed)	1 Age 2 Sex 3 Rank 4 Troop 5 Task 6 Time spent performing SDAs in the habituation phase 7 SN strength	Experimental ID Individual ID

				8 Previous knowledge of task success (1/0)	
Predictors of participating for long SDA bouts	P3. Individuals with more experience of cognitive challenges would participate for cumulative daily short SDA bouts.	Model 3. LMM	Cumulative daily duration of SDA bouts > 60 seconds (log transformed)	1 Age (quadratic) 2 Sex 3 Rank 4 Troop 5 Task 6 Time spent performing SDAs in the habituation phase 7 SN strength 8 Previous knowledge of task success (1/0)	Experimental ID Individual ID
Predictors of task preference	P4. Individuals with more experience would spend more time performing SDA bouts on the choice task	Model 4. Binomial GLMM	Proportion (%) of total time spent performing SDAs, performing SDAs on the choice task	1 Age 2 Sex 3 Rank 4 Troop 5 SN strength	Individual ID

3.4 Results

3.4.1 The likelihood of participation

Troop participation in the experimental phase was voluntary and touchscreen deployment was opportunistic. As such, the two troops differed in the number of encounters with the experimental area (J troop: N = 8 occasions totalling 8 h 37 min; L troop: N = 17 occasions totalling 21 h 21 min). By the end of the study, 63% of J troop individuals and 58% of L troop individuals had participated in the experimental phase at least once. Within the choice task, 56% of J troop and 45% of L troop participated, and 51% of J troop and 49% of L troop participated in the sequence task at least once. For further details of the number of SDA bouts (period of activity during which an individual continuously touched or directed actions towards the touchscreen) for each sex and the different age classes, see Table 3.3. Across the experimental phase, there was a total of 33 h and 30 min of SDAs recorded with 28,409 separate SDAs triggering automatic detection of screen presses by the touchscreens.

Individuals from all age/sex classes from both troops showed SDAs in all tasks presented during the experimental phase at least once, other than infants in J troop. Out of 45 males in total, only one male (a low-ranking juvenile in L troop) did not participate in either the choice or sequence tasks. Within the choice task, 43 males participated at least once, and 42 males participated in the sequence task. Conversely, 30 females did not participate in the experimental phase at any point; 16 of 68 females showed SDAs at least once in both the choice and sequence tasks. A total of 27 females participated in the choice task and 28 females in the sequence task. Only one sub-adult (a high-ranking but severely

injured male in J troop) did not participate in the choice task, with all other sub-adults participating in all tasks. Juveniles represented the next highest proportion of age class that interacted with the touchscreens at least once, followed by adults. One infant performed SDAs on both the choice and sequence tasks, the low-ranking mother of this infant did not perform any SDAs.

The mean distance travelled (km) by baboons on days that the troop encountered the experimental area (mean = 8.106, range = 13.2) did not differ from the mean distance travelled on days that the troop did not encounter the experimental area (mean = 9.194, range = 14.1; $T(75.532) = -1.829$, $p = 0.071$). Similarly, the mean daily distance travelled on days that the troop encountered the experimental area did not differ from the mean daily travelled on the same dates for the following two field seasons in 2023 and 2024 (mean = 7.97, range = 10.9; $T(55.643) = 0.289$, $p = 0.775$). Overall, the presence of the touchscreens did not impact the foraging movement of baboon troops.

To test Predictions 1a-c, we examined the influence of age, sex and rank on the likelihood of individuals performing SDAs at least once during the experiment using a binomial GLMM (model 1). This model showed a negative correlation between age and participation: younger animals were more likely to exhibit SDAs (Estimate = -0.155, SE = 0.076, $z = -2.040$, $p < 0.05$; Table 3.3). There was no effect of touchscreen use during the habituation phase, troop, sex or rank on the likelihood of performing at least one SDA in the experimental phase. Further to this, neither the strength of social connections nor the observation of a rewarded SDA impacted the likelihood of performing an SDA (Table 3.3).

Table 3.3: Composition and sample size of L-troop and J-troop according to age class (defined in Roatti et al., 2023). Although age was used as a continuous variable in analyses, age classes are used in this table for descriptive purposes. Individuals are categorised according to age/sex groups with adult (A), sub-adult male (SA), juvenile (J), unsexed infant (I), male (M) and female (F) reported. The percentage of individuals in a category that participated are italicised. A bout of screen-direction actions (SDAs) was categorised as a period of activity during which an individual continuously touched or directed actions towards the touchscreen. Numbers in parentheses represent the total number of bouts sampled in the related category. The asterisk indicates that a single sub-adult male emigrated from L troop to J troop between the habituation and experimental phases.

	Troop breakdown	Age/sex	Total number of individuals in category	Total number of participants in category	Individuals sampled in habituation	Individuals sampled in choice task	Individuals sampled in sequence task
J Troop	Troop total		64	40 *63%*	19 *29%* (63)	36 *56%* (406)	33 *52%* (378)
	Age group total	A	26	12 *46%*	4 *15%* (5)	13 *50%* (62)	12 *46%* (36)
	Age group total	SA (male only)	12*	12 *100%*	10 *83%* (46)	11* *92%** (297)	12* *100%** (289)
	Age group total	J	15	13 *86%*	5 *33%* (12)	12 *80%* (47)	9 *60%* (53)
	Age group total	I	11	11 *100%*	0 *0%* (0)	0 *0%* (0)	0 *0%* (0)

	Sex group total	M	23*	23* *100%*	18 *78%* (62)	22* *96%** (371)	20* *87%** (348)
	Sex group total	F	30	16 *53%*	1 *3%* (1)	14 *47%* (35)	13 *43%* (30)
L Troop	Troop total		77	46 *60%*	32 *42%* (437)	35 *45%* (680)	38 *49%* (884)
	Age group total	A	30	14 *47%*	9 *30%* (123)	11 *37%* (356)	14 *47%* (389)
	Age group total	SA (male only)	13*	12 *100%*	13* *100%* (286)	12 *100%* (279)	12 *100%* (454)
	Age group total	J	20	16 *80%*	11 *55%* (28)	11 *55%* (43)	11 *55%* (39)
	Age group total	I	15	1 *7%*	0 *0%* (0)	1 *7%* (2)	1 *7%* (1)
	Sex group total	M	23*	22* *96%*	22* *96%** (421)	21 *96%* (648)	22 *100%* (853)
	Sex group total	F	39	23	10	13	15

				59%	*26%* (16)	*33%* (30)	*38%* (30)

Table 3.4: Model outputs from the (G)LMM analyses of the likelihood of participation (1), the cumulative daily time spent participating in <60 second bouts (2) and >60 second bouts (3), and task preference (4). Age was inputted as a continuous variable in the models. Bold indicates variables that achieved statistical significance above 95%. All analyses included observations from 21 days and 25 experiments, with models including 1752 observations from 142 individuals (1), 181 observations from 76 participants (2), 1521 observations from 76 participants, 86 data points from 86 participants (3) and 86 data points from 86 participants (4).

Model	Nobv / Nind	Term	Estimate	Std. Error	T value (2 and 3), Z value (1 and 4)	P
(1)	1752 / 142	Intercept	1.438	1.364	1.054	0.292
		Age	**-0.155**	**0.076**	**-2.040**	**<0.05**
		Sex: Male	-1.409	3.613	-0.390	0.697
		Rank	1.518	1.367	1.111	0.267
		Troop: L	-0.240	0.662	-0.362	0.717
		Habituation	-0.072	0.769	-0.093	0.926
		Social Network: Strength	-0.337	0.616	-0.546	0.585
		Experienced Rewarded SDA	*1.383*	*0.790*	*1.751*	*0.080*
(2)	181 / 76	Intercept	3.020	0.475	6.352	<0.001
		Age	-0.038	0.036	-1.050	0.297
		Sex: Male	0.103	0.230	0.446	0.658
		Rank	<0.001	0.451	0.001	0.999

		Troop: L	0.009	0.200	0.049	0.961
		Task: sequence	-0.073	0.138	-0.530	0.597
		Habituation	<0.001	<0.001	1.373	0.174
		Social Network: Strength	-0.030	0.174	-0.175	0.862
		Experienced Rewarded SDA	0.004	0.171	0.204	0.839
(3)	1521 / 76	**Intercept**	**2.284**	**0.697**	**3.275**	**0.001**
		Age	**0.673**	**0.165**	**4.071**	**<0.001**
		Age^2	**-0.048**	**0.011**	**-4.222**	**<0.001**
		Sex: Male	**0.939**	**0.261**	**3.604**	**<0.001**
		Rank	-0.329	0.457	-0.720	0.472
		Troop: L	0.153	0.145	1.052	0.299
		Task: Sequence	**-0.215**	**0.103**	**-2.092**	**<0.05**
		Habituation	**<0.001**	**<0.001**	**7.208**	**<0.001**
		Social Network: Strength	0.217	0.141	1.539	0.125
		Experienced Correct SDA	-0.286	0.152	-1.878	0.06
(4)	86 / 86	Intercept	-0.435	1.287	-0.338	0.736
		Age	-0.095	0.098	-0.971	0.332
		Sex: Male	-0.372	0.632	-0.588	0.556
		Rank	-0.352	1.220	-0.289	0.773
		Troop: L	-0.507	0.538	-0.942	0.346
		Habituation	<0.001	< 0.001	0.969	0.332

		Social Network: Strength	0.616	0.494	1.248	0.212

3.4.2 Predictors of short daily SDA bouts

To test Predictions P2a-c, we examined the influence of age, sex, and rank on the duration of short SDA bouts with an LMM (model 2). There was no association between any of the explanatory variables and the cumulative daily time spent performing short SDA bouts (Table 3.3).

3.4.3 Predictors of long daily SDA bouts

We explored the influence of age, sex and rank on the time spent engaged in SDAs using a LMM (model 3). The median time spent performing SDAs for individuals within these data was 236 s (IQR = 453 s, range = 3163 s). The model identified a quadratic relationship between age and the cumulative time spent performing SDAs per day in the experimental phase (Figure 3.3a). The predicted participation time peaked at 7.33 years of age, with 179 s spent performing SDAs during a single bout (age (linear): Estimate = 0.673, SE = 0.165, t = 4.071, p <0.001, age (quadratic): Estimate = -0.048, SE = 0.011, t = -4.222, p < 0.001). The model identified an effect of sex, with males performing long cumulative daily SDA bouts for longer periods per day than females (males median = 263 s, IQR = 485 s; females median = 81 s, IQR = 51 s; Estimate = 0.939, SE = 0.261, t = 3.604, p < 0.001; Fig. 3.3b.). Rank did not have a significant impact on high daily participation with touchscreen tasks, and both J- and L-troops spent similar time per day performing SDAs for longer periods of time. The inclusion of task type as an explanatory variable produced a model with greater explanatory power than a model without it ($\chi^2(1) = 4.432$, $p < 0.05$). The duration of participation in the sequence task (median = 216 s, IQR = 380 s) was lower than the choice task (median = 289 s, IQR = 600 s; Estimate = -0.215, SE = 0.103, t = -2.092, p < 0.05; Fig. 2c.). The time spent performing SDAs in the habituation phase was

positively associated with the time spent performing SDAs in the experimental phase (Estimate = < 0.001, SE = < 0.001, t = 2.961, p = 0.007). The strength of social connections within a proximity social network, and the experience of either performing, or observing a conspecific performing, a rewarded SDA, were all unrelated to the duration of participation (Table 3.3).

Figure 3.3: Factors impacting long daily SDA bouts in touchscreen tasks.

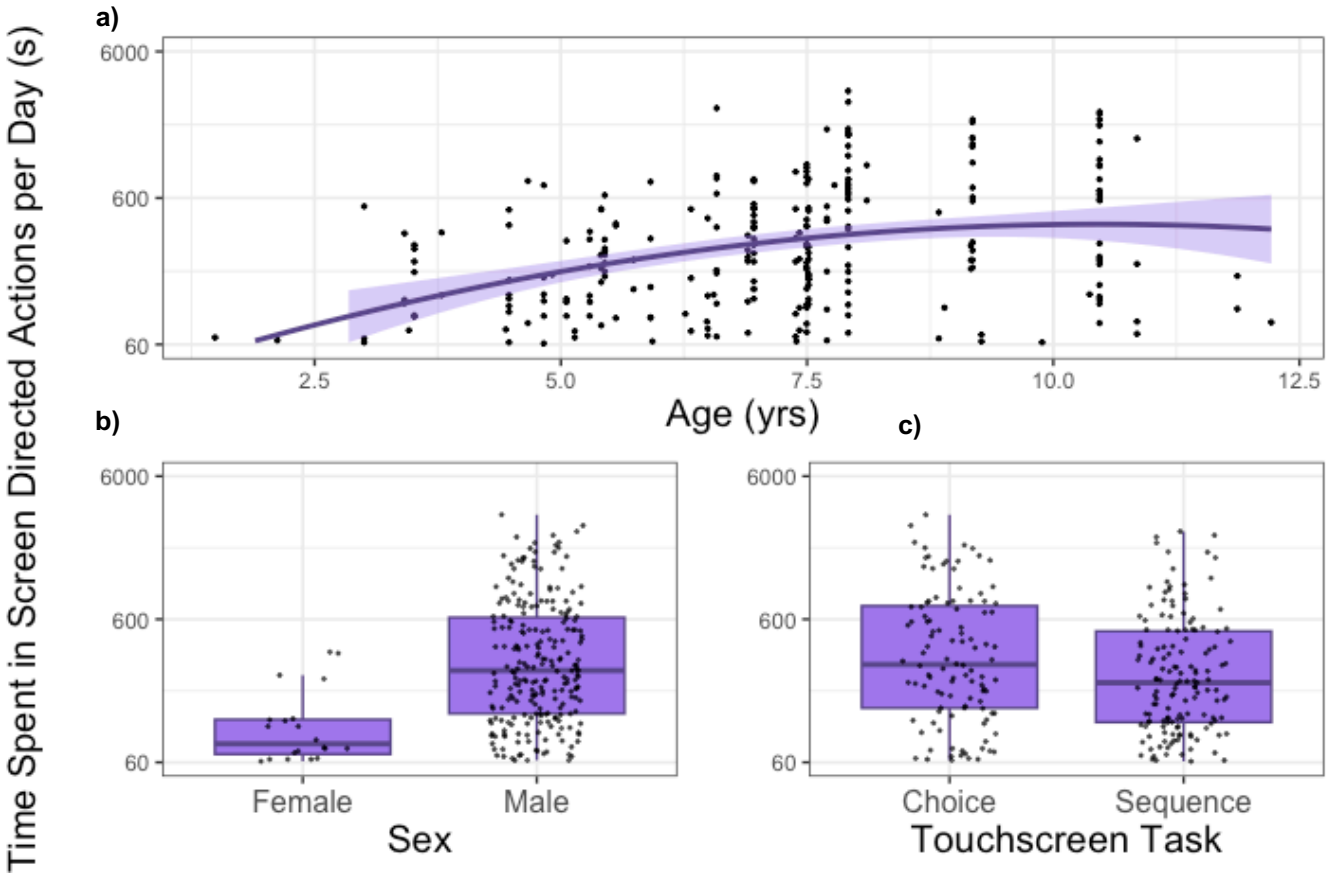


Figure 3.3: (a) A scatter graph showing the quadratic relationship between cumulative time spent (s) performing screen directed actions (SDAs) per day for long SDA bouts and age of participants in the experimental phase. (b) A boxplot of cumulative time spent (s) performing SDAs per day according to the sex of the participant. (c) A boxplot of cumulative time spent performing SDAs per day on either the choice task or the sequence task. For all, raw data is shown. Relationships are inclusive of both J and L troops combined.

3.4.4 Did age, sex or rank predict task preference?

We explored the influence of age, sex, and rank using a binomial GLMM (model 4) on the proportion of time an individual spent performing SDAs on the two-choice task (s) compared to the total time the same individual spent performed SDAs on both tasks (s). This model found no effect of age, sex or rank on task preference (Table 3.3). Furthermore, there was no effect of troop, time spent performing SDAs in the habituation period or social network strength on task preference.

3.5 Discussion

In this study, we evaluated individual variation in wild baboons' participation in a multi-task, multi-touchscreen experiment. Specifically, we investigated how age, sex, and rank: (P1a-c) affected whether individuals interacted with the touchscreens; (P2a-c) affected the cumulative time individuals participated in short SDA bouts (< 60 s); (P3a-c) affected the cumulative time individuals participated in long SDA bouts (> 60 s); and (P4a-c) were associated with any individual preference for attempting a relatively easy or difficult task. In line with our predictions, younger animals were most likely to engage with the touchscreen at least once. Although we were unable to identify any predictors of the cumulative amount of time individuals spent in short SDA bouts, we found multiple predictors for individual participation in the cumulative time individuals spent performing long SDA bouts. Specifically, we found that older individuals were more likely than younger individuals to engage with touchscreens for a longer cumulative SDA bouts per day (although this relationship reaches an asymptote at around 10 years of age), and males engaged in long cumulative daily SDA

bouts for longer than females. In contrast to our predictions, we found no impact of rank on any measure of participation. Participants spent longer participating in the easier (choice) task than the more difficult (sequence) task, but neither age, sex nor rank affected the proportion of time participating in the choice task compared to the sequence task. Below we discuss the implications of our findings for the design of cognitive experiments with wild primates as well as discussing the differences in participation (or lack thereof) in cognitive tasks that range in difficulty.

In total, 61% of 142 potential participants (68% of non-infants) participated in the experiment. This is similar recruitment (60%) to a large captive population of Guinea baboons (*Papio* papio) within a touchscreen study (Claidière et al., 2014), but a much lower proportion than some studies of small captive population sizes (Egelkamp and Ross, 2019). This demonstrates that wild baboons are motivated to interact with static touchscreen tasks despite the presence of natural foraging opportunities because the corn kernels used to reward task success are highly valued due to their nutritional content (Ranum et al., 2014). Despite this level of participation, baboons did not alter their daily movement when touchscreens (and associated rewards) were encountered by the troop compared to days when touchscreens were not encountered. Collectively, this indicates that the touchscreens represented highly valued resources, but the rewards gained only contributed a small share of the total daily intake of the baboons – due to their need to travel for other forage opportunities irrespective of touchscreen presence. The deployment of touchscreens in wild conditions within this study therefore represented a valued component of the natural foraging behaviour of the study troops. Future applications of similar methods could facilitate comparative studies

between wild and captive populations whereby a similar proportional participation can be captured.

As predicted, we found that age predicted likelihood of interaction with the touchscreens. Similar to captive Guinea baboons (Fagot and Bonté, 2010) and barbary macaques (*Macaca sylvanus*: Almeling et al., 2016), the likelihood that individuals interacted with the novel tasks at least once decreased with age. Young individuals may be more explorative and neophillic in early life as they need to acquire information due to their relative inexperience compared to older individuals (Biondi et al., 2010). Further to this, younger individuals often have limited access to resources, both due to inexperience in obtaining and exploiting them, and lack of ability to defend resources (Johnson and Bock, 2004), and may thus be motivated to explore new opportunities. Infants were also free to access the touchscreens, with one infant participating in the choice and sequence tasks (although its mother did not). Poor participation from infants is not surprising considering young infants lack the motor skills necessary to sustain interaction with the screen in addition to their dependence on mothers for travel and nutrition (Roatti et al., 2023). Despite the lack of participation from infants, our findings signal high motivation of younger individuals to interact with novel tasks and sample their environment. This means that the likelihood of capturing young participants with freely accessible cognitive tasks is high, allowing targeted studies towards younger age ranges. Alternatively, more experienced (older) individuals are unlikely to interact with tasks, presenting issues in analyses of subsequential task performance as inexperienced individuals are most likely to be sampled.

Despite the greater tendency for younger individuals to engage in SDAs, they did not perform short cumulative daily SDA bouts any more intensively than older individuals. This is surprising as young individuals are most likely to display exploratory behaviour and such behaviour tends to be of short duration (Kummer and Goodall, 1985). Our findings are also in contrast to touchscreen studies conducted with captive Guinea baboons, where younger individuals represented the most active participants through the 85 day experimental period (Fagot and Bonté, 2010). A possible explanation of the paradox of higher likelihood of touchscreen interaction of younger individuals and the similarity in touchscreen use in short cumulative daily SDA bouts could be that younger individuals are performing more long SDA bouts. However, younger individuals did not perform longer daily SDA bouts than older individuals. Together, this shows that although younger individuals are more likely to contact novel cognitive tasks, they do not sustain participation for long periods of time during an experimental day. Instead, younger individuals displayed mainly short SDA bouts at a similar engagement level to older individuals. One explanation for this level of participation could be that larger (and older) baboons are constraining long SDA bouts of younger individuals through displacements (Bean, 1999; van Horik et al., 2017), cancelling out the high motivational participation of young participants. Due to our multi-touchscreen experimental design, younger individuals were able to utilise neighbouring touchscreens to perform SDAs but were constrained to short SDA bouts if a larger baboon inevitably displaced them. However, we found no impact of rank on likelihood of participating, nor time spent participating in short or long SDA bouts. An alternative explanation therefore might be that younger individuals were less motivated to perform long daily SDA bouts, perhaps due to boredom or distractions. If this interpretation is correct, it suggests that cognitive studies may

struggle to engage younger individuals for lengthy time periods, even when multiple resources are presented. This could limit the ability of younger individuals to learn cognitive tasks through trial-and-error and necessitate such participants to acquire information on task completion via other learning routes, such as social learning, in order to maximise task efficiency.

Males in this study demonstrated higher cumulatively long daily SDA bouts than females, supporting our prediction. However, contrary to our prediction, sex did not predict the likelihood of participation or the intensity of performance of short SDA bouts. Together, this indicates that males were focusing their participation towards long daily SDA bouts to a greater extent than females. Male baboons are larger than females of similar ages, and therefore require more energy (Key and Ross, 1999). The touchscreens in this study dispensed a high quality and concentrated reward (corn kernels), whereas the immediate surrounding area contained scattered seeds interspersed within substrate (§1.2). Males attaining the largest share of concentrated resources is consistent with previous studies in this population (King et al., 2008). This not only has consequences for cognitive experiments with wild primates such as causing sampling biases, but also sheds light on the learning environment of baboon troops. With mainly male engagement, males are more likely to learn cognitive tasks through trial and error than females. In turn, this means that males should be the focus of observations from females intending to learn cognitive tasks through social learning (Martina et al., 2020). By observing males, females could exploit touchscreen resources quickly and efficiently in short timeframes where they were able to participate.

Contrary to our predictions, we found no impact of rank on the likelihood to interact with the touchscreens or the cumulative time spent participating in short and long bouts, indicating that rank had no impact on touchscreen monopolisation. Although no effect of rank on measures of participation in this study were found, dominance interactions were observed in the experimental arena by researchers when lower ranked individuals attempted to participate. Such behaviours were also observed by Harrison et al. (2023), where high-ranking adult female vervet monkeys monopolised the touchscreen. However, in the current study, displaced individuals were able to participate in tasks on neighbouring touchscreens, and so a potential impact of displacement on the cumulative time performing short- and long SDA bouts was minimised. Therefore, by presenting multiple touchscreens simultaneously, our study made it difficult for high-ranking individuals to monopolise multiple touchscreens and allowed lower-ranking individuals to access at least one touchscreen. A lack of rank effect on participation was also observed in rhesus macaques using four simultaneously-presented touchscreens (Gazes et al., 2019); however, high- and low-ranking individuals portioned their time to avoid using touchscreens together. This was also observed in Guinea baboons, where a single high-ranking female inhibited the use of touchscreens by lower-ranking females, and subsequently low-ranking females interacted with the touchscreens when high-ranking females were less active around them (Fagot and Paleressompoulle, 2009). This represents a future research direction within wild baboon populations. Together, this demonstrates that by simultaneously presenting multiple touchscreens to wild primates, low-ranking individuals can access touchscreens not only to explore briefly but can engage for comparable time periods to high-ranking individuals. Furthermore, this study builds upon studies in captivity by showing that even though participants

have free access to food resources far from the touchscreens, participants engaged with touchscreens where potential rank conflict could take place. This suggests a high motivation for novel cognitive task participation in wild baboons. In cognitive research, presenting multiple touchscreens could lower sampling biases within despotic animal societies where monopolisation may exclude low-ranked individuals. In turn, this will allow researchers to investigate factors that may impact performance and learning of cognitive tasks in low-ranked individuals.

We found no effect of age, sex, or rank on the proportion of time individuals spent on the easier (choice) task compared to the more difficult (sequence) task. This suggests that a preference for the choice task was ubiquitous across the participants. Overall, the choice task was associated with more active performance of long daily SDA bouts than the sequence task, suggesting that the participating baboons preferred to engage with the less cognitively demanding task for longer durations. As the first half of the sequence remained on the screen even after a correct action was made, this required participants to remember the first SDA performed to complete the sequence task. This differs to some studies in which the first portion of a sequence disappears after a correct choice, making it easier for the participant to complete the second choice (Chen et al., 1997; Conway and Christiansen, 2001; Jiang et al., 2018). The higher likelihood of success by chance on the choice task (50 %) could have contributed to the motivation of individuals to continue engaging with it over the sequence task (which only had a 33 % likelihood of success by chance). A ubiquitous preference for easier tasks in this study is consistent with other species such as vervet monkeys (van de Waal et al., 2015; van de Waal and Bshary, 2011), African

elephants (*Loxodonta africanus*: Greco et al., 2013) and otters (*Lutrogale perspicillata* and *Anonyx cinereus*: Ladds et al., 2017). Further to this, the choice task was more rewarding than the sequence task due to fewer actions required to complete it and a lower likelihood of unrewarded SDAs. In other words, participants sought to maximise energy intake whilst minimising effort, in line with optimal foraging theory. Such a preference for time efficient tasks is also consistent with previous studies using freely accessible touchscreens, where rhesus macaques dedicated a lower proportion of their time engaging with tasks that took longer to complete compared to shorter tasks (Calapai et al., 2017). Further studies could provide greater rewards for more difficult tasks to shed light on reward- and effort relationships and how these vary across age, sex and rank. These findings could inform established and ongoing research surrounding animal decision-making (Brosnan et al., 2013), landscape use (Fehlmann et al., 2017), and foraging strategies (Marshall et al., 2012); as well as in cognition research that aims to understand when and why primates choose to participate in tasks of varying difficulty and how free-choice links to cognitive performance (Perdue et al., 2014; Washburn et al., 1991).

This study found that age was a key driving factor in the likelihood of interaction with touchscreen tasks in wild baboons. Along with sex, age also determined the cumulative daily time over which individuals engaged with touchscreen tasks. Because we found no effect of rank, we suggest that including a multi-touchscreen layout may be helpful in allowing individuals that may have otherwise been unable to access a single touchscreen, for instance due to monopolisation, access alternative touchscreens. We also demonstrated that wild baboons are able to use touchscreen devices and ubiquitously prefer prolonged engagement

with an easier task compared to a more difficult task with the same rewards. This study adds to a growing body of scientific work that presents cognitive experiments to large populations of wild animals, ensuring cognitive experiments occur in contexts that are representative of the social and ecological conditions that wild animal groups experience.

4.0 Wild primate cognition: Predictors of performance on easy and difficult touchscreen tasks in wild chacma baboons

4.1 Abstract

There has been a recent surge in conducting cognitive experiments in large social groups in wild settings, to uncover factors that may influence the evolution of cognitive abilities in natural conditions. However, in wild conditions, animals are faced with a variety of situations that present different cognitive challenges to individuals compared to captivity. In addition, wild individuals have differing experiences of cognitive challenges depending on demographic and social characteristics. To better understand how cognitive performance is impacted by the varying difficulty of cognitive challenges and individual heterogeneity in wild animal groups, we presented two troops of free-roaming wild chacma baboons (N = 142) with four rewarded touchscreens displaying an easy and a relatively difficult task. Using a mixed-models approach, we found that overall individuals showed greater task success on the easy task, with older individuals and those of higher-rank showing greatest success. Furthermore, we found that the presence of high-ranking individuals at neighbouring touchscreens decreased task success of a lower-ranked neighbour. In the difficult task, individual task success decreased over the course of the experiment, with the memory of previous success impacting task success. These results suggest that predictors of cognitive performance can be identified. Future research should aim to disentangle the contributions of age and social dominance using task specific challenges to cognitive evolution, bridging the gap between ecological validity and experimental precision.

4.2 Introduction

Cognition encompasses an animal's capacity to gather information from its environment, process and interpret it, store it for future use and ultimately apply it to guide behaviour and decision-making. Research into animal cognition has aimed to determine how and why individuals or species differ in their cognitive abilities, which are measured through cognitive tests (Schwartz and Beran, 2022). Cognitive testing has been conducted across many taxa, with a particular research focus on non-human primates (hereafter primates) which are of great interest due to research applications for human evolution and the evolution of complex behaviours such as tool-use (Yamamoto et al., 2013). Cognitive tests can be targeted toward interdisciplinary research, with tests presented to primates used to investigate proximate causes of cognitive behaviours (Abu-Akel and Shamay-Tsoory, 2011; Carrington and Bailey, 2009; Sallet et al., 2011) and ultimate consequences (Cronin et al., 2017; Huebner et al., 2018). Most cognitive testing on primates has been conducted in research centres or zoological collections (Cronin et al., 2017; Hopper, 2017; Martin et al., 2022; Pritchard et al., 2016), with only 25% of primate cognitive studies occurring in the wild (McEwen et al., 2022). There are two major advantages of studying cognition in captive settings. Primarily, captive experimentation allows conditions to be controlled, such as subjects' experience of cognitive tasks, and the timing and amount of information given to subjects. These approaches allow researchers to investigate the cognitive capacities of animals more accurately than if such conditions were more naturalistic (Fischer, 2022). Secondly, problems and scenarios that the wild counterparts of captive animals will be unlikely to or rarely encounter can be presented to captive participants. This reveals behavioural capacities of animals to deal with exceptional situations that would be unlikely to be observed under

natural conditions (Leavens et al., 2010; O'Malley and McGrew, 2000), and shed light on how important such behaviours may be to the survival and reproduction of individuals. Together, cognitive studies in captivity demonstrate an easily accessible and flexible method of conducting animal cognition research.

Despite the benefits of studying cognition in captivity, using exclusively captive animals poses limitations that can hinder the ecological validity of the findings. As a result, conclusions drawn may misrepresent the evolution of cognitive behaviours under natural conditions (Fischer, 2022; Pritchard et al., 2016). Three particular issues that may mean cognitive studies in captivity lack ecological validity include firstly, the enticement of captive individuals into participation through food deprivation (Hopper, 2017). Hunger is a major factor in influencing the motivation to participate in cognitive tests (Thornton and Samson, 2012). Therefore, motivation to persist in participating in cognitive testing may vary within wild populations where not all individuals are equally satiated. This may mean that captive individuals have greater time and motivation to learn cognitive tasks compared to wild populations who can easily obtain food from elsewhere. Secondly, captive animal groups are artificially curated by humans, with access to cognitive tasks only afforded to select individuals. Demographic variables strongly impact test participation (see chapter 3 and Dean et al., 2011) and therefore the time available to learn cognitive behaviours. When cognitive tasks are freely accessible to all individuals in wild populations, social and demographic factors that can influence task participation may emerge, making comparisons between captive artificial groups and wild populations difficult (Harrison et al., 2023). Thirdly, captive animals are unlikely to be presented with situations during their development that would stimulate the acquisition of the foraging and social

skills necessary for survival in the wild (Boesch, 2012, 2021). In turn this may impede cognitive development in problem-solving behaviours that are most commonly experienced by wild individuals (Bard et al., 2014), and instead encourage cognitive development in problem-solving using enrichment that has little parallel in the wild. The ecological and evolutionary validity of cognitive testing in captive conditions is therefore a topic of debate due to the disparities between the social and environmental differences that captive and wild animals face (Fischer, 2022; Pritchard et al., 2016).

The ability of researchers to conduct detailed cognitive testing has benefitted from technological advances. Computerised touchscreen devices have been used in cognitive testing for decades (for review, see Egelkamp and Ross, 2019) and give researchers several advantages over 'traditional' testing. Firstly, touchscreens can allow detailed control over the presented stimuli whilst ensuring any effect of experimenter presence is minimised (Fischer, 2022). This means that tasks can be changed remotely without interfering with either the equipment or the test subjects, which may be dangerous. Secondly, touchscreens allow novel tasks to be displayed on the screen whilst the apparatus remains constant. While habituation to the physical touchscreen is required prior to cognitive testing to alleviate neophobia and train participants regarding touchscreen function, subsequent presentations of novel tasks can be presented on the familiar apparatus. Thirdly, touchscreens can be used in conjunction with traditional observations of natural behaviours, with novel tasks devised quickly that can be tailored towards testing mechanisms underlying natural cognitive behaviours. Together, touchscreens demonstrate a flexible mode of presenting novel tasks

whilst minimising the need for habituation periods and researcher interaction with study subjects.

Although conducting cognitive testing in wild conditions offers ecological validity, controlled conditions cannot be completely obtained, making it difficult to eliminate all confounding variables that may influence the expression of cognitive behaviours. Field experiments instead tend to focus on addressing what natural behaviours can influence performance in cognitive tests, what the adaptive value of such behaviours may be, and how the cognitive processes supporting such behaviours may have evolved (Fischer, 2022). With these aims, wild studies fall into two main categories. Firstly, naturalistic studies can engage in the targeted observation of natural behaviours. For instance, in chacma baboons (*Papio ursinus*), social knowledge has been tested by observing foraging decisions (Marshall et al., 2012) and leadership (King et al., 2008; King and Cowlishaw, 2009). Targeted observations can therefore be used to investigate how animals use physical and social information to inform decision-making. A second method in which cognitive studies are conducted in wild populations is through presenting subjects with novel items, thereby controlling for subjects' previous exposure to the cognitive task, allowing researchers to investigate problem-solving (Morand-Ferron et al., 2016). This procedure, although more controlled than naturalistic observations, suffers from the impact of participation (or lack thereof) with the cognitive task. Participation may vary according to age (Benson-Amram and Holekamp, 2012; Biondi et al., 2010; Martina et al., 2021), sex (Harrison et al., 2023; Thornton and Samson, 2012), rank (Bercovitch and Strum, 1993; Reader and Laland, 2001), social network position (Carter et al., 2015) or task difficulty (see chapter 3). Despite this obstacle, previous studies have presented puzzle

boxes of varying difficulty to wild participants (van de Waal et al., 2015; van de Waal and Bshary, 2011), as well as novel food items (Martina et al., 2020) and touchscreen devices (Harrison et al., 2023). When cognitive testing is conducted with wild populations, the fitness consequences of variation in cognitive abilities can be inferred using surrogates found in natural environments (Fischer, 2022), such as body condition and how cognitive performance links to survival following the presentation of cognitive tests (Fichtel et al., 2023; Huebner et al., 2018). Taken together, conducting cognitive studies in the wild can add valuable ecological validity to established theories and results obtained from tried and tested cognitive studies in captivity, opening a window into ultimate fitness consequences of cognitive variation.

Within wild populations, touchscreens have been presented to vervet monkeys (*Chlorocebus pygerythrus*), comparing their participation and performance with those of captive populations (Harrison et al., 2023). Among those individuals that participated in the vervet study, no differences in cognitive performance were found between captive and wild populations. An explanation for this is that wild groups were larger than captive groups and so had greater competition for the single touchscreen. This counteracted the captivity effects whereby captive animals are more likely to outperform their wild counterparts in cognitive tests (Forss et al., 2022). Furthermore, there were no differences between age or sex in completing 30 simple associative tasks presented, but no data was analysed on the subsequent performance (Harrison et al. 2023). Linking heterogeneities with cognitive performance in wild populations would give great insights into potential fitness consequences of cognitive variation that could stem from motivation to engage in cognitively demanding tasks.

In this study, we explored individual variation in performance in two simultaneously deployed cognitive tasks presented to wild chacma baboons (see chapter 3). We firstly aimed to assess whether (1) performance (hereby known as task success), measured as the number of correct choices made, differed between a relatively easy and more difficult task (a choice task and sequence task, respectively). Secondly, we aimed to investigate the impact of demographic predictors of task success and learning the task, including (2a) age, (2b) sex and (2c) rank across the two tasks. Thirdly, we aimed to assess (3) whether and how the presence of other individuals at neighbouring touchscreens impacted the performance of focal individuals.

For each of these three sets of analyses, we tested specific predictions. In the first case, we predicted that individuals would perform a greater number of correct choices on the easier choice task than the more difficult sequence task (P1a). Unexpectedly during the study, we observed individuals attempting alternative solutions to both touchscreen tasks in order to gain food rewards without touching the screen. We therefore predicted that more time would be spent performing alternative solutions on the sequence task than the choice task (P1b). Secondly, we predicted that individuals more experienced in problem-solving, such as older individuals (Galef and Laland, 2005), males (King et al., 2008), or higher-ranked individuals (Harrison et al., 2023; Laland, 2004) would perform the greatest number of correct choices overall (P2a, P2b, P2c respectively). In addition to experience, previous studies have shown than high-ranking individuals can be better than low-ranking individuals at performing sequence tasks (MacLean et al., 2008; Paz-y-Miño C et al., 2004). We therefore predicted that rank would

positively correlate with performance in the sequence task as well as the easier choice task (P2c). Finally, chacma baboons are despotic, and high-ranking individuals often monopolise concentrated resources (King et al., 2008). The threat of aggressive interactions from high-ranking individuals could cause acute stress in low-ranking individuals and impact their performance (Abbott et al., 2003; Hoffman et al., 2010; Zhang et al., 2018). Therefore, we predicted that the presence of higher-ranked individuals at neighbouring touchscreens would correlate negatively with the performance of a lower-ranked participant in both the choice and sequence tasks (P3).

4.3 Methods

4.3.1 Study site, species and subjects

This study took place at Tsaobis Nature Park, Namibia (22°23'S, 15°45'E) as part of the Tsaobis Baboon Project between 21st July and 3rd October 2022. Two habituated troops (J and L) of wild chacma baboons were the subjects, comprising a total of 64 and 78 individuals in J and L, respectively. Of these potential participants, 86 (61%) individuals interacted at least once with a touchscreen, touching the screen via a screen-directed action (SDA), and therefore comprise the participating sample size in this study (see chapter 3). The experimental arena was located within an ~800 m^2 unenclosed area near a permanent artificial waterhole within 1 km of three commonly used sleeping cliffs of the study troops.

Age (in years) of the participants were calculated using methods from Dezeure et al., (2021) as time from the known or estimated date of birth to the beginning

of the experimental phase of this study. Dominance interactions were collected during full day follows (May – October 2022) and did not include dominance interactions involving the experimental apparatus. Dominance ranks were calculated for each individual through the 'I&SI' method (De Vries, 1998; Schmid and de Vries, 2013). Ranks were standardised within troops between 0 (low-ranking) and 1 (high-ranking) using the formula 1-((1-*r*)/(1-*n*)), where *r* is the absolute rank of an individual ranging from 1 to the group size of *n* (Baniel et al., 2018). Proximity associations were collected between May and October 2022 through sampling all individuals within 10 m of a randomised focal individual (Roatti et al., 2023). Weighted social networks were then calculated, from which the strength of social connections was used in later analyses (Croft et al., 2009). Baboons readily gather information about cognitive task completion (Carter and Cowlishaw, 2021) and associate with conspecifics that they have strong social connections with (Roatti et al., 2023). It was therefore possible that baboons could learn how to complete the cognitive tasks via social learning between task attempts, rather than exclusively through personal experience of the task. Furthermore, individuals could be more likely to experience personal learning of a task if a strong social partner previously used the touchscreen. Social network strength was therefore used in later analyses as a predictor of how social ties explained task performance, and such as an indicator of social learning.

4.3.2 Ethical statement

All research regarding the presentation of touchscreens to chacma baboons as part of the Tsaobis Baboon Project was conducted under ZSL Ethical Review 412-PCE-0120.

4.3.3 Touchscreen set-up and general procedure

This study utilised four simultaneously presented 15-inch open-frame LCD Elo 1950L touchscreens with an integrated automatic feeding mechanism, with a battery life of two hours. The touchscreens were contained in Pelican cases and housed in metal cages (grid width of 20 cm). These were placed in a semi-circle pattern 20 m apart to reduce visibility from neighbouring screens, and oriented south to reduce screen glare. Cage legs were secured into PVC tubes that were held in place with 1 m^3 of concrete and rocks to a depth of 1 m to prevent baboons lifting the cages out of the ground. Natural substrate was replaced covering the concrete to ground level (Figure 4.1).

Figure 4.1: Touchscreen Setup

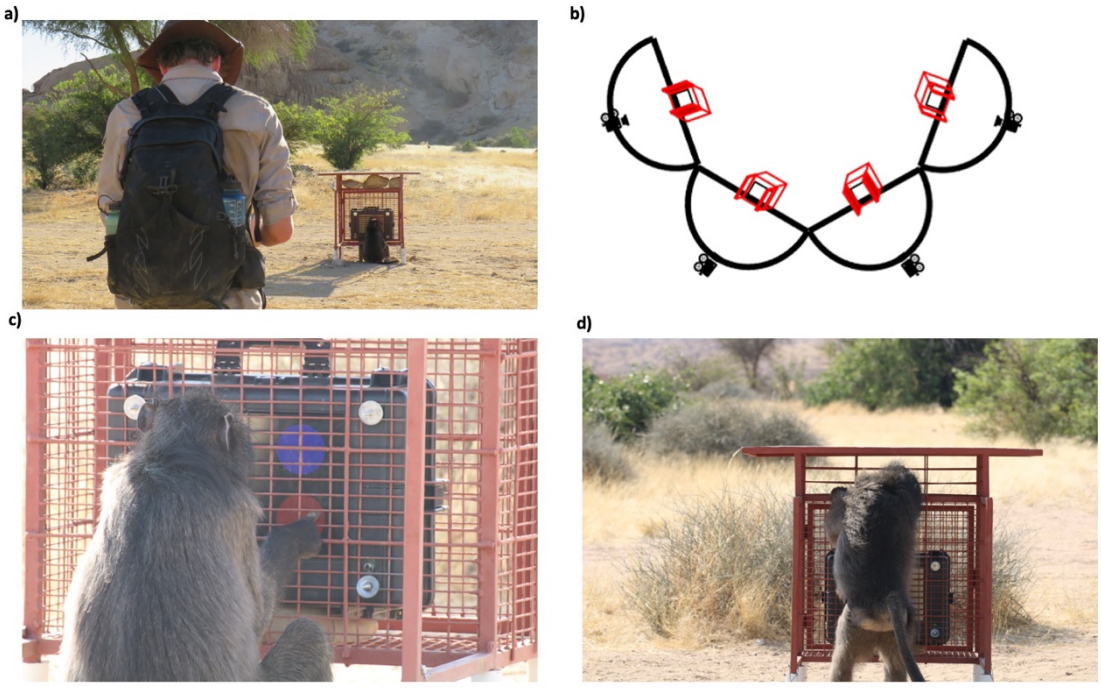


Figure 4.1: Experimental set-up. Shown are (a) a photograph of the data collection, recording participant behaviour from over 10 m distance from the cage in which touchscreens were housed, set into a hole ~80 cm deep with cage legs held within PVC tubes. The PVC tubes were held in place with a mix of concrete and rocks. PVC tubes were used so that the cages could be removed at the end of the experiment. (b) A schematic of the experimental area with red cages housing touchscreens; the semicircles indicating the observer area with camcorders positioned outside the area in front of the touchscreen. Touchscreen cages were static and remained in the same locations throughout the study. Touchscreens were randomly allocated to each cage on every experimental day. (c) A photograph showing a juvenile male baboon doing screen-directed actions (SDAs) on a touchscreen displaying the sequence task. The photograph shows the touchscreen at eye height to a sitting baboon. (c) A photograph of an adult male baboon attempting to shake the cage (§4.4.2).

Touchscreen units were deployed when baboons were within 1 km of the experimental arena and remotely started when a baboon was within 50 m of the experimental area. This occurred mostly between 12pm and 2pm as at this time, baboons often looked for water sources near to the experimental area. A researcher stood 15 m in front of each of the four touchscreens and recorded the identity of all baboons interacting with the units using Cybertracker (Liebenberg, 2022). One tripod-mounted camcorder (model Sony hdr-cx240e) was placed

besides each observer to record all experiments and ensure the baboon identities of touchscreen users were accurate.

The touchscreens were presented for a maximum of two hours to a participating troop, after which point, the screens were put to sleep remotely. The touchscreens were removed after a troop had left the experimental area, and the cages remained in place. If a technical issue arose with the touchscreens (such as the reward dispenser becoming blocked), the screens would be remotely put to sleep. Usually only one experiment was run per day with a single troop (n=18), but on a small number of occasions (n=3) we ran two experiments within a single day when both troops visited the experimental arena on two different occasions (at least two hours apart to allow touchscreen recharging).

The same bespoke touchscreen software was used on all touchscreens, which was able to present different tasks according to the phase of the experiment (see below for more details; Figure 4.2). The touchscreens automatically recorded presses to the screen, with the location of the touch, time, and whether the touch was successful or not depending on the pre-set task. These data were supplemented by researchers recording screen-directed actions (SDAs), ensuring that a press to the touchscreen was reliably recorded automatically by the touchscreen as well as a researcher (as residual moisture on the screen could cause the touchscreen to register a press).

Further to data regarding behaviours directed at the touchscreen, dominance interactions were collected *ad libitum* between May and October 2022 during full-day follows of both troops during long-term data collection, and did not include

dominance interactions involving the experimental apparatus. Dominance ranks were calculated for each individual through the 'I&SI' method (De Vries, 1998; Schmid and de Vries, 2013). Ranks were standardised within troops between 0 (low-ranking) and 1 (high-ranking) using the formula 1-((1-*r*)/(1-*n*)), where *r* is the absolute rank of an individual ranging from 1 to the group size of *n* (Baniel et al., 2018). Rank differences between individuals on neighbouring touchscreens were calculated by subtracting the rank of the highest ranked individual present at a touchscreen next to the touchscreen of a participant during a bout (20 m away) from the rank of the participant. This resulted in a negative difference if the highest rank of neighbours was greater than that of the participant (-1 < 0) and a positive value if the participant was a higher rank than its neighbour (0 < 1). The neighbour was not required to be performing SDAs to be included in this sample.

Social networks were built using proximity data. Proximity associations were collected between May and October 2022 through recording all individuals within 10 m of a randomised focal individual (Roatti et al., 2023). Weighted social networks were then calculated, from which the strength of social connections was used in later analyses as a proxy for social learning – the learning of a behaviour from the observation of another – that may have contributed to task success (Croft et al., 2009). A full ethogram of behaviours recorded in the touchscreen study can be found in Appendix 3.

4.3.4. Habituation phase

Prior to beginning the experiments, it was necessary to accustom the baboons to the touchscreen units to decrease neophobia and familiarise them with the action of touching the screen to obtain a food reward (Schmitt, 2018). Between 21st July

and 25th August 2022, the baboons were habituated to the presence of the touchscreens and familiarised with the action of touching the screen to obtain a food reward. During this habituation phase, participants were required to press a randomly located yellow hexagon to obtain a familiar and highly preferred food reward (1 - 4corn kernels) from one of two simultaneously presented touchscreens (Figure 4.2a). Following a correct choice, 1-4 corn kernels was dispensed through one of two chutes and accompanied by a small green light on the touchscreen exterior. An incorrect choice resulted in a disappearance of the shapes from the screen for one second and accompanied by a red light in the same location as the green light. After an SDA registered by the screen at any location, shape/s reappeared again in a random configuration after 1 second. The two touchscreens were deployed in the second and fourth positions of the experimental arena (with position one being closet to the watering hole) simultaneously throughout the habituation phase. Both troops had the opportunity to encounter the habituation task, although equal individual exposure to the touchscreens was unlikely given the voluntary nature of participation. Unequal exposure was therefore controlled statistically in the analyses. Due to time constraints, the habituation phase lasted for 21 days, giving baboons equal exposure to the experimental area in the habituation and experimental phases.

4.3.5 Experimental phase

During the experimental phase (31st August – 3rd October 2022), four touchscreens arranged randomly were deployed simultaneously, with two touchscreens displaying a relatively easy task (choice task) and two touchscreens displaying a relatively difficult task (sequence task) to obtain a food reward of 1-4 corn kernels. During the choice task, participants were

simultaneously presented with a white five-pointed star that was rewarded when pressed, and a white cross that was not rewarded, both on a black background (Figure 4.2b). The sequence task required participants to select coloured shapes in an exact sequence to obtain a food reward; a red circle followed by a blue circle (Figure 4.2c). Both circles were presented simultaneously on a black background and the red circle remained on the screen after being pressed. Touches to the black background surrounding the shapes as well as selecting incorrect shapes resulted in a test failure and the shape locations were reset to random quadrants with a 1-s delay.

Task success was measured as the number of correct choices an individual made per SDA bout. A bout was defined as the time spent continually making SDAs, with a bout ending after at least 10 seconds of SDA inactivity (for instance if an individual left the touchscreen or stopped using the touchscreen). The number of correct choices made during a bout was the only measure of task success in the choice and sequence tasks within this study.

Figure 4.2: Touchscreen Tasks Presented

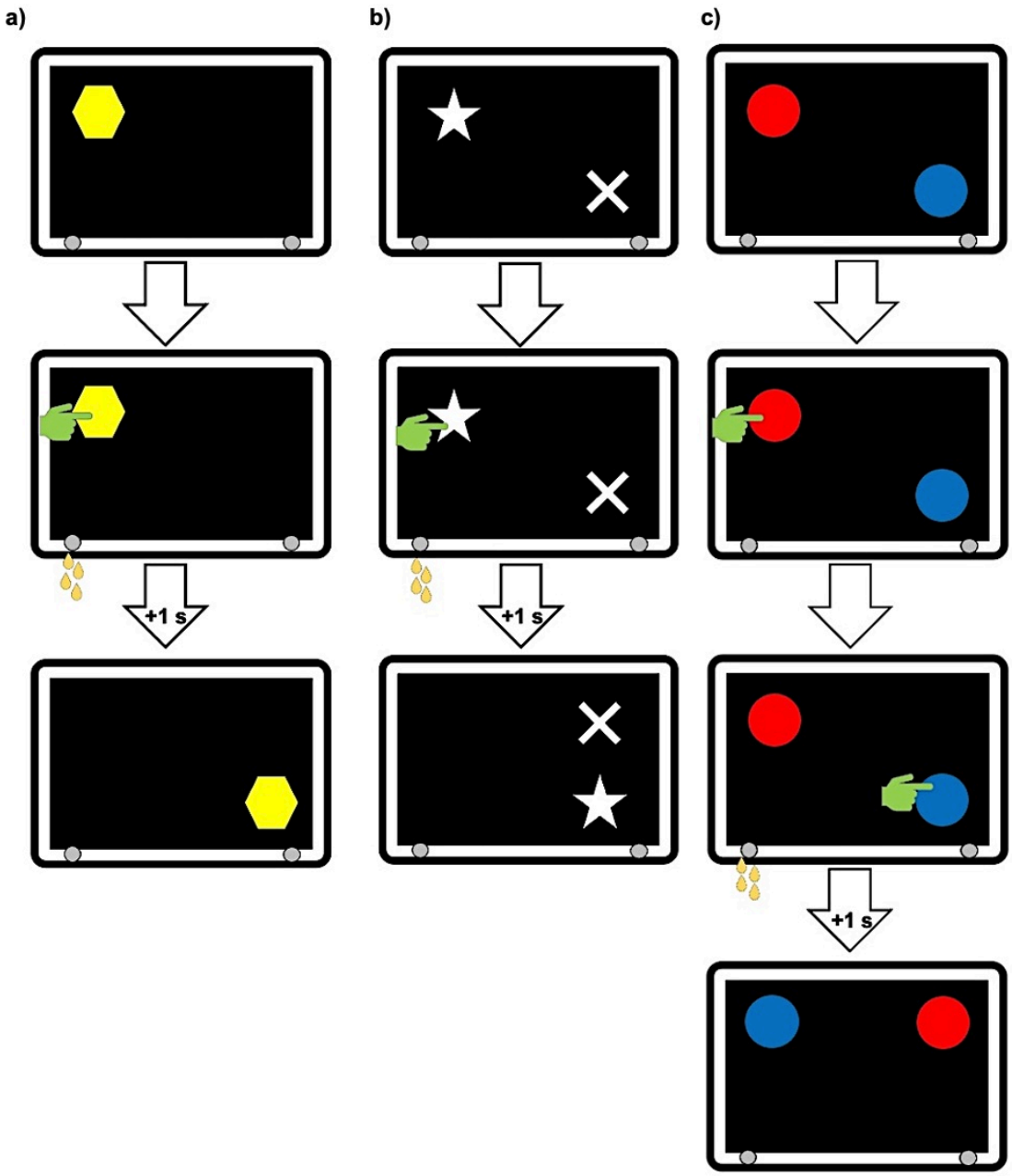


Figure 4.2: Touchscreen tasks presented. Shown are schematics of the touchscreens presented to baboons in this study. Corn reward is depicted as delivered from a random chute at the base of the touchscreen. Tasks consisted of (a) the habituation task presented on two touchscreens simultaneously. The habituation task consisted of a yellow hexagon that was rewarded when pressed. (b) The choice task presented on two of four simultaneously deployed touchscreens in the experimental phase. The choice task consisted of a white star and cross, whereby the star was rewarded when pressed and the cross was not. (c) The sequence task presented on two of four simultaneously deployed touchscreens in the experimental phase. The sequence task consisted of a red circle and a blue circle, whereby only a press to the red circle followed by a press to the blue circle would result in a reward. The red circle remained on the screen after the initial press. After a correct or an incorrect press was made to either the shapes or the background, shapes would disappear from the screen for 1 s and reappear in randomised quadrants. The tasks would therefore be reset, and for the sequence task, any previous attempt

would not carry over to the next attempt (for example if red was chosen followed by another red choice, selecting blue after a task reset would not count as a completed sequence).

4.3.4 Statistical analysis

All analyses were performed on R v2023.06.02 build 561. We ran one generalised linear mixed-effects model (GLMM) and six linear mixed-effects models (LMM) to address our aims using the R package “lme4” (Bates et al., 2015). We did not complete any model simplification as all explanatory variables were of interest. To evaluate the fit of GLMMs and LMMs, we visually inspected the residuals for normality, homoscedasticity and the absence of patterns that might indicate model misspecification. Residual plots, including Q-Q plots, were used to assess whether residuals conformed to the assumptions of the model. Specifically, we checked for a lack of systematic trends in residuals versus fitted values, as well as the approximate normality of residuals (Zuur et al., 2009). We assessed multicollinearity among predictors by calculating variance inflation factors (VIFs) with the package “car” (Fox et al., 2023). All fixed effects were of importance to our research questions, therefore any multicollinearity, if present, was taken into consideration before interpreting results. All models are summarised in table 4.1. These diagnostic checks ensured that the models were appropriate for the data and that parameter estimates were unbiased and reliable. The explanatory power of each variable was determined by comparing the ‘full’ model to a null model (excluding the variable of interest) through ANOVA.

Table 4.1: A summary of statistical models used to address P1-3. To test these predictions, the explanatory power of models was assessed by comparing full models with all biologically relevant variables to models with variables removed (ANOVA). All models presented are full models as the removal of any variable did not improve model fit without creating difficulties for biological interpretation. VIFs were checked for all models and non-displayed any significant collinearity.

Research questions	Predictions	Model	Response	Fixed effects	Random effects, etc
Differences between tasks	P1a. More correct choices with the simpler task P1b. Alternatives sought for the sequence task	Model 1a. LMM Model 1b. LMM	Correct choices per bout Cumulative time spent shaking cage	Task type + offset bout time 1 Task type 2 Cumulative incorrect choices, choice task 3 Cumulative incorrect choices, sequence task 4 Time since last correct choice 5 Cage type + offset cumulative screen time	Experimental ID Individual ID Experimental ID Individual ID
Individual predictors of learning	Males (P2a) and older individuals (P2b) more likely to make correct choices; high rank individuals better at sequence tasks (P2c)	Model 2a. Binomial GLMM, Choice task Model 2b. Binomial GLMM, Sequence task	Learning criteria reached, 0/1 Learning criteria reached, 0/1	1 Age 2 Sex 3 Rank 4 Cumulative screen time (choice, sequence)	Individual ID

		_____ Model 2c.LMM, choice task Model 2d. LMM, sequence task	_____ Correct choices per bout Correct choices per bout	5 Troop 6 Social network strength _____ 1 Age (choice quadratic, sequence linear) 2 Sex 3 Rank 4 Social network strength 5 Cumulative screen time (choice linear, sequence quadratic) 6 Troop 7 Time since last correct choice 8 Time spent in habituation + offset bout time	_____ Experimental ID Individual ID
Effects of individuals at neighbouring touchscreens	P3. Presence of higher ranked neighbours will reduce performance in both tasks	Model 3a. LMM, choice task _____ Model 3b. LMM, sequence task	Correct choices per bout _____ Correct choices per bout	1 Rank difference with neighbours 2 Cumulative screen time (choice, sequence) 3 Troop + offset bout time	Experimental ID Individual ID

To address our first prediction (P1a; model 1a), a LMM was used to determine whether performance differed between task type. The response variable used was task success, with task type (choice and sequence) as a fixed effect. The model also included a log offset of bout length (s) to control for participation. This offset was required as time spent using the touchscreens differed between individuals according to age, sex and task (see chapter 3), meaning some individuals gained greater opportunities to learn tasks via trial and error. Random effects of experiment number and participant identification to control for environmental variability across the experiment and repeated measures respectively.

To investigate alternative strategies used to obtain food rewards from the touchscreens (P1b), cumulative time spent performing alternative strategies (s) was used as our response variable in an LMM (model 1b). The main alternative strategy was identified following the experiment as shaking the cage vigorously, which would dislodge 1 – 4 corn kernels from their internal housing and onto the ground. Therefore, the cumulative time spent shaking the cage was used as the response variable with a fixed effect of task type (log transformed to account for positive skew). We also included three predictors of prior task success experience as fixed effects. If a greater number of incorrect choices were performed, this may have motivated individuals to seek alternative solutions to gain rewards. Therefore, we included the cumulative number of incorrect choices performed in the choice task as a first fixed effect and similarly in sequence tasks as a second fixed effect. Thirdly, we were interested in assessing if memory of previous task success impacted the time spent performing alternative strategies, and so time since the last correct choice was made (s) was included as a fixed

effect. A further fixed effect of the cage type was included as two of the four cages were heavier than the others. To control for a greater cumulative time using the screen impacting the cumulative time spent shaking the screen, cumulative screen time was included as an offset. Experiment number and participant identity were included as random effects. No collinearity between fixed effects were found.

To address our second predictions, learning criteria were established to categorise whether participants consistently performed correct choices above chance (P2a-c; models 2a-b). Learning criteria were defined by achieving two performance measures (relating to over 75% percentage correct and consecutive correct responses above chance), which is standard across cognitive literature (Claidière et al., 2014; Fagot and Bonté, 2010). Firstly, baboons were required to complete a task to above chance level at least once over the course of the experiment to be categorised as learning the task. Baboons had a 50% chance of completing the choice task, and a 25% chance of completing the sequence task randomly. Therefore, in order to achieve above chance levels (< 5% probability of completing the task randomly), baboons were required to complete at least five consecutive choice tasks correctly to achieve learning criteria for the choice task. For the sequence task, baboons were required to perform at least three consecution sequence tasks correctly to achieve learning criteria. Due to the multi-touchscreen design of this study, baboons were able to move to a different touchscreen but still attempt the same task. Furthermore, the categorisation of bouts meant that individuals could attempt a task, rest (or consume rewards) and then resume task activity on the same touchscreen. To account for freedom in task participation, learning criteria assessment

encompassed consecutive bouts regardless of touchscreen. However, this could misrepresent high touchscreen users as achieving learning criteria when their overall task success is consistently poor. For example, a baboon may perform 100 choices on one touchscreen displaying a choice task, of which the only correct choices made were the final two (2% correct). If the baboon then moves to another touchscreen and performs another 100 choices of which the only correct choices were the first three (3% correct), it will appear as though the baboon has completed five correct choice tasks consecutively despite only 2.5% of choices being correct. Therefore, the second requirement to reach learning criteria, to account for frequent (but poor) touchscreen users, was that baboons were required to perform at least 75% of choices within a single bout correctly, within all bouts that the consecutive correct choices occurred within. This percentage measure is the minimum across cognitive literature (Claidière et al., 2014; Fagot and Bonté, 2010). To assess the impact of age, sex and rank on reaching the learning criteria, two binomial GLMMs with a logit link function (one for each task) were used with an individual reaching learning criteria coded as 1, and not reaching learning criteria coded as 0. Age (yrs), sex (male or female), rank, troop (J or L) and social network strength were included as fixed effects. To assess if participation predicted reaching learning criteria, the cumulative time spent performing SDAs on the task was included as a fixed effect although it was not possible to control for bout length or experimental day due to the binary nature of the models. Participant identity was used as a random effect.

Two LMMs (models 2c-d) were used to investigate the impacts of age (P2a), sex (P2b) and rank (P2c) on performance regardless of learning criteria, with the same measure of performance as the LMM within P1a, but with performance in

the choice and sequence tasks analysed separately. These models were used so that predictors of performance of low touchscreen users who could never achieve learning criteria, such as those that performed fewer than three choices on the sequence task could be included in our analyses. Age was used as a fixed effect in these models, with models using a linear and quadratic fit compared using an ANOVA and the model best explaining the variation in the data used. Fixed effects for these models also included sex, rank, social network strength and troop. Furthermore, cumulative screen time on the task (s) (choice = linear, sequence = quadratic identified as best fit for the data using ANOVA as previous) was included as a fixed effect to control for baboons that used the touchscreens more gained greater opportunities to learn the correct choices (and thus may mask any impacts of other predictors). In addition, baboons may have forgotten correct choices if a significant time had passed since a baboon's last correct choice, meaning they would need to relearn the task which in turn would impact their performance compared to a previously knowledgeable state. Consequently, time since the last correct choice was included as a fixed effect. Finally, baboons who spent longer using the touchscreens during the habituation period were more familiar with the workings of the touchscreen, than baboons who had not experienced the touchscreen until the experimental period. As there was no way to give baboons equal exposure to the touchscreen (although a different task) during the habituation phase, time spent performing SDAs in the habituation phase (s) was included as a fixed effect. A log offset of bout length was included to control for time spent at the touchscreen, and random effects of experiment number and participant identification were also included.

To address our third prediction (P3), two LMMs were used (one per task) to predict the impact of the rank of conspecifics at neighbouring touchscreens on the performance of a participant at a touchscreen (model 3a-b). For this model, the number of correct choices made when a shape was chosen at least once during a bout (log transformed) was used as the response variable. Fixed effects in these models included rank differences, cumulative time spent performing SDAs and troop, along with a log offset of bout length. Random effects of experiment number and participant identification included.

4.4 Results

4.4.1 Overall task performance

In total, the touchscreens recorded 28,409 touches to the screen. Within the choice task, this included 4220 correct shapes and 2589 incorrect shapes pressed. Within the sequence task, this included 894 correct shapes chosen (resulting in 447 completed sequences of red - blue) and 525 incorrect sequences completed (inclusive of all incorrect possibilities; red – red, red – nothing, blue first). In the experimental phase, 38 individuals across 754 bouts of SDAs performed at least one correct choice in both tasks inclusive. Through our examination of the impact of task type on the number of correct choices made (Figure 4.3), we found that performance on the sequence task was lower than on the choice task (Estimate = -1.020, SE = 0.082, t = -12.370, $p < 0.001$; Table 4.2). As discussed previously (§3.4.1), daily distance travelled by baboons was not impacted by the presence of the touchscreens. By integrating performance into these analyses, we could assess whether baboons gained high degrees of nutrition from touchscreens (Ranum et al., 2014) that may have

impacted their foraging strategies. The minimum number of correct choices that participants made in a session was one, resulting in 1.2 – 4.8 kCal gain. The maximum calorific gain during a session by a single individual was 22.45 – 89.79 kCal (troop median = 1.2 – 4.8 kCal per session, IQR = 7.2 – 28.8 kCal per session).

Figure 4.3: Task success according to task type

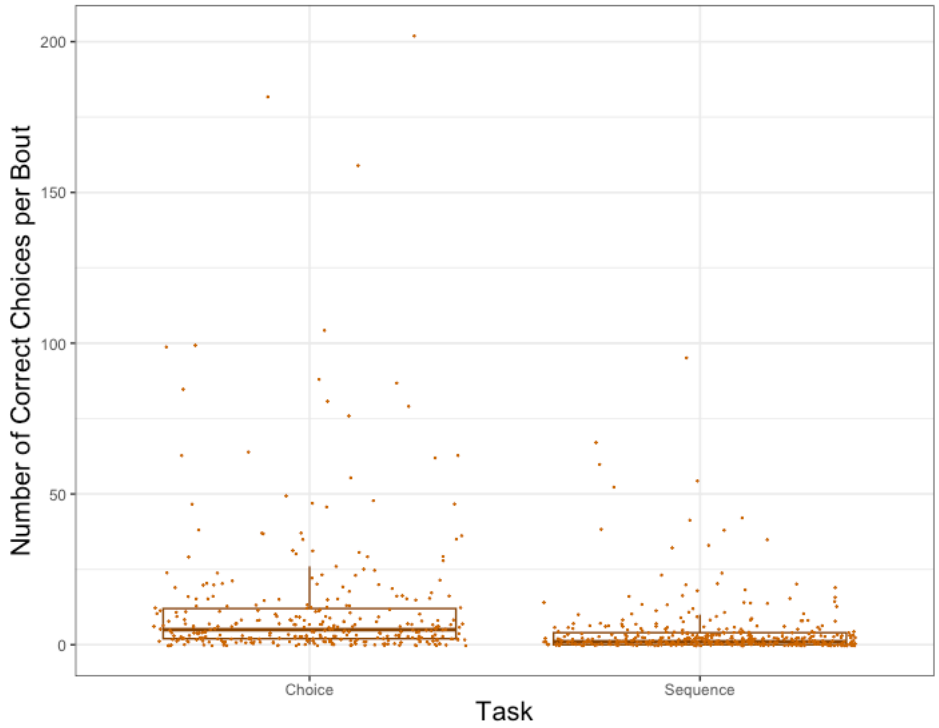


Figure 4.3: Boxplot of the number of correct choices made during a bout on the choice and sequence tasks. A bout was defined as the time between a participant's first SDA when within arm's reach of a touchscreen and the last SDA with a minimum 10 s gap before the next SDA. The correct number of choices per bout was defined as number of correct choices or full sequences a participant made, with non-shape touchscreen SDAs omitted. Data represented are raw data and are inclusive of all SDA bouts across all participants.

Table 4.2: Model outputs for (1) differences in performance across both tasks (P1), (2) time spent performing alternative actions (P2), (3a) predictors of reaching learning criteria for the choice (3b) and sequence tasks (P3a-c), (4a) predictors of performance for the choice (4b) and sequence task (P3a-c) and (5) impact of rank differences with neighbours on task success (P4). Table items in bold represent model outputs of statistically significant values ($p < 0.05$).

Model	Nobv / Nind	Term	Estimate	Std. Error	T value (1a, 1b, 2c, 2d, 3a, 3b), Z value (2a, 2b)	P
(1a) Task diff	754 / 38	**Intercept**	**-2.348**	**0.123**	**-19.09**	**<0.001**
		Task: sequence	**-0.635**	**0.077**	**-8.24**	**<0.001**
(1b) Alternative	792 / 38	Intercept	28.990	94.000	0.308	0.758
		Task: sequence	**159.900**	**69.800**	**2.290**	**<0.05**
		Cumulative incorrect choices: choice task	**1.374**	**0.499**	**2.747**	**<0.05**
		Cumulative incorrect choices: sequence task	**1.295**	**0.453**	**2.858**	**<0.05**
		Time since last correct	0.002	0.001	1.427	0.154
		Heavier cage	-113.868	68.664	-1.658	0.125
(2a) Learning criteria: choice task	65 / 65	Intercept	-33.991	820.292	-0.041	0.967
		Age	0.494	0.664	0.745	0.457
		Sex: M	18.164	832.267	0.022	0.983
		Rank	-2.992	7.388	-0.405	0.686
		Cumulative time: (choice)	**0.003**	**0.001**	**2.156**	**<0.05**
		Troop: L	15.707	795.807	0.020	0.984
		Social network strength	-2.912	2.342	-1.243	0.214
(2b) Learning criteria: sequence task	72 / 72	Intercept	-18.670	873.30	-0.021	0.983
		Age	-0.461	0.620	-0.743	0.458

		Sex: M	15.550	873.30	0.018	0.986
		Rank	6.955	7.399	0.940	0.347
		Cumulative time (seq)	<0.001	<0.001	1.892	0.058
		Troop	-1.937	1.645	-1.199	0.231
		Social network strength	-1.111	1.421	-0.782	0.435
(2c) Performance: choice task	319 / 22	Intercept	1.023	1.779	0.575	0.568
		Age (linear)	**-1.41**	**0.466**	**-3.037**	**<0.01**
		Age (quadratic)	**0.087**	**0.027**	**3.228**	**<0.01**
		Sex: M	-0.252	0.975	-0.259	0.796
		Rank	**3.569**	**1.143**	**3.123**	**<0.01**
		Social network strength	-0.192	0.184	-1.039	0.328
		Cumulative screen time	-0.033	0.055	-0.604	0.548
		Troop: L	**-0.409**	**0.185**	**-2.207**	**<0.05**
		Time since last correct	-0.009	0.015	-0.601	0.548
		Time in habituation	0.058	0.048	1.219	0.230
(2d) Performance: sequence task	379 / 23	Intercept	0.118	1.519	0.078	0.938
		Age (linear)	-0.062	0.119	-0.521	0.620
		Sex: M	-1.025	1.324	-0.774	0.445
		Rank	0.289	1.396	0.207	0.842
		Social network strength	0.009	0.287	0.032	0.977
		Cumulative screen time (linear)	**-0.721**	**0.341**	**-2.116**	**<0.05**
		Cumulative screen time (quadratic)	**0.049**	**0.024**	**2.029**	**<0.05**
		Troop: L	-0.168	0.230	-0.729	0.496
		Time since last correct	**-0.054**	**0.015**	**-3.694**	**<0.001**
		Time in habituation	**0.179**	**0.077**	**2.332**	**<0.05**

(3a) Neighbour effect: choice task	136 / 20	Intercept	0.173	0.569	0.304	0.764
		Rank difference to neighbour	**0.998**	**0.435**	**2.293**	**<0.05**
		Cumulative screen time	**0.245**	**0.073**	**3.393**	**< 0.01**
		Troop	-0.022	0.277	-0.081	0.938
(3b) Neighbour effect: sequence task	134 / 24	Intercept	-0.288	0.774	-0.372	0.712
		Rank difference to neighbour	0.627	0.382	1.643	0.103
		Cumulative screen time	0.123	0.104	1.184	0.244
		Troop	0.785	0.413	1.899	0.068

4.4.2 Alternative strategies

The only alternative strategy that individuals employed to gain food reward without the need to attempt touchscreen tasks was to aggressively shake the cage that contained the screen (Fig 4.1d). This would dislodge corn rewards from their internal housing, and they would fall through the dispenser tubes onto the ground. Overall, 25 individuals attempted to shake the touchscreens of which all were males except an ambitious shake attempt by an unsexed infant. Of the males, two were juveniles, 18 were sub-adult males and five were adults. In our LMM (model 1b), we found that individuals shook the cage containing a touchscreen displaying the sequence task for a greater cumulative time than touchscreens displaying the choice task (Fig 4a; Estimate = 159.9, SE = 69.8, T = 2.290, $p < 0.05$). In addition, individuals shook the touchscreens displaying the choice task (Estimate = 1.374, SE = 0.499, T = $p < 0.05$) and the sequence task (Estimate = -1.295, SE = -0.453, $p < 0.05$) for a longer cumulative time when more incorrect choices were made on the task. We found no relationship between the time since the last correct choice was made and the cumulative time spent shaking the touchscreens. Furthermore, individuals did not shake heavier cages for less cumulative time than lighter cages.

Figure 4.4: Factors impacting the use of alternative touchscreen strategies

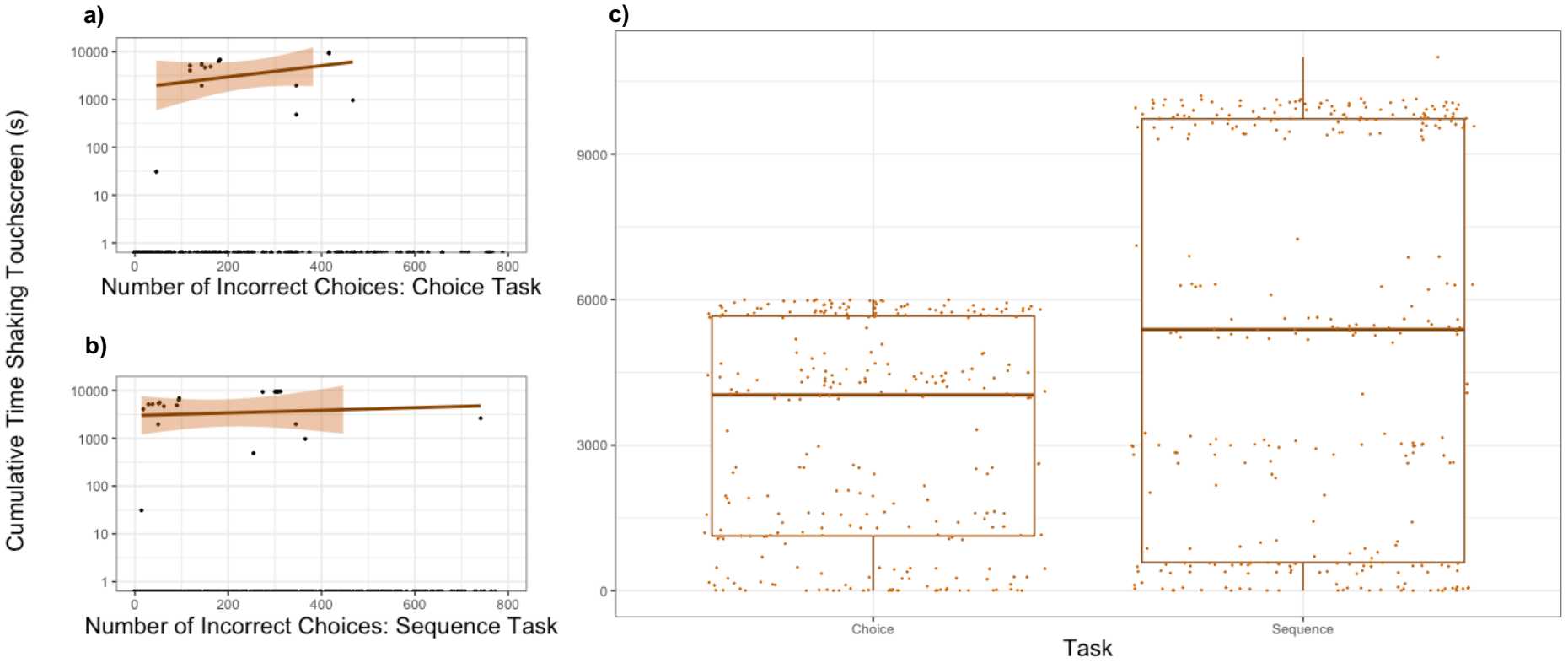


Figure 4.3: a) A scatter graph showing the relationship between the cumulative time spent shaking the cage containing the touchscreen and b) the cumulative number of incorrect choices made in the choice task and the sequence task. c) A boxplot depicting the cumulative time spent shaking the cage containing the touchscreen according to the task displayed on the touchscreen. Data depicted are raw data and inclusive of both J and L troops.

4.4.3 Reaching learning criterion

Out of all participants, only males reached full learning criterion. In the choice task this included seven sub-adult males and one adult male. Four sub-adult males reached full learning criterion in the sequence task, with only two sub-adult males reaching full learning criterion in both tasks. Our binary GLMMs (models 2a and 2b) demonstrated that only cumulative time spent on tasks impacted the likelihood of reaching full learning criterion (choice: Estimate = 0.003, SE = 0.002, $p<0.05$; sequence: Estimate < 0.001, SE < 0.001, $p = 0.058$; Table 4.2).

4.4.4 Factors impacting performance

We ran two LMMs (models 2c and 2d) to investigate the impact of predictors such as age, sex and rank on performance within the touchscreen tasks, regardless of reaching learning criteria or not. Within the choice task (Figure. 4.5; Table 4.2), we found a quadratic effect of age on performance, with performance increasing with age, plateauing between 8 and 9 years old (linear: Estimate = -1.41, SE = 0.466, T = -3.037, $p < 0.01$; quadratic: Estimate = 0.087, SE = 0.027, T = 3.228, $p < 0.01$). We found no impact of sex on performance during a bout, but we found that performance positively correlated with social rank (Estimate = 3.569, SE = 1.143, T = 3.123, $p < 0.01$). In addition, we observed a troop difference in performance (Estimate = -0.049, SE = 0.185, T = -2.207, $p < 0.05$) with J troop performing a greater number of correct choices than L troop per bout.

Within the sequence task (Figure 4.6; Table 4.2), we found no impact of age, sex or rank on performance. Participants increased task success per bout within

low cumulative touchscreen use in a quadratic relationship but then performance decreased at around one hour (3600 s) of cumulative touchscreen use in a linear relationship (linear: Estimate = -0.721, SE 0.341, T = -2.116, $p < 0.05$; quadratic: Estimate = 0.049, SE = 0.024, T = 2.029, $p < 0.05$). In addition, we found a negative correlation between performance and the time passed since the participant performed a correct SDA (Estimate = -0.054, SE 0.015, T = -3.694, $p < 0.001$). Individuals that attempted the habituation task for a longer cumulative duration also choice more correct shapes (Estimate = 0.179, SE = 0.077, T = 2.332, $p < 0.05$).

Figure 4.5: Factors impacting performance in the choice task.

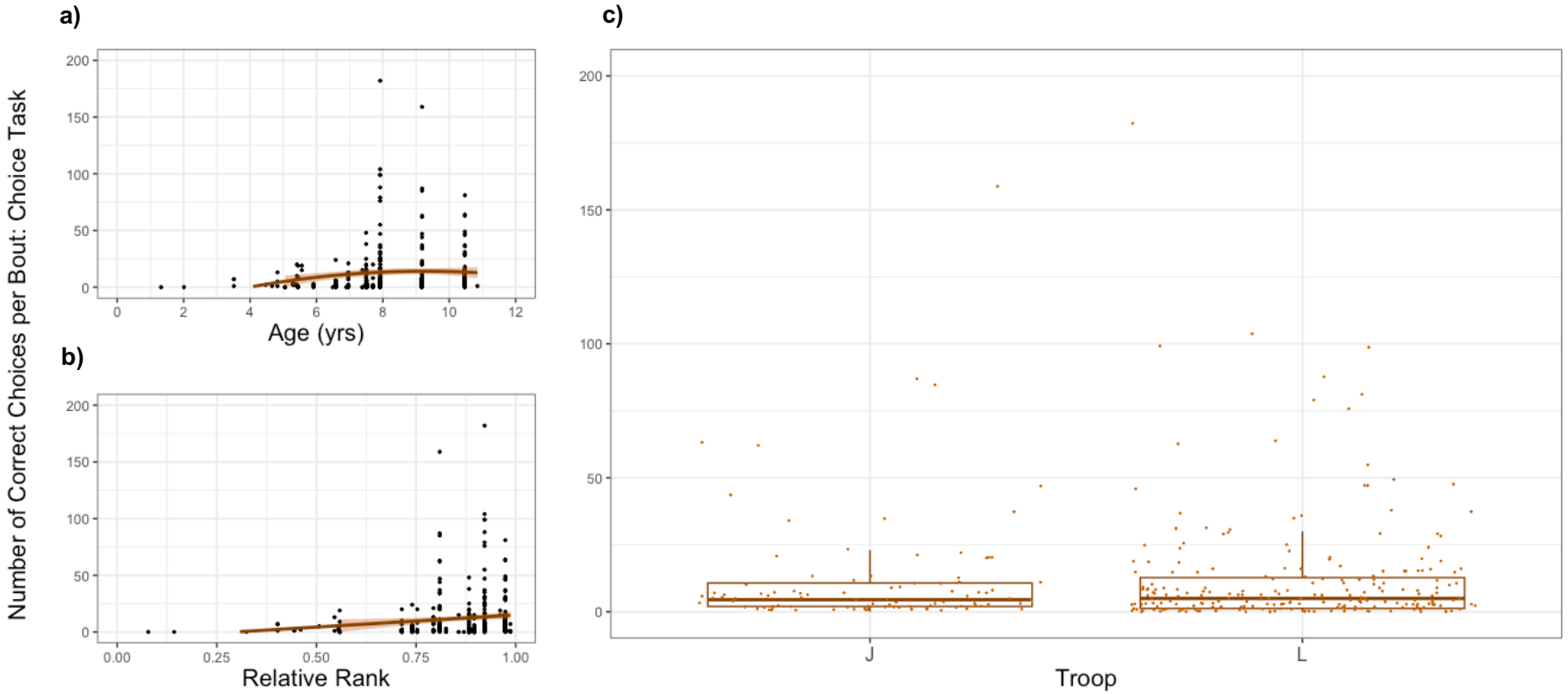


Figure 4.5: Scatterplots depicting the number of correct choices made per bout in the choice task according to the age (a) and rank (c) of the touchscreen users. In addition, is a boxplot of the number of correct actions chosen per bout in the choice task according to the resident troop of the touchscreen user (c). Data depicted is raw data.

Figure 4.6: Factors impacting performance in the sequence task.

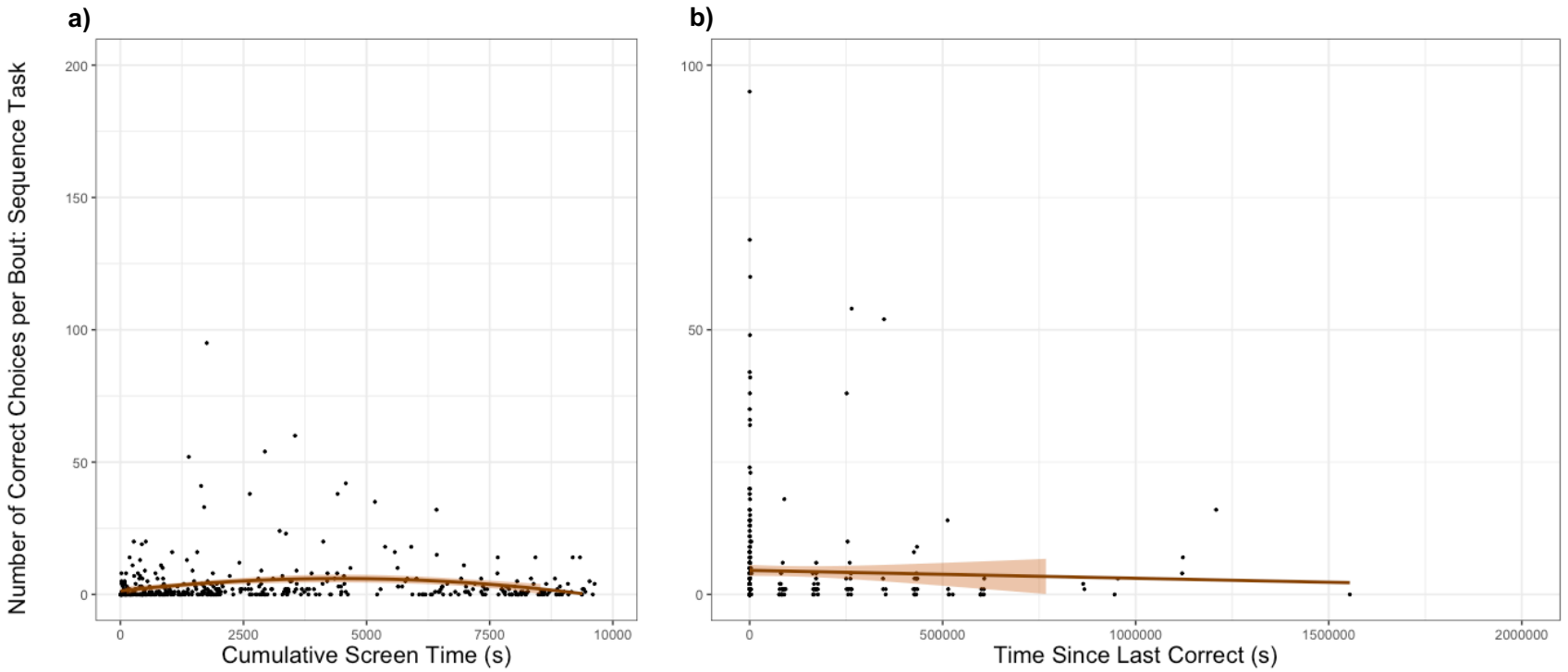


Figure 4.6: Scatterplots depicting the number of correct actions chosen per bout in the sequence task according to the cumulative time spent attempting the sequence task at time of the attempt (a) and the time passed since the last correct sequence was completed by the touchscreen user at the time of the task attempt (b). Data depicted is raw data.

4.4.5 The Neighbour effect

The impact of the presence of higher-ranked and lower-ranked baboons at neighbouring touchscreens through an LMM. Within this model (model 3), we found that participants showed a greater number of correct choices per bout on the choice task when lower-ranked individuals were present on an adjacent touchscreen (Figure 4.7; Table 4.2), and fewer correct choices per bout if their neighbour was of higher-rank than themselves (Estimate = 0.998, SE = 0.435, T = 2.293, $p < 0.05$). In addition, the number of correct choices made on the choice task was positively correlated with cumulative time spent attempting the choice task (Estimate = 0.245, SE = 0.073, T = 3.393, $p < 0.001$).

Figure 4.7: Neighbour effect on the choice task.

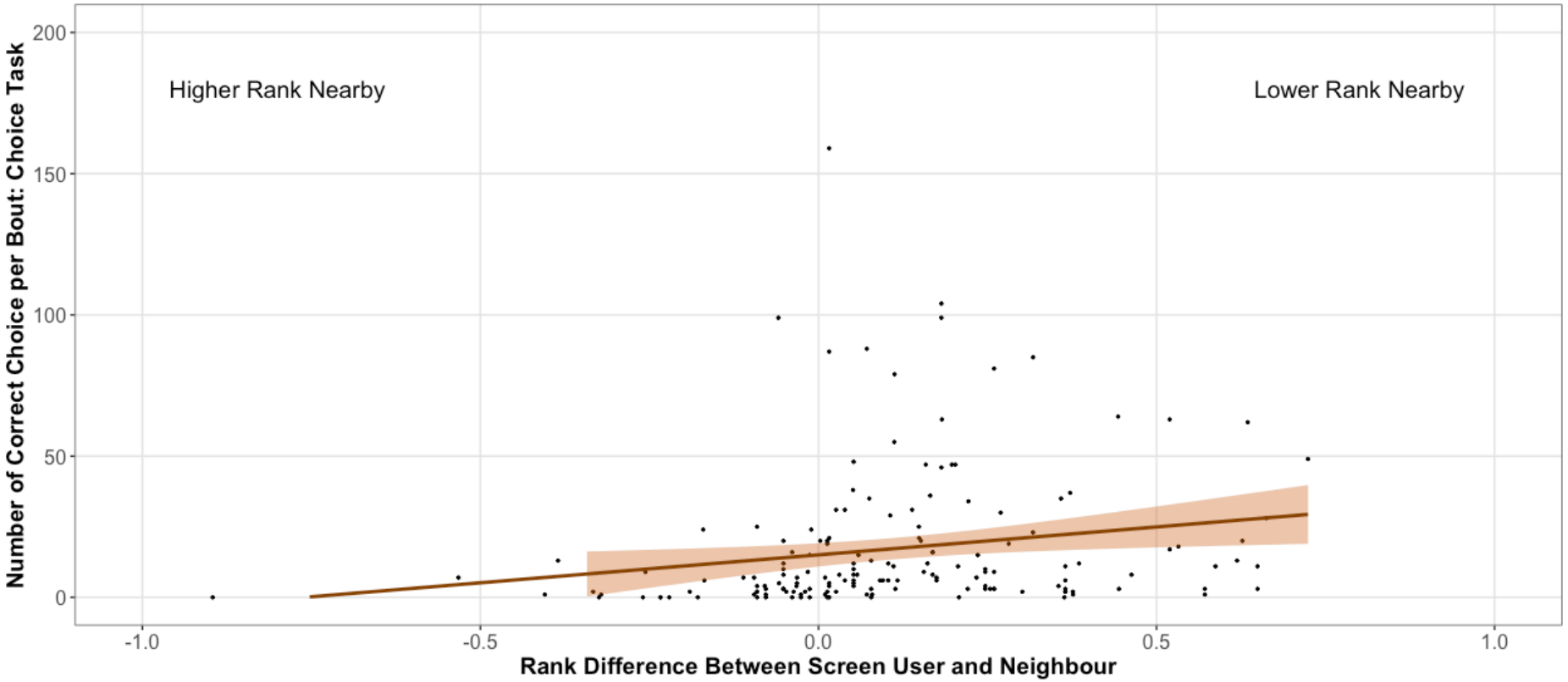


Figure 4.7: A scatterplot depicting the linear relationship between the rank difference of a participant and a baboon on a neighbouring touchscreen and the number of correct choices made by the participant per bout in the choice task. Rank difference was calculated as the relative rank of the participant minus the highest relative rank of the individual on a neighbouring touchscreen. A rank difference of 0 < 1 indicated the participant was of lower-rank than its neighbours and a rank difference of -1 < 0 indicated the participant was of higher-rank than its neighbour. Data depicted are raw data inclusive of both J and L troops.

4.5. Discussion

The purpose of this study was to assess factors that impacted task success in a relatively easy and difficult touchscreen task, including task difficulty (P1a), the use of alternative strategies (P1b), the likelihood of learning according to age, sex and rank (P2), overall performance according to age, sex and rank (P3) and the impact of high-ranking neighbours on performance (P4). Overall, individuals chose around 10 times more correct touchscreen shapes per bout on the easy (choice) task than the difficult (sequence) task. Individuals also sought alternative solutions (shaking the touchscreen) to obtain food rewards from touchscreens, with a greater duration of shaking dedicated to the more difficult task. The duration of shaking was also positively correlated with the number of incorrect choices made on both tasks. Only greater time spent attempting touchscreen tasks (§3.4.3) predicted the likelihood of reaching learning criteria, but only on the choice task. In the choice task, more correct choices were made by older individuals and those of higher rank, as well as those residing in J troop performing a greater number of correct choices per bout than L troop. Furthermore, when individuals on neighbouring touchscreens were of higher rank than a participant, the number of correct choices made by the participant decreased in the choice task. In the sequence task, the number of correct choices increased initially with greater time attempting tasks, but then decreased after around 1 hr of attempting the sequence task. A major contributor to decreasing task success in the sequence task was memory, with fewer correct choices being made when more time had passed since the last correct choice an individual made.

A greater task success on the choice task is not surprising because the choice task was easier to complete than the sequence task. This result evidences results from Chapter 2, whereby individuals across all taxa included in the analyses (including primates) showed greatest improvement in task success in tasks with fewer steps (§2.3.2.2). One major factor that impacted task success in the sequence task was memory, as when more time passed from an individual's last completed sequence, they made fewer correct choices. It is suggested that baboons are able to hold four to five items at a time within their working memory – a temporary system that holds and manipulates information for short periods – used in tasks such as reasoning, decision-making and problem-solving (Botvinick et al., 2009; Cowan, 2017; Maugard et al., 2013; Wright, 2007). However the working memory of baboons is greatly impacted by task complexity, with more difficult tasks exerting a greater load on the working memory, evidenced by a negative correlation between task success and working memory load of baboons across three touchscreen tasks (Maugard et al., 2013). It is therefore not surprising that memory impacted task success in the task with the greatest working memory load (sequence task) in this study. In addition to working memory, previous studies presenting touchscreen tasks to captive baboons have demonstrated that a small proportion of participants can consolidate complex touchscreen tasks into long-term memory, and complete tasks successfully after a 12-month hiatus (Fagot and Thompson, 2011). However, this required the exposure of tens of thousands of trials to individual baboons, and a similar study to other captive baboons whom already had experience of completing previous sequence tasks, whereby it still took several months to learn new sequence tasks (Claidière et al., 2014; Malassis et al., 2020). This means that baboons in this study were unlikely to be able to commit

task actions to consolidated memory as the greatest number of touchscreen attempts of a single baboon in this study was 5163 over 21 days (see Chapter 3). However, as this study was the first to present touchscreens to baboons outside of controlled conditions, other factors such as social, demographic, or environmental may have influenced task success in addition to the restraints of memory.

As predicted, out of the task participants (1 to 11 years of age), older individuals had greater task success than younger individuals, but only in the choice task. This result is not surprising as older individuals are more experienced in problem-solving than younger individuals (Biondi et al., 2010; Galef and Laland, 2005). Although older individuals used the touchscreen for longer periods of time per day than younger individuals (§3.4.3), participation in the experimental tasks were controlled for in these analyses. Therefore, increasing age not only predicted greater use of cognitive tasks, but also cognitive performance of those that did participate (1 to 11 years of age). However, age did not predict task success in the sequence task, showing that age is not a factor in the completion of complex tasks but introduces variability in completing simple tasks. A lack of age-related variation in task success (attempts to reach learning criteria) was also found in Harrison et al., (2023), suggested to be explained by an effect of competition within frequent touchscreen users.

As predicted, rank affected task success, with higher-ranking individuals having greater task success on the choice task. Within previous research involving the baboon population in this study, high-ranking individuals have been shown to gain the best access to resources (King et al., 2008), although this was not the

case for this experiment in isolation (§3.4). This means high-ranking individuals likely have the best prior experience of problem-solving in novel foraging tasks, which has been suggested as an explanation for their greater task success in cognitive experiments (MacLean et al., 2008; Paz-y-Miño C et al., 2004). Another explanation for greater cognitive performance of high-ranking individuals comes from the social intelligence hypothesis (Dunbar, 1998; Shultz and Dunbar, 2007). Although contested (DeCasien et al., 2017; Holekamp, 2007; Sayol et al., 2016), the social intelligence hypothesis suggests that human and non-human primate cognitive performance increases as a result of navigating increasingly complex social landscapes, that includes remembering sequences and structure of hierarchical relationships. Some evidence for this comes from anatomical changes within primate brains associated with rank, with a greater thickness of grey matter (synaptic density) in rhesus macaque (*Macaca mulatta*) brain regions associated with social cognition and perception when an individual was of higher social rank (Sallet et al., 2011). In addition, Australian magpies (*Cracticus tibicen dorsalis*) residing in larger social groups demonstrated greater task success in four cognitive experiments compared to those in smaller social groups (Ashton et al., 2018), as did ring-tailed lemurs (*Lemur catta*; Maclean et al., 2013). These findings highlight the need for further research to disentangle the influence of experience and the social dynamics of high-ranking individuals on cognitive performance in wild groups. Such studies are crucial, as both experience and social contexts in wild populations differ markedly from these typically observed in established cognitive research conducted in captivity.

Within this study, one factor that impacted choice task success of low-ranking individuals was the presence of high-ranking individuals at neighbouring touchscreens. However, no such neighbour effect (Cornelius et al., 2010; Niu et al., 2023; Ostner et al., 2021) was observed in the sequence task, likely due to the already low task success regardless of the presence of high-ranking neighbours. In the presence of an individual of higher relative rank, a low-ranking touchscreen user would likely experience a high degree of acute stress, increasing their attentiveness towards their neighbour through social monitoring, rather than the touchscreen task (Gaynor and Cords, 2012; M. Barros et al., 2008; Tkaczynski et al., 2014). Stress has a profound impact on cognitive performance (Oliveira et al., 2018; Tuckey et al., 2024) and is exacerbated by social and environmental factors (Mendl, 1999; Soravia et al., 2021). Although the highest ranked male in a baboon troop may show a high degree of long-term stress related to consortship and maintenance of his dominant position in the hierarchy (Gesquiere et al., 2011), low-ranking individuals often present high degrees of chronic, and regular acute stress associated with subordination (Abbott et al., 2003; Hoffman et al., 2010). The combination of chronic stress associated with a low rank, combined with likely acute stress faced at touchscreens due to the neighbour effect and social monitoring, likely contributed to the poor task success of low-ranked individuals on the choice task when higher-ranking individual were nearby.

In the sequence task, 20 individuals developed an alternative strategy – shaking the cage housing the touchscreen to gain food rewards – and spent greater cumulative time shaking touchscreens that displayed the difficult task than the easier task. A primary motivation for this strategy appeared to be the

accumulation of incorrect choices that consequently reduced the food rewards the baboon received. For both tasks, a higher number of incorrect choices was associated with more time spent shaking the touchscreen. This difference reflects individuals' preference for alternative strategies over attempting a challenging task they were unlikely to succeed in (van de Waal et al., 2013; Waal and Whiten, 2012). Only large individuals (males) were sufficiently strong to shake the cage and faced minimal pressure to make consecutive correct task choices by using an alternative strategy instead. Therefore, males who discovered the alternative strategy were able to gain rewards without needing to achieve either requirement for the learning criteria. However, no individuals that were unable to shake the cage (young individuals) reached learning criteria. Younger individuals were less likely than older (larger) individuals to use touchscreens for long periods (see chapter 3). This means that young individuals were only able to form consecutive streaks of task success by switching or returning regularly to touchscreens. This meant that they faced additional challenges to performing consecutive task successes (for instance if regularly switching screens and tasks) than individuals that remained at a single screen for long time periods. This hindered the ability of younger individuals to reach our learning criteria. Together, the presence of an alternative strategy likely reduced pressure on completing consecutive task successes for larger individuals and younger individuals lacked the problem-solving experience to solve tasks with required consistency to reach learning criteria.

One surprising result from this study was a difference in troop task success on the choice task. Both troops within this study inhabit the same geographical area, with overlapping territories containing the same resources, with intertroop

migrations occurring every year. Environmental factors are unlikely to explain troop differences in cognitive performance – such as a greater exposure to problem-solving in one troop than another due to their environment. If one troop contained more older individuals than another, this could create greater task success in one troop. However, the troop with a higher task success in the choice task contain five fewer mature adults than the other troop, meaning that fewer successful old individuals were unlikely to have influenced group differences in task performance. As previously outlined, cognitive performance has been suggested to improve with increasing group size (Ashton et al., 2018), and indeed cognitive performance in primates improves with group size (Ashton et al., 2015; MacLean et al., 2013). However, within this study, the better performing troop contained 12 fewer individuals. It is possible therefore that cognitive differences between groups could simply be a product of low sample sizes (two troops), and further research integrating more groups of varying group sizes could uncover factors than impact cognitive performance in specific group contexts such as social learning.

In conclusion, baboons were more successful at completing a relatively easy choice task compared to a relatively difficult sequence task. Within the easy task, success was influenced by heterogeneous factors, including the age and rank of the learner, as well as the proximity to a higher ranked individual. However, within the more difficult task, poor task success drove exclusively large learners to seek a simpler alternative strategy to obtain the same food reward. This means within the baboon troops in this study, the ability to successfully gain food rewards from the novel touchscreen tasks varied significantly. Therefore, individuals that gained experience solving tasks in this

study may possess proven problem-solving skills that could enable the exploitation of resources upon encountering a future novel cognitive task. Together, this study highlights how heterogeneity within primate troops can lead to the development of novel behaviours and the cognitive limitations that prevent rapid learning in baboon troops.

5.0 Social learning patterns and predictors of observation in touchscreen tasks in wild chacma baboons

5.1 Abstract

Social learning allows animals to gain and adapt behaviours by observing conspecifics and can lead to the formation of cultures. However, the mechanisms and individuals' traits influencing this process remain poorly understood in wild populations. Understanding the drivers of social learning is particularly relevant when individuals face novel challenges requiring rapid adaptation. To investigate these drivers, we explored the predictors of observation (a multi-model approach) and the diffusion of novel touchscreen task behaviours (network-based diffusion analysis) in two wild troops of chacma baboons (N = 142 individuals) in Namibia. Using a multi-touchscreen, multi-task experimental setup, we presented an easy task and a difficult task to baboons for 21 days. We also manipulated social learning opportunities by introducing opaque panels to restrict visibility of certain touchscreens and tasks. The total duration of observation was greater when panels were absent, with younger individuals observing others most often. However, observers were not able to successfully apply and exploit social information to improve task success despite regularly touchscreen users being most observed by others. Using network-based diffusion analysis, we also found no evidence for social learning of task success, although social models explained the order of touchscreen use. These findings suggest that while baboons show interest in observing others, the application and exploitation of social learning may be constrained by individual heterogeneity, a reliance on asocial learning or disinterest in acquiring such behaviours. This means that innovations are unlikely to spread through

baboon troops outside of asocial learners, limiting the formation of cultural variants.

5.2 Introduction

Social learning – learning that is facilitated by the observation of, or interaction with, another individual or the products of an individuals' behaviour (Hoppitt and Laland, 2013) – allows animals to exploit novel resources without gathering costly personal information, and also improve efficiency in current resource use (Laland, 2004). Studying how individuals learn from one another is of interest to ethologists and behavioural ecologists as social learning allows animals to make adaptive decisions and learn about their environment efficiently (Lefebvre and Giraldeau, 1996). Subsequently, social learning is a key evolutionary tool for animals to acquire potentially adaptive behaviours from knowledgeable individuals (§1.6). However, social information is not always reliable (e.g. due to foraging patch depletion; Giraldeau et al., 2002) and can lead to the acquisition of inefficient behaviours (Luncz et al., 2018). Understanding how and when individuals use social learning as opposed to individual / personal learning (asocial learning) is therefore of great evolutionary importance, particularly when animals face unprecedented threats to which they must adapt rapidly to survive (Brakes et al., 2025, 2021).

Socially learned behaviours may have social (Rekdahl et al., 2018) or ecological (Hobaiter et al., 2014) applications for learners, allowing researchers to link the social transmission of the behaviour to functionality. Traditional studies investigating social learning fall into three main groups, with a mosaic of social

information transmission occurring between dyads, within small groups and large groups, and also between species. Firstly, diffusion studies – the patterns of transmission of behaviours within a group – attempt to seed a behaviour into a group by training (an) individual/s to perform a specific behaviour (the demonstrator) and assess how this behaviour spreads (controlled diffusion). Controlled diffusions are more commonly conducted in controlled conditions such as laboratories or zoological collections (Hoppitt and Laland, 2013), as these settings enable researchers to reduce confounding variables that may impact the expression of a novel behaviour. However, introducing trained behaviours through human intervention may compromise the ecological validity of such studies, prioritising controlled conditions and reproducibility over real-world applicability (Fischer, 2022; Kendal et al., 2010; Pritchard et al., 2016). Secondly, it may be possible to seed behaviours into captive, free-ranging, or wild populations and observe how the behaviour spreads through the population. Seeding behaviours in this way allows researchers to investigate natural facilitators and barriers to social information diffusion (van de Waal et al., 2013). A third method of assessing the spread of behaviours via social learning is through natural diffusions, where researchers observe how a naturally-innovated behaviour spreads (Allen et al., 2013). Natural diffusions offer the greatest insight into the evolution of socially learned behaviours due to the minimal interference of humans. However, there can be no guarantee that learners have not previously performed behaviours prior to observation by researchers (and therefore individuals may have acquired a behaviour via other learning pathways). Furthermore, there is a low likelihood of replicability across groups, as innovations may be linked to local environments and pressures, and innovations are unlikely to be observed by researchers being in the right place

at the right time. Comparisons of natural diffusions are therefore difficult, meaning that to understand how behaviours spread through a group by social learning, a combination of seeding novel behaviours within natural groups is a popular method of investigating social learning (Reader and Biro, 2010).

To assess individual variation in capturing socially transmitted behaviours, the process of social learning can be deconstructed into three phases: acquisition, application and exploitation (Carter et al., 2016a). At each of these stages, phenotypic constraints such as social, behavioural, ecological, demographic as well as the cognitive abilities of the observer and demonstrator may prevent the dissemination of novel behaviours (Hoppitt and Laland, 2013). In the first phase, individuals must acquire information from others to discover the benefits or consequences of a behaviour. Social networks influence this process by structuring opportunities for information acquisition, with individuals more likely to gather information from those with whom they frequently interact or are in close proximity (Atton et al., 2012; Claidière et al., 2013; Coussi-Korbel and Fragaszy, 1995). This can lead to social information becoming trapped within a group of closely associated individuals that share a similar phenotype, known as homophily (Carter et al., 2015). Furthermore, the necessity to acquire new information drives the motivation to observe others; for instance, young individuals lack the experience of older conspecifics to exploit certain resources (Galef and Laland, 2005). This leads to younger individuals dedicating more time to acquiring social information (Carter et al., 2014; Huffman, 1996) whilst combining this with gaining personal information through exploring novel resources (see chapter 3; Martina et al., 2021).

In the second phase, opportunities to apply an acquired behaviour can be impacted by social and demographic factors; for example, high-ranking individuals can monopolise resources (King et al., 2008). This can limit available opportunities for low-ranking individuals to apply socially learnt information to those occasions when high-ranking individuals are not present (Drea and Wallen, 1999). Similarly, competition at resources can limit the participation of one sex in sex-despotic societies (see chapter 3; Harrison et al., 2023). Furthermore, stronger social bonds between individuals can allow access to resources and facilitate the application of behaviours (Fruteau et al., 2009; Henzi and Barrett, 2002).

In the third phase, there is no guarantee that an applied behaviour can be exploited consistently by the same individual. For instance, if younger individuals acquire a behaviour either through observation or exploratory participation in a cognitive task (see chapter 3), they may lack the cognitive ability to perform the task effectively to exploit consistent rewards (see chapter 4). In addition, any rewards gained may be scrounged by others, which may decrease the motivation of scrounging victims (such as low-ranking individuals) to apply behaviours and also making victims the target of social information gathering from scroungers (King et al., 2009). Such high-ranking individuals possess the greatest choice with how to gain rewards from social information, either via scrounging or being able to monopolise resources and are therefore highly experienced in exploiting social information. Together, this may mean that individuals who are inexperienced or unable to exploit resources could strategise to observe knowledgeable individuals (such as high-ranking

monopolisers) to gain high-quality social information that will allow them to quickly exploit resources when a short window of opportunity is presented.

Although social learning allows individuals to quickly obtain behaviours, copying others in an undiscriminating manner is often not an optimum solution to solving novel tasks (Hoppit and Laland, 2013). For instance, Randell et al. (2010) modelled simulated fitness payoffs of different social learning strategies – the methods by which individuals choose to learn socially and how – finding that social learners have higher fitness than asocial learners only when copying is rare. This is because when environmental variables change, the value of social information declines if few individuals sample their environment. This means that social learners employ different strategies to adaptively decide when and who to copy (Boyd and Richerson, 1985). Generally, individuals may choose to copy when their current behaviour (or lack thereof) is inefficient (Boyd and Richerson, 1988) – the strategy of copy when uncertain (or unproductive) – or when asocial learning is costly, such as learning about a novel predator (Chivers and Smith, 1995). Who individuals copy is dependent on the ability to access quality social information (Kendal et al., 2015), balanced with pressures to conform to a common behaviour (Leeuwen et al., 2013). Collectively, social learning is not inherently adaptive but is utilised contextually alongside asocial learning (Kendal et al., 2005).

Network-Based diffusion analysis (NBDA) is a statistical tool that tests whether the links in a social network predict the flow of information within a group (Dufour et al., 2011; Franz and Nunn, 2009; Hoppitt et al., 2010; Wey et al., 2008). NBDA has been used to assess social learning in multiple species

including ring-tailed lemurs (*Lemur catta;* Kendal et al., 2010), humpback whales (*Megaptera novaengliae*; Allen et al., 2013), squirrel monkeys (*Saimiri sp.*; Claidière et al., 2013) and bearded capuchins (*Sapajus libidinosus*; Coelho et al., 2024). NBDA assumes that social learning opportunities are determined by the social network, such that the probability of learning from another is impacted by the strength of connections between the observer and the demonstrator.

In this study, we explore phenotypic predictors of opportunities to acquire social information through observing conspecifics and information diffusion in two troops of wild chacma baboons. We aimed to assess to what extent individuals learned socially or re-innovated behaviours by experimentally restricting social learning opportunities but not others. The novel behaviour of interest in our study was the completion of two touchscreen tasks, one relatively easy and one relatively difficult. Our first aim was to assess the predictors of observing conspecifics participating in touchscreen tasks (1a) and the predictors of being observed by conspecifics while participating in touchscreen tasks (1b). Secondly, we aimed to assess the extent to which social or asocial learning influenced the order that participants learnt touchscreen tasks and interacted with the touchscreens through NBDA (2). Thirdly, we aimed to assess whether observing successful task behaviours influenced the subsequent task performance of the observer (3). Finally, we aimed to evaluate whether restricting social learning affected how individuals observed one another (4a) and their subsequent replication of task behaviours (4b). We predicted that in line with previous studies, younger individuals (Tan et al., 2018; Wobber and Warneken, 2013) as well as females (Martina et al., 2020) and low-ranking

individuals (Canteloup et al., 2021, 2020) would dedicate most time to observing others (P1a) due to their inexperience and limited access to personal learning on touchscreen tasks (see chapter 3). Conversely, we predicted that older, male and high-ranking individuals would be observed for the longest durations, as these individuals are most likely to complete touchscreen tasks due to prior problem-solving experience, and are most likely to be observed by others (see chapter 4; Kendal et al., 2015). We also predicted that social networks based on proximity would predict the diffusion of touchscreen task information, as has been demonstrated previously in this population (Carter et al., 2015; Carter and Cowlishaw, 2021) (P2). Thirdly, we predicted that individuals' performance would subsequently improve according to their observations of successfully-completed tasks (Hoppitt and Laland, 2013) (P3). Finally, we predicted that the presence of physical restrictions to observation would decrease the total duration of observation at those touchscreens (4a) and consequently performance at those screens would be lower (4b) in line with prediction 3.

5.3 Methods

5.3.1 Ethics

All research regarding the presentation of touchscreens to chacma baboons as part of the Tsaobis Baboon Project was conducted under ZSL Ethical Review 412-PCE-0120.

5.3.2 Study site and subjects

This study took place at Tsaobis Nature Park, Namibia (22°23'S, 15°45'E) as part of the Tsaobis Baboon Project between 21st July and 3rd October 2022. Two habituated troops (J and L) of wild chacma baboons were the subjects, comprising a total of 64 and 78 individuals in J and L, respectively. The experimental arena was located within an ~800 m^2 unenclosed area near a permanent artificial waterhole within 1 km of three commonly used sleeping cliffs of the study troops.

Age (in years) of the baboon participants were calculated using methods from Dezeure et al., (2021) as time from the known or estimated date of birth to the beginning of the experimental phase of this study. Dominance interactions were recorded *as libitum* during full day troop follows (May – October 2022) and did not include dominance interactions involving the experimental apparatus. Dominance ranks calculated for each individual using the 'I&SI' method (De Vries, 1998; Schmid and de Vries, 2013). Ranks were standardised within troops between 0 (low-ranking) and 1 (high-ranking) using the formula 1-((1-*r*)/(1-*n*)), where *r* is the absolute rank of an individual ranging from 1 to the group size of *n* (Baniel et al., 2018). A full ethogram of behaviours recorded in the touchscreen study can be found in Appendix 3.

5.2.3 Social network construction

All analyses and data handling were performed on RStudio v2023.06.02 build 561. To build a social network, we collected proximity associations between

May and October 2022 through instantaneous scan sampling (Altmann, 1974) every 30 mins during daily troop follows. To guarantee sampling independence within troops that were not able to be sampled at one time point due to being spread over a wide area, the neighbours of focal individuals were taken (Roatti et al., 2023). During each focal, all individuals within a 10-meter radius of the focal individual were recorded as members of the focal individual's proximity subgroup. If no individuals were within 10 m of the focal, the individual was recorded as being alone. A proximity network of 10 m was chosen as an established predictor of social information diffusion within the study groups (Carter et al., 2015; Roatti et al., 2023). To ensure independence between samples, focal individuals were selected from a randomised list of all individuals present in the troop. A focal individual was not re-sampled within one hour if their name appeared again on the list, and individuals recorded as neighbours in proximity subgroups were also excluded from being selected as focal individuals within that same hour. In instances where group composition remained stable for an extended period, such as during resting or foraging bouts, sampling was paused until significant group movement occurred, ensuring that new scans reflected changes in subgroup composition. This approach allowed us to standardise data collection and ensure the reliability of proximity measurements across all individuals in the troop.

To represent the strength of association between individuals, we employed a Simple Ratio Index (SRI), which calculates the proportion of scans in which two individuals were observed together within the same proximity subgroup. The SRI values ranged between 0 (indicating no association) and 1 (indicating constant association). This index is appropriate for systems where group

membership is relatively stable and all individuals are identifiable, as is the case at Tsaobis, where visibility is generally high due to sparse vegetation (Hoppitt and Farine, 2018).

For each troop, an undirected and weighted proximity network was created using the igraph package in R. Nodes in the network represented individual baboons, while edges represented the strength of social ties between them, as determined by their SRI values. We retained all associations, regardless of the strength of the SRI, to avoid the removal of potentially important weak ties, which could otherwise bias our understanding of social network structure. Each troop's network was represented as an adjacency matrix, with individuals as both rows and columns, and the SRI values populating the matrix cells.

5.2.4 Touchscreen experimental procedure

We utilised four simultaneously presented 15-inch open-frame capacitive LCD Elo 1950L touchscreens to indiscriminately seed novel information to two wild troops of baboons within a between-group, open diffusion framework. The touchscreens used contained an integrated automatic feeding mechanism, with a battery life of two hours during active use. The touchscreens were contained in Pelican cases and housed in metal cages (grid width of 20 cm) and were placed in a semi-circular pattern 20 m apart, to reduce visibility from neighbouring screens, and oriented south to reduce screen glare. Cages were static and placed in an unenclosed area (~800 m^2) within 100 m of an artificial waterhole and 1 km of two commonly used sleeping cliffs of the study troops.

Touchscreen units were deployed when baboons were observed within 1 km of the experimental arena and remotely turned on when a baboon was within 50 m of the experimental area. This occurred mostly between 12pm and 2pm as at this time, baboons often looked for water sources near to the experimental area. A human observer was located 15 m in front of each of the four touchscreens and dictated to a tripod-mounted camcorder (model Sony hdr-cx240e) the identities of participants that attempted to touch the screen of the touchscreens, henceforth described as screen-directed actions (SDAs). Touchscreens were remotely turned off after a maximum of two hours or if a technical issue arose with the touchscreens (such as damage or blockage). Usually only one experiment was run per day with a single troop (n = 18), but on a small number of occasions (n = 3) we ran two experiments within a single day when both troops visited the experimental arena on two different occasions (at least two hours apart to allow touchscreen recharging).

The touchscreens displayed multiple-coloured shapes of 20 cm length within randomly assigned quadrants. Between 21st July and 25th August 2022, the baboons were habituated to the presence of the touchscreens and familiarised with the action of touching the screen to obtain a food reward. Within the habituation phase, participants were required to press a randomly located yellow hexagon to obtain a familiar and highly preferred food reward (corn kernels) from one of two simultaneously presented touchscreens (Figure 5.1a). Unequal exposure to touchscreens during the habituation phase was controlled statistically in the analyses. Following a correct SDA, a food reward of 1-4 corn kernels was dispensed through one of two chutes and accompanied by a small green light on the touchscreen exterior. An incorrect choice resulted in a

disappearance of the shapes from the screen for one second and accompanied by a red light in the same location as the green light. After an SDA registered by the screen at any location, shapes reappeared again in a random configuration after 1 second. Touchscreens automatically recorded any contact with the screen, including the location of the touch, time, and whether the touch resulted in success or failure of the task.

During the experimental phase (31st August – 3rd October 2022), four touchscreens were deployed simultaneously, with two touchscreens displaying a relatively easy task (choice task) and two touchscreens displaying a relatively difficult task (sequence task) to obtain a food reward of 1-4 corn kernels. During the choice task, participants were simultaneously presented with a white five-pointed star that was rewarded when pressed, and a white cross that was not rewarded, both on a black background (Figure 5.1b). The sequence task required participants to select coloured shapes in an exact sequence to obtain a food reward; a red circle followed by a blue circle (Figure 5.1c). Both circles were presented simultaneously on a black background and the red circle remained on the screen after being pressed. Touches to the black background surrounding the shapes as well as selecting incorrect shapes resulted in a test failure and the shape locations were reset to random quadrants with a 1-s delay.

Figure 5.1: Tasks presented to baboons in the habituation and experimental phases

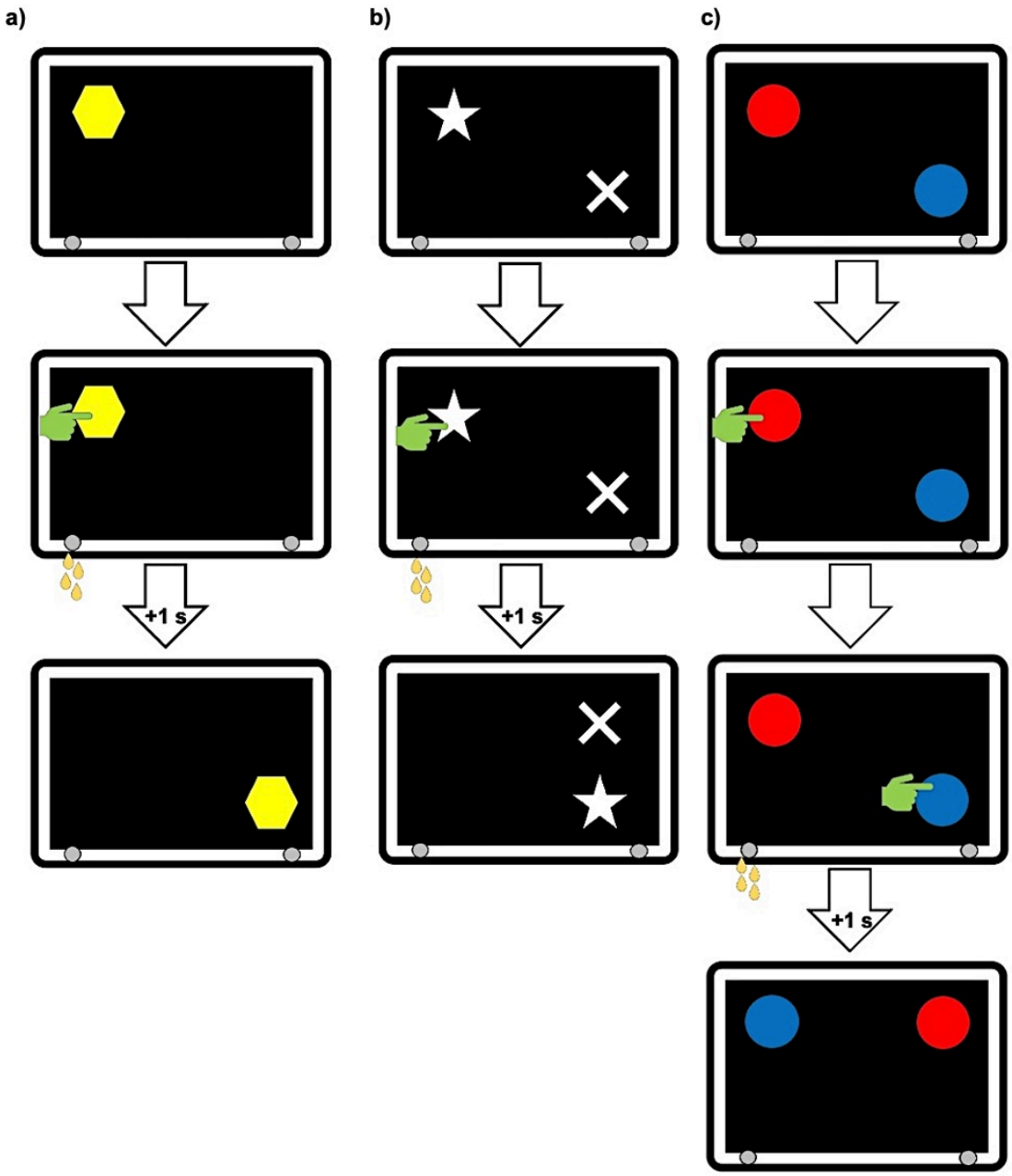


Figure 5.1: Touchscreen tasks presented. Shown are schematics of the touchscreens presented to baboons in this study. Corn reward is depicted as delivered from a random chute at the base of the touchscreen. Tasks consisted of (a) the habituation task presented on two touchscreens simultaneously. The habituation task consisted of a yellow hexagon that was rewarded when pressed. (b) The choice task presented on two of four simultaneously deployed touchscreens in the experimental phase. The choice task consisted of a white star and cross, whereby the star was rewarded when pressed and the cross was not. (c) The sequence task presented on two of four simultaneously deployed touchscreens in the experimental phase. The sequence task consisted of a red circle and a blue circle, whereby only a press to the red circle followed by a press to the blue circle would result in a reward. The red circle remained on the screen after the initial press. After a correct or an incorrect press was made to either the shapes or the background, shapes would disappear from the screen for 1 s and reappear in randomised quadrants. The tasks would therefore be reset, and for the sequence task, any previous attempt

would not carry over to the next attempt (for example if red was chosen followed by another red choice, selecting blue after a task reset would not count as a completed sequence).

Task performance (hereafter called task success) was measured as the number of correct SDAs an individual made when at least one shape was selected per SDA bout. An SDA bout was defined as the time spent performing SDAs between when a participant first performed an SDA and when they stopped performing SDAs for a period of 10 s (either due to inactivity or moving away from the touchscreen). The number of correct SDAs was calculated as the sum of completed tasks within a bout, but participants using the touchscreen who did not select any shapes during their SDA bout were excluded from the performance analyses. This performance measure was chosen because our aim was to assess whether participants learned to distinguish between shapes and colours on the touchscreen rather than learning to touch the screen (including the black background) in general.

To measure the observation of touchscreen users by conspecifics, a semi-circle of diameter 10 m was lightly hoed into the substrate surrounding each cage, with the cage at the centre of the straight edge of the semi-circle (Figure. 2a). Any baboon entering this semi-circle was designated as being able to observe the SDAs of an individual at the touchscreen at the centre of the semi-circle. When the head of a baboon in the observation area was oriented toward a conspecific performing SDAs (participant), the observing baboon was categorised as an observer of the participant, and the participant was categorised as being observed by the observer (Table 5.1). At all times, two cages were fitted with opaque panels that obstructed the view of the touchscreen from 180° without the panels, to 60° with the panels in place

(Figure 5.2a). These panels were placed on cages with touchscreens presenting the choice task for L troop and the sequence task for J troop. Lines emanating from the panels to the curved edge of the semi-circle were lightly hoed into the ground to aid in the visibility of the observation area for researchers. From between these lines (60° < 120°) it was possible to observe the screen, from outside these lines (0° < 60° and 120° < 180°) the view of the screen was obstructed by the panels. Therefore, when the panels were in place, only baboons between the 60° and 120° lines were categorised as observers when their heads were oriented towards a participant performing SDAs.

Figure 5.2: Observability of touchscreens

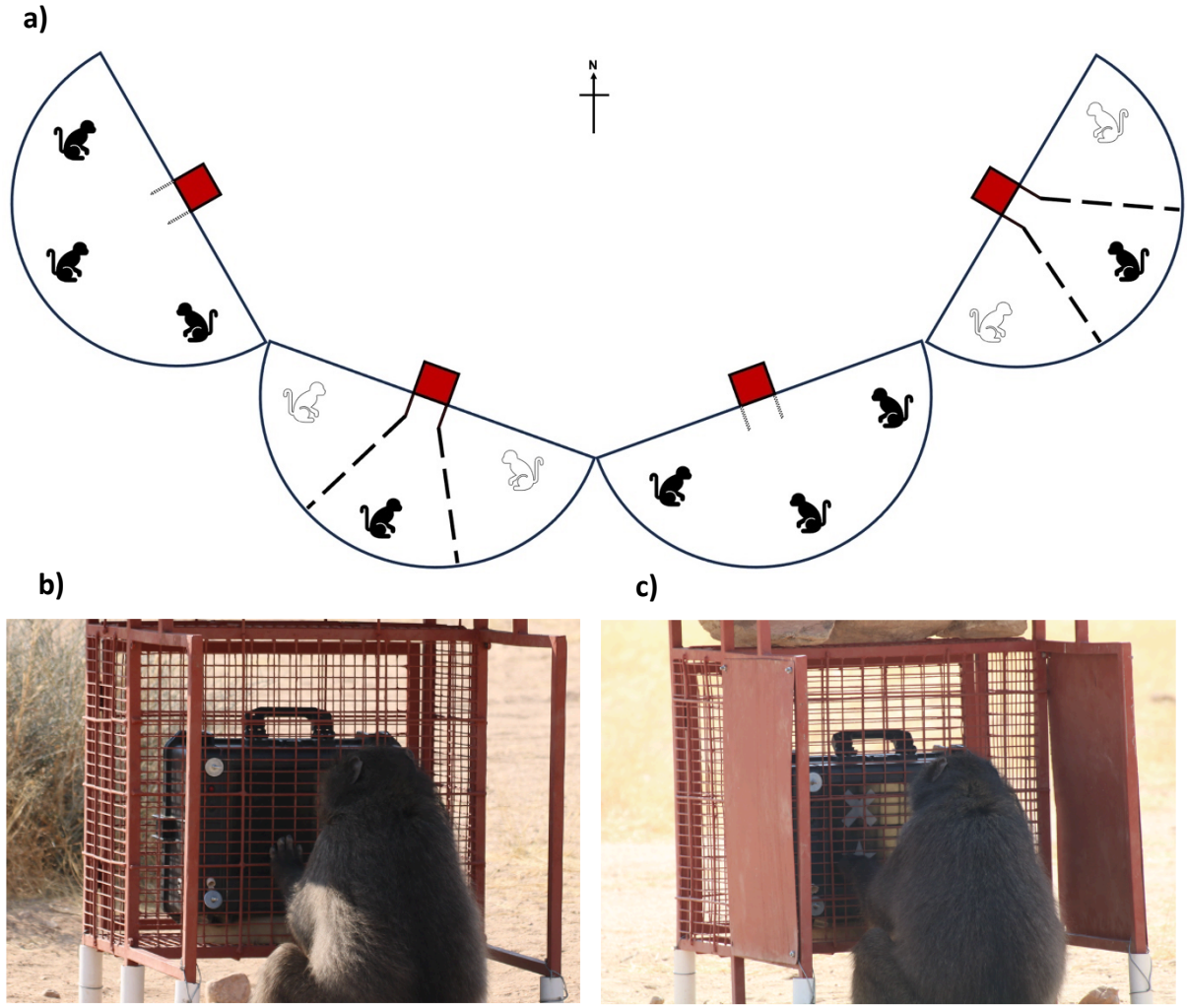


Figure 5.2: Touchscreen arrangement and observability. Shown is a schematic of the touchscreen layout within the experimental phase (a) with photographs of touchscreens without (b) and with (c) panels attached that restrict observability of the screen. Depicted in the schematic are four touchscreens (red) with screens facing the semicircles. The semicircles represent 10 m radius observation areas whereby a baboon within that area with their head oriented toward another baboon using the touchscreen were categorised as observers, and the touchscreen users as observed. Starting from the left of the schematic, the second and fourth touchscreens contain observation restricting panels, as shown in (c). The dashed lines within these semicircles represent the observation area in which a baboon can observe the screen without being obstructed by the panels (an arc of 60°). Within each observation area on the schematic white baboons cannot see the screen, and black baboons can see the screen.

Table 5.1: List and explanation of touchscreen behaviours and observation measurements used in analyses.

Behaviour / measure of interest	Explanation	Model
Observation	An individual was present within the 10 m diameter semi-circle surrounding a touchscreen and whose head was oriented toward a touchscreen participant performing SDAs. If a touchscreen contained restrictive panels, only individuals between the 60° and 120° were counted as observers.	1a, b
Screen-directed action (SDA)	An action of an individual that was directed towards a touchscreen, such as touching the screen with the hand or muzzle. This measure indicated interaction with a touchscreen. The touchscreen automatically recorded SDAs and the success or failure regarding task completion.	2
SDA bout	A bout was defined as the time spent continually making SDAs, with a bout ending after at least 10 s of SDA inactivity (i.e., if an individual left the touchscreen or stopped using the touchscreen).	2, 3, 4b
Time spent observing others	A measure of the total duration (s) that an individual spent observing conspecifics performing SDAs from within the observation area.	1a
Time spent being observed	A measure of the total duration (s) that an individual spent being observed by conspecifics in the observation area whilst that individual was performing SDAs.	1b
Number of correct choices observed	The cumulative number of correct SDAs that were observed by an individual at the point the individual performed SDAs themselves.	3
Number of correct choices in the choice task	Sum of the number of stars touched within the choice task, when at least one star or cross was touched during an SDA bout. The variable was log transformed to account for positive skew.	2, 3, 4b
Number of correct choices in the sequence task	Sum of the number of completed sequences (red circle followed by a blue circle) within the sequence task, when at least one circle was touched during an SDA bout. This measure therefore excluded SDA bouts of participants that only selected the black background and never touched any circles. Incorrect choices included the following touches: red circle, red circle; red circle, background press; red circle, no subsequent touch; blue circle first touch. The variable was log transformed to account for positive skew.	2, 3, 4b
Correct choices above chance in the choice task	The participant was required to select five stars in a row to be considered to have performed the task above chance. This is due to a 50 % probability of correctly choosing a star rather than a cross by chance. Therefore, selecting five stars consecutively represented a	2

	lower than 5 % probability of doing so by chance. This measure was not restricted to single bouts on a single touchscreen but included SDAs across touchscreen transitions and across sequential bouts.	
Correct choices above chance in the sequence task	The participant was required to complete three sequences in a row to be considered to have performed the task above chance. This is due to a 25 % probability of correctly completing a sequence by chance. Therefore, completing three sequences consecutively represented a < 5 % probability of doing so by chance. This measure was not restricted to single bouts on a single touchscreen but included SDAs across touchscreen transitions and across sequential bouts.	2

5.2.5 Statistical analysis

5.2.5.1 Predictors of observation

Predictors of observing conspecifics and being observed

All Statistical analysis was conducted on R v2023.06.02 build 561. Within all analyses, all troop and task combinations were analysed separately (J troop choice task, J troop sequence task, L troop choice task and L troop sequence task). We ran eight linear models (LM) to address our aims within P1a and b. To evaluate the fit of GLMMs and LMMs, we visually inspected the residuals for normality, homoscedasticity and the absence of patterns that might indicate model misspecification. Residual plots, including Q-Q plots, were used to assess whether residuals conformed to the assumptions of the model. Specifically, we checked for a lack of systematic trends in residuals versus fitted values, as well as the approximate normality of residuals (Zuur et al., 2009). When variables showed positive skew, variables were transformed using *log* or *sqrt* functions. We assessed multicollinearity among predictors by calculating

variance inflation factors (VIFs) with the package “car” (Fox et al., 2023). All fixed effects were of importance to our research questions, therefore any multicollinearity, if present, was taken into consideration before interpreting results. All models are summarised in Table 5.2. These diagnostic checks ensured that the models were appropriate for the data and that parameter estimates were unbiased and reliable. The explanatory power of each variable was determined by comparing the ‘full’ model to a null model (excluding the variable of interest) through ANOVA.

To address prediction P1a, our response variable was the total duration spent observing participants (s) for each baboon within both troops. To address prediction P1b, we ran four LMs with the total time a participant was observed by others (s) as the response variable. The same fixed effects were included in all models; the total duration of observations, fixed effects of age (yrs), sex (male or female), rank (relative to conspecifics), social network strength and troop. Both 1a and 1b included an offset of the cumulative time spent using the touchscreens to account for a higher likelihood of observations taking place with greater screen time (Table 5.2).

Table 5.2: A summary linear models (LM) used to answer P1a, P1b and P4a, and linear mixed-effects models (LMM) used to address P3 and P4b. To test these predictions, the explanatory power of models was assessed by comparing full models with all biologically relevant variables to models with variables removed (ANOVA). All models presented are full models as the removal of any variable did not improve model fit without creating difficulties for biological interpretation.

Research questions	Predictions	Model	Response	Fixed effects	Random effects, etc
Predictors of observation	P1a. Younger, females and low-ranking will spend longer observing others	Models 1a. LM; Choice, J-troop Sequence, J-troop Choice, L-troop Sequence, L-troop	Total time spent observing others (log transformed)	1 Age 2 Sex 3 Rank 4 SN strength 5 Cumulative screen time on task (log transformed)	n/a
	P1b. Observers will observe older, males and high-ranking for longer	Models 1b. LM; Choice, J-troop Sequence, J-troop Choice, L-troop Sequence, L-troop	Total time spent being observed by others (log transformed)	1 Age 2 Sex 3 Rank 4 SN strength 5 Cumulative screen time on task (log transformed)	n/a

Observer performance	P3. Individuals that observed more correct choices will show greater task success	Models 3. LMM; Choice, J-troop Sequence, J-troop Choice, L-troop Sequence, L-troop	Number of correct task choices made in a bout (log transformed)	1 Cumulative correct choices previously observed 2 Cumulative screen time on task (log transformed) + offset bout time	Experimental ID Individual ID
Effects of restricting observability of the touchscreens	P4a. Restrictive panels will decrease the time spent observing individuals attempting touchscreen tasks _____ P4b. Task success at touchscreens with restrictive panels will be lower than touchscreens without panels	Models 4a. LM; Choice, Sequence _____ Models 4b. LMM; Choice, J-troop Sequence, J-troop Choice, L-troop Sequence, L-troop	Total time spent observing others (log transformed) _____ Total time spent being observed by others (log transformed)	1 Absence of panels 2 Cumulative screen time on task (log transformed) _____ 1 Age 2 Sex 3 Rank 4 SN strength 5 Cumulative screen time on task (log transformed)	n/a _____ Experimental ID Participant ID

5.2.5.2 Assessment of social learning

Network-Based Diffusion Analysis

To address P2, we conducted 12 NBDAs to assess the influence of social learning on the order the individuals acquired SDA behaviours. The behaviours of interest in this study were performing correct SDAs above chance (P2a; see table 1), performing at least one correct SDA (P2b) and performing any SDA during the experiment (P2c). These behaviours represented different degrees of application of learned touchscreen behaviours following potential information acquisition.

NBDA requires data on the social relationships between individuals in the group and the timing of when individuals performed a learned behaviour. These data can be structured in different ways. Firstly, social networks can be undirected, such as proximity-based networks that assume individuals in close proximity are most likely to observe one another, or directed, such as grooming networks that reflect one-way interactions. Secondly, diffusion data is typically represented by the order that individuals acquired a behaviour, allowing researchers to investigate the mechanisms driving this sequence. Two key approaches for analysing these mechanisms in NBDA are the order of acquisition analysis (OADA; Hoppitt et al., 2010), which examines how individuals acquire a behaviour in a specific sequence, and the time of acquisition analysis (TADA; Franz and Nunn, 2010), which focuses on when individuals acquire a behaviour over time. Both approaches enable the evaluation of whether the spread of a behaviour is driven by social transmission within a network.

We used NBDA to determine whether the acquisition of the touchscreen task was driven by social transmission. NBDA models the spread of a behaviour through a social network, allowing us to quantify the relative contributions of social and asocial learning by comparing a model with differentiated social relationships to a model where all social connections are equal. We used a static NBDA model due the limited temporal data within the short timeframe of the study. Using the OADA method, we modelled the probability that an individual would acquire the task as a function of its social connections to others who had already learned the behaviour. The social transmission parameter (S) was estimated to quantify the influence of social ties on adopting the behaviour of interest. The OADA model assumes that individuals are more likely to learn the behaviour if they are connected to others who have already acquired the skill, with the strength of this likelihood determined by the social transmission parameter. All individuals that were present in the troops during the experimental phase were included in the social network as all individuals had the opportunity to participate and observe others during the study.

To account for the possibility of asocial learning, we also fitted an asocial model in which the parameter for social transmission was fixed at zero ($S = 0$), implying that the behaviour spread independently of the social network. This model served as a null hypothesis for comparison against the social transmission model.

For each troop, we created nbdaData objects in R containing the adjacency matrices of the proximity social networks and the order of acquisition vectors.

We fitted both social and asocial OADA models using the oadaFit function from the "NBDA" package (Hasenjager et al., 2021). Maximum likelihood estimates (MLEs) were obtained for the social transmission parameter (*S*) in the social model, and the Akaike Information Criterion corrected for small sample sizes (AICc) was used to evaluate model fit. We performed model comparison using AICc values, with the difference in AICc scores between the social and asocial models (ΔAICc) indicating the relative support for social transmission. The likelihood ratio test (LRT) was used to assess whether the social model provided a significantly better fit to the data than the asocial model. The test statistic was calculated as twice the difference in the log-likelihoods between the social and asocial models, and the resulting p-value was obtained by comparing the statistic to a chi-squared distribution with one degree of freedom. We generated profile likelihood plots to visualize the uncertainty around the estimated social transmission parameter (*S*) and computed 95% confidence intervals (CIs) for the parameter. The proportion of acquisition events attributable to social transmission (%ST) was calculated using the nbdaPropSolveByST function, which estimates the proportion of learning events that can be explained by social connections in the network.

Observation vs Performance

To address our third prediction (P3), we ran four linear mixed-effects models (LMM) to determine whether the cumulative number of correct task-specific SDAs observed by an individual before they attempted the same touchscreen task predicted their performance on the task. The response variable for these models was the number of correct choices recorded by the touchscreen (see

chapter 4) in the choice or sequence task by J troop and L troop, with task and troop combinations analysed separately. This measure of performance was log transformed to account for positive skew. All models included a fixed effect of the cumulative number of correct SDAs seen at the time of touchscreen use and an offset of the cumulative time spent performing SDAs at the time of touchscreen use to account for differential participation (see chapter 3). Random effects of experimental day and participant identity were included to control for possible differences between testing days (such as environmental variability) and repeated measures of participants.

Impact of obstructions of observation

To address our fourth prediction (4a), we ran two LMs (one for each task) to access whether obstructing the visibility of the screens with panels impacted the duration of observations toward participants for the obscured screen. The response variable for these models was the total duration that each individual spent observing participants on each task. A fixed effect of troop was included in both models, as well as an offset of total time spent performing SDAs to control for participation in tasks potentially driving motivation to observe others or be present within the observation area.

To address our final prediction (4b), we ran two LMs (one for each task) to assess whether the presence of panels impacted task performance. The response variable for these models was the same measure of performance as used in P3 with a fixed effects of panel presence, an offset of cumulative time

spent performing SDAs and random effects of experimental day and participant ID.

5.3 Results

5.3.1 Predictors of observation

Overall, 77 of the 142 baboons present within this study observed another baboon performing touchscreen SDAs at least once, for a total of 15120 s (252 min). Between troops and tasks, this was represented by J troop observing participants for 5150 s in the choice task and 3151 s in the sequence task. Within L troop, individuals observed participants for 1487 s in the choice task and 5332 s in the sequence task. To test predictions within 1a, we examined whether age, sex, rank or social network strength predicted the total time spent observing conspecifics performing SDAs at touchscreens using two LMs (Table 5.3, model 1a). Within J troop, age negatively correlated with time spent observing choice task participants (Estimate = -0.525, SE = 0.158, T = 1.772, $p < 0.05$). Within L troop, the was a positive correlation between the cumulative time spent attempting touchscreen tasks and time spent observing others (choice; Estimate = 0.3352, SE = 0.123, T = 2.734, $p < 0.05$, sequence; Estimate = 0.338, SE = 0.147, T = 2.296, $p < 0.05$).

Table 5.3: Model outputs for linear models (LM) and linear mixed-effects models (LMM). Model outputs include (1a) predictors of observing others in both tasks and troops, (1b) predictors of being observed by others in both tasks and troops, (3) the impact of the number of correct SDAs observed and subsequent task success of the observer, (4a) the impact of panel absence on the duration of observations at that touchscreen in both tasks and (4b) the impact of panel absence on task success. Table items in bold represent model outputs of statistically significant values ($p < 0.05$)

Task	Troop	Model	Nobv / Nind	Term	Estimate	Std. Error	T value (3, 4a, 4b), Z value (1a, 1b,)	P
Choice	**J**	1a) Observers	64 / 64	Intercept	0.219	2.430	0.090	0.929
				Age	**-0.525**	**0.158**	**-3.318**	**<0.05**
				Sex	0.121	1.657	0.073	0.942
				Rank	0.251	2.496	0.101	0.920
				SN strength	1.642	0.927	1.772	0.083
				Screen time	0.213	0.158	1.351	0.183
	L	1a) Observers	78 / 78	Intercept	-0.147	2.022	-0.073	0.942
				Age	-0.184	0.116	-1.587	0.118
				Sex: M	-1.732	1.420	-1.219	0.228
				Rank	-0.376	2.025	-0.186	0.853
				SN strength	0.119	1.091	0.109	0.914
				Screen time	**0.335**	**0.123**	**2.734**	**<0.001**
Sequence	**J**	1a) Observers	64 / 64	Intercept	1.073	2.867	0.374	0.710
				Age	-0.096	0.175	-0.547	0.587
				Sex: M	0.161	1.794	0.090	0.929
				Rank	0.018	2.812	0.007	0.995

				SN strength	-0.937	1.114	-0.841	0.405
				Screen time	0.275	0.162	1.696	0.096
	L	1a) Observers	78 / 78	Intercept	-2.731	2.350	-1.162	0.250
				Age	-0.257	0.134	-1.917	0.060
				Sex: M	-0.540	1.652	-0.337	0.737
				Rank	0.356	2.389	0.107	0.915
				SN strength	1.654	1.284	1.288	0.203
				Screen time	**0.338**	**0.147**	**2.296**	**<0.05**
Choice	**J**	1b) Observed	64 / 64	**Intercept**	**-4.347**	**1.941**	**-2.239**	**<0.05**
				Age	0.164	0.126	1.300	0.200
				Sex: M	0.291	1.324	0.220	0.827
				Rank	3.466	1.994	1.739	0.087
				SN strength	-0.982	0.740	-1.327	0.191
				Screen time	**0.324**	**0.126**	**2.572**	**<0.001**
	L	1b) Observed	78 / 78	**Intercept**	**-5.940**	**1.276**	**-4.654**	**<0.001**
				Age	0.039	0.073	0.529	0.599
				Sex: M	0.898	0.897	1.001	0.321
				Rank	-0.271	1.278	-0.212	0.833
				SN strength	0.836	0.689	1.214	0.230
				Screen time	**0.165**	**0.077**	**2.130**	**<0.05**
Sequence	**J**	1b) Observed	64 / 64	Intercept	-1.297	2.166	-0.599	0.552
				Age	0.082	0.132	0.624	0.536
				Sex	0.608	1.355	0.449	0.655

				Rank	1.372	2.124	0.646	0.522
				SN strength	-1.534	0.842	-1.823	0.075
				Screen time	**0.293**	**0.122**	**2.397**	**<0.05**
	L	1b) Observed	78 / 78	**Intercept**	**-7.162**	**1.692**	**-4.233**	**<0.001**
				Age	0.078	0.097	0.807	0.423
				Sex	1.856	1.153	1.609	0.113
				Rank	0.392	1.720	0.228	0.821
				SN strength	1.138	0.924	1.231	0.223
				Screen time	**0.301**	**0.106**	**2.839**	**<0.05**
Choice	**J**	3) Correct observed vs task success	2266 / 9	Intercept	-1.450	0.664	-2.181	0.066
				Correct seen	0.062	0.086	0.726	0.473
				Screen time	-0.054	0.086	-0.623	0.557
	L	3) Correct observed vs task success	4543 / 18	**Intercept**	**-3.026**	**0.689**	**-4.391**	**<0.001**
				Correct seen	0.058	0.151	0.388	0.699
				Screen time	**0.124**	**0.058**	**2.130**	**<0.05**
Sequence	**J**	3) Correct observed vs task success	1539 / 13	**Intercept**	**-2.590**	**0.775**	**-3.344**	**<0.05**
				Correct seen	0.050	0.074	-0.674	0.501
				Screen time	-0.099	0.101	-0.985	0.328
	L	3) Correct observed vs task success	3695 / 18	**Intercept**	**-2.661**	**0.526**	**-5.055**	**<0.001**
				Correct seen	0.005	0.052	0.101	0.921
				Screen time	-0.055	0.067	-0.820	0.418
Choice		4a) Panels vs observation	142 / 142	Intercept	0.388	0.469	0.828	0.409
				Panels absent	**1.848**	**0.636**	**2.902**	**<0.05**

				Screen time	**0.350**	**0.064**	**5.479**	**<0.001**
Sequence		4a) Panels vs observation	142 / 142	**Intercept**	**1.981**	**0.494**	**4.009**	**<0.001**
				Panels absent	0.187	0.670	-0.279	0.781
				Screen time	**0.355**	**0.067**	**-5.312**	**<0.001**
Choice		4b) Panels vs task success	6809 / 27	**Intercept**	**-2.871**	**0.344**	**-8.351**	**<0.001**
				Panels absent	0.333	0.247	1.351	0.193
				Screen time	0.064	0.047	1.361	0.179
Sequence		4b) Panels vs task success	5234 / 31	**Intercept**	**-2.419**	**0.433**	**-5.594**	**<0.001**
				Panels absent	-0.069	0.324	-0.212	0.834
				Screen time	-0.086	0.056	-1.518	0.135

5.3.2 Predictors of being observed by others

Overall, out of 86 individuals that performed at least one SDA and 23 individuals that selected a shape on either task at least once, 20 individuals were observed by another baboon within the observation area. To test predictions within 1b, we examined whether age, sex, rank or social network strength predicted the total time spent observing conspecifics performing SDAs at touchscreens using two LMs (Table 5.3). The cumulative time spent attempting touchscreen tasks positively correlated with the time that an individual was observed by others across all tasks and troops (L troop choice; Estimate = 0.165, SE = 0.774, T = 2.130, $p < 0.05$, L troop sequence; Estimate = 0.301, SE = 0.106, T = 2.839, $P < 0.05$, J troop choice; Estimate = 0.324, SE = 0.126, T = 2.572, $p < 0.05$, J troop sequence; Estimate = 0.293, SE = 0.122, T = 2.397, $P < 0.05$).

5.3.3 NBDA

To assess whether behaviours of interest in this study; performing correct SDAs above chance (P2a), performing at least one correct SDA (P2b), and performing any SDA during the experiment (P2c; see table 5.1) could be explained by social learning, we employed NBDA to analyse the patterns of social transmission over the 21-d period of the experiment using static proximity social networks (Table 5.4). In L troop, the social model did not differ in explaining the order of acquisition of completing the touchscreen tasks above chance levels (learn the task) than an asocial model. There was no evidence of social transmission in J-troop for completing either touchscreen task above chance. The social model, however, was 30.57 times more likely to explain the order

that individuals performed of at least one correct SDA in the choice task in L troop than the asocial model (Fig. 5.3c; $\chi^2 = 9.240$, $p < 0.01$), but there was no difference between the social and asocial model in completing at least one sequence in the sequence task in L- troop. There was no evidence of social transmission impacting the performance of at least one correct SDA in either task in J-troop. The social transmission model 42.911 times more likely explained in what order individuals within L- troop used the touchscreen performed at least one SDA in the choice task (Fig. 5.3e; $\chi^2 = 9.740$, $p < 0.01$) and by 13.792 times in the sequence task (Fig. 5.3f; $\chi^2 = 7.396$, $p < 0.01$) than the asocial model. The social model did not differ from the asocial model in explaining in what order individuals within J troop used the choice task, and there was no evidence of social transmission impacting the use of the sequence task in J troop.

Figure 5.3: Social network of J troop with individuals who learned.

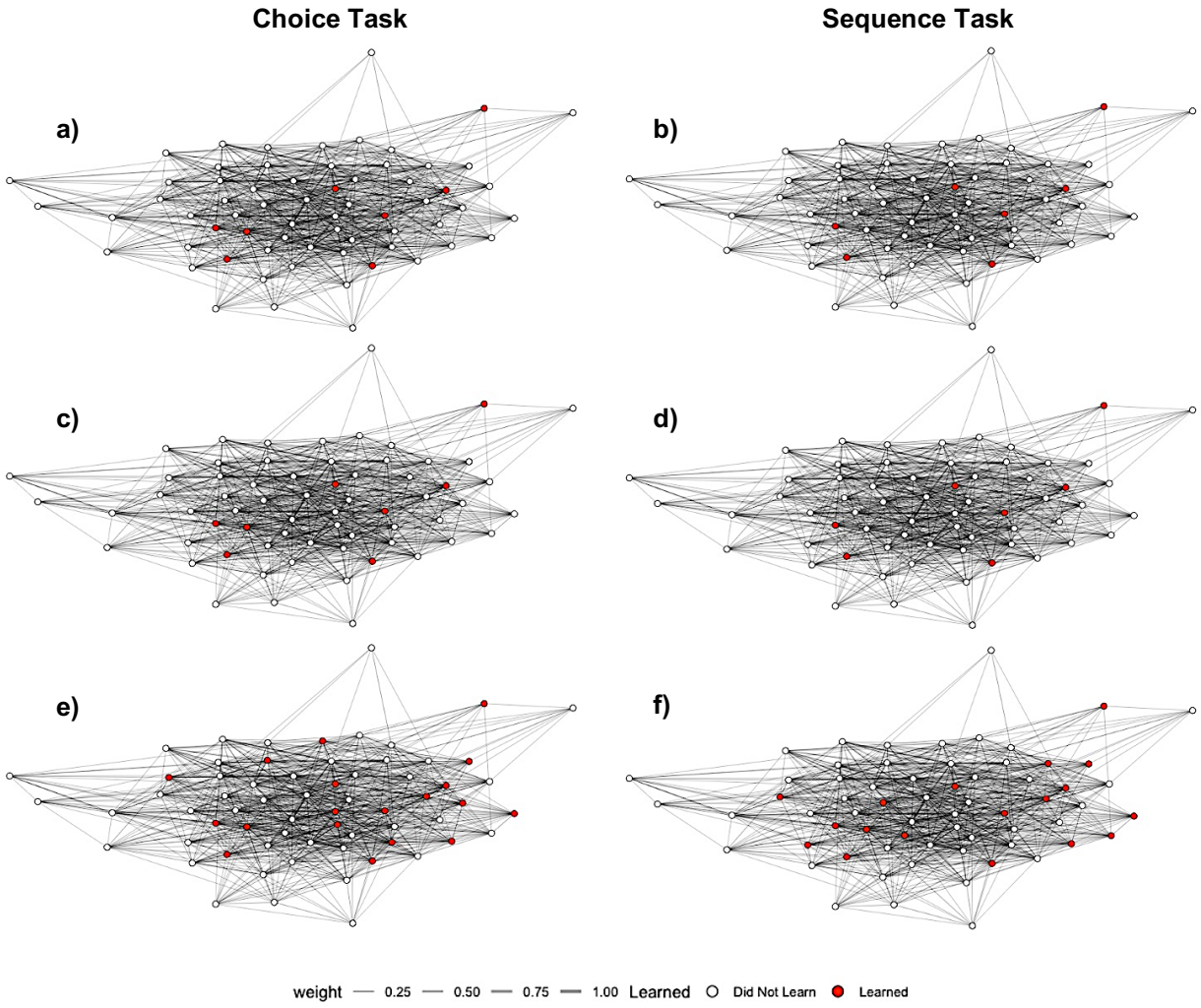


Figure 5.3: Weighted social networks for J troop generated from proximity scan sampling data (individuals within 10 m) between May and October 2022. Nodes highlighted in red represent individuals that learned to complete touchscreen tasks above chance for the (a) choice task and the (b) sequence task. Depicted in (c) and (d) are individuals highlighted in red that completed at least one correct choice task and sequence task respectively, and (e) and (f) shows individuals that performed at least one screen-directed action towards a touchscreen at least once for the choice and sequence tasks respectively. No social networks support the order in which nodes acquired the learned behaviour more than an asocial model of learning.

Figure 5.4: Social network of L troop with individuals who learned

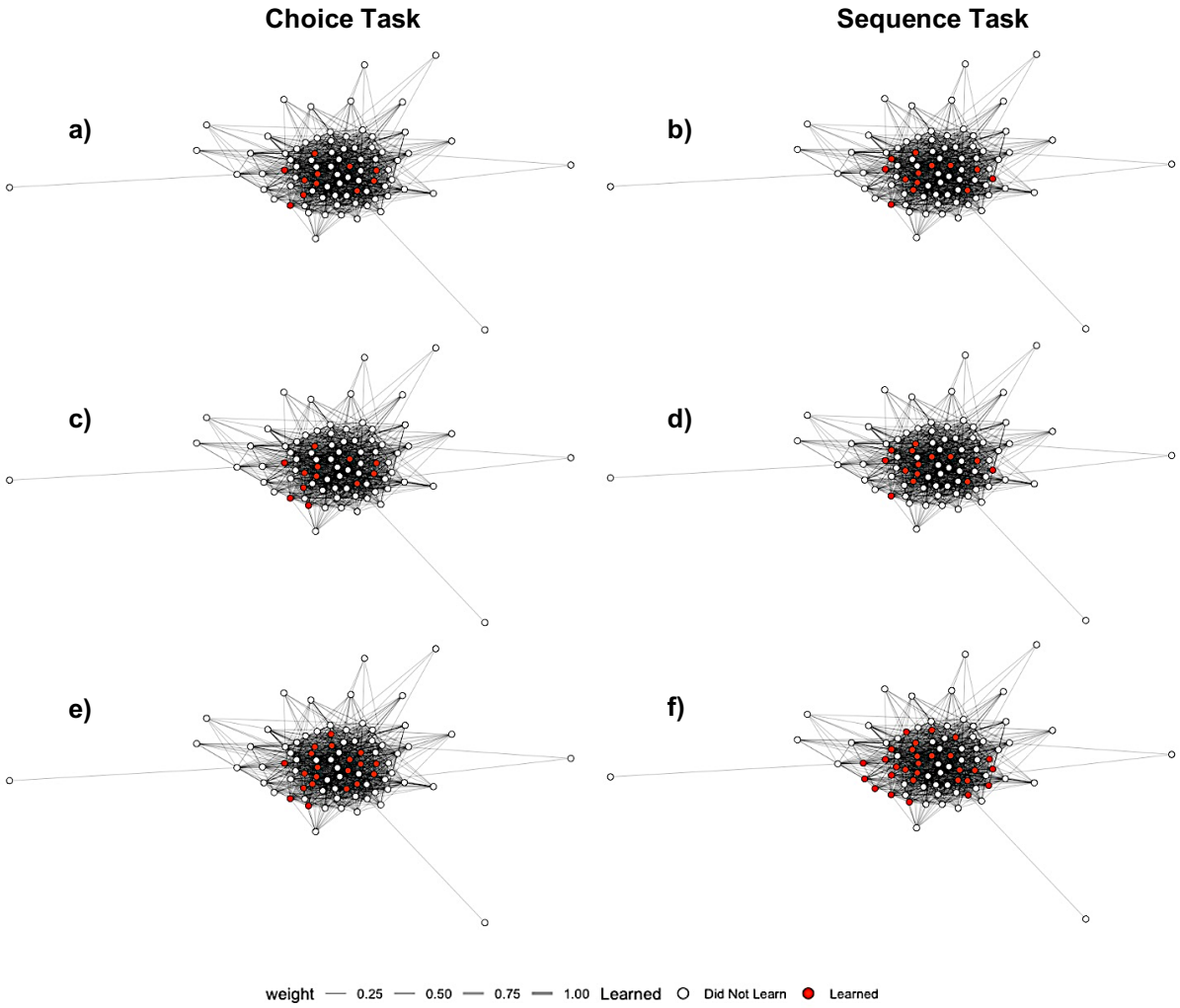


Figure 5.4: Weighted social networks for L- troop generated from proximity scan sampling data (individuals within 10 m) between May and October 2022. Nodes highlighted in red represent individuals that learned to complete touchscreen tasks above chance for the (a) choice task and the (b) sequence task. Depicted in (c) and (d) are individuals highlighted in red that completed at least one correct choice task and sequence task respectively, and (e) and (f) shows individuals that performed at least one screen-directed action towards a touchscreen at least once for the choice and sequence tasks respectively. Only in (c), (e) and (f) do the social networks support the order in which nodes acquired the learned behaviour more than an asocial model of learning.

Table 5.4: Model outputs for Network-Based Diffusion Analysis. Table items in bold represent statistically significant values ($p < 0.05$).

Troop	Task	Learned behaviour	ΔAIC	Social model explains data better than asocial model	Behaviour occurred via social transmission	Chi-squared	P
J	Choice	Task success above chance	-2.667	0.027 x	0 %	0	1
		Task success once	-2.667	0.027 x	0 %	0	1
		Attempt task	-1.048	0.592 x	41.199 %	1.187	0.276
	Sequence	Task success above chance	-2.8	0.247 x	0 %	0	1
		Task success once	-2.8	0.247 x	0 %	0	1
		Attempt task	-2.25	0.325 x	0 %	0	1
L	Choice	Task success above chance	0.143	1.075 x	65.335 %	2.588	0.108
		Task success once	**8.840**	**30.57 x**	**100 %**	9.240	**< 0.01**
		Attempt task	**7.518**	**42.911 x**	**100 %**	9.740	**< 0.01**
	Sequence	Task success above chance	-0.121	-0.941 x	68.549 %	2.243	0.134
		Task success once	-0.936	-0.626 x	62. 58 %	1.397	0.237
		Attempt task	**5.248**	**13.792 x**	**70. 794 %**	7.396	**< 0.01**

5.3.4 Correct seen vs performance

Within 15120 s of time spent observing touchscreen users perform SDAs, 167 completed choice tasks and 125 completed sequences were observed by conspecifics. To test whether the number of correct SDAs observed by participants at the point of touchscreen use (P3), we performed four LMMs (one for each troop and task combination). We did not find any impact of the number of correct SDAs observed by a baboon on their consequent task performance across all tasks and troops. Cumulative time spent using the touchscreen predicted task success in L- troop on the choice task (Estimate = -3.026, SE = 0.689, T = -4.391, $p < 0.05$). No other variable predicted the number of correct choices made by an individual.

5.3.5 Panels vs observations

In total, 4638 s of observation was undertaken by baboons observing participants performing SDAs on touchscreens with restricted observable view, whereas the total duration of observation towards unrestricted touchscreens was 10482 s. To assess whether the absence of the restrictive panels impacted the duration of observation (4a), we conducted two LMs, one for each task. Although there was no impact of the panel absence on observation duration in the sequence task, the absence of the panels had a positive impact on the total duration of observations in the choice task (Estimate = 1.848, SE = 0.637, T = 2.902, $p < 0.04$; Figure. 5.5). The cumulative time spent attempting touchscreen tasks had a positive effect on the time spent observing others in both tasks (choice; Estimate = 0.350, SE = 0.064, T = 5.479, $p < 0.001$).

Figure 5.5: The impact of restricting observation on the total duration of observation

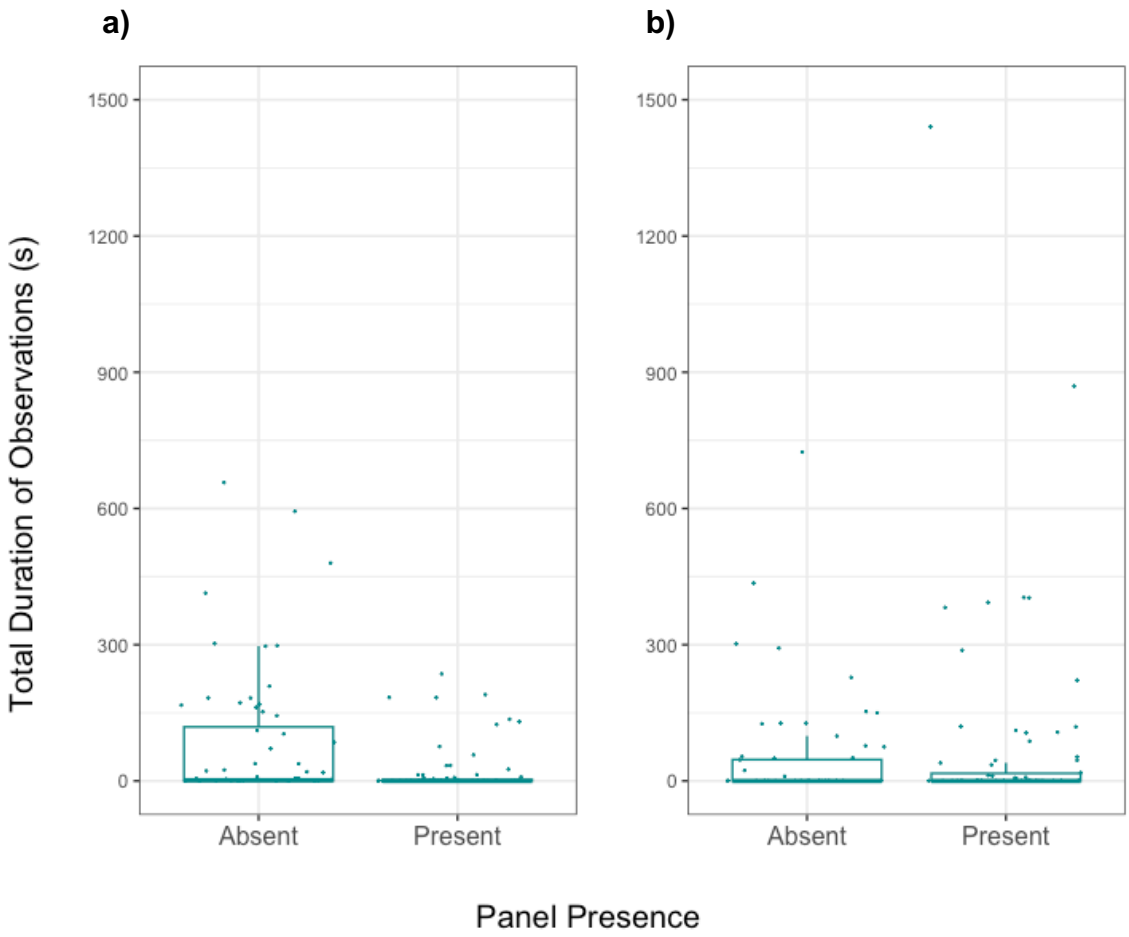


Figure 5.5: Boxplots depicting the total duration of observations made by baboons within the observation area toward touchscreen users attempting the a) choice task and b) sequence task. When panels were present on the cage, the view of the screen was restricted to 60° and when panels were absent, observable views of the touchscreen extended to 180° field of vision. Depicted are raw cumulative data for each observer.

5.3.6 Panels vs performance

To test our predictions within 4b, we conducted two LMMs (one per task) to assess whether the presence of the restrictive view panels on a touchscreen cage impacted the task performance of the task participant. We found no impact of the absence of the panels, or cumulative time spent attempting touchscreen tasks on the number of correct SDAs made by participants in the either task.

5.4 Discussion

The purpose of this study was to assess to what extent baboons utilised social learning to complete two touchscreen tasks: an easier “choice” task and a more challenging “sequence” task. We aimed to manipulate the social information available to observers to disentangle social and asocial leaning, by restricting access to social information about one task in each troop. To do this, we fixed opaque panels to the touchscreen cages to obscure the view of touchscreen users and their SDAs from observers. Our manipulation was only partly successful: baboons spent more time observing touchscreen users when panels were absent, but only during the choice task in L troop. We found little evidence of social learning regardless of panel absence, with an asocial model (and therefore factors discussed in Chapter 4) better explaining the order that baboons in both troops learnt the choice and sequence tasks (task success above chance level). In addition, the baboons did not show greater task success when they observed others completing touchscreen tasks, giving further evidence for asocial learning. Despite this, baboons were presented with opportunities for social learning, with younger individuals in J troop most likely

to observe others in the choice task. Observation was also predicted by touchscreen use, with a positive correlation between time spent attempting touchscreen tasks and observing others (in L troop), as well as being observed by others (in both troops). The impact of these results on strategies baboons used to learn touchscreen tasks in this study is discussed below, in addition to factors that hindered the flow of information in baboon troops.

Individuals in L troop spent more time observing others attempting the choice task, where there was an absence of restrictive panels. However, the absence of panels did not influence the duration of observation of J troop individuals of the sequence task. This observation preference may be attributed to higher task success rates on the choice task compared to the sequence task (§4.4.1), similar to task success being greater following social learning opportunities on tasks with fewer steps across taxa (§2.3.2.1). Observers were likely more motivated to watch users on the choice task as these users were more frequently rewarded, providing a greater attraction to these touchscreens due to the presence of food and reliable demonstrations of task success. Therefore, as only L troop could observe the choice task unrestricted, the positive impact of panel absence on observation was only experienced when the choice task and panel absence were combined – leading to high observation times in L troop.

By focusing observations on the choice task, observers maximised their chances of acquiring useful knowledge (Agee and Monfils, 2018; Dunlap et al., 2016). In contrast, the sequence task posed greater challenges for asocial learning due to the longer time required for task completion and greater load on working memory §4.5; Maugard et al., 2013). Theoretically, social learning

would be more advantageous in this context, as copying successful demonstrators could reduce the costs of asocial learning (Boyd and Richerson, 1985; Coolen et al., 2005, 2003). Additionally, with lower success rates in the sequence task, an effective social learning strategy would involve copying demonstrators when observers were uncertain, or their current behaviours were ineffective (Grueter et al., 2010; Grüter et al., 2011; Kendal et al., 2009). Evidence for this strategy can be seen in callitrichid monkeys, during a series of puzzle box presentations of varying difficulty. Here, individuals learned easier tasks asocially and more difficult tasks through social learning (Kendal et al., 2009). Despite these advantageous social learning strategies, baboons did not spend more time observing others during the sequence task. This suggests that baboons either did not actively seek social learning opportunities for the sequence task, they were unable to access them, or that no useful information was produced at these touchscreens. Such deviation from adaptive social learning strategies (if useful information was produced) highlights potential limitations in how baboons utilise or prioritise social learning in more challenging contexts.

We found little evidence using NBDA that baboons used social information to learn to solve the touchscreen tasks, with the social model explaining the order of touchscreen learning no better than the asocial model. This is not surprising, as although observations did occur, only 20 of the 86 participants were observed performing an SDA by another baboon – indicating baboons were either unmotivated or unable to observe a broad range of participants. Furthermore, out of the 4667 rewarded SDAs performed throughout the experimental phase (§4.4.1), only 292 were observed by another baboon. In

addition, task success was not affected by restricting visual access to social information, suggesting that individuals were using personal information to solve the task. Together, this suggests that baboons did not seek, or were unable to gain quality social information regarding task completion and that greater opportunities for social learning did not influence the number of correct choices made. However, in L troop, the social model in NBDA was 13 to 43 more likely to explain the order the baboons first used the touchscreen than the asocial model. It appears therefore that baboons were learning via stimulus enhancement (Heyes, 1994) that touchscreens provided a reward, but did not socially learn how to obtain the reward. Despite the screen being obstructed by panels and participants, the rewards were visible to all observers as the chutes dispensed the kernels onto the ground either side of the participant and between the panel and the ground (~10 cm gap: see figure 3.1a). Consequently, it was much easier for observers to learn the association between rewards and the touchscreen apparatus than between the rewards and SDAs by observing others. The greatest number of rewards hitting the ground would have been observed in the choice task (§4.4.1). Within L troop, the greatest number of correct SDAs would have also been observed in the choice task due to panel absence. Collectively, this means that observers in L troop were more likely than observers in J troop (where panels obstructed the choice task) to associate rewards with performing an SDA – even if they did not learn specifically what SDA to perform. This means that baboons were able to acquire social information about touchscreens as a food resource, and then apply this information by performing at least one SDA. Therefore, the limit to social learning in this experiment was the ability to fully exploit touchscreen tasks.

Individuals observed others indiscriminately of their demographic or social characteristics. This is a social learning strategy that is typically not adaptive (Rendell et al., 2010) unless the accumulated knowledge of conspecifics represents a more reliable source of information than any one individual can provide (Giraldeau et al., 2002). A logical strategy to maximise social learning opportunities in this study would have been to direct observations towards reliably successful touchscreen users – such as older or higher-ranking individuals in the choice task (see chapter 4) – by directly monitoring payoffs (Schlag, 1998). Within the sequence task, task success was so low (see chapter 4) that observers were unlikely to witness sufficient correct choices to acquire task information or identify knowledgeable individuals, which was possible in captive experiments (Claidière et al., 2013; Fagot and Bonté, 2010; Fagot and Paleressompoulle, 2009). Consequently, indiscriminate observation of touchscreen users offered no disadvantage. When observers did witness correct choices made by others, this did not translate to task success when they came to attempt the same task. There are four possible explanations for this poor application of social information: firstly, observers (initially) observed the touchscreen user and not their use of the touchscreen. Secondly, individuals had insufficient time to identify who was knowledgeable over the course of the experiment. Thirdly, individuals may have lacked the cognitive capacity to process, apply and exploit social information regarding correct touchscreen choices. Fourthly, task success of observers may have been inhibited by high-ranking individuals at neighbouring touchscreens (see chapter 4; Drea and Wallen, 1999), and so socially acquired behaviours were not successfully applied. These explanations may have contributed to the lack of social learning in either task. Together, the findings from NBDA and the lack of a relationship

between observations and subsequent task success suggest that task success – both in the easier and more challenging task – was driven primarily by asocial learning, highlighting the limited role of social learning in the context of this experiment.

As predicted, younger individuals spent longer than older individuals observing others using the touchscreens; however, this pattern was only present in J troop on the choice task. This aligns with previous research suggesting that younger individuals rely on information from others due to their limited personal experience (Biro et al., 2006; Carter et al., 2014; Tan et al., 2018; Wobber and Warneken, 2013), and have sufficient free time to do so (Grampp et al., 2019). In the choice task, younger individuals were the most likely to participate (indicating explorative behaviours) but were least likely to use the touchscreens for long periods of time (see chapter 3). Moreover, when younger individuals did use the touchscreen, they did not complete tasks as successfully as older individuals (see chapter 4), reflecting their limited personal experience with successful task completion. This behaviour underscores their reliance on social learning opportunities to supplement their limited personal experience.

Social learning opportunities were sought by the longest touchscreen users and observations directed toward the longest touchscreen users. This circular observation pattern meant that touchscreen users were attempting to scrounge social information from those that produced the greatest information, potentially to supplement their own personal experience of touchscreen tasks. Individuals tend to associate with those that they share similar phenotypes, termed positive assortment or homophily (Aplin et al., 2013; Croft et al., 2009, 2006; Massen

and Koski, 2014). Such associations mean that the association and proximity of individuals is a good indicator of social transmission (Claidière et al., 2013; Kendal et al., 2010). Individuals who produce social information are therefore more likely to associate with others of a similar phenotype that also generate social information, and not those that tend to rely on gathering such information (Carter et al., 2015). A lack of association with those of differing phenotypes that rely on social information (heterophily), therefore limits the flow of social information in a network. However, the task success of observers did not improve with the number of correct choices they had observed in others. These mixed results indicate that information available during observations was not acquired or applied. Instead this pattern of observation can be explained by touchscreen users waiting their turn and queueing within the observation area (Carter et al., 2016). The homophily of touchscreen users in this study, either due to scrounging social information or by queueing for touchscreen access, meant that social information flow was constrained.

In conclusion, while this study effectively manipulated social learning opportunities using opaque panels, we found no evidence that information regarding task success was transmitted socially. Instead, baboons in this study predominantly relied on personal experience to navigate complex tasks. Although, inexperienced individuals such as young baboons, invested time in observing others, they were ultimately unable to apply or exploit the information effectively. Notably, social information gathering was mainly utilised by already knowledgeable individuals rather than naïve ones, limiting its transmission through the social network. These findings underscore the role of individual

heterogeneity and a reliance on asocial learning in inhibiting the spread of complex behaviours within these groups.

6.0 General Discussion

6.1 Importance of the study

Social learning is widespread across the animal kingdom, forming a vital transmission mechanism for behaviours key to survival and reproduction. Although some consider cultural behaviours that are transmitted via social learning unique to humans (Dean et al., 2012), the diversity of social learning in animals is clear with a classification of behaviours and species as cultural hindered primarily by definitions and consensus (Brakes et al., 2021; Kendal et al., 2018; Schuppli and Schaik, 2019). Inherently therefore, culture is deeply rooted within the evolutionary history of social animals (Allen, 2019).

The wide variety of cultural and potentially cultural behaviours across taxa, although extensive, poses the question of how such variety arises. By general definitions, cultural behaviours are inherited via social learning and are transmitted across generations (Hoppitt and Laland, 2013). The evolution of culture is therefore highly sensitive to individual variation in social learning, namely the ability to acquire, apply and exploit social information (Carter et al., 2016), and the factors that determine the demographic composition of individuals in a group (Fogarty et al., 2019). By comparing information use across species, tasks and experimental settings (see chapter 2), in addition to the various factors that influence them (chapters 3-5), the reasons that some species but not others sustain cultural behaviours can be elucidated (van Schaik, 2010).

To understand how different factors facilitate or impede the transmission of social information, and may thus affect the evolution of culture, I addressed the possible constraints on social information flow in chacma baboons (*Papio ursinus*). Baboons readily gather social information from conspecifics (Carter et al., 2014, 2016; Carter and Cowlishaw, 2021; Martina et al., 2020). Furthermore, they are frequently faced with cognitively demanding challenges tied closely with their omnivorous diet (van Schaik et al., 1999) and large social group (Sallet et al., 2011; Seyfarth and Cheney, 2013).

In the next sections, I summarise the main findings of this thesis (§6.2) and highlight their implications for the formation of culture in heterogeneous social networks (§6.3). Secondly, I evaluate the applications of the findings of this thesis to the emerging field of cultural conservation (§6.4). Finally, I address the future directions that have emerged from this research specific to the evolution of culture and the application of the fields of social learning and culture to current biological debates (§6.5).

6.2 Summary of findings

To understand the drivers of cultural evolution, I first assessed whether the shared mechanism of cultural behaviours – social learning – can be compared across species. Within chapter 2, I compared the success of learners in completing a task or behaviour following social learning opportunities in a meta-analysis across 185 studies. These studies showed a distinct taxonomic bias towards mammals (particularly primates) and birds (particularly perching birds).

Further trends in the literature showed that simple social learning tasks were the most common, and that most took place in captive conditions, limiting ecological validity. A comparison of task success rates, pooled across all taxa and settings, revealed that simple task performance (one-step) showed the greatest increase following social learning opportunities compared to complex task performance (two- and three-step). These results confirm previous studies that found task success was greatest in tasks with fewer steps (Kendal et al., 2009). Task improvement was also greatest if individuals were in wild settings compared to being captured and brought into captivity, where in turn captured individuals completed tasks faster than individuals raised in captivity. This means that presentations of both simple and complex to wild learners would give the greatest ecological validity to social learning studies. By investigating species differences in social learning abilities in appropriate settings, we can get closer to understanding why some species have culture and others do not, given that species with strong social abilities are more likely to show cultural traditions.

For my third, fourth and fifth chapters, I presented the first multi-touchscreen study to wild primates to understand how heterogeneities in individual traits affected how individuals accessed, used, and learned an easy and difficult touchscreen task. In this experiment, I presented two troops of chacma baboons with four rewarded touchscreens that displayed an easy choice task and a relatively difficult sequence task, with restricted social learning opportunities on half of the touchscreens. These touchscreens represented a foraging opportunity that was integrated within the natural foraging behaviour of the troops – as daily distance travelled was unaffected by touchscreen presence. The median calorific gained for troops during a touchscreen session

was negligible (1.2 – 4.8 (IQR = 7.2 – 28.8 kCal per session) and therefore explains why troop movements and foraging behaviour was not impacted by the experiment.

For my third chapter, I analysed how demographic and social factors influenced who participated in the experiment. These results showed that all participants showed a preference for attempting easier touchscreen tasks than difficult tasks. Although younger individuals were most likely to participate at least once, older individuals participated for the longest durations. Furthermore, males showed the greatest duration of touchscreen use compared to females in the easier task. This means that opportunities to access resources where social information was being produced were not equal across baboons, likely due to motivational differences rather than touchscreen access being limited by dominants (where rank had no effect on participation). These results support previous studies showing the neophilic nature of younger individuals (Martina et al., 2021). In addition, similar to previous studies, baboons that used the touchscreens were able to complete simple and complex tasks (Claidière et al., 2014; Malassis et al., 2020) and older individuals and males participated in touchscreen tasks for longer durations (Fagot and Bonté, 2010).

For my fourth chapter, I analysed how demographic, social, and cognitive factors affected task success in the experiment, whilst controlling for differential participation. The results showed that overall, baboons chose more correct choices on the easier touchscreen task than the more difficult task. Within the more difficult task, task success decreased over time, most likely because the memory of task success impacted performance, with a longer time since an

individual's last correct choice reducing current task success. This poor performance may be why an effect of age, sex, or rank could not be detected in the more difficult task, or that the ability to perform a complex task is independent of age, sex, or rank. However, in the easier task, older individuals showed the greatest task success and higher-ranked individuals outperformed lower-ranked individuals. A neighbour effect was also seen regarding rank, with lower-ranked individuals having lower task success when a relatively higher-ranked individual was at the neighbouring touchscreen, a pattern similar to that described in previous studies (Drea and Wallen, 1999; Nicol and Pope, 1994). Finally, some baboons discovered an alternative solution to gaining food rewards from the touchscreen without attempting the touchscreen tasks. This alternative solution was performed for longer durations on the more difficult task and was performed for longer durations when a greater number of incorrect choices were made. This suggests that the ability to successfully complete novel tasks is not uniform within large social groups, impacted by the age and rank of the actor as well as the characteristics of those within close proximity.

For my fifth chapter, I analysed a range of factors that might predict how baboons obtain social information, and from whom (using an experimental design that permitted or restricted social learning opportunities). I then used network-based diffusion analysis (NBDA) to estimate the degree to which social learning explained the order that the baboons learnt to complete the touchscreen tasks. Collectively, I then analysed whether social learning opportunities affected the later task success of the observers. The results from these analyses showed that task success was best explained by asocial learning, with a greater duration of observation time directed from high

touchscreen users towards other high touchscreen users. However, the observation of others' touchscreen success did not improve the subsequent performance of the observers. This physical separation between demonstrators and naïve individuals in the observation network meant social information was unlikely to be transmitted to those who could not access or exploit the touchscreen tasks.

6.3 Culture in heterogeneous social networks

The results obtained from the touchscreen experiment and following analyses may have important implications for our understanding of the spread of social information in baboons. In particular, a variety of factors may constrain the transmission and maintenance of cultural behaviours in baboons due to limitations to acquiring, applying and exploiting social information. These factors (discussed below) prevented the transmission of social information through the whole group (see chapter 5), whilst also limiting how individuals accessed (see chapter 3) and utilised resources (see chapter 4). Together, these findings highlight factors that likely play a role in the lack of culture found in baboons (Whiten and van de Waal, 2017).

6.3.1 Those that produce social information

Social information is produced by individuals that acquire behaviours individually (Giraldeau et al., 2002; Lee et al., 2016), either by personal learning (through trial and error) or by innovation (Amici et al., 2019). Innovation requires invention – the initial creation of a novel behaviour or solution (Hoppit and Laland, 2013). A multitude of factors can influence the likelihood of innovation at

the individual level due to individual trait variation, but also due to the social and ecological environment that potential innovators inhabit (Hopper, 2016). First and foremost, individuals must have the cognitive capacity to invent novel behaviours or solutions (§Chapter 4) but also must show motivation and persistence in problem-solving (§Chapter 3). The latter, as demonstrated in chapter 3, can be impacted by age and sex in chacma baboons, but also by rank in other primates (Drea and Wallen, 1999) as well as personality whereby bolder individuals are more likely to approach novel tasks (Hoppit and Laland, 2013). Further to this, as discussed in §1.3.3, low-ranking individuals may innovate more often in some contexts as they are excluded from other resources and must find alternative methods to access their requirements (Perry et al., 2017). Similarly, social tolerance (§1.5.4) may influence the motivation of individuals to perform novel behaviours in public view – for fear of agonisms or kleptoparasitism (Hopper, 2016). Finally, individual traits and social dynamics in a population can interplay with environmental factors to drive pressures to innovate. During periods of ecological variability, innovation forms an adaptive pathway to buffer against unpredictable resource acquisition – as was suggested in Japanese macaques (Imanishi, 1953) – and when resources are particularly scarce orangutans have been observed modifying tool use in response to necessity (Laumer et al., 2019). Together, a greater experience of innovating can mean a group with shared characteristics or individuals may produce high quality social information in innovations are adaptive.

Innovation rates, and therefore the likelihood of producing social information about new behaviours, is greatest in individuals with more experience (Reader and Laland, 2001). This means that in primates, adults show higher innovation

rates than immature individuals (Amici et al., 2019). However, a lack of experience in younger individuals may motivate exploratory behaviour and neophilia, making innovation sometimes more likely in younger individuals (Perry et al., 2017). Within sexually dimorphic species, the larger sex may be more willing to discover foraging opportunities due to their greater foraging demands and, as such, become producers of social information about food patch location and quality (Amici et al., 2019; Perry et al., 2017). This is true in chacma baboons, whereby males are more likely to apply and exploit social information about foraging patches (Carter et al., 2016). In addition, low-ranking individuals are more likely to innovate than high-ranking individuals (Perry et al., 2017; Reader and Laland, 2001), in order to exploit novel resources not yet monopolised by higher-ranking individuals, who consistently produce social information at resources that lower-ranks cannot access (King et al., 2008). This makes low-ranking individuals the target of information gathering from high-ranking individuals who are able to scrounge resources.

My results are in line with previous studies regarding the production of social information. Younger baboons were most likely to participate in the touchscreen study, demonstrating their neophilia and motivation to learn about their environment. However, more experienced older individuals were able to use the touchscreens for longer periods of time and showed the highest task success. This meant that older individuals were the major producers of social information in the easier task according to age, in line with previous studies (Camacho-Alpízar and Guillette, 2023; Perry et al., 2017; Reader and Laland, 2001; Tan et al., 2018). I also corroborated sex differences found in previous studies, as male baboons (the larger sex) used the touchscreens for a longer duration than

females (Fagot and Bonte, 2010). However, I found no sex differences in task success, meaning that a greater quantity of social information about the task was produced by males, but it was of equal quality to that produced by females. These results present a possible attention bias against producers of social information, as those that produced social information in this study (older individuals and males) may not remain in the troop for long periods. Male baboons tend to disperse between the ages of 8 and 10 years of age (Bergman et al., 2008; Washburn and DeVore, 1961). My results showed that older individuals produced social information of a high quality and quantity – with most social information produced by individuals of dispersal age - and males (the dispersing sex) produced social information in high quantities. Consequently, although older males should be the target of social information gathering from conspecifics. However, older males of dispersal age do not make reliable demonstrators due to their potential to leave troops. Therefore, any personal investment made by conspecifics in building network relationships with demonstrators that produce high quality and quantity of social information may be wasted. Instead, individuals may show conformity within demographic groups that are most likely to remain in the troop. This potential dynamic is likely reversed when a new male enters a troop, as the immigrant may possess novel and useful information that may lead to conformity within the group once the new male has become established. Despite the apparent reliability of older and male individuals as producers of social information, the social system of baboons may limit their effectiveness as reliable producers.

My results deviated from previous studies in that I found no monopolisation of resources (i.e., touchscreens) by high-ranking individuals (Harrison et al.,

2023), meaning that the quantity of social information produced was similar across ranks. However, high-ranking individuals produced higher quality social information than low-ranking individuals through their higher task success on the easier task. The quality of social information produced by low-ranking individuals was also reduced by the presence of high-ranking individuals at neighbouring touchscreens. This meant that the quality of information produced depended on the proximity of other actors as well as the characteristics of the producer. Overall, this means that only older individuals produced social information of both the greatest quantity and quality, whereas males produced only a high quantity of social information, and dominant individuals produce only high-quality social information.

6.3.2 Those reliant on social information

Social information is gathered by individuals to gain knowledge that would either be otherwise inaccessible or to improve the efficiency of a known behaviour (Laland, 2004). Younger individuals have the least experience of their environment and solving novel problems, and so are generally more explorative of their environments than older individuals (Martina et al., 2021). However as discussed (§6.3.1), younger individuals may not have frequent access to resources for long periods of time that would facilitate personal learning (see chapter 3). It would therefore be expected that younger individuals would readily gather social information so resources can be exploited quickly when an opportunity to do so is presented (Carter et al., 2014; Tan et al., 2018; Wobber and Warneken, 2013). The same can be said about the smaller sex (female baboons) who also lack access to resources and would require social information to increase their chances of successful exploitation of resources.

This is evidenced in previous studies with females tending to gather social information whilst males produce information (Amici et al., 2019; Canteloup et al., 2020; Reader and Laland, 2001; Watson et al., 2018). Collectively, the most efficient social learning strategy for inexperienced learners (young individuals and females) would be to direct observations towards producers a high quantity as well as a high quality of social information (Camacho-Alpízar and Guillette, 2023; Laland, 2004; Tan et al., 2018).

My results showed that a high quantity of social information about the touchscreens was produced by older individuals and males, and social information of high quality was produced by older individuals and those of high rank. It was therefore predicted (§5.2) that individuals who would dedicate most time to observing others would be inexperienced in cognitively demanding tasks (younger individuals, females and those of low rank), and they would direct their observations toward more experienced conspecifics (older individuals, males and those of high rank). In line with general trends (Hoppitt and Laland, 2013), younger individuals spent longer observing others than older individuals, but this was only the case in J troop during the easy task. Within L troop, and during the difficult task in J troop, touchscreen use positively predicted the duration of observation of others irrespective of age, sex or rank. Consequently, when individuals disperse, one strategy for obtaining valuable social information would be to observe immigrant males (who produce a high quantity of high-quality social information). However, as no dispersal occurred during this study, such strategies cannot be investigated but pose an interesting avenue for future research. These findings suggest that an individual's knowledge of the touchscreen tasks might influence their likelihood of observing others at the

touchscreen. This opposes the theory that inexperience motivates the gathering of social information, but instead touchscreen users could have sought to increase the efficiency of their own touchscreen behaviours. To this end, touchscreen use also predicted the duration that an individual was observed by others, demonstrating that experienced individuals were more likely to observe other experienced individuals. This result also opposes directed social learning strategies that inexperienced individuals will seek social information from those who have demographic characteristics associated with the quality and quantity of information production (Camacho-Alpízar and Guillette, 2023; Laland, 2004). Although my results are indicative of an absence of known social learning strategies, it must be considered that the experimental design (chapters 3-5) did not allow enough time for such strategies to develop. As chacma baboons are a despotic species (Fischer et al., 2019), it would be predicted that social learning would be directed as opposed to nonspecific, given that nonspecific social learning is more common in egalitarian species (Coussi-Korbel and Fragaszy, 1995). Instead, observers sought social learning opportunities from individuals they knew to be knowledgeable, rather than assuming knowledge of a conspecific based upon age, sex or rank alone.

6.3.3 Barriers to information flow

The flow of social information around a network depends on the characteristics of the actors within the network as discussed (their ability to acquire, apply and exploit social information), as well as the network structure (Castles et al., 2014; Hasenjager et al., 2021; Hoppitt, 2017; Wild and Hoppitt, 2019). Although most animals are associated with a network to some degree (mother-offspring or mating for instance), an interrogation of information flow through these networks

may not be representative of how a species lives and expresses behaviour due to the life history of the species. Instead, there may be limited value for some species in acquiring specific social information because the information is not useful to enhance survival and/or reproduction, or individuals have few opportunities to acquire it. In the first instance, social information may not be representative of novel situations that a species may face in natural conditions – an explanation given by some studies as to why individuals did not learn a task socially. One example of such a study is Schmelz et al., (2017), whereby giant otters (*Aonyx cinerea*) did not learn to solve a 'loose string' task where two individuals must temporally coordinate pulling a rope to gain resources. However, it is uncommon for giant otters to hunt cooperatively in ways similar to the loose string task (Leuchtenberger et al., 2020), and therefore investigating barriers to social information flow may be uninformative. Within Chapter 2, some tasks represented in the sample were presented to species that may not experience such tasks naturally. For example, two-step tasks (Table 2.1) were presented to domesticated chickens (*Gallus gallus*; Nicol and Pope, 1993, 1994, 1998) and pigeons (*Columba livia*; Bouchard et al., 2007), species that do not require complex and multi-step problem solving for survival and reproduction. This means that, as suggested in Chapter 2, comparative assessments should carefully consider the ecological relevance and validity of social learning tasks presented to species and groups (wild vs captive) before investigating factors that influence social information flow. Secondly, the social structure or lifespan of some species may mean that social learning opportunities are infrequent, unreliable or carry little information during short-lived interactions. Such species that such instances may apply to include short lived species (e.g. guppies) whereby complex social information requiring long

durations to acquire, apply and exploit (e.g. sequence tasks or tool use) may not have sufficient time to diffuse through networks. Equally, in solitary animals and those that do no exhibit parental care (e.g. Port Jackson sharks; Vila Pouca et al., 2020), conspecific interactions may be infrequent and therefore reliance on social information less important for the species. Consequently, a barrier to information flow in these species may not be similar to those identified in baboons but are present as a result of the life history of the species. Although life history must be considered when designing studies that interrogate social information flow, it is not currently known how/when some species use social information – to which thoughtfully designed studies can shed light on the importance of social learning across taxa.

I applied NBDA to estimate the importance of social learning for the order that touchscreen users learned touchscreen tasks according to their proximity social networks (§5.3.3). My results found no evidence of social learning in the completion of either touchscreen task. Further evidence for a lack of social learning stems from social network strength having no influence either on who observed who, or on task success following these social learning opportunities (Hoppitt, 2017; Sosa et al., 2021; Wild and Hoppitt, 2019). These results show that the flow of social information relating to task success may have been impeded in both troops, of which four possible causes are discussed below.

One major factor in the ability of observers of touchscreen users to acquire social information about touchscreen use was the presence of panels, intended to restrict social learning opportunities, at some touchscreens but not others. My results showed that the total duration of observations per observer was greater

at touchscreens without panels. This suggests that the panels were successful at restricting social learning opportunities for others without impeding access to the touchscreens or task success (via asocial learning) for the current touchscreen user. This indicates that baboons maximised their observable view of conspecifics that they sought to gather social information from. However, the absence of the panels did not lead to any change in task success following social learning opportunities, giving further evidence to the asocial model of learning. Through NBDA, my results showed that the asocial model explained the order that baboons acquired the ability to solve the touchscreen tasks better than the social model. Due to the between-group design of this study, I was able to conclude that the absence of the panels had no impact on social learning within the choice task or the sequence task.

A second factor that may have formed a barrier to social information flow was task difficulty. As described above (§6.3.1), high touchscreen users both attempted the easier task for longer durations than the more difficult task, but also achieved higher overall task success on the easier task. These results show a distinct preference for gaining the same food reward from an easier task instead of a more difficult task, in line with previous studies (Gazes et al., 2019). In addition, individual predictors of task participation and success were only found in the easy task. This was likely due to the baboons more readily forgetting how to solve the more difficult sequence task, decreasing the sample size and thus statistical power of knowledgeable individuals in that task. What is most interesting is that task difficulty did not impact whether baboons used asocial or social learning to solve the task. This indicates that, despite a markedly greater quality of social information produced at the easier task, the

baboons still failed to learn this task socially. In contrast, since task success was so poor in the difficult task, baboons might have been expected to dedicate more time to gathering social information about this task. However, the presence of an easier task with the same reward as the difficult task (and an alternative strategy of shaking the touchscreens to obtain the reward for the difficult task without solving it) reduced the incentives for the baboons to invest time in seeking out such information.

A third barrier to the flow of social information may have been a neighbour effect. As outlined previously, the task success of low-ranking individuals was lowest when a relatively high-ranking individual was at the neighbouring touchscreen (within 20m). Although the presence of high-ranking individuals did not limit touchscreen participation (see chapter 3) it did reduce touchscreen performance (see chapter 4). This shows that, unlike in previous studies with baboons and other primates (Drea and Wallen, 1999; Fagot and Paleressompoulle, 2009), low-ranking baboons did not limit their time attempting touchscreen tasks to those occasions when high-ranking individuals were absent. Instead, low-ranking individuals attempted to interact with the touchscreen in the presence of high-ranking individuals even at the risk of increased agonism. This likely added acute stress to regular stresses and higher social monitoring associated with a low dominance rank (Abbott et al., 2003), which led to decreased cognitive performance (Mendl, 1999; Oliveira et al., 2018; Soravia et al., 2021; Tuckey et al., 2024). However, Drea and Wallen (1999) suggested that low-ranking primates can ‘play dumb’ in the presence of high-ranking individuals so that they are not the target of aggressive

behaviours. Although I cannot rule out this possibility, low-ranking individuals consistently performed worse than high-ranking individuals in the choice task.

Finally, another barrier to information flow through the whole troop may have been the circular observations of touchscreen users. My results showed that the cumulative time spent attempting touchscreen tasks positively correlated with both the time spent observing others and the time spent being observed. This means that knowledgeable touchscreen users observed one another, although opportunities to acquire social information did not improve their subsequent task success. This limited the diffusion of social information through the entire troop as inexperienced individuals with little or no task experience were unlikely to gain social information from knowledgeable conspecifics. Consequently, high quality social information was clustered within a sub-group of successful asocial learners and did not spread to those who would have benefitted greatest from social information. This meant that those reliant upon social information did not acquire high-quality social information, and when combined with their poor experience of the tasks, were unable to learn the tasks. When applied more broadly, these results indicate that touchscreen users who also produced high quality social information – males / those of dispersal age – were not actively observed by those predicted to be reliant on social information (young individuals, females, and low-ranked individuals. One explanation for this (§6.3.1) is that individuals who will be present within their current troop, due to philopatry (females) or young age, don't actively seek social learning opportunities from those that could disperse. As no immigrant males entered either troop during the touchscreen study, attention biases towards immigrants who may possess high quality social information could not be tested.

Nevertheless, the potential of older males to disperse may have created a barrier to the flow of social information through the troops after knowledge of touchscreen tasks became clustered within the demographic that was most capable of dispersal.

Combined, these four barriers to social information flow through the baboon troops highlight that there may have been several reasons why the baboons learnt the touchscreen tasks asocially rather than socially, including limitations on social learning opportunities, task difficulty, a neighbour effect and a clustering of high-quality information by high-quality producers. Although social information regarding task success did not flow through troops, baboons did acquire novel behaviours – completing choice and sequence tasks to learning criteria (§4.4.3). This suggests that baboons were able to individually acquire novel behaviours, but the social information produced simply did not spread. Individuals were given substantial opportunities to gain social information from participants (up to 2 hrs per session totalling 42 hrs over the experimental period), as touchscreen shapes were visible from within 10 m even when a participant was present (although restricted in some conditions). Although repetitive observations were possible, the repetitive exposure to the same tasks was greater in captive studies than within this experiment. For example, it tens of thousands of trials given to captive baboons over several months to learn new sequence tasks and show cultural transmission (Claidière et al., 2014; Malassis et al., 2020). Despite the suggestion of barriers to information flow in Chapter 5, the relatively short exposure of touchscreens to baboons within this study compared to captive conditions may not have been sufficiently long enough for observers to develop social learning strategies. However, in light of

rapid environmental change – including accelerating desertification (Farren, 2024), the dissemination of adaptive behaviours may be hindered in baboons if lasting and repeated exposure is a pre-requisite for social learning. As a consequence, baboons who are least likely to individually acquire novel behaviours (§4.4.1; 4.4.3) may be vulnerable to rapid environmental change.

In addition, it is important to note that although barriers to information flow were present, this does not preclude the disinterest of individuals in paying attention to social information as a result of the experimental design. Firstly, the touchscreens represented an abnormal resource for baboons at Tsaobis. This means that baboons may have been more cautious of entering the experimental area and also no baboon was experienced on how to gather social information from touchscreen users. This means that normal patterns of conspecific observation may have been compromised in this experiment as the experimental design is not optimal for the species. Secondly, unlike Harrison et al. (2023), the touchscreens that were used in this study were static. This meant that participation in the touchscreen experiment relied upon baboons staying within the experimental area. Therefore, if baboons were moving transiently through the experimental area, there were few opportunities to gather social information from conspecifics. Finally, the experimental area was located within 1 km of two commonly used sleeping cliffs and a water source, to maximise the likelihood that baboons would see the experimental area. However, this meant that these other resources could have been of greater interest to baboons than the observation of conspecifics at touchscreens. Despite these possibilities, the experimental design still managed to recruit a similar proportion of touchscreen users as captive studies, that both encourage participation and have fewer

environmental and social distractions then are present at Tsaobis. Overall, this study shows that baboons were highly interested in participating in the touchscreen experiment, but potential barriers to gathering social information and a potential disinterest of doing so hindered the flow of social information through the troops.

6.3.4 Strategies in cognitive challenges

Animals do not exclusively learn socially or asocially, but rather show an adaptive learning strategy in response to their personal experience as well as the physical and social environment that surrounds them (Kendal et al., 2005). There are a multitude of studies both theoretical and experimental that address this adaptive use and investigate the optimum learning strategy of animals (Hoppitt and Laland, 2013). By contrasting optimal learning strategies suggested in previous studies to the learning strategies utilised in this study, an explanation for the patterns of learning in baboon learning of touchscreen tasks may be found.

Social learning becomes a beneficial mechanism of learning when asocial learning is difficult or costly (Hoppitt and Laland, 2013; Laland, 2004). This is most true when acquiring behaviours that would result in the demise of the learner if they were to make a mistake during asocial learning, such as learning to avoid a novel predator (see chapter 2). There was no significant cost (in obtaining rewards) in this study to baboons learning asocially, as touchscreen rewards (and likely aggressive interactions with high-ranking conspecifics) were equal no matter the learning mechanism (social or asocial) utilised to obtain rewards. Therefore, because there was no cost of asocial learning, social

learning did not represent an advantageous mechanism for learning in this study.

In cases where asocial learning is less efficient than social learning, such as when the task or behaviour is too difficult to learn by trial and error (e.g. tool-use; Hobaiter et al., 2014), social learning is often preferred (Kendal et al., 2009). However, there are a number of social learning strategies that animals can employ, with the optimal strategy dependant on context and who or what is being observed in order to gather social information (Hoppitt and Laland, 2013). One social learning strategy is to 'copy when uncertain' (Boyd and Richerson, 1988; Galef, 2009), employed when an individual either does not understand the task or does not understand the solution or behaviour needed to complete the task (Kendal et al., 2009). My results show that younger individuals had limited access to touchscreen tasks and therefore obtained few opportunities to learn asocially. This ultimately led to younger individuals choosing the least number of correct choices on the easier task. Although low-ranking individuals also performed poorly, their access to tasks was equal to high-ranking individuals and so their opportunities for asocial learning remained high. This meant that young individuals, but not low-ranking individuals, were most likely to be uncertain about touchscreen tasks and thus most likely to benefit from using social learning to overcome this uncertainty. Indeed, younger individuals observed others for a longer duration than older individuals, but only within J troop on the more difficult task. This pattern was likely observed on the difficult task in J troop as social learning opportunities were not restricted by opaque panels. Furthermore, as suggested previously (§6.3.3), if individuals employed a social learning strategy to 'copy when uncertain', a greater proportion of

observation time should be dedicated to tasks that an individual finds most difficult. It appears therefore that younger individuals in J troop may have employed this strategy to gather social information from a difficult task. This pattern was not seen in L troop as the difficult task was obstructed by opaque panels and therefore information gathering by uncertain individuals was impeded. Gaining social information ultimately was an unsuccessful social learning strategy as task success did not improve following an observation of a correct choice.

A further social learning strategy is to 'copy when the established behaviour is unproductive' (Grueter et al., 2010; Grüter and Ratnieks, 2011). For this strategy to be successful, individuals who are inefficiently performing an established behaviour (such as randomly choosing correct choices on touchscreen tasks) should choose to copy successful individuals (Boyd and Richerson, 1985; Schlag, 1998). This creates a 'success bias' in who observers choose to scrounge social information from (Hoppitt and Laland, 2013). Contextual evidence for success can be seen within some primates, with naïve chimpanzees more likely to follow knowledgeable individuals to hidden food items than less knowledgeable chimpanzees (Menzel, 1974). However, a success bias can be masked by a transmission bias favouring a social or demographic characteristic that is used as a proxy for knowledge (Boyd and Richerson, 1985). In the present study, older individuals and those of higher rank were the most successful, and so individuals whose behaviour was unproductive should have directed attention to conspecifics with these characteristics. Such a transmission bias has been seen in chimpanzees where individuals preferred to copy the more successful foraging method of older and

higher-ranked individuals over younger and lower-ranked conspecifics (Horner et al., 2010). However, such a transmission bias was not the case in this study, as observations were directed towards all high touchscreen users, irrespective of age or rank. This means that baboons were using a success bias strategy to gain the needed/correct social information. Despite this strategy, observers did not improve task success following social learning opportunities and so if this strategy of gathering social information was employed, it was unsuccessfully applied and exploited.

Although the baboons observed each other on the touchscreens, there was no evidence of social learning or the transmission of social information regarding task success through the baboon groups. This suggests that the baboons may have attempted to acquire social information but were ultimately unsuccessful either in the initial acquisition or in applying and exploiting that information subsequently. An alternative explanation might be that the baboons used a combination of asocial and social learning to first attempt the touchscreen tasks, and then asocial learning to complete them. First the baboons learnt to interact with the touchscreens socially (evidenced from NBDA) but learnt how to complete tasks asocially (evidenced by NBDA and the lack of social network strength as a predictor of whether or not individuals reached the learning criteria). Following this, social information was restricted to these asocial learners. Although high touchscreen users observed other high touchscreen users, the acquisition of social information regarding task success was assumed, measured only by the orientation of the observer's head towards a touchscreen user. It is therefore plausible that the social learning opportunities that high touchscreen users found themselves in was not intentionally for the

purpose of observing conspecifics, but was a queueing system for access to the touchscreen (Carter et al., 2016). As baboons waited for their turn, they periodically watched the current touchscreen user to see when a touchscreen was available but were not paying attention to what that user was doing. However, according to this interpretation, even if not intentional, queuing baboons still gained social learning opportunities from touchscreen users while queuing, and therefore the barrier to social information transmission lay with a lack of motivation to acquire social information. If the timeframe of the experiment was increased to comparable levels to captive studies (e.g. Claidière et al., 2018, 2014), baboons may have had more time to identify individuals that produce high quality social information (§6.3.1) and selectively observed them to obtain social information, thus boosting their task efficiency. Equally, adjustments to the experimental design to better mimic natural movements and behaviours of foraging baboons - such as placing touchscreens on the ground and facing up – may facilitate social information transmission when familiarity with strategies for gaining such information is increased.

In conclusion, the baboons in this study showed an impressive ability to solve easy and difficult touchscreen tasks. They showed great ingenuity in seeking alternative solutions when possible and adaptability in prioritising their cognitive efforts towards simpler tasks with the same reward. In addition, the presence of significant barriers to the transmission of social information observed in this study suggests that some cultural behaviours may be unlikely to diffuse through baboon groups. This is due to two major factors; firstly, the variability in the ability to acquire, apply and exploit social information due to individual variation in these abilities, and secondly due to a preference for asocial learning in

completing complex tasks. Collectively, the presence of individual heterogeneity in social networks means that the spread of information through those networks becomes increasingly difficult to predict, with major implications for cultural evolution in those groups.

6.4 Applications to conservation

Social learning is an adaptive behaviour that allows animals to learn about their environment efficiently (Feldman and Laland, 1996; Laland et al., 2010; Lefebvre and Giraldeau, 1996). It is also a requirement for defining culture in animals (§1.2). Culture has recently been recognised by the Convention on the Conservation of Migratory Species (CMS) as a conservation priority and recommended by the Cultural Expert Group for integration into the development of conservation strategies for animals with culture (Brakes et al., 2019). In 2020, special concerted action was announced by the CMS to categorise Western African chimpanzees and Eastern Pacific sperm whales (*Physeter macrocephalus*) as cultural conservation units (UNEP, 2020). This decision was made due to the unique cultural behaviours exhibited by these populations; nut-cracking and unique vocal clans respectively (Biro et al., 2006; Rendell and Whitehead, 2003). This means that both populations require a specific conservation action plan that may differ from species-wide conservation policy in order to preserve the adaptive potential of behavioural diversity within the species (Brakes et al., 2019; Gruber et al., 2019).

Most recently at CMS 2024, the Cultural Expert Group recommended that CMS rapidly explores standardised methods for identifying social learning and incorporating social learning into conservation management (CMS, 2024). This

was requested because social learning is a prerequisite for cultural behaviours and their identification. Through interrogating potentially adaptive behaviours transmitted via social learning, conservationists could ensure that current and future behavioural diversity that is dependent on social learning remains. Such behavioural diversity, much like genetic diversity (Mable, 2019), increases the likelihood that an adaptive behavioural variant exists in a population that would aid in the survival and reproduction of those that possess it. However, unlike evolution via genetic means, socially-learned behaviours can be transmitted within generations and so allow for rapid adaptive change in relation to the scale of global species population declines (Brakes et al., 2025, 2021; WWF and ZSL, 2024).

As social learning and culture are increasingly integrated into conservation management and policy (Schuppli and Schaik, 2019), conservation efforts and funding is unlikely to be equally shared between cultural species. This will inevitably create discussions regarding what cultural behaviours are most important to conserve, what species displays the most ‘beneficial’ cultural behaviours and how likely cultural behaviours are lost or gained, in order to prioritise conservation efforts. However, there is no standardised way to compare cultural behaviours or social learning across taxa, or compare behaviours transmitted via social learning even within species. This was an issue that I discussed in chapter 2, where I found significant issues in data measurement and reporting that hindered comparative analyses. After identifying common inconsistencies within social learning literature that limited comparability, I designed a comparative experimental social learning paradigm that unites implementation simplicity and conceptual sophistication to

systematically investigate the emergence and spread of solutions to increasingly difficult cognitive tasks following social learning across a variety of different species. This work is still ongoing, but I present a brief overview in the Appendices (see Appendix 2). This ongoing study could represent a standardised methodology for future comparisons of social learning across taxa and tasks, further enhanced by the avoidance of some technical terminology that can hinder cross-study comparisons (§2.1).

Although the inclusion of animal culture in conservation policy could form a useful new tool in protecting the behavioural diversity of endangered species, it's application in conservation should be approached with caution (Carvalho et al., 2022). The main focus of conservation efforts is species preservation, with the identification and management of the biggest threats to population decline paramount to ensuring species persistence (Cowlishaw and Dunbar, 2021). Across vertebrates (§ Chapter 2), habitat-loss / land-use change is a key driver of population decline, with disease also a major threat to primates (WWF and ZSL, 2024). Social learning and cultural behaviours offer a potential buffering system to adapt to these changes (Brakes et al., 2025, 2021, 2019), but the identification of potentially adaptive cultural behaviours may complicate conservation strategies. Within West African chimpanzees (those covered by CMS cultural conservation concerted action), cultural nut-cracking skills are acquired over extended periods through social learning (CMS, 2020). Acquisition of these behaviours is impacted by several factors, such as disruptions to social structure or interruptions during social learning processes (Berdugo et al., 2024). Consequently, conservation actions that integrate cultural behaviours must consider the time and social structures necessary for

social transmission. Considering the main drivers of chimpanzee population decline – habitat loss and disease – the addition of cultural behaviours into conservation action plans could detract focus and time away from more pressing factors. Ultimately, as is covered in Chapter 1, approaches to identifying cultural behaviours are not yet universally agreed, creating further barriers to conservation applications. The pandisciplinarity of animal culture is a major factor in disjointed terminological definitions and may further hinder progression into a unified application of animal culture due to the need (King, 2024). One further difficulty is linking cultural behaviours to survival (King, 2024), whereby such information would be informative to assessing the worth of cultural behaviours to conservation actions when balancing other priorities such as tackling poaching. Quantifying the survival value to cultural behaviours may be a lengthy process – particularly in relatively long-lived species such as chimps and sperm whales within current CMS legislation. Consequently, it may be difficult to justify a conservation focus including cultural behaviours when decreasing the impacts of other threats such as habitat destruction has clearer and measurable goals. What is more, the dynamics of how cultural behaviours emerge, are maintained, or disappear are specific to species and groups due to the requirement for social learning (§1.2). The context-specific nature of culture therefore makes it difficult to firstly produce ‘one size fits all’ guidance or legislation (King et al., 2024) and adds to the latency of cultural conservation action due to the need to identify and assess the conservation value of cultural behaviours in each species and group. Finally, if cultural behaviours are identified, linked to survivability and species- / group-specific action plans agreed, there is currently no paradigm to facilitate prioritisation if resources are limited. Such discussions could consider how likely novel cultural behaviours

may emerge (§6.3.1), how behaviours spread and are maintained, any survival benefits of behaviours and how likely behaviours are to be lost. To allow for such discussion, a comparative metric should be employed within social learning and cultural research (§ Appendix 2). However, interpretations of such a paradigm may reveal that some cultural behaviours may be 'less worthy' of conservation action, muddying the water further regarding the use of culture in conservation opposed to tried and tested measures (e.g. genetic or demographic). Nevertheless, discussions regarding the conservation of animal culture is in its relevant infancy (Brakes et al., 2025). Although it's integration into current conservation practice should be approached with caution, considering unique and potentially adaptive behaviours may be a valuable tool for conservation. To shed light on the complex dynamics of social information transmission and maintenance will only serve to enlighten our understanding of culture and consider how best to conserve it.

Within the touchscreen analyses, my results demonstrated that the spread of social information (or lack thereof) was greatly dependent upon the characteristics of heterogeneous actors within the social network. Namibia, particularly the Erongo region where Tsaobis is located) is predicted to warm drastically as a result of climate change (Farren, 2024). Accelerating desertification of the environment that troops included in my results inhabit will likely increase resource scarcity. As a consequence, there may be an increased selective pressure to innovate, with the emergence and maintenance of novel adaptive behaviours necessary during time of environmental variability as desertification accelerates. Although these results are indicative of a lack of social learning and diffusion of novel behaviours, the study was temporally

limited and so cannot fully predict the maintenance of such behaviours long-term. However, if environmental pressures change at a faster rate than the time needed for innovations to be maintained in populations, baboons may be unable to develop behavioural adaptations that may aid their survival. My results indicate that heterogeneous actors within populations designated as special concerted action by CMS may also impede the diffusion of social information. As threatened populations become increasingly smaller and fragmented, social networks in more threatened populations will become altered compared to their previous state due to demographic changes in group composition (Shizuka and Johnson, 2020). This means that the transmission of potentially adaptive social information could drastically change, rendering inefficient social learning in some groups but not others (Momennejad, 2022; Sosa et al., 2021). Consequently, it would be advisable to take heterogeneity in social networks into account concurrently with the conservation of animal culture to best understand how cultural behaviours evolve and can be conserved effectively.

6.5 Future directions

This thesis explored the impact of heterogeneity within social networks on the spread of social information through two troops of baboons. I presented multiple touchscreens simultaneously to subjects, alongside a choice of an easy and difficult task. In addition to replicating and expanding this research in other study systems, several further factors could also be addressed in future work. Firstly, my results showed a significant preference for attempting the easy task (culminating in a higher task success). In this study, both easy and difficult tasks were equally rewarded, and so it was more efficient for baboons to engage with

the easier task. By increasing the reward in the difficult task but not the easy task, a simultaneous presentation of an easy-low reward task and a difficult-high reward task may generate different patterns of individual task preference than found in this study. Furthermore, inexperienced individuals may be more motivated to seek social information in the difficult-high reward task than the easy-low reward task, as the acquisition of such information would maximise payoffs. Secondly, although the panels were successful at restricting the acquisition of social information, access to touchscreens was not restricted. Unlike touchscreen studies in captive populations (Claidière et al., 2014), dominant individuals were observable at neighbouring touchscreens, decreasing the task success of subordinates (see chapter 4). By restricting touchscreen access by rank, the neighbour effect could be eliminated if low-ranking individuals can participate in the absence of high-ranking neighbours. This would allow individuals who are typically not observed by others generating an adaptive innovation that could diffuse through a group. By reversing the patterns of individual heterogeneity among touchscreen users found within this study and only granting touchscreen access to those typically most reliant on social information (younger individuals, females and low-ranking individuals), the extent to which typical producers of social information have the capacity to gather information from others can be investigated. Finally, due to the pioneering experimental design of chapters 3-5, no prior knowledge of how optimal the experimental design was for investigating social transmission in the baboon groups studies could have been obtained. Therefore, it must be considered that the experimental design, and subsequent results, may not truly represent social learning dynamics within chacma baboons. To validate the results found in this thesis, in addition to optimising the experimental design of

further touchscreen experiments, future studies could incorporate a between-group design. Within the TBP, data are collected *ad libitum* regarding the emergence of innovations, but no further investigations are undertaken for their diffusion through troops. As an indication of troop differences were found in this thesis (§ Chapters 4 and 5), assessments of why different (or the same) innovations do / do not diffuse naturally through troops may reveal demographic and social factors that may provide further evidence for those found in this thesis (or provide alternative evidence). These data from natural diffusions – although unlikely to be observed (§1.2.1) – can be reinforced through experimental approaches such as presenting different tasks to different troops using touchscreens. One further experimental approach could quantify natural diffusion chains that baboons follow when learning about novel foraging patches (patch flows). By comparing natural diffusion chains (either innovation diffusions or experimentally induced diffusions through patch flows) to those found in touchscreen studies, the ecological validation of this thesis can be increased.

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AUTHOR CONTRIBUTION STATEMENT

The research chapters (2-5) of this thesis are a series of manuscripts that are intended for publication. Although I performed the majority of work that forms this thesis, a number of colleagues contributed to this research (see specific contributions below). Data collection was funded by different grants (indicated below). Finally, this work was possible thanks to many people who worked at / supported the Tsaobis Baboons Project and colleagues at the Zoological Society of London (see Acknowledgements).

Chapter 2:

- Simon Paul Kenworthy: conceptualisation, literature gathering and refinement, data curation, data analysis, writing drafts and final manuscript, visualisation.
- Alecia Carter: conceptualisation, review and editing.
- Guy Cowlishaw: conceptualisation, review and editing.

Chapters 3 - 5:

- Simon Paul Kenworthy: conceptualisation, data collection, data curation, data analysis, writing drafts and final manuscript, visualisation, project funding (Natural Environmental Research Council, London NERC Doctoral Training Program).
- Alecia Carter: conceptualisation, review and editing, project administration, project funding (Templeton World Charity Foundation Grant – TWCF0509)
- Guy Cowlishaw: conceptualisation, review and editing, project administration, project funding (Research England).

Appendices

Appendix 1 Meta-analysis supplementary material

Table A1.1: Refinement categories for literature refinement in chapter 2.

Refinement Category	**Refinement Criteria**
Search engines	Web of Science | Google Scholar
Search terms	Social learn*| Social information| Public information| (Learn*) AND (Demonstrat*)| (Social*) AND (Transmit*)| cultur* AND (transmit* OR evol*)| Learn* AND rate*
Literature type	Exclude: review| preprint| meta-analyses
Categorical refinement	Inclusion of categories listed under 'refine': Behavioural Sciences| Zoology| Ecology| Environmental Studies| Agriculture Dairy Animal Science| Rehabilitation| Acoustics| Fisheries| Marine Freshwater Biology| Development Studies| Genetics Heredity| Mathematical Computational Biology| Biodiversity Conservation| Environmental Sciences| Communication| Neurosciences| Biochemistry Molecular Biology| Biology| Agriculture Multidisciplinary| Multidisciplinary Sciences| Veterinary Sciences| History Philosophy of Science| Evolutionary Biology| Statistics Probability| Anthropology| Endocrinology Metabolism| Biochemistry| Molecular Biology| Cell Biology| Physiology| Physiology Applied| Psychology Multidisciplinary| Psychology Biological| Cultural Studies| Reproductive Biology| Ornithology | Entomology
Abstract refinement	Include: If title and/or abstract contained named species or taxonomic group | reference to social learning (defined under search terms) Exclude: Interspecies social learning | duplicate study/article
Extractable data refinement	Exclude: data not available/extractable| interspecies social learning| duplicate data | no control group if naïve task performance cannot be 'expected'| theoretical models only

Research question appropriation refinement	Include: Only novel tasks with no prior experience Exclude: Invertebrate subject | Task performance not recorded | Social learning 'opportunity' only with no task | Grouping/herding/shoaling behaviour only | Within a choice task, if the choice was made due to 'personality' of the observer | Human participants in experiment | Non-animal demonstrator/model | Cannot rule out individual learning as explanatory variable

Table A1.2: Full list of studies included in chapter 2.

Taxonomic Class	Taxonomic Order	Taxonomic Family	Species	Task presented	Experimental setting	% or Latency	Reference
Actinopterygii	Cichliformes	Cichlidae	Julidochromis transcriptus	Transitive inference	Captive	%	Hotta et al., (2015)
	Cypriniformes	Cyprinidae	Cyprinus carpio	Anti-predator behaviour	Captive	%	Lovén Wallerius et al., (2020)
	Cypriniformes	Cyprinidae	Danio rerio	Route choice	Captive	Latency	Lindeyer and Reader, (2010)
	Cypriniformes	Cyprinidae	Danio rerio	Route choice	Captured	Latency	Roy and Bhat, (2017)
	Cypriniformes	Cyprinidae	Danio rerio	Route choice	Captive	Both	Attaran et al., (2020)
	Cypriniformes	Cyprinidae	Pimephales promelas	Anti-predator behaviour	Captured	%	Chivers and Smith, (1995)
	Cypriniformes	Cyprinidae	Pimephales promelas	Anti-predator behaviour	Captured	%	Crane et al., (2015)
	Cyprinodontiformes	Poeciliidae	Poecilia latipinna	Mate choice	Captive	%	Gierszewski et al., (2018)
	Cyprinodontiformes	Poeciliidae	Poecilia mexicana	Patch choice	Captive	%	Fuss et al., (2021)
	Cyprinodontiformes	Poeciliidae	Poecilia reticulata	Route choice	Captive	%	Brown and Laland, (2002)
	Cyprinodontiformes	Poeciliidae	Poecilia reticulata	Patch choice	Captive	%	Hasenjager et al., (2020)
	Cyprinodontiformes	Poeciliidae	Poecilia reticulata	Route choice	Captive	%	Laland and Williams, (1997)
	Cyprinodontiformes	Poeciliidae	Poecilia reticulata	Patch choice	Wild	Both	Reader et al., (2003)
	Gasterosteiformes	Gasterosteidae	Gasterosteus aculeatus	Patch choice	Captured	Both	Trapp and Bell, (2017)
	Gasterosteiformes	Gasterosteidae	Gasterosteus aculeatus	Patch choice	Captive	Both	Borcherding et al., (2020)
	Gasterosteiformes	Gasterosteidae	Gasterosteus aculeatus	Patch choice	Captured	%	Coolen et al., (2003)
	Gasterosteiformes	Gasterosteidae	Gasterosteus aculeatus, Pungitius pungitius	Patch choice	Captured, Captive	%	Webster et al., (2019)

	Gasterosteiformes	Gasterosteidae	Pungitius pungitius	Patch choice	Captured	%	Duffy et al., (2009)
	Gasterosteiformes	Gasterosteidae	Pungitius pungitius	Patch choice	Captured	%	Webster and Laland, (2011)
	Gasterosteiformes	Gasterosteidae	Pungitius pungitius	Patch choice	Captive	%	Webster and Laland, (2015)
	Perciformes	Percidae	Perca fluviatilis	Novel food choice	Captured	%	Magnhagen and Staffan, (2003)
	Perciformes	Pomacentridae	Pomacentrus amboinensis	Anti-predator behaviour	Captured	%	Manassa et al., (2014)
	Salmoniformes	Salmonidae	Salmo salar parr	Novel food capture	Captive	%	Brown et al., (2003)
	Salmoniformes	Salmonidae	Salvelinus alpinus	Anti-predator behaviour	Captive	%	Vilhunen et al., (2005)
	Salmoniformes	Salmonidae	Salvelinus fontinalis	Novel food choice	Captured	%	White and Gowan, (2014)
Amphibia	Anura	Ranidae	Rana sylvatica	Anti-predator behaviour	Captive	%	Chivers and Ferrari, (2014)
	Urodela	Ambystoma	Ambystoma annulatum	Novel food choice	Captured	%	Crane et al., (2018)
Aves	Accipitriformes	Accipitridae	Circus aeruginosus	Novel food capture	Wild	%	Kitowski, (2009)
	Anseriformes	Anatidae	Branta canadensis	Anti-predator behaviour	Captured	%	Blackwell et al., (2019)
	Columbiformes	Columbidae	Columba livia	Two-step	Captured	Latency	Bouchard et al., (2007)
	Columbiformes	Columbidae	Streptopelia risoria	Two-step	Captive	%	Hatch and Lefebvre, (1997)
	Columbiformes	Columbidae	Zenaida aurita	Anti-predator behaviour	Wild	%	Barrera et al., (2011)
	Galliformes	Phasianidae	Gallus gallus	Novel food choice	Captive	Both	Cloutier et al., (2002)
	Galliformes	Phasianidae	Gallus gallus	Patch choice	Captive	%	McQuoid and Galef, (1994)
	Galliformes	Phasianidae	Gallus gallus	Two-step	Captive	%	Nicol and Pope, (1993)
	Galliformes	Phasianidae	Gallus gallus	Two-step	Captive	%	Nicol and Pope, (1994)
	Galliformes	Phasianidae	Gallus gallus	Two-step	Captive	%	Nicol and Pope, (1999)

	Galliformes	Phasianidae	Gallus gallus	Novel food choice	Captive	%	Sherwin et al., (2002)
	Galliformes	Phasianidae	Lagopus leucurs	Novel food choice	Wild	%	Allen and Clarke, (2005)
	Galliformes	Phasianidae	Coturnix japonica	Mate choice	Captive	%	Ophir and Galef, (2004)
	Falconiformes	Falconidae	Milvago chimango	One-step	Captured	Both	Biondi et al., (2010)
	Passeriformes	Corvidae	Aphelocoma coerulescens	Novel natural behaviour	Wild	%	Midford et al., (2000)
	Passeriformes	Corvidae	Corvus corax	Two-step	Captive	Both	Fritz and Kotrschal, (1999)
	Passeriformes	Corvidae	Corvus corax	Novel object choice	Captive	%	Schwab et al., (2008)
	Passeriformes	Corvidae	Calocitta formosa	One-step, Three-step	Captured	%	Langen, (1996)
	Passeriformes	Corvidae	Corvus macrorhynchos	Two-step	Captive	%	Izawa and Watanabe, (2011)
	Passeriformes	Estrildidae	Lonchura punctulata	Patch choice	Captive	%	Rieucau and Giraldeau, (2009)
	Passeriformes	Estrildidae	Taeniopygia guttata	Novel food choice	Captive	%	Katz and Lachlan, (2003)
	Passeriformes	Estrildidae	Taeniopygia guttata	Mate choice	Captive	%	Kniel et al., (2015)
	Passeriformes	Estrildidae	Taeniopygia guttata	Novel food choice	Captive	%	Guillette and Healy, (2017)
	Passeriformes	Estrildidae	Taeniopygia guttata	Novel natural behaviour	Captive	%	Guillette and Healy, (2019)
	Passeriformes	Estrildidae	Taeniopygia guttata	Novel natural behaviour	Captive	%	Guillette et al., (2016)
	Passeriformes	Estrildidae	Taeniopygia guttata	Patch choice	Captive	%	Riebel et al., (2012)
	Passeriformes	Estrildidae	Taeniopygia guttata	Mate choice, Novel food choice	Captive	%	Rosa et al., (2012)
	Passeriformes	Estrildidae	Taeniopygia guttata	Mate choice	Captive	%	Swaddle et al., (2005)
	Passeriformes	Icteridae	Dolichonyx oryzivorus	Patch choice	Wild	%	Nocera et al., (2006)

	Passeriformes	Icteridae	Molothrus bonariensis	One-step	Captured	Latency	May and Reboreda, (2005)
	Passeriformes	Icteridae	Quiscalus lugubris	Anti-predator behaviour	Captured	%	Griffin and Galef, (2005)
	Passeriformes	Maluridae	Malurus cyaneus	Anti-predator behaviour	Wild	%	Feeney and Langmore, (2013)
	Passeriformes	Meliphagidae	Phylidonyris novaehollandiae	Anti-predator behaviour	Wild	%	McLachlan et al., (2019)
	Passeriformes	Paridae	Cyanistes caeruleus	Two-step	Captured	%	Aplin et al., (2013)
	Passeriformes	Paridae	Cyanistes caeruleus	Novel food choice	Captured	%	Hamalainen et al., (2017)
	Passeriformes	Paridae	Cyanistes caeruleus	Patch choice	Captured	%	Hamalainen et al., (2019)
	Passeriformes	Paridae	Parus major	Patch choice	Captive	%	Marchetti and Drent, (2000)
	Passeriformes	Paridae	Parus atricapillus	One-step	Captured	%	Sherry and Galef, (1990)
	Passeriformes	Paridae	Parus major	Patch choice	Wild	%	Jaakkonen et al., (2015)
	Passeriformes	Paridae	Parus major	Novel food choice	Captive	%	Landová et al., (2017)
	Passeriformes	Paridae	Parus major	Three-step	Captive	%	Smit and van Oers, (2019)
	Passeriformes	Parulidae	Cardellina rubra	Anti-predator behaviour	Wild	%	Thorogood and Davies, (2016)
	Passeriformes	Parulidae	Dendroica caerulescens	Patch choice	Wild	%	Betts et al., (2008)
	Passeriformes	Passeridae	Passer domesticus	Novel food choice	Captured	%	Greig-Smith and Fryday, (1994)
	Passeriformes	Ploceidae	Euplectes afer	One-step	Captive	Both	Danel et al., (2019)
	Passeriformes	Sturnidae	Acridotheres tristis	Anti-predator behaviour	Captured	%	Griffin, (2008)
	Passeriformes	Sturnidae	Acridotheres tristis	Anti-predator behaviour	Captured	%	Griffin et al., (2010)
	Passeriformes	Sturnidae	Sturnus vulgaris	Novel natural behaviour	Captured	%	Fernandez-Juricic and Kacelnik, (2004)

	Passeriformes	Sturnidae	Sturnus vulgaris	Novel food capture	Captured	%	Rafacz and Templeton, (2003)
	Passeriformes	Thraupidae	Cactospiza pallida	Tool use	Captured	%	Tebbich et al., (2001)
	Passeriformes	Turdidae	Catharus fuscescens	Patch choice	Wild	%	Kelly and Schmidt, (2017)
	Passeriformes	Turdidae	Turdus merula	Patch choice	Wild	%	Smith et al., (2001)
	Pelecaniformes	Pelecanidae	Pelecanus onocrotalus	One-step	Captive	Both	Danel et al., (2020)
	Psittaciformes	Nestoridae	Nestor notabilis	Two-sequence	Wild	Both	Gajdon et al., (2004)
	Psittaciformes	Nestoridae	Nestor notabilis	Four-sequence	Captive	Both	Huber et al., (2001)
	Psittaciformes	Psittaculidae	Melopsittacus undulatus	Two-step	Captive	%	Heyes and Saggerson, (2002)
Chondrichthyes	Carcharhiniformes	Carcharhinidae	Negaprion brevirostris	One-step	Captured	%	Guttridge et al., (2013)
	Heterodontiformes	Heterodontidae	Heterodontus portusjacksoni	Route choice	Captive	Both	Vila Pouca et al., (2020)
	Myliobatiformes	Potamotrygonidae	Potamotrygon falkneri	One-step	Captured	%	Thonhauser et al., (2013)
Mammalia	Artiodactyla	Bovidae	Bos taurus	Novel food choice	Captive	%	Jackson et al., (2010)
	Artiodactyla	Bovidae	Capra hircus	Patch choice	Captive	%	Baciadonna et al., (2013)
	Artiodactyla	Bovidae	Ovis canadensis	Migration	Wild	%	Jesmer et al., (2018)
	Artiodactyla	Suidae	Sus scrofa	Novel food choice	Captive	%	Figueroa et al., (2013)
	Artiodactyla	Suidae	Sus scrofa	Novel food choice	Captive	%	Figueroa et al., (2021)
	Artiodactyla	Suidae	Sus scrofa	Novel food choice	Captive	Both	Oostindjer et al., (2011)
	Carnivora	Herpestidae	Suricata suricatta	Novel food choice	Wild	%	Thornton, (2008)
	Carnivora	Herpestidae	Helogale parvula	Anti-predator behaviour	Wild	%	Kern et al., (2016)

	Carnivora	Hyaenidae	Crocuta crocuta	One-step	Captive	Both	Benson-Amram et al., (2014)
	Carnivora	Mustelidae	Lutrogale perspicillata , Aonyc cinereus	One-step	Captive	Both	Ladds et al., (2017)
	Chiroptera	Phyllostomidae	Carollia perspicillata	Novel food choice	Captive	%	Ratcliffe and ter Hofstede, (2005)
	Chiroptera	Phyllostomidae	Glossophaga soricina	Patch choice	Captive	%	Rose et al., (2016)
	Chiroptera	Phyllostomidae	Trachops cirrhosus	Patch choice	Captured	%	Jones et al., (2013)
	Chiroptera	Phyllostomidae	Uroderma bilobatum	Novel food choice	Captured	%	Teague O'Mara et al., (2014)
	Chiroptera	Vespertilionidae	Eptesicus fuscus	Novel food capture	Captured	%	Wright et al., (2011)
	Diprotodontia	Macropodidae	Macropus eugenii	Anti-predator behaviour	Semi-wild	%	Griffin and Evans, (2003)
	Perissodactyla	Equidae	Equus caballus	One-step	Captive	Both	Krueger et al., (2014)
	Primate	Callitrichidae	Callithrix jacchus	One-step	Captive	%	Burkart et al., (2009)
	Primate	Callitrichidae	Callithrix jacchus	One-step	Captive	%	Caldwell and Whiten, (2003)
	Primate	Callitrichidae	Callithrix jacchus	Two-sequence	Captive	%	Caldwell and Whiten, (2004)
	Primate	Callitrichidae	Callithrix jacchus	Novel food choice	Captive	%	Dell'Mour et al., (2009)
	Primate	Callitrichidae	Callithrix jacchus	Two-step	Wild	%	Gunhold et al., (2014a)
	Primate	Callitrichidae	Callithrix jacchus	Two-step	Wild	%	Gunhold et al., 2014b)
	Primate	Callitrichidae	Saguinus oedipus	Patch choice	Captive	%	Moscovice and Snowdon, (2004)
	Primate	Callitrichidae	Callithrix jacchus	Patch choice	Captive	Both	Voelkl and Huber, (2007)
	Primate	Cebidae	Cebus capucinus	Novel food manipulation	Wild	%	Barrett et al., (2017)
	Primate	Cebidae	Saimiri boliviensis	Two-step	Captive	%	Hopper et al., (2013)

	Primate	Cebidae	Saimiri sciurea	Two-step	Captive	%	Claidière et al., (2013)
	Primate	Cebidae	Sapajus apella	One-step	Captive	%	Wood and Whiten, (2017)
	Primate	Cebidae	Sapajus spp.	Tool use	Wild	%	Coelho et al., (2015)
	Primate	Cercopithecidae	Chlorocebus aethiops	Two-step	Wild	%	Botting et al., (2018)
	Primate	Cercopithecidae	Chlorocebus aethiops	Two-step, three-step	Wild	%	van de Waal and Bshary, (2011)
	Primate	Cercopithecidae	Chlorocebus aethiops	Two-step	Wild	%	van de Waal and Whiten, (2012)
	Primate	Cercopithecidae	Chlorocebus aethiops	Three-step	Captive	%	van de Waal et al., (2013)
	Primate	Cercopithecidae	Chlorocebus aethiops	Three-step	Wild	%	van de Waal et al., (2015)
	Primate	Cercopithecidae, Hominidae	Macaca fuscata, Chlorocebus aethiops, Pan troglodytes	Novel food choice	Wild, unlisted	%	Lefebvre, (1995)
	Primate	Cercopithecidae	Macaca mulatta	Patch choice	Captive	%	Monfardini et al., (2012)
	Primate	Cercopithecidae	Macaca nemestrina	Two-step	Captive	%	Custance et al., (2006)
	Primate	Hominidae	Pan paniscus	Novel food choice	Captive	%	Shorland et al., (2019)
	Primate	Hominidae	Pan troglodytes	Two-step	Captive	%	Call et al., (2005)
	Primate	Hominidae	Pan troglodytes	One-step	Captive	%	Hopper et al., (2015)
	Primate	Hominidae	Pan troglodytes	One-step	Captive	%	Hopper et al., (2011)
	Primate	Hominidae	Pan troglodytes	Two-step	Captive	%	Horner et al., (2010)
	Primate	Hominidae	Pan troglodytes	Tool use	Semi-wild	%	Marshall-Pescini and Whiten, (2008)

	Primate	Hominidae	Pan troglodytes	Matching stimuli	Captive	%	Martin et al., (2011)
	Primate	Hominidae	Pan troglodytes	Patch choice	Captive	%	Vale et al., (2014)
	Primate	Hominidae	Pan troglodytes	Two-step	Captive	%	Watson et al., (2017)
	Primate	Hominidae	Pongo pygmaeus , Pongo abelii	Two-step	Captive	Both	Dindo et al., (2011)
	Primate	Lemuridae	Lemur catta	Novel natural behaviour	Captive	%	Hosey et al., (1997)
	Primate	Lemuridae	Varecia variegata	Two-step	Captive	%	Dean et al., (2011)
	Proboscidea	Elephantidae	Loxodonta africana	Two-step	Captive	%	Greco et al., (2013)
	Rodentia	Muridae	Mus musculus	Novel food choice	Captured	%	Clipperton et al., (2008)
	Rodentia	Muridae	Rattus rattus	Novel food choice	Captive	%	Donhoffner et al., (2017)
	Rodentia	Muridae	Rattus norvegicus	Novel food choice	Captive	%	Galef, (1993)
	Rodentia	Muridae	Rattus norvegicus	Novel food choice	Captured	%	Galef et al., (1998)
	Rodentia	Muridae	Rattus norvegicus	Novel food choice	Captured	%	Galef et al., (1999)
	Rodentia	Muridae	Rattus norvegicus	Novel food choice	Captured	%	Galef and Whiskin, (2004)
	Rodentia	Muridae	Rattus norvegicus	Novel food choice	Captured	%	Galef et al., (2008)
	Rodentia	Muridae	Peromyscus maniculatus	Anti-predator behaviour	Captive	Both	Kavaliers et al., (2005)
	Rodentia	Muridae	Rattus norvegicus	Novel natural behaviour	Captive	%	Laland and Plotkin, (1990)
	Rodentia	Muridae	Rattus norvegicus	Novel food choice	Captive	%	Laland and Plotkin, (1991)
	Rodentia	Sciuridae	Cynomys ludovicianus	Anti-predator behaviour	Captured	%	Shier and Owings, (2007)
Reptilia	Squamata	Agamidae	Pogona vitticeps	Two-step	Captive	%	Kis et al., (2015)

	Squamata	Lacertidae	Podarcis sicula	Patch choice	Captured	Both	Damas-Moreira et al., (2018)
	Squamata	Scincidae	Liopholis whitii	Patch choice	Captured	Both	Munch et al., (2018)
	Squamata	Scincidae	Eulamprus quoyii	Patch choice	Captive	%	Noble et al., (2014)
	Testudines	Testudinidae	Geochelone carbonaria	Route choice	Captive	%	Wilkinson et al., (2010)

Appendix 2: Comparative Social Learning

A2.1 Cognitive research in zoos

The majority of zoos are committed to preserving animal diversity both within their collections and through endorsing and funding conservation efforts. Furthermore, zoo-based research involving animal welfare regarding cognitive enrichment is plentiful (Clark, 2017; Herrelko et al., 2012; Hopper, 2021; Jones and Pillay, 2004). However there remains significant gaps in conducting cognitive research in zoos that could benefit facilitate a mutually beneficial relationship between cognitive researchers and cognitive enrichment programs in zoos (Clark, 2022; Hopper, 2017). Studies that have attempted to bridge this gap are not equally represented across taxa or zoological collections (see McEwen et al., 2022 for review). However these studies, including touchscreen studies (see Egelkamp and Ross, 2019 for review), show inconsistencies in experimental design and data reporting that hinders comparative analyses (see chapter 2). Such analyses could shed light on cognitive and cultural evolution whilst enhancing the development of welfare practices in captive populations (Clark, 2017; Cronin et al., 2017; Hopper, 2021; Whitehouse et al., 2013). To ensure comparative analyses are informative, three major issues must first be addressed (see chapter 2 and 6 for further detail). Firstly, biases in taxonomic representation and cognitive tasks presented must be addressed. Secondly, consensus must be reached regarding the classification of social learning and culture to facilitate multidisciplinary research (Hoppitt and Laland, 2013; Kendal et al., 2018). Finally, a measure of social learning (as well as data reporting) should be standardised to facilitate cross-study analysis that aid in addressing

wider biological questions and the conservation of culture (CMS, 2024; UNEP, 2020).

A2.2 Rationale

Through standardisation of the cognitive tests presented, task performance and ethograms, as well as open and clear data reporting, I intend to demonstrate that social learning experiments can be comparable and informative. I designed and capitalised on a novel paradigm that unities implementation simplicity and conceptual sophistication to investigate the emergence and spread of solutions to increasingly difficult cognitive tasks. This paradigm stems from one key principle, that social learning occurs along spectrum, and the continuation of field-specific social learning classification serves no applicable purpose towards wider inter-disciplinary goals such as conservation.

A2.3 Ethical approval

Ethical approval for this study was granted on 19th June 2023, for the integration of all primate species within the zoological collection of the Zoological Society of London (ZSL). Ethical approval can be found using project code IOZ196.

A2.4 Methods

<u>Task design</u>

To standardise the cognitive task presented across species, all species receive the same cognitive task scaled to match the species' size. These tasks are also placed within an enclosure that best matches the enclosure use of that species

(for instance cognitive tasks presented to arboreal are mounted to vertical surfaces or suspended). All care was taken to ensure that all tasks were novel to subjects. During the control and experimental phases (outlined below), all individuals gained their first puzzle box exposure at the same time.

The tasks presented to subjects are positive reinforcement rewarded puzzle boxes (Appendix Figure A2.1). These puzzle boxes increase in task difficulty with each round of experiments, beginning with the simplest cognitive task. This incremental scale of task difficulty is implemented as our understanding of the cognitive abilities of some included species is poor, and so every effort is made in task design to maximise the likelihood that all primates within this study could solve at least the simplest puzzle box. At the current stage of the study (06/12/2024), four puzzle boxes types of increasing difficulty have been designed, with the two simplest presented to subjects (Appendix Table A2.1). All puzzle boxes are made from 9 mm plywood and painted with non-toxic paint. There were three sizes of puzzle boxes made to match species size: 15 cm x 15 cm, 20 cm x 20 cm and 30 cm x 30 cm. Each box contains a hole placed at the centre of one side that had a diameter equal to the radius of the side (e.g. the 20 cm x 20 cm box contained a hole of 10 cm diameter).

The simplest puzzle box experiment (patterned, Appendix Figure A2.1a) consists of four boxes painted in monochrome patterns (stripes, large spots, checkered and small dots). Mashed food items were smeared on the underside of the face of the puzzle box that contained the hole. This ensured that the food item was hidden from view when subjects investigated the box from above or from the side. This means that subjects could obtain the food reward by passing their hand through the hole and reaching back upwards towards the underside

of the hole side. After controls had been completed (see below), the food reward was only placed in the checkered box, meaning subjects must associate a pattern with food reward.

The second puzzle box design (substrate, Appendix Figure A2.1b) consists of the same four puzzle boxes as the simplest puzzle box. However, instead of smearing food rewards directly onto the underside of a box face, food items were hidden within substrate. This substrate was inedible (straw or leaves) and filled the box completely. Solid food items were then placed only into the striped box. This means that to access food rewards, subjects were required to place their hand through the hole and into the substrate, feeling around for solid food items. Subjects therefore must associate a pattern with a food reward. This task represents an increase in difficulty compared to the 'patterned' experiment as the identification of the lack of food rewards via personal learning was more time consuming than previous. Therefore, dedicating a large amount of time searching for food rewards in unrewarded boxes became inefficient.

The third puzzle box design (door, Appendix Figure A2.1c) consists of four unpatterned boxes (painted in a neutral colour) that have a physical restriction to box access. This restriction consists of a wooden door that can be rotated clockwise to reveal the hole in the box. The door can be rotated either with the palm of the hand or by placing a finger in a depression on the edge of the door. A spring prevented the door from rotating by gravitational force alone and allowed the door to return to a close position if not force was enacted upon it. Food was placed inside every puzzle box. This cognitive task represents an increase in difficulty as it incorporates learning a single actionable step, rather than testing foraging decisions.

The fourth puzzle box design (lock, Appendix Figure A2.1d) consists of the same four puzzle boxes as the 'door' boxes, expect a single stage lock prevents the door from opening. This lock consists of a sliding door bolt that releases the door. This task represents an increase in task difficult from the 'door' box as two actionable steps must be completed in a specific sequence.

Controls

As boxes are placed in enclosures known to subjects, subjects may have personal preferences for foraging or engaging in cognitive tasks in specific locations (Daoudi et al., 2017). To control for this, four unpatterned boxes are placed in the designated locations around the enclosure, of which all are rewarded using the 'pattern' technique described above. Within a 30-minute data collection window, the time each individual spent within arm's reach of each box at each location was recorded. Boxes are then rotated between locations (to account for an unknown box preference), meaning that the location control consisted of four 30-minute exposures. As some boxes in this study are patterned, the preference for subjects attempting cognitive tasks due to a preference for a certain pattern was addressed. Similar to the location control (and using the same reward system), boxes of each pattern are placed in the designated locations and the time each individual spent within arm's reach of each patterned box was recorded. The pattern control lasted for four 30-minute trails.

Experimental phase – inferred asocial / social comparison.

As subjects are released into the enclosure containing the puzzle boxes, the first individual to discover the solution to the puzzle box becomes the

demonstrator, with all other individuals categorised as learners. The acquisition of the task solution is then tracked through the group as an open diffusion experiment. To evidence the acquisition of social information, I quantify social learning opportunities by recording the head orientations of learners and demonstrators towards conspecifics attempting solve puzzle boxes, using two GoPros placed inside or outside of enclosures. After a 30-minute period, puzzle boxes are removed to prevent unrecorded learning between experiments. After each 30-minute experimental trial, puzzle boxes are rotated around the designated locations (see location control), meaning each puzzle box experiment is repeated four times. The first individual to discover the solution to the puzzle box remains as the demonstrator for each trial.

In addition to observations of learners and demonstrators, the proportion of observed behaviours performed successfully is also quantified. By not exclusively quantifying puzzle box solutions (gaining food rewards) and from whom individuals learn, I am able to instead quantify the impact of social learning at each stage of solving the puzzle box. There are five key steps required to solve any cognitive task: firstly, individuals must first learn where the task / reward is located. I quantify this measure by recording the proportion of time individuals spend within arm's reach of the rewarded box compared to unrewarded boxes (P = presence). Secondly, individuals must interact with / touch with box to ascertain where an action can be made. I quantify this measurement by recording the proportion of time individuals spend touching the rewarded box when within arm's reach (I = interaction). Thirdly, within all cognitive tasks, individuals must perform an action/s (such as opening a lock or performing a behaviour). I quantify these behaviours by recording the proportion

of time spent interacting with the puzzle box that is designated as a correct action (A = action). Fourthly, even if an individual performs a correct action, they may not necessarily obtain a reward (for instance if they do not notice the presence of a reward). I quantify this behaviour by measuring the proportion of actions that are rewarded (C = consequence). Finally, an individual may obtain a reward, but they may not consume or use it, perhaps due to kleptoparasitism. To measure this, I quantify the proportion of food rewards that were consumed (R = response).

Resets

If puzzle boxes solutions require subjects to associate a specific pattern with food rewards, pattern preferences are 'reset' before a different pattern association can be tested (for example between the 'pattern' and 'substrate' experiments). To reset pattern preferences, all patterned boxes are placed into enclosures at random locations and loaded with an equal quantity of food rewards in each that require no cognitive effort to attain. These boxes are placed in enclosures for eight days. On the final day, data is collected regarding the time each individual spends within arm's reach of each box. When the time spent within arm's reach of each box is not statistically different (Chi-squared), a new pattern association experiment can begin.

Figure A2.1: Standardised Cognitive Tests Within Comparative Social Learning Study

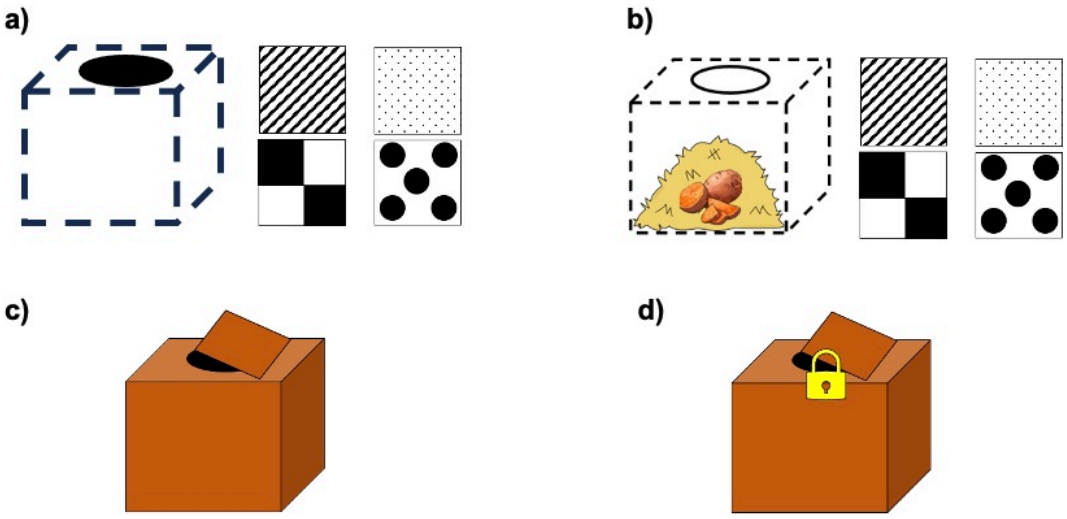


Figure A2.1: Schematics of the four puzzle box designs within the comparative social learning study. The puzzle boxes depicted are the patterned box (a), substrate (b), door (c) and lock (d).

A2.5 Intended analysis

P, I, A, C and R can be performed by any subject, but most crucially can be observed being performed by any individual. There is a clear distinction between an observer witnessing a demonstrator complete an action, obtain a reward, and then consume it (A, C and R) compared to an observer witnessing a demonstrator only interact (I) with a puzzle box. It is therefore paramount to quantify the behaviours than observers have witnessed and compare this to their behaviour following this social learning opportunity (see intended analysis for more detail). By measuring social learning in this way, social learning is placed on a spectrum as a proportion of observed behaviours performed successfully. Consequently, a learner can be described as a successful social learner if they interacted (I) with a box after observing a demonstrator only

perform this behaviour (I). This differs from typical social learning studies where the observer is characterised as not completing the task, and therefore social learning didn't take place, which would be an unfair description of the social learning opportunities available to the learner.

After summing P, I, A, C and R of demonstrators and observers, the proportion of observed behaviours performed successfully can be calculated. These data can then be analysed as a response variable with generalised linear mixed-effects models (Bates et al., 2015). To understand how heterogeneous factors (of both demonstrator and learner) impacted social learning, fixed effects of taxonomy, age, sex, rank, social network metrics, kinship and time since last task success can be included in models alongside random effects of subject identification, experiment number, weather, and disruption (such as enthusiastic members of the public).

A2.6 Preliminary results

Table A2.1: Stage of Completion for Species and Social Learning Tasks (as of 06/12/2024).

Species	**# Individuals Male: female**	**Task**	**Data coded**	**Data analysed**
Chimpanzee (WZ)	3:2	1 - Patterned	✓	✓
		2 - Substrate	✓	
Ring-tailed lemur (LZ)	8:0	1 - Patterned	✓	✓
Ring-tailed lemur (WZ)	3:4	1 - Patterned	✓	
White-naped mangabey (LZ)	2:4	1 - Patterned	✓	✓
		2 - Substrate	✓	
Western lowland gorilla (LZ	2:5	1 - Patterned	✓	✓
		2 - Substrate	✓	
Squirrel monkey (LZ)	10:0	1 - Patterned	✓	
Black and white colobus (LZ)	-	1 - Patterned		
Hanuman langur (LZ)	-	1 - Patterned		
Suluwesi crested macaque (WZ)	-	Pending		
Francois langur (WZ)	-	Pending		
Other mammals	-	In discussion		
Birds	-	In discussion		
Reptiles	-	In discussion		
Amphibians	-	In discussion		
Fish	-	In discussion		

A2.7 Collaborative framework

Table A2.2: A species-wide ethogram used to collect data during social learning experiments. These data will be used by other researchers and staff at ZSL to inform several research projects including captive management and translocation protocols.

Category	Data collected	Description
Aggressive	Physical	Hit, bite, grab, drag, throw, throw at, push
Aggressive	Chase	Run after them
Aggressive	Vocal	Shout, scream, directed
Aggressive	Gestural	Usually hand or face used, species variable eg head bobbing
Affiliative	Groom	Moving head or hands through the fur / over the skin of another, usually accompanied with feeding and reciprocation
Affiliative	Vocal	Directed vocalisations - species specific
Affiliative	Gestural	Usually hand or face used, species variable eg lip smacking or mounting
Affiliative	Share	Actively giving food, moving a viable food source to another or eating the same food source with another
Anxious	Self-groom	Groom self
Anxious	Pace	Move back and forth continuously
Anxious	Vigilance	Looking around / scanning environment / looking at individual whilst showing anxious behaviour
Anxious	Vocal	Distress
Dominance	Displace	Movement of one individual causes another individual to move out of their proximity or path
Dominance	Supplant	Movement of one individual causes another individual to move out of their proximity or path, the first individual then stands/sits in the location of the displaced individual
Dominance	Submissive gesture	Submissive gestures that are non-sexual
Neutral	Vocal	Vocal where the meaning is unclear
Other	Back turn	Eating or using puzzle box with back turned to another individual in order to conceal the food or solution from them
Other	Peering	Standing near another and staring with intent at another's actions regarding the puzzle boxes. The other individual doing the action would acknowledge the other one peering and allow them to watch.
Other	Sniff mouth	Sniffing mouth of another
Other	Lick mouth	Licking mouth of another
Other	Sniff hand	Sniffing hand of another
Other	Lick hand	Licking hand of another
Unknown	Vocal	Intentional but don’t know for what
Other	Scrounge	Taking food from another / making another drop the food (and then eating it) without themselves obtaining it from the puzzle box
Other	Scent mark	Scent mark
Other	Mounting	Mounts individual

Other	Breeding	Mating attempt
Other	Flirting	Advertising calls or gestures
Forage	Forage	Forage for food NOT in the puzzle boxes
Browse	Browse	New behaviour for foraging - preferred by SK, includes both stationary and moving browsing
Rest	Rest	Not moving - basically doing nothing, stationary but can look around
Move slow	Move slow	Walk
Move fast	Move fast	Run
Other	Tool use	Using a tool (e.g. tree branch/stick) to retrieve food reward from the box, or outside the box.
Other	Alternative enrichment	Engaging in enrichment activity provided in enclosure other than the puzzle boxes.

Appendix 3: Ethogram of behaviours with touchscreen experimental area

Table A3: An ethogram used to collect data during touchscreen studies in chapters 3 - 5.

Behaviour	**Description**
Begin / End session	The time whereby a baboon first entered the experimental area and when the last baboon left the area.
Baboon ID	The identity of the baboon either using the touchscreen or observing others.
Begin / End bout	The time whereby a baboon first began continuously touching or inspecting the touchscreen until they stopped doing so for a period of < 10 seconds.
Touch screen	When a baboon could be visibly seen touching the screen by the researcher.
Inspect screen	When a baboon was within arm's reach of the screen and looking at it or making movements towards the screen – used when it was unclear to the researcher (due to obstructed views) whether a baboon was touching the screen or not.
Shake screen	When a baboon physically attempted to or shake the cage that housed the touchscreen.
Rest	When a baboon was within arm's reach of the screen but making no attempt to interact with the screen either physically or visually.
Observe	When a baboon was within 10 m radius of the touchscreen – when a participant was engaged in touching or inspecting the screen – and their head was orientated towards the direction of the participant.
Malfunction	When the touchscreen encountered an issue such as reward blockage, low battery or was damaged.

Appendix 4: Further demographics details during touchscreen study

Table A4: A breakdown of troop demographics at the end of the touchscreen study (Chapters 3 – 5). Listed are the age and sex of individuals as well as their reproductive states. Some pregnancies were unknown at the time of the study, as pregnancy was only identified following the conclusion of the study during a period of amenorrhea and so pregnancies where the conception data is unknown are marked as pregnant (unk). Identifications used as part of the TBP are anonymised as standard practice. Infant sex is marked as unknown as this is confirmed during trapping, which did not occur during the period of this thesis and so infant sex could not be later confirmed.

Troop	ID	Age	Sex	Reproductive state	Troop	ID	Age	Sex	Reproductive state
J	1	8.11	M		L	1	6.49	M	
J	2	8.84	M		L	2	16.98	F	Pregnant (unk)
J	3	7.59	F	Lactating	L	3	1.49	M	
J	4	0.61	Unk	Dorsal infant	L	4	8.9	F	Lactating
J	5	7.78	M		L	5	0.5	Unk	Ventral infant
J	6	5.4	F	Swelling	L	6	1.83	F	Non-swelling
J	7	6.55	M		L	7	4.83	F	Non-swelling
J	8	5.91	M		L	8	9.89	M	
J	9	7.39	F	Lactating	L	9	8.11	F	Lactating
J	10	0.79	Unk	Dorsal infant	L	10	0.81	Unk	Dorsal infant
J	11	5.29	M		L	11	1.32	M	
J	12	4.47	M		L	12	4.83	F	Non-swelling
J	13	9.66	F	Pregnant (unk)	L	13	7.41	F	Lactating
J	14	6.71	F	Pregnant (unk)	L	14	0.91	Unk	Dorsal infant
J	15	16.19	F	Lactating	L	15	12.21	M	
J	16	0.03	Unk	Ventral infant	L	16	6.64	F	Lactating
J	17	1.58	M		L	17	0.7	Unk	Dorsal infant
J	18	6.96	M		L	18	4.07	F	Non-swelling

J	19	5.13	F	Non-swelling	L	19	9.16	M	
J	20	6.9	M		L	20	6.26	M	
J	21	13.88	F	Lactating	L	21	3.39	M	
J	22	0.48	Unk	Ventral infant	L	22	6.32	M	
J	23	11.6	F	Lactating	L	23	16.98	F	Lactating
J	24	1.02	Unk	Dorsal infant	L	24	0.65	NA	Dorsal infant
J	25	8.99	F	Lactating	L	25	2.01	F	Non-swelling
J	26	0.92	Unk	Dorsal infant	L	26	7.38	M	
J	27	5.14	M		L	27	1.38	F	Non-swelling
J	28	8.58	F	Lactating	L	28	5.06	M	
J	29	0.56	Unk	Ventral / Dorsal infant	L	29	4.83	M	
J	30	4.67	M		L	30	3.63	F	Non-swelling
J	31	1.71	F	Non-swelling	L	31	1.65	M	
J	32	18.59	F	Lactating	L	32	9.6	F	Lactating
J	33	0.15	Unk	Ventral infant	L	33	0.27	Unk	Ventral infant
J	34	4.31	F	Non-swelling	L	34	7.7	M	
J	35	5.93	F	Non-swelling	L	35	11.16	F	Lactating
J	36	3.79	M		L	36	0.71	Unk	Dorsal infant
J	37	5.3	F	Swelling	L	37	7.92	M	

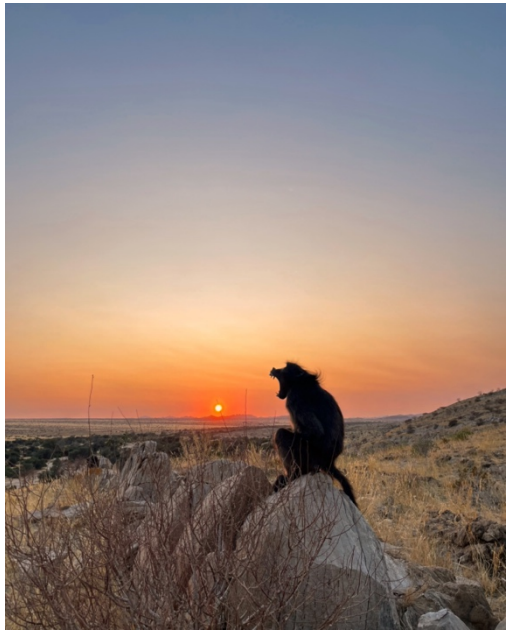
J	38	3	M		L	38	7.52	M	
J	39	10.37	M		L	39	4.75	F	Non-swelling
J	40	1.82	M		L	40	5.79	F	Swelling
J	41	18.78	F	Pregnant (unk)	L	41	6.74	F	Lactating
J	42	4.85	F	Non-swelling	L	42	0.21	Unk	Ventral infant
J	43	7.56	F	Swelling	L	43	6.9	F	Swelling
J	44	7.73	F	Non-swelling	L	44	3.24	F	Non-swelling
J	45	18.31	F	Lactating	L	45	1.81	F	Non-swelling
J	46	0.02	Unk	Ventral infant	L	46	3.41	F	Non-swelling
J	47	10.85	M		L	47	1.88	F	Non-swelling
J	48	6.96	M		L	48	3.51	M	Non-swelling
J	49	12.16	F	Lactating	L	49	6.58	M	
J	50	0	Unk	Ventral infant	L	50	5.56	M	
J	51	9.27	F	Non-swelling	L	51	6.48	F	Non-swelling (recent infanticide)
J	52	1.86	F	Non-swelling	L	52	2.12	F	Non-swelling
J	53	7.42	F	Swelling	L	53	5.45	M	
J	54	5.41	M		L	54	1.37	F	Non-swelling
J	55	4.91	M		L	55	21.71	F	Lactating
J	56	5.74	M		L	56	0.31	Unk	Ventral infant

J	57	3.46	F	Non-swelling	L	57	9.39	F	Lactating
J	58	9.18	M		L	58	0.03	Unk	Ventral infant
J	59	3.41	M		L	59	4.79	F	Lactating
J	60	7.87	F	Swelling	L	60	0.09	Unk	Ventral infant
J	61	7.79	F	Lactating	L	61	9.54	F	Pregnant (unk)
J	62	0.66	Unk	Dorsal infant	L	62	10.47	M	
J	63	1.54	F	Non-swelling	L	63	18.27	F	Lactating
J	64	4.44	F	Non-swelling	L	64	0.11	Unk	Ventral infant
					L	65	11.87	M	
					L	66	4.44	F	Non-swelling
					L	67	10.26	F	Lactating
					L	68	0	Unk	Ventral infant
					L	69	7.5	M	
					L	70	4.53	F	Non-swelling
					L	71	13.76	F	Lactating
					L	72	0.38	Unk	Ventral infant
					L	73	9.18	M	
					L	74	16.67	F	Pregnant (unk)
					L	75	8.11	F	Lactating
					L	76	0.93	Unk	Dorsal infant

					L	77	12.94	F	Pregnant (unk)
					L	78	8.11	F	Pregnant

Appendix 5: A Babbling, Bumbling Band of Baboons

Throughout my time in time in Tsaobis, I have gotten to know some interesting characterises in the baboon world. Below are some photographs of those characters that serve as an acknowledgment and remembrance of their contributions to this thesis.



Credit: Rachel Thomson



Credit: Vittoria Roatti



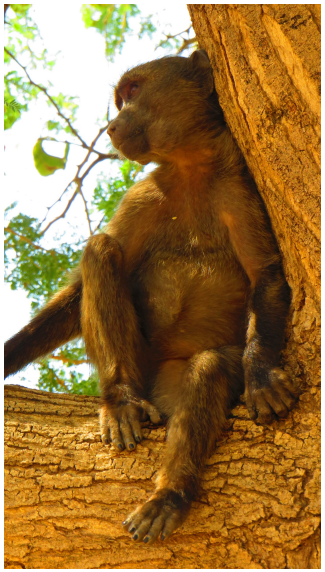
Credit: Rachel Thomson



Credit: Rachel Thomson



Credit: Rachel Thomson



Credit: Amelia Ramage