Social learning of a foraging task in great tits: Population patterns and underlying mechanisms

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Abstract

Certain bottlenose dolphin pods forage using sponges, while a subset of Japanese macaque troops wash sweet potatoes. These are just some examples of group-level patterns of behaviour that could have arisen by social learning. Understanding the scale at which social learning acts to result in such traditions can be informative of underlying mechanisms. In addition, studying how social learning can influence the occurrence and distribution of behaviour over space and time enables a better understanding of how selection acts on populations. Thus, in this thesis, I investigate the role of social learning on spatiotemporal foraging patterns and the underlying mechanisms in wild great tits (*Parus major*). To do this, I employed both field and captive experiments to examine learning at experimentally introduced foraging tasks. I found individual and spatial variation in coarse and fine-scale techniques used to solve a bidirectional control procedure task. Social learning of fine-scale solving behaviours was focused on location rather than actions, suggesting fine-scale local enhancement. I also found that social learning influences temporal behavioural patterns, with learning individuals benefiting from the improving skill levels of demonstrators. This however, was masked at a local scale by competition. Temporal changes in behaviour were influenced by potential 'habit forming', with individuals acting to increase their foraging efficiency of preferred techniques rather than adopting more efficient techniques. Finally, results from a captive open diffusion experiment using a two-action task, though inconclusive, supported fine-scale local enhancement in great tits when foraging. This thesis highlights the importance of examining the impact of social learning on behavioural patterns at different scales. It also emphasises the need to examine not only how social learning influences novel skill acquisition and the distribution of behaviour in populations, but also how it influences temporal changes in behaviours already within the repertoire of individuals.

Author Contributions

Kai L. R. Kam designed and performed the experiments, obtained the video footage for all data chapters, and analysed the data. Had independent intellectual contributions, wrote the drafts for all chapters and incorporated the comments from co-authors into the final thesis.

Ben C. Sheldon supervised, obtained funding for, and co-conceived the main project. Had intellectual contributions, offered advice on the design of experiments and analysis methods, and provided constructive comments on drafts of all chapters.

Lucy M. Aplin supervised the main project, co-conceived the main project, had intellectual contributions, and developed the puzzle-box used in Chapters 2 and 3. Contributed towards the modification of the puzzle-box and catching of birds in Chapter 4, gave advice on the design of experiments and analysis methods, and provided constructive comments on drafts of all chapters.

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CHAPTER 1

General Introduction

Chapter 1: General Introduction

1.1 Why study social learning?

All animals need to respond to changes in their environment to survive. One of the ways to do so is to alter their behaviour as a result of experience - a process also known as learning (Rescorla, 1988). Individuals can learn from direct experience, which largely operates through reinforcement (Bandura, 1971), or through the observation or interaction with another individual or its products, which is termed 'social learning' (Heyes, 1994). Social learning is important to the life history of a wide diversity of animals, particularly among vertebrates (Heyes & Galef, 1996) but also in many invertebrates (Leadbeater & Chittka, 2007). Individuals often rely in part on information from others to make decisions such as how to find food, which mate to choose, or where to settle (Galef & Giraldeau, 2001; White, 2004; Freeberg, 2000; Parejo, White & Danchin, 2007). Social learning does not just enable individuals to acquire new skills and innovations, such as red squirrels (*Tamiascurus hudsonicus*) learning to open hickory nuts after seeing conspecifics doing so (Weigl & Hanson, 1980), but is also one potential way individuals can improve existing skills. For example, Norway rats (*Rattus norvegicus*) have been found to socially learn from

conspecifics how to forage more efficiently for buried carrot pieces (Laland & Plotkin, 1990).

Social learning has been a topic of interest in a variety of fields, including economics, psychology, anthropology and behavioural ecology. Economists seek to discover how it increases efficiency and performance, psychologists are curious about cognitive mechanisms underlying social learning, while anthropologists are interested in what it might reveal about the roots of human culture and intelligence (Hoppitt & Laland, 2013). Within the field of behavioural ecology, scientists are particularly interested in the implications social learning has for the way animals acquire patterns of behaviour that help them to adapt to their environment (Heyes & Galef, 1996; Galef & Giraldeau, 2001). Learning from others is often seen as an adaptive strategy (Galef, 1995), allowing individuals to bypass the risks involved in, and time needed for, trial-and-error learning by adopting the behaviours that had been tested by others (Galef & Laland, 2005). However, social learning can also result in the spread of apparently maladaptive behaviour, as demonstrated in experiments where guppies and dogs will follow others in choosing a longer route to access food (Laland & Williams, 1998; Pongrácz et al., 2003 respectively). Indiscriminately adopting others' behaviours may lead to the acquisition of obsolete or less reliable information in a rapidly changing environment (Boyd & Richerson, 1985; Giraldeau, Valone & Templeton, 2002; Franz &

Matthews, 2010). However, the selective employment of social learning can still allow it to be adaptive, for example if individuals only copy when it is costly to use asocial learning (Laland, 2004). Thus, it is useful to study how social learning shapes behaviour, gaining a greater glimpse into its potential impacts on reproductive fitness and survival (Heyes & Galef, 1996).

1.2 The role of social learning in tradition and culture

Reports of the emergence and spread of innovations in wild animals have sparked interest within the scientific community over the past half a century, and led to research examining how social learning mediates the spread of novel behaviours through animal populations. Novel behaviours had been observed in wild populations across a wide range of taxa – from the famous milk bottle opening innovation in British tits (Fisher & Hinde, 1949) and the use of sponges as foraging tools in bottlenose dolphins (Krützen et al., 2005), to the washing of sweet potatoes in Japanese macaques (Kawai, 1965). In all cases these innovations appeared to spread within groups of individuals and were restricted to certain geographical areas or populations. This pattern could potentially be the result of multiple individuals responding independently to the same environmental factor in the same way. However many of the studies on such observed behavioural patterns have found that social learning is at least partly

responsible. For example, Lefebvre (1995) modelled the spread of the milk bottle opening in British tits, and found accelerated rates of learning, supporting a social effect on the acquisition of this behaviour. Also, Mann et al. (2012) supported the role of social learning in the spread of 'sponging' behaviour in bottlenose dolphins by analysing their social networks and finding that individuals that foraged using sponges associate more with others that also used sponges to forage.

Distinctive group behavioural patterns that are transmitted at least partially through social learning and endure across generations are termed traditions (Fragaszy & Perry, 2003). More specifically, the form of social learning most likely to result in tradition is social transmission, where there is a positive, causal influence of an individual on another's behaviour such that the latter behaves more similarly to the former (Galef, 1988; Lonsdorf & Bonnie, 2010), as opposed to social inhibition, where individuals learn not to perform the same action as others upon seeing an aversive result (Hoppitt & Laland, 2013). I also consider tradition interchangeable with the term 'culture' (Hoppitt & Laland, 2013), even though there is on-going debate on what truly constitutes culture (Laland & Janik, 2006). Definitional and conceptual disagreements over what types of social learning may lead to culture have contributed towards the conflict in the literature over whether animals have culture, and if so, which taxa have culture (Byrne et al., 2004; Laland & Hoppitt, 2003). The use of a relatively broader

definition of culture, such as that employed in this thesis, may mislead some to believe that animal and human cultures are the same, when they may in fact have different underlying mechanisms (Galef, 1992). However, a broad definition is more operational, allowing the use of empirical data to investigate the presence of culture in animals and for comparisons between taxa (Laland & Hoppitt, 2003; Ramsey, 2013).

One of the motivations behind the study of animal traditions has been to investigate the roots of human culture (Perry, 2011). This has resulted in a general research focus on primates. However, social learning has been recorded in a wide range of taxa (Brown & Laland, 2003; Coolen, Dangles & Casas, 2005), as have potential cases of traditions (e.g. in cetaceans, Cantor & Whitehead, 2013; and in birds, Hunt & Gray, 2003). While studying the role of social learning and traditions in other taxa may not reveal as much about the evolutionary origins of human culture, it is still valuable in other aspects. It is helpful for understanding how differences between groups develop, and also increases our understanding of population-level consequences of social learning, which has ecological and evolutionary implications (Fragaszy & Perry, 2003; Richerson & Boyd, 2005). For example, the effect of social learning on population patterns of behaviour is informative of the types of selective pressure that shapes behaviour – not just the ecological environment but also through social influences (Laland, 2008). In addition, by moulding behavioural patterns, social learning can

modify the local environment and so alter the evolutionary processes affecting populations, a phenomenon known as 'niche construction' (Odling-Smee, Laland & Feldman, 1996).

Whiten (2009) summarised three main ways to study animal traditions: (i) by quantifying traditional behaviours, (ii) understanding variation in these behaviours across space and time, and (iii) understanding the mechanisms underlying the formation of traditions. However the first two questions can be examined at different scales, potentially changing the results. For example in keas (*Nestor notabilis*), the coarse-scale behaviour of opening a box to receive a food reward was learnt by observing conspecifics, but not the exact fine-scale method of opening (Huber, Rechberger & Taborsky, 2001). Studying behaviour at the coarser scale may lead to overgeneralisation, while studying behaviour at a fine scale, despite its greater resolution, risks introducing greater noise and measurement error (Wiens, 1989; Levin, 1992). Thus, to study behaviour in a biologically meaningful way, it is important to ensure that the behaviour is quantified at a scale where the behaviour is repeatable within individuals, as selection can only act on repeatable traits (Boake, 1989). While selection could potentially also act on plastic traits, there has to be a limit to the plasticity of a trait such that individuals remain consistently different across space and time.

After identifying socially learnt behaviours that might also be traditional, it is important to observe how these behaviours vary spatiotemporally, and to consider the potential underlying causes for these patterns. A common method employed to do this is the ethnographic approach, where researchers attempt to isolate the contribution of genetics, environmental conditions and social learning to between-group behavioural variation (Whiten et al., 1999). However, it is difficult to completely separate the contribution of these three potentially interacting sources of behavioural variation, and thus recently non-exclusive methods have been introduced to complement this approach. This includes the partitioning of behavioural variation based on the relative contribution of genetic, ecological and social factors (Laland & Janik, 2006), and inferring social learning by the use of social network analysis (Franz & Nunn, 2009).

1.3 Social learning mechanisms

It is important to understand the way in which social learning influences behaviour not just at the functional or population level, but also at the mechanistic level. Mechanisms underlying social learning can provide insights to the type of information that individuals obtain from their environment (Webster & Laland, 2013). Furthermore, those interested in studying the roots of human culture need to understand the degree of homology between the mechanisms underlying humans and non-humans cultures

(Galef, 1992). Comparing the underlying mechanisms with that of humans could also shed light on the limits to cumulative and complex culture in animals (Boyd & Richerson, 1996), and on the stability of traditions (Tomasello, 1994; Schnoell, Dittmann & Fichtel, 2014). In particular, some have argued that imitation is required for culture (Galef, 1992), while others have shown that other forms of social learning, such as local and stimulus enhancement, can result in the formation of traditions (Slagsvold & Wiebe, 2011; Heyes, 1993); note however, this is often a result of definitional differences in the term "culture" used, as discussed previously (Laland & Galef, 2009).

Despite multiple reviews attempting to classify them, there is, to date, no agreed set of terminology for social learning mechanisms (Heyes, 1994; Zentall, 2001; Hoppitt & Laland, 2008; Hoppitt & Laland, 2013). There is often overlap between social learning categories, possibly because underlying mechanisms can work in parallel or conjunction (Hoppitt et al., 2012), and so experiments often can not firmly identify the operation of one mechanism and rule out others completely (Hoppitt & Laland, 2013). Thus, in this thesis, I choose to only focus on the most commonly examined categories of mechanisms, rather than to exhaustively consider all possible mechanisms suggested in the literature. The six social learning mechanisms examined in this thesis are: local enhancement (Thorpe, 1963), stimulus enhancement (Spence, 1937; Heyes, 1994), social facilitation (Zajonc, 1965), imitation (Zentall, 2006; Heyes, 2001), emulation

(Tomasello, 1990), and response facilitation (Byrne, 1994). The definitions are summarised in Table 1.1. Although this parsimonious approach means that there may be some mechanisms that might be missed out, it enables me to contribute a piece of work that could be compared to the majority of existing studies on social learning mechanisms in a diverse range of taxa. Furthermore, due to the aforementioned overlapping of terms and possibility of combinations of mechanisms, not every single mechanism needs to be examined (or even can be experimentally deduced) to infer its operation.

Table 1.1 Social learning mechanisms considered in this thesis

Social learning mechanism	Definition	Reference(s)
Local enhancement	Observing another individual at a location or interacting with objects at that location causes an attraction towards that specific location.	Thorpe (1963)
Stimulus enhancement	Observing another individual interacting with a stimulus causes an individual to change its behaviour towards the same type of stimulus	Spence (1937) & Heyes (1994)
Social facilitation	An individual changes its behaviour as a result of the presence of others	Zajonc (1965)
Imitation	After observing another individual perform a novel action, or an action in a specific context, an individual mimics the action	Zentall (2006) & Heyes (2001)
Emulation	An individual behaves in a way to achieve the same effect or goal that it has seen another individual accomplish	Tomasello (1990)
Response facilitation	An individual becomes more likely, only in the short term, to perform the same action that it observed another individual performing	Byrne (1994)

Of all the mechanisms considered in this thesis, imitation has had the least consensus in the literature regarding its definition. Byrne (2002) proposed three potential reasons for this: there is disagreement on (i) whether imitation needs to include intentionality (Zentall, 1996), (ii) how exact imitative copying must be (Nehaniv & Dautenhahn, 2002), and (iii) whether the behaviour that is copied needs to be completely novel. I agree with Hoppitt & Laland (2013) that a definition of imitation that can be verifiable through experimentation is more useful, and thus intentionality should not be an essential part of imitation. The second point is a question of the scale of behaviour, which has been discussed earlier in this chapter – imitation should be the copying of a behaviour quantified at a biologically meaningful scale. Finally, in a bid to address the last point, Byrne (2002) split imitation into production imitation, where a novel act is copied, and contextual imitation, where an existing action is applied in a new context. I chose to use a single definition of imitation based on Zentall (2006) and Heyes (2001), but incorporating both aspects mentioned by Byrne (2002), as in practice, it is difficult distinguish between the two. Thus, I defined imitation as instances where an individual mimics a novel action, or an action in a specific context, that it has observed another individual perform.

Response facilitation, where individuals are more likely to perform the action they see others performing, can be a simpler explanation for instances of apparent

imitation (Byrne, 1994; Byrne, 1999). A key difference between the two, however, is that response facilitation is short-lived and not context-specific (Hoppitt & Laland, 2013). Emulation is another mechanism by which animals can learn by direct observation (also known as observational learning), either by observing others' actions or the products of those actions. Unlike imitation, individuals emulate the same end product as that which they had observed others attain, without necessarily copying the exact action (Tomasello, 1990). Finally, local and stimulus enhancement are similar but distinct mechanisms (Webster & Laland, 2013; Arbilly & Laland, 2014), where individuals are attracted to a specific location or particular stimulus respectively, by other individuals or their products (see Table 1.1 for full definitions). Together with social facilitation, where the mere presence of others influences an individual's behaviour (Zajonc, 1965), these are considered indirect social learning mechanisms, as individuals learn by using trial-and-error after the initial social influence.

Distinguishing between social learning mechanisms is often not straightforward, and multiple mechanisms may be involved in a single learning event. Nonetheless, there have been several attempts to design experiments that can do so, particularly concerning imitation, a mechanism thought of as mainly confined to humans (Tomasello, 1999). One of the most frequently used and successful methods used to identify imitation is the two-action method first developed by Dawson & Foss (1965). In

this approach, animal subjects are given a task that can be solved in two alternative ways, with both alternatives gaining an identical reward. In the classical two-action method, these alternatives were different motor actions used to contact the same manipulandum, thus controlling for emulation, local and stimulus enhancement. If the subjects are significantly more likely to solve the task using the solution they had observed others perform, imitation is assumed to be the underlying mechanism. However, this method has been criticised for potential differences in the inherent preferences for certain types of actions that could bias the results (Hopper et al., 2007).

More recently, a bidirectional procedure was developed by Heyes & Dawson (1990), where the two solutions to the task were performed using the same action but projected in different directions, allowing for response symmetry. This method, too, has its limitations, as it cannot rule out fine-scale enhancement when the different solutions have different points of contact. There are two ways to overcome the limitations of these established methods. First, the two methods could be combined such that each method could resolve the issues of the other in uncovering the underlying social learning mechanism at work. Second, the solving actions of a subject could be compared to that of its demonstrator at a finer resolution, such as in a study on marmosets (*Callithrix jacchus*) that used video analysis to examine the precise motor actions used by individuals' when opening a twist-lid container (Voelkl & Huber, 2007).

1.4 Field versus laboratory approaches

The first studies of social learning were based on observations of animal behaviour in the wild, such as for spatial variation in chaffinch (*Fringilla coelebs*) song (Marler, 1952). These group or spatial variations in patterns of behaviour are suggestive, but it is difficult to infer conclusively that there is a contribution of social learning to the development of the patterns just through observation alone (Galef, 2004). Furthermore, field observations in isolation are unable to tease apart the cognitive mechanisms of social learning, as they cannot control each individual's learning experience (Hoppitt et al., 2012).

In contrast to field observations, captive experiments have allowed researchers to discern a capacity for social learning in a wide range of taxa, including in fish, reptiles, and insects (Brown & Laland, 2003; Noble, Byrne & Whiting, 2014; Kis, Huber & Wilkinson, 2015; Leadbeater & Chittka, 2007). Such experiments can also inform wild studies - traditions can be deduced with greater confidence when the behaviours observed in free-living populations were also shown to be socially transmittable between individuals in the laboratory (Sherry & Galef, 1984; Sherry & Galef, 1990; Terkel, 1996). In addition, the use of clever experimental designs has elucidated social learning mechanisms by controlling for certain mechanisms in order to identify the presence of others, such as in the two-action method described previously. However,

laboratory approaches are also limited, as they are performed in artificial conditions, which decrease the ecological relevance of the results. One way to increase the ecological validity of captive studies without forgoing too much experimental control is through the use of open diffusion captive experiments (Whiten & Mesoudi, 2008; Kendal, Galef & van Schaik, 2010). In these experiments, a trained demonstrator is used to introduce a novel behaviour into a group of naïve individuals, and the diffusion of information is subsequently tracked. This provides a more naturalistic setting compared to the traditional dyadic designs, as the spread of social learning in wild populations occurs at the group level (Whiten & Mesoudi, 2008), yet provides control over the demonstrations and group composition. Nonetheless, as this is still a captive approach, it alone cannot prove that the same mechanisms are at work in free-living populations (Kendal, Galef & van Schaik, 2010). In free-living populations, the animal's behaviour may be shaped primarily by personal information instead (Kendal et al., 2005). For example in keas, social learning was demonstrated in captivity but not in the field (Gajdon, Fijn & Huber, 2004).

Neither field observations nor laboratory approaches alone are sufficient for us to confidently demonstrate the presence of social learning, its underlying mechanisms, and its consequences for group behaviours in free-living populations. Recently, researchers have turned to the use of field experiments in an attempt to overcome this

problem, by performing experiments on animal populations in the wild (reviewed in Reader & Biro, 2010; Kendal, Galef & van Schaik, 2010). This has the advantage of (at least some of) the rigour of laboratory approaches, yet is carried out in natural settings, enabling more thorough investigation of the ecology and evolution of social learning (Galef, 2004). Combined with recent advances in statistical techniques, these methods have enabled social learning to be identified in the wild in over 20 species (Reader & Biro, 2010), although only a handful have used them to investigate the underlying social learning mechanisms to date (e.g. Schnoell, Dittmann & Fichtel, 2014; Hoppitt et al., 2012). Identifying social learning mechanisms in the wild remains a challenge, often requiring a higher degree of experimental control than field experiments could offer (Kendal, Galef and van Schaik, 2010). Thus, a better approach would be to supplement field experiments with captive studies (e.g. Raine & Chittka, 2008; Morand-Ferron et al., 2015), and draw conclusions based on a consideration of the results from both.

1.5 Great tits (*Parus major*): a model species for studying social learning

Great tits (*Parus major*) form loose fission-fusion flocks in the winter (Aplin et al., 2012), are innovative (Cole, Cram & Quinn, 2011), and forage opportunistically (Aplin et al., 2015). These are traits often associated with social learning of foraging

behaviours (Lachlan, Crooks & Laland, 1998; Reader, 2003; Lefebvre & Palameta, 1988). In fact, a long history of studies have shown that great tits use social information in a variety of contexts, not just in the development of foraging behavior (Slagsvold & Wiebe, 2011), but also in song learning (Johannessen, Slagsvold & Hansen, 2006; Fayet et al., 2014) and when making decisions about habitat settlement and breeding sites (Seppänen et al., 2007; Forsman et al., 2008; Parejo, White & Danchin, 2007). Furthermore, observational and experimental evidence suggests that innovations can spread to form foraging traditions in this species, for example in the famous 'milk bottle innovation', when a novel behaviour (prising open foil-capped milk bottles to access cream) spread across Britain and persisted over almost two decades (Fisher & Hinde, 1949; Aplin, Sheldon & Morand-Ferron, 2013). Thus, great tits are an excellent model species to investigate social learning and traditions, particularly in terms of foraging.

A recent study has experimentally induced persistent foraging traditions in free-living great tits, where conformist social learning was found to be a main contributing factor to the establishment and persistence of group behaviours (Aplin et al., 2015). Conformity is defined as the preferential adoption of the most frequently performed behavioural variant (Boyd & Richerson, 1985), and has previously been shown in wild vervet monkeys (van de Waal, Borgeaud & Whiten, 2013). The study by Aplin et al. (2015) was significant as it was the first time conformity has been empirically

demonstrated in wild non-primates. The study employed a bidirectional task, where birds solved a puzzle-box by sliding a door either left or right to obtain a mealworm reward. However this method is limited, as it cannot distinguish the social learning mechanisms responsible for the conformist bias (as discussed previously in this chapter). Therefore, in this thesis, I aim to use several alternative and complementary approaches to elucidate the likely social learning mechanisms underlying the population-level patterns observed in this study.

1.6 Study system

This thesis builds on the study by Aplin et al. (2015), and furthers our current understanding of the social learning of foraging behaviours in great tits. It consists both of field and captive experiments, so as to combine the ecological validity gained from wild observations with results from more rigorous captive work. All of the work has been reviewed by the Department of Zoology ethical committee, University of Oxford, and all captive work was done under Natural England licenses 20123075 and 20131205.

The field experiment is based on the same study system as Aplin et al. (2015). It was performed on the long-term study population of great tits in Wytham Woods, Oxfordshire (51˚46'N, 1˚20'W), a predominantly broadleaf deciduous woodland 385ha

in size. Approximately 90% of the great tit population had been previously caught, due to annual mist-netting efforts in winter and the trapping of birds in nest-boxes during the breeding season (Aplin et al., 2013). Once caught, individuals are each fitted with a British Trust for Ornithology metal leg ring and a plastic leg band attached to a passive integrated transponder (PIT) tag (IB Technology), enabling their unique identification. They are also aged as birds in their first year or adults (second-year or older), and are sexed according to plumage characteristics (Svensson, 1994).

1.7 Thesis aims and overview

In this thesis, I aim to investigate the role of social learning in the development of spatiotemporal foraging patterns in free-living great tits, and to elucidate the underlying social learning mechanisms involved. This thesis contains three data chapters:

In Chapter 2, I provide a detailed investigation of the social learning processes behind the patterns observed in Aplin et al. (2015). I explore: (i) the scale at which social learning operates, (ii) spatial and social variation in the acquired foraging behaviours, and (iii) the underlying social learning mechanisms. I do so by quantifying the range of individual behaviours involved with performing the artificially introduced foraging techniques – not just the side of door contact as examined in Aplin et al. (2015),

but also the fine-scale body movements when solving the foraging task. To infer the relative role of social learning in these foraging behaviours, I couple an ethnographic method with two complementary methods: modelling the immediate effect of personal and social information on individuals' decision-making, and social network analysis to investigate potential social assortment in the expressed behaviours. For the first time, I aim to gain insights into social learning mechanisms in the wild by examining fine-scale body movements, a method only used previously in captivity (Voelkl & Huber, 2007). Depending on what type and scale of behaviour where social learning is identified, it will suggest particular candidate learning mechanisms; for example if social learning were found to occur for body movements, it would be suggestive of potential imitation.

In Chapter 3, I look at the relationship between social learning and foraging efficiency in two main ways. First, I investigate how social learning influences foraging efficiency. Often, social learning has been focused on the acquisition of skills, even though it can influence fitness through its impact on skill improvement (Raine & Chittka, 2008; Dukas, 2008). Thus, this chapter aims to fill this gap in the literature by examining the relative role of personal and social information on both initial foraging efficiency at a new task, and the change in efficiency over time. Second, I expand on the results in Chapter 2 by investigating whether the observed population patterns in behaviour are explained by the relative efficiency of different foraging techniques

instead of social learning. Doing so provides a clearer picture of the role of social learning (as opposed to other factors) in influencing the range of behaviours associated with the observed foraging tradition.

In Chapter 4, I investigate the underlying social learning mechanisms using a captive open-diffusion experiment with a two-action task. The two-action task complements the bidirectional control procedure in the field study by additionally controlling for fine-scale local enhancement, as the point of contact on the manipulandum is the same for both actions. Thus, this chapter complements that of Chapter 2, which provided initial insights into the possible underlying social learning mechanisms. Being a captive experiment, yet still maintaining some ecological validity by using an open-diffusion design, this approach provides a greater experimental control than that in Chapter 2. It thus has more power to better elucidate the social learning mechanisms involved in acquiring the behaviour (Kendal, Galef & van Schaik, 2010).

Finally, I conclude the thesis with a General Discussion chapter (Chapter 5). In this chapter, I bring together the results of my data chapters and discuss how they collaboratively address the aims of this thesis. I then extend the results of the data chapters by exploring how my work informs the potential pathways for future research.

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CHAPTER 2

Individual and spatial variation in experimentally induced foraging techniques in a wild bird population

Chapter 2: Individual and spatial variation in experimentally induced foraging techniques in a wild bird population

Abstract

The social transmission of information can lead to the formation of persistent behavioural patterns within populations, resulting in traditions. Understanding this process can help us understand the link between cultural behaviour and the ecology and evolution of species. In this paper, I examine how social learning influences behavioural patterns of a free-living great tit population, in the solving of an experimentally introduced foraging task involving a bidirectional control procedure. I found that individual variation, spatial variation and the use of social information all inform decision-making processes, not just in the direction of solving, but in the fine-scale body movements used when doing so. However, social network assortment by behaviour occurred only for the side preference and contact position of the manipulandum, suggesting that social learning when foraging mainly involves location-based rather than action-based cues. This paper thus highlights the importance for social learning studies to examine behavioural patterns at different scales, as this can potentially be informative of underlying social learning mechanisms and the way animals make use of information from their environment.

Keywords: animal traditions, bidirectional control procedure, culture, great tits, social learning.

2.1 Introduction

In humans, differences in behaviour between groups are oft-noted phenomena, with cultural diversity in languages, customs and practices across societies. Similarly in animals, certain behaviours– such as sponging behavior in bottlenose dolphins or sweet potato-washing behavior in Japanese macaques — are seen in only a subset of pods or troops (Krützen et al., 2005; Hirata, Watanabe & Kawai, 2001). This observed within-group similarity and between-group differences in behavioural repertoire has sparked much interest in the possibility of animal 'cultures', although this has been a matter of great contention, in part due to disagreements over what constitutes culture (Laland & Janik, 2006; Laland & Galef, 2009). Between-group differences and within-group similarity in behaviour can be due to any combination of genetic, ecological and social factors (Whitehead, 2009). However, for such shared behaviours to be a tradition or culture, they must be at least partly acquired by social learning (Ramsey, 2013). Social learning, where an individual learns by observing another individual or the products of its behaviour (Hoppitt & Laland, 2013), can be a potentially important component of behavioural ecology (Laland, 2008, but see van Schaik, 2010). For example, using social learning can enable animals to be more efficient in foraging (Galef & Giraldeau, 2001), and aid in mate selection (White, 2004). Studying social learning outcomes, such as traditions and cultures, can thus enable a better understanding of the influence of these processes on evolution and ecology (Fragaszy & Perry, 2003; Richerson & Boyd, 2005; Whiten, 2009).

In this paper, I use the most common definition for 'tradition' – a characteristic pattern of behavior common to a social group of individuals that endures across generations, having been transmitted at least partially through social learning (Fragaszy & Perry, 2003), and consider the term interchangeable with 'culture' (Hoppitt & Laland, 2013). There are various dimensions to the study of tradition, including investigating underlying transmission mechanisms, cultural content, and spatiotemporal behavioural patterns (Whiten, 2009). The starting point for all these is most often to identify behavioural variation across relatively isolated groups (McGrew, 2003; Leca, Gunst & Huffman, 2007), before investigating the reason behind the variation. This could be social learning, but could equally be genetic differences, environmental conditions, or a combination of all three (Laland & Janik, 2006). While it is important to quantify between-group behaviours in the study of tradition, doing so without considering within-individual consistency of the behaviours studied would confound its interpretation. Behaviours that are not repeatable within individuals may not be single traits, resulting in greater error when they are examined at the between-individual or group level (Hayes & Jenkins, 1997). Furthermore, individual variation is important when considering the adaptive and evolutionary consequences of social learning and traditions, as selection can only act upon behavioural traits that are repeatable (Boake, 1989).

A standard way to take into account both between and within-individual variation is by measuring the intra-class correlation coefficient (ICC), often called 'repeatability' (Dingemanse & Dochtermann, 2013). The repeatability of a behaviour is a measure of how consistently individuals behave over time when the behaviour varies across individuals (Bell, Hankison & Laskowski, 2009).

Hence, knowledge of repeatability enables a better appreciation as to how behavioural differences can arise or be sustained across time (Dingemanse et al., 2002). Such behavioural variation can be quantified across multiple scales, for example from the general behaviour 'lid opening', to exact motor actions employed when opening lids. However, few studies have examined fine-scale behavioural variation, even though these can be potentially informative of the underlying mechanisms (e.g. Voelkl & Huber, 2007). It is important for us to examine the mechanisms underlying social learning, as it can better allow us to understand how traditions and culture develop (Franz & Matthews, 2010) and the specific cues that are brought to an individual's attention as a result of other individuals' actions or products of those actions, which is informative of where selection may act to shape the acquisition socially-learnt behaviours. Studying fine-scale behavioural variation can thus potentially be useful in overcoming some of the limitations of field observations, where an investigation of mechanisms has often been difficult (Heyes, 1993; van de Waal & Bshary, 2011). Indeed, only a handful of studies have examined social learning mechanisms in the wild, even though it is essential in placing our understanding in appropriate ecological and social contexts (Sargeant & Mann, 2009). Examining behavioural variation at finer scales may not allow us to fully deduce the underlying mechanisms, but it can give us useful insights. For example, many of the studies in the wild have used Dawson & Foss' (1965) bidirectional control procedure (e.g. Schnoell, Dittmann & Fichtel, 2014), but this procedure is unable to rule out fine-scale local enhancement, as the specific area of contact is not the same for both sides of the apparatus (Hoppitt & Laland, 2013).

If within- and between-individual variation has been quantified and significant differences in behaviour found between groups, we can then attempt to identify whether these differences can be described as traditions (McGrew, 2003; Leca, Gunst & Huffman, 2007). This can be done by examining the role of social learning in the formation of those behavioural differences (Whiten, 2009) relative to genetic and ecological factors (Laland & Janik, 2006; Thornton & Clutton-Brock, 2011). Previously, studies have often attempted to find cases where potential genetic or ecological explanations can be minimised or excluded, in order to conclude that differences between groups are due to within-group cultural transmission (Whiten et al., 1999). However it is difficult to completely exclude genetic or ecological factors (Laland & Janik, 2006). It would thus be useful to employ complementary methods - one of which is to examine the relative influence of others' behaviour on an individual's behavioural decision. If an individual bases its choice of behaviour at least in part on others' behaviour, this would support a case for cultural transmission and consolidation. Another method is to investigate whether there is behavioural assortment within social networks. With social learning, individuals should be more likely to be socially connected to other individuals using similar behaviours. However, it should be noted that part of behavioural assortment could be a reflection of ecological assortment, and this needs to be controlled for when using this method.

Great tits (*Parus major*) form loose fission-fusion flocks in the winter, are innovative and forage opportunistically (Aplin et al., 2015). A long history of studies have shown that great tits use social information in a variety of contexts, from when foraging (Slagsvold & Wiebe, 2011) and in song (Fayet et al., 2014), to when making decisions about habitat settlement and breeding sites (Seppänen et

al., 2007; Forsman et al., 2008; Parejo, White & Danchin, 2007). Further, observational and experimental evidence suggests that novel innovations can spread to form traditions in parids, for example in the famous 'milk bottle innovation', when a novel behaviour, the prising open of foil capped milk bottles, spread across Britain and persisted over almost two decades (Fisher & Hinde, 1949; Aplin, Sheldon & Morand-Ferron, 2013).

This paper builds on a previous study by Aplin et al. (2015), which investigated artificial foraging traditions in free-living great tits. In the winters of 2012-13 and 2013-14, 24 automated puzzle-boxes containing live mealworms were introduced into 8 replicated subpopulations in Wytham Woods, Oxfordshire (Aplin et al., 2015). These puzzle-boxes had a bidirectional door and could be accessed using either of two equally difficult and rewarding solutions – either by sliding the door left or right to reveal a mealworm reward. Puzzle-boxes reset after each solve and an incorporated radio-frequency identification (RFID) antennae registered the identity of visiting birds that wore passive integrated transponder (PIT)-tags. Two individuals in each of 5 subpopulations were taught to solve the puzzle-boxes to obtain the food reward, and the solving behaviour spread rapidly throughout these subpopulations. Both knowledge about the puzzle-box, and use of the arbitrary solution seeded by each demonstrator, persisted over 2 years, suggesting that the behaviour was retained as a tradition (Aplin et al., 2015). That study was designed to examine group differences in the direction of solving (sliding the door left or right; a two-option paradigm) after the introduction of a demonstrator trained in one of the two solving options. Any finer-scale behaviours when at the puzzle-box were not quantified or controlled, but were free to vary within or across subpopulations.

This present study focuses on quantifying any fine-scale differences within this experimentally induced foraging behaviour across 4 subpopulations, and examines the implications of potential differences on our understanding of the possible social learning mechanisms underlying this foraging tradition. Using a mix of automated tracking puzzle-boxes and video footage of attempts to solve the puzzle-boxes, I scored individual solving attempts according to 7 fine-scale solving technique measures which characterised the behaviour. I summarised the measures into two specific dimensions: the side preference and fine-scale body movements used when solving. I then calculated the repeatability of those two dimensions, and quantified behavioural variation at different spatial scales – individual, site and subpopulation levels.

2.2 Methods

2.2.1 Study System

This study was conducted within a long-term study population of great tits at Wytham Woods, Oxfordshire (51˚46'N, 1˚20'W), which is a largely deciduous woodland spanning 385ha. The majority of individuals in this population had been caught previously, either by the use of mist-nets in the winter to catch immigrants, or in nest-boxes during the breeding season (Aplin et al., 2013). They were fitted with British Trust for Ornithology (BTO) metal leg rings and plastic rings with unique passive integrated transponder (PIT) tags upon capture, which enabled the identification of each individual (Firth & Sheldon, 2015). Individuals were aged according to differences in the primary coverts between first-years and adults (second year or older), and were sexed either according to their plumage characteristics or by the presence of a brood patch (Svensson, 1994). This work was reviewed by the Department of Zoology ethical committee, University of Oxford, and was conducted under relevant licenses from the British Trust for Ornithology and Natural England.

2.2.2 Data Collection

I collected data from 12 sites over 4 subpopulations – Great Wood (GW: sites 2B, 2C, 2D), Common Piece (CP: sites 1B, 1C, 1D), Brogden's Belt (BB: sites 1G, 1H, 3E) and Marley Plantation (MP: sites 7F, 7G, 7H), between 24th November 2014 and 9th January 2015. The sites within each subpopulation were located approximately 250m apart (Figure 2.1) and each had a puzzle-box (see below)

installed for the entire 4-week duration. These 12 sites had also been exposed to the puzzle-boxes in the previous one (BB and MP) or two (GW and CP) winters (Aplin et al., 2015). The BB and CP subpopulations had originally been seeded with the solving technique of sliding the door right on the blue side, while the GW and MP subpopulations had been seeded with the solving technique of sliding the door left on the red side. At the end of the last experimental period in the winter of 2013-14 (a snapshot of the last 5 days of puzzle-box exposure), the solution used in the majority of attempts by great tits at each subpopulation followed that of the original demonstrators (Table 2.1). Subpopulations were isolated from each other to variable degrees, from MP (completely isolated) to CP and BB (where 22.7% of the combined number of individuals were shared; Table 2.2). Given the previous exposure, I expected that approximately 40% of each subpopulation would already be knowledgeable about how to access the puzzle-boxes, by calculating the percentage of PIT tags belonging to individuals that had solved in previous years (Aplin et al., 2015).

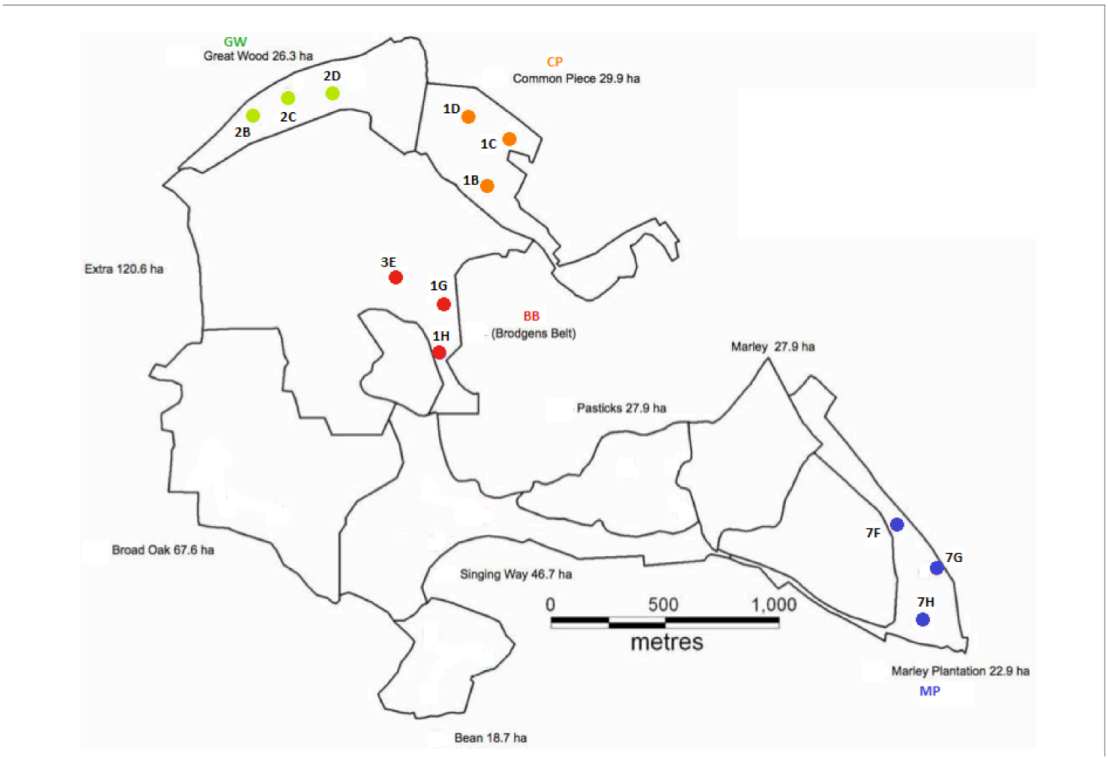

Figure 2.1 Map of Wytham Woods, Oxford, with the location of puzzle-boxes (sites) demarcated by circles that are colour-coded according to subpopulations: Great Wood (green), Common Piece (orange), Brogden's Belt (red) and Marley Plantation (blue).

Table 2.1 Percentage of each subpopulation solving the puzzle-box task by sliding the door on the blue (left) or red (right) side, in the last 5 days of exposure to the puzzle-box in the winter of 2013-14.

Sub-population	**Percentage of attempts solved using blue/red side (%)**	
	Blue	Red
Brogden's Belt (BB)	99.8	0.2
Common Piece (CP)	94.8	5.2
Great Wood (GW)	0	100
Marley Plantation (MP)	3.7	96.3

Table 2.2 The number of ringed individual great tits shared between pairwise (a) sites (1G to 7H) and (b) areas (BB to MP), with numbers in the diagonal (in bold) representing the total number of ringed individuals known to have been present at the puzzle-box within each site or area. Shared ringed individuals are individuals whose presence was recorded by puzzle-boxes in both sites and areas over the course of 20 days, within the period of 24th November 2014 and 9th January 2015.

(a)

		BB			**CP**			**GW**			**MP**		
		1G	1H	3E	1B	1C	1D	2B	2C	2D	7F	7G	7H
BB	1G	**107**											
	1H	93	**156**										
	3E	35	36	**46**									
CP	1B	31	38	7	**84**								
	1C	13	21	1	32	**68**							
	1D	7	14	3	11	29	**49**						
GW	2B	4	8	0	0	3	3	**54**					
	2C	7	14	2	1	5	6	33	**72**				
	2D	16	18	4	2	4	7	14	31	**53**			
MP	7F	0	0	0	0	0	0	0	0	0	**44**		
	7G	0	0	0	0	0	0	0	0	0	30	**54**	
	7H	0	0	0	0	0	0	0	0	0	14	33	**53**

(b)

	BB	**CP**	**GW**	**MP**
BB	**176**			
CP	58	**137**		
GW	28	11	**115**	
MP	0	0	0	**87**

Puzzle-boxes consisted of a white plastic box with a bidirectional sliding door (coloured blue on the left and red on the right) in front of an opening that allowed access to live mealworms. A perch attached to the box contained PIT tag-reading RFID antennae. This was linked to an internal printed circuit board within the box, connected to a 12V battery. For each visit, it recorded: the duration (arrival and departure timings of PIT-tagged individuals), success of a solving event (whether the door was slid), and the side to which the door was slid (blue or red side). The door reset a second after the solving bird stopped being detected at the antennae perch. Puzzle-boxes were swapped randomly between different sites each week to reduce any potential equipment bias. To prevent entry by larger, non-target species, the box was enclosed by a 1 x $1m^2$ cage with a 5 x 5 cm^2 mesh, which only allowed small birds to enter. There was also an openly accessible peanut feeder located within the cage. Peanut granules are a much less preferred food resource to mealworms (Aplin et al., 2015), but this feeder served to attract flocks to the location.

A single puzzle-box was placed at each of the sites two days before the filming began in order to allow for enough time for the discovery of the food patch. Filming was done between 10am and 2pm, within the period of greatest foraging activity in mid-winter (N.D. Milligan, 2014, pers. comm., 13 Oct). In particular, I filmed one site in each subpopulation (2C [GW], 1D [CP], 1G [BB] and 7H [MP]) twice a week for 4 weeks, while the other sites were sampled once or twice in the first week (and last week, if sampled twice) to obtain finer spatial resolution. I used three CamOne Infinity cameras containing 32GB QUMOX/SanDisk microSD cards for the purposes for this study. Each camera was fitted onto a tripod and was adjusted to face the door of the puzzle-box at each

site. Cameras were small (10 x 8 x 13 cm) to reduce the possibility of neophobia. I filmed the puzzle-box at each site for approximately 1h during each sample.

2.2.3 Video Analysis

A total of 47h 34min 22s of video footage was used for this study and analysed in iMovie (vers. 10.0.3, Apple Inc. 2014). Within this footage, I classed all instances where a bird had any contact with the door of the puzzle-box as a solving attempt. For each solving attempt, I recorded: (1) date and time of solving, (2) time taken to solve (time from landing to when the bird gained access to the mealworm, in seconds), (3) position of door contact, (4) initial landing position, (5) perching position when solving, (6) solving action, (7) side of door contact, (8) number of door contacts, and (9) variety of solving actions used (see Table 2.3 and Figure 2.2 for scoring protocols). This scoring protocol was decided based on identifying as many discrete fine-scale aspects of the solving behaviour as possible in the video footage. Although a small number of PIT-tagged individuals of other species also used the puzzle-boxes, for the purposes of this study I only included great tits, as although great tits learn observationally from other species, previous work suggests that they learn better from conspecifics (Sasvári, 1985).

Table 2.3 Descriptions and protocols for scoring solving technique variable groups for each solving attempt.

Variable group	Description	Scoring protocol
Position of door contact	Position on the door which the individual contacts (possible to have more than one position per attempt – depends on number of door contacts)	5 possible positions: See Figure 2.2 for four of these positions. The final position is any other position that is not shown in Figure 2.2 (i.e. door front).
Initial landing position	Position on antenna perch when the bird first lands	11 possible positions: See Figure 2 for ten of these positions. The final position is any other position that is not shown in Figure 2.2.
Solving perching position	Position on antenna perch when the individual contacts the door (possible to have more than one position per attempt – depends on number of door contacts)	11 possible positions: See Figure 2.2 for ten of these positions. The final position is any other position that is not shown in Figure 2.2.
Solving action	Type of action individuals employ to slide the door (possible to have more than one action per attempt – depends on number of door contacts)	5 possible actions: Bite – Side of door wedged between the individual's beak Flick – Individual's beak moves outward (towards camera) Foot – Individual contacts the door with its foot Peck – Individual's beak contacts the door then recoils Push – Individual's beak is in contact with the door as it moves
Side of door	Side of the bidirectional door which is contacted (possible to have more than one side per attempt)	2 sides: Blue (contacts left side of door) Red (contacts right side of door)
Number of door contacts	Number of contacts with the door in an attempt	As described
Variety of solving actions	Number of different solving actions used in an attempt	As described

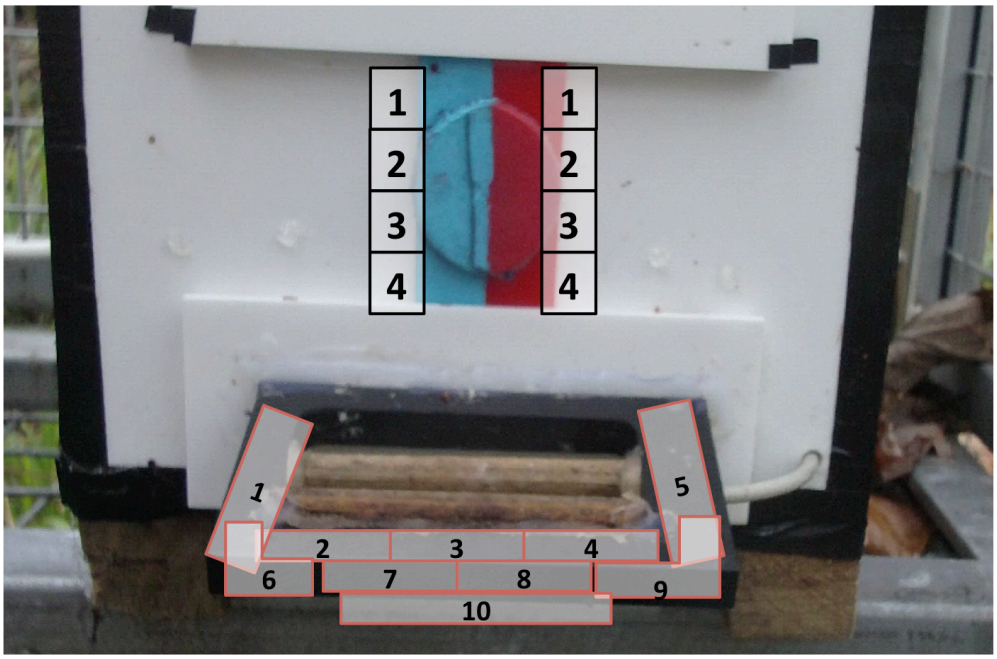

Figure 2.2 Different possible positions in which individuals could contact the door and antennae (perch). Positions of door contact (boxes with black borders) are at the sides of the door, which is divided into quarters, with no side distinction in scoring. Landing positions (boxes with red borders) are on the perch containing the antenna reader. There are 5 main positions (1-5), and positions 6-10 represent instances where the feet of individuals are found in more than one of the 5 main positions.

I used two methods to minimise any scoring bias on the part of the observer. First, I scored videos without knowledge of the individuals' identity. I then matched the date and time of each attempt to the data obtained from the puzzle-boxes, so that the individual identities detected by the antenna readers on the puzzle-boxes could be matched to the respective attempt in the scored data. Second, four different observation periods (one from each subpopulation: 1G [BB], 1D [CP], 2C [GW], 7H[MP]) totalling 4h 56min 11s (10.4% of all footage) were analysed independently by a second observer (S.D.J. Lang). This was done after I had provided this second observer with a scoring protocol and demonstrated a few examples using attempts outside of those 4 observation periods. I then checked for agreement in scoring outcomes in order to test the robustness of the scoring protocol (see Section 2.2.4.1).

When examining population variation in solving techniques, I excluded solving attempts where the door was off-centre or stuck, and other instances of equipment malfunction. These represented 5.6% of all attempts. A total of 3267 solving attempts remained, of which 3078 were successful (94.2% success rate). In addition, 1458 of 3267 (44.6%) attempts were performed by individuals who were either unringed or whose PIT-tag did not register at the device. Excluding these individuals, there was a total of 149 unique great tits across all four subpopulations (Table 2.4). Most attempts by ringed individuals were performed by males (64.2% of those with known sex) and adults (74.2%; Table 2.5a), which is reasonably reflective of the actual demographic of the solvers (71.1% adult and 60.2% male solvers; Table 2.5b).

Table 2.4 A summary of the data obtained from the video data collection. Table shows the amount of footage (in seconds), number of solving attempts, rate of solving attempts (number of solving attempts divided by amount of footage), rate of success of solving, and the number of identified individuals (total and successful) for great tits at each site.

Sub-population	Site	Footage (s)	Number of solving attempts	Rate of solving attempts (min^{-1})	Success rate (%)	Number of ringed individuals	Number of successful ringed individuals
CP	1B	7416	127	1.03	0.94	17	16
CP	1C	7387	94	0.76	0.99	9	9
CP	1D	31858	697	1.31	0.95	17	16
GW	2B	3730	87	1.40	1.00	12	12
GW	2C	26219	467	1.07	0.93	30	29
GW	2D	7449	99	0.80	0.94	18	18
BB	3E	7643	113	0.89	0.96	15	15
BB	1G	31872	500	0.94	0.96	41	39
BB	1H	7914	170	1.29	0.89	20	18
MP	7F	4641	103	1.33	0.91	10	10
MP	7G	3327	69	1.24	0.84	8	7
MP	7H	31806	741	1.40	0.93	16	15
Total		**171262**	**3267**	**1.14**	**0.94**	**149**	**147**

Table 2.5 Age and Sex demographics of the (a) 1808 solving attempts and (b) 149 identifiable great tit solvers.

a) Solving attempts	Male	Female	Sex unknown*	Total
First-years	372	47	48	467
Adults (Second year or older)	705	554	83	1342
Total	1077	601	131	**1808**

b) Solvers	Male	Female	Sex unknown*	Total
First-years	27	7	9	43
Adults (Second year or older)	53	46	7	106
Total	80	53	16	**149**

* Sex was unknown for individuals that were ringed or tagged as nestlings but not caught again after their post-juvenile moult.

2.2.4 Statistical Analysis

All statistical analyses were carried out in R version 3.1.1 (R Development Core Team, 2014).

2.2.4.1 Inter-rater reliability

To calculate the inter-rater reliability for categorical solving techniques, I used Cohen's (1960) kappa (κ). For the number of door contacts and variety of solving actions used per attempt, I used linearly weighted Cohen's (1968) kappa (κ_w). I used the concord package (Lemon & Fellows, 2007) for calculating Cohen's kappa, and the irr package (Gamer et al., 2010) to calculate weighted Cohen's kappa.

2.2.4.2 Multiple factor analysis

The solving attempt for each individual was characterised by 7 different variables of a mix of statistical data types, totalling 36 options (Table 2.2). I thus used multiple factor analysis (MFA) to reduce the dimensionality of variables (Pagès, 2015), using the FactoMineR package in R (Lê, Josse & Husson, 2008). This was advantageous as it allowed for: (1) taking into account all of the variation in the data; (2) unbiased consideration of all variables; and (3) production of continuous dimension scores (equivalent to principle components loadings), summarising the main aspects of solving technique for each solving attempt. A preliminary MFA performed on all 7 groups of scoring technique variables showed that position of door contact had relatively low loadings (all

eigenvalues <0.04) on the first two dimensions, and so I added it as a supplementary rather than active variable in the final MFA performed.

2.2.4.3 Factors influencing foraging behaviour

I used linear mixed models (LMMs) to investigate factors influencing foraging behaviour, and fitted them using the lme4 package in R (Bates et al., 2014). As all LMMs had individual identity as a random effect (see below), I generally only included data obtained from uniquely identifiable individuals (see exceptions below). Although 44.6% of solving attempts were by birds that were not uniquely identifiable, this could be due to the RFID antennae malfunctioning or individuals landing at a position where their PIT tags could not be read by the antennae, since over 90% of this population were estimated to have been ringed (Aplin et al., 2013; Farine et al., 2015). Thus, I would not expect this to bias the results significantly as it should still be representative of the population. Nonetheless, I included birds that were not uniquely identifiable where appropriate in the analyses.

To investigate whether age or sex influenced solving technique, I added age and sex as fixed effects independently to a random intercept LMM with individual, puzzle-box and site identities as random effects. I fitted the models using ringed individuals with known age and sex respectively. I conducted a likelihood ratio test to examine the effect of adding the fixed effect term using models fitted with maximum likelihood estimators (Pinheiro & Bates, 2000).

For an initial exploration of whether there were likely to be significant spatial differences in solving technique, I conducted a likelihood ratio test

between the random intercept LMM with individual and puzzle-box identities as random effects, and an LMM with site or subpopulation (dependent variables) added as an additional random effect. Models were fitted with restricted maximum likelihood estimators (Pinheiro & Bates, 2000). For this analysis, I grouped unidentifiable individuals according to their sites or subpopulations respectively and additionally included them.

Finally, to examine the relative influence of the behaviour of others on an individual's behaviour, I fitted both personal and social information measures as fixed effects, together with individual and site identity as random effects in an LMM to explain each MFA dimension. Two measures were used for personal and social information each – one based on the dimension score of the previous solve, and another based on the mean dimension score of previous solves. Both the previous and mean solve measures of social information were calculated using the last recorded solve by another individual or prior solves by others respectively (inclusive of solves by unidentifiable individuals), within the last 245s at the same date and site, to increase the likelihood that the focal individual had observed the solve(s) (for more details, see Aplin et al., 2015). In contrast to this, the personal information measures were not limited by site or timing.

2.2.4.4 Repeatability

Repeatability was taken as the between-group variance divided by the sum of the between-group variance and within-group variance (Sokal & Rohlf, 2012). To investigate within-individual repeatability in solving technique, I ran a random intercept LMM, with individual identity as a random effect. In addition,

to correct for the confounding effect of time (taken as the number of minutes of access to the puzzle-box since it was first introduced in the winter of observation), spatial location (site), and puzzle-box identity, I included time as a fixed effect and site and puzzle-box identity as random effects. I then calculated an adjusted repeatability (for methodology, refer to Nakagawa & Schielzeth, 2010). I obtained 95% confidence intervals through the use of parametric bootstrapping (Faraway, 2006). Finally, to investigate whether there were differences in within-individual repeatability across different ages and sexes, I calculated conditional repeatabilities. These were adjusted for time, site and puzzle-box identity. I then took pairwise differences between parametric bootstrapped values (1000 simulated iterations) of the conditional repeatability values and checked the resultant confidence intervals for overlaps with zero (Nakagawa & Cuthill, 2007; English, Nakagawa & Clutton-Brock, 2010).

2.2.4.5 Behavioural assortment in social network

Another way of examining the possible effect of social learning on the formation of behavioural differences between groups in this paper is to observe whether the solving behaviours were socially assorted. To do this, I used social networks for each site. Data on the social interactions between birds was collected as part of a larger on-going project (see for example Farine et al., 2015). Social networks were calculated by J.A. Firth as part of this wider project, using the R package asnipe (Farine, 2013). I then calculated Newman's (2003) assortativity coefficient using weighted edge nodes for both MFA dimensions and each of the solving techniques. To test for significance of the assortativity

coefficient, I used the node permutation method described in Farine (2014), controlling for individuals solving on the same date. I used the assortnet package (Farine, 2014) to calculate Newman's (2003) assortativity coefficient and its standard error based on the jackknife method, and the asnipe package (Farine, 2013) to perform node permutations for significance testing.

2.3 Results

2.3.1 Inter-rater reliability

When the ratings of two observers watching the video footages were compared, the solving technique measures ranged from fair (variety of solving actions: κ_w=0.29, p<0.001) to perfect agreement (side: κ=1, p<0.001) between observers (Table 2.6). This suggests that the ratings are relatively repeatable across observers.

Table 2.6 Inter-rater reliability calculated using Cohen (1960)'s kappa (κ) and weighted Cohen's (1968) kappa (κ_w) for solving technique measures.

Solving technique measure	Inter-rater reliability statistic	Z	p-value
Solving action	κ=0.559	110	<0.001
Initial landing position	κ=0.907	734	<0.001
Solving perching position	κ=0.902	702	<0.001
Position of door contact	κ=0.912	163	<0.001
Side of door contact	κ=1	53.5	<0.001
Number of door contacts	κ_w=0.293	23.1	<0.001
Variety of solving actions	κ_w=0.559	7.14	<0.001

2.3.2 Overall variation in foraging technique

There was an overall population-level preference for a subset of solving techniques in all measures other than for side of door contact (Figure 2.3). There were also approximately equal numbers of contacts on both the blue and red side of the door (Figure 2.3a), although there were slightly more contacts on the blue/left than the red/right side (blue: 54.3%, red: 45.7%; blue/red ratio of 1.19). That there was no overall preference for the side of door contact is

unsurprising, as two sub-populations were seeded with blue/left and two with red/right. Most initial landing positions were in positions 1, 2, 3 and 4, while there were two major solving perching positions – 2 and 4 (see Figure 2.3b and 2.3c). 46.6% of the solving perching positions were on the left side (1, 1A, 2 and 2A), compared to 40.4% of solving perching positions on the right (4, 4A, 5 and 5A); a left/right perching ratio of 1.15. This likely reflects the side choice detailed above, with individuals standing on the perch position closest to their preferred side of door, especially when comparing the blue/red and left/right perching ratios. In terms of the body actions individuals used to solve, the most frequently used action was a push (55.6%; Figure 2.3d), and most of the solving attempts were performed with just one type of action (73.0%; Figure 2.3e). 89.7% of door contacts were in the middle two positions (Figure 2.3f). 75.6% of successful attempts involved a solution within the first two seconds (Figure 2.3g), and 86.1% of solving attempts had three or fewer door contacts (Figure 2.3h).

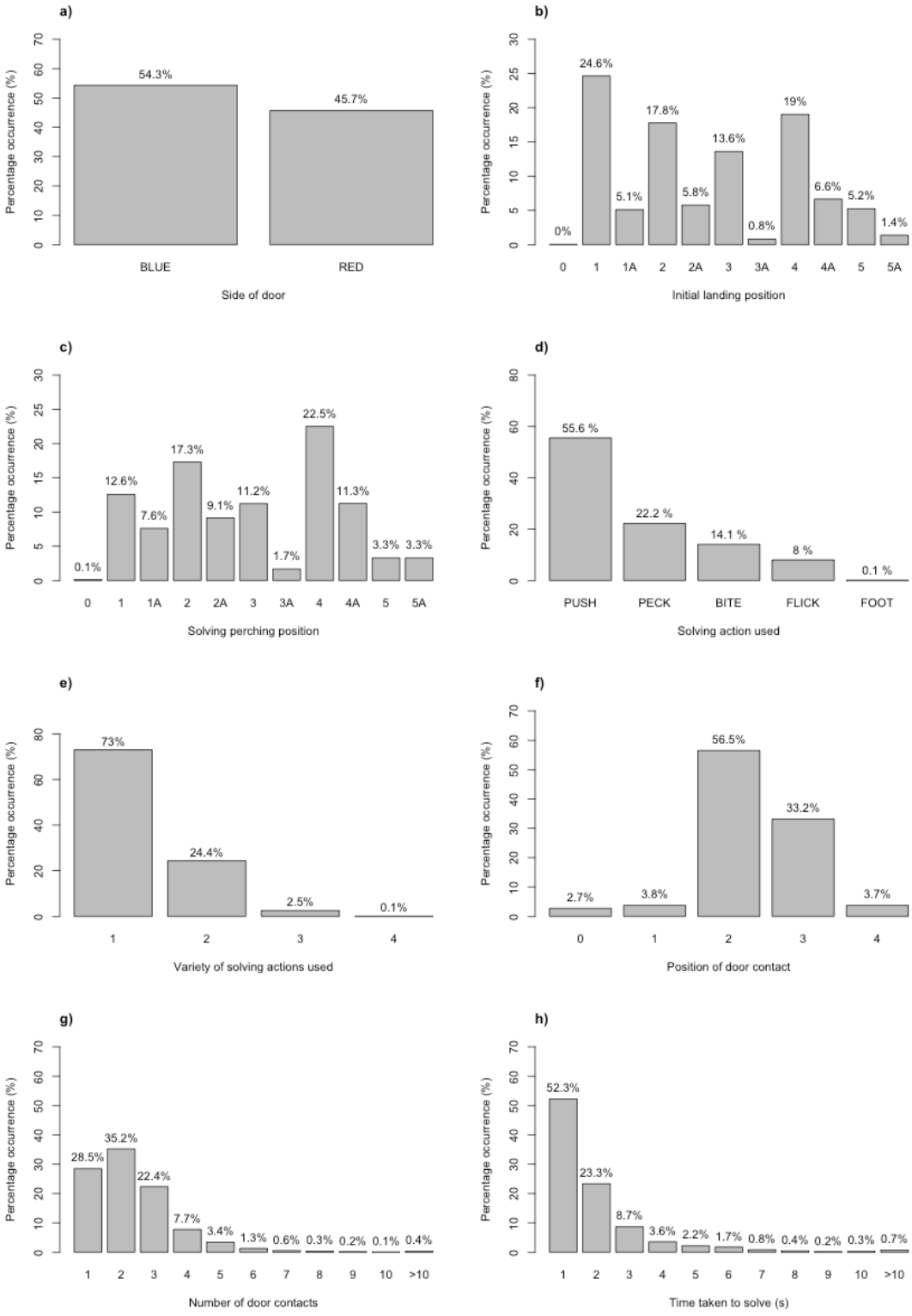

Figure 2.3 Variation in the techniques used to solve a foraging task. Percentage occurrences of the (a) side of door contacted, (b) initial landing positions, (c) solving perching positions, (d) solving actions used, (e) variety of solving actions used, (f) positions of door contact, (g) numbers of door contacts and (h) time taken to solve in each solving attempt.

2.3.3 Multiple factor analysis of behavioural variation

There was high dimensionality in the data, with 11 dimensions that had an eigenvalue of greater than 1 (Table 2.7). Of these, the first two dimensions represented 9.80% and 7.29% of the variation of the data respectively. Using multiple factor analysis (MFA) meant I could extract the dimensions that are most important and relevant to the study in question; here the side preference and fine-scale movement used in solving. As the side of door contact, initial perching position and perching position when solving all had the highest scores on dimension 1 (Figure 2.4), I took dimension 1 to represent the sidedness of solving techniques. There was a relatively equal loading of all variable groups except for side of door contact on dimension 2 (Figure 2.4), hence I took dimension 2 to represent the finer-scale movements (labelled "micro-techniques") used when opening the door.

Table 2.7 Table of eigenvalues and dimension scores for each group of variables for dimensions with eigenvalue of greater than 1.

Dimensions	**Eigenvalues**			**Results for variable groups**					
	Eigenvalue	Percentage of variance	Cumulative percentage of variance	Initial landing position	Solving perching position	Side of door	Solving action	Variety of solving actions	Number of door contacts
Dim.1	2.32	9.80	9.80	0.43	0.76	0.72	0.10	0.14	0.16
Dim.2	1.73	7.29	17.09	0.33	0.33	0.06	0.31	0.36	0.33
Dim.3	1.49	6.28	23.37	0.64	0.65	0.03	0.03	0.09	0.05
Dim.4	1.40	5.92	29.29	0.59	0.67	0.00	0.08	0.05	0.01
Dim.5	1.30	5.49	34.78	0.59	0.66	0.19	0.02	0.02	0.00
Dim.6	1.29	5.42	40.20	0.54	0.58	0.01	0.10	0.04	0.03
Dim.7	1.24	5.23	45.43	0.57	0.62	0.00	0.02	0.01	0.02
Dim.8	1.21	5.09	50.52	0.58	0.62	0.00	0.00	0.00	0.00
Dim.9	1.20	5.05	55.57	0.57	0.63	0.00	0.00	0.00	0.00
Dim.10	1.17	4.92	60.49	0.54	0.60	0.00	0.02	0.01	0.00
Dim.11	1.16	4.88	65.37	0.54	0.59	0.00	0.02	0.01	0.00

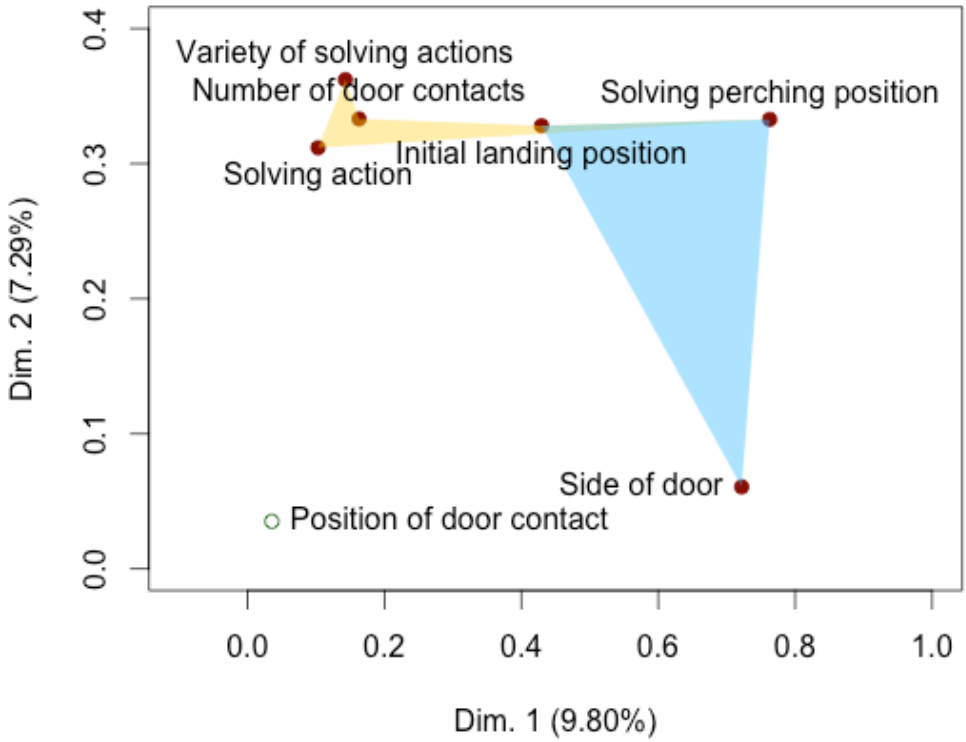

Figure 2.4 The group representation plot of the Multiple Factor Analysis (MFA). The active groups are represented in red (closed circle), while the supplementary group is in green (open circle). The points represent the coordinates of each variable group on the first two MFA dimension scores (exact values are given in Table 2.6). The variable groups most associated with MFA dimension 1 (side preference) are connected by a blue polygon, while those most associated with MFA dimension 2 (micro-technique) are joined by a yellow polygon.

2.3.4 Variation in micro-technique and sidedness

There were no age or sex difference in the values for MFA dimension 1 (sidedness): age: χ^2=0.555, df=1, p=0.456, sex: χ^2=0.552, df=1, p=0.457). By contrast, MFA dimension 2 (micro-technique) showed significant differences by age and sex, with first-years (LMM: est=0.552, se=0.136; LRT: χ^2 =14.9, df=1, p<0.001) and males having a higher dimension score (LMM: est=0.317, se=0.133; χ^2 =5.56, df=1, p=0.018). When the five fine-scale technique measures most associated with MFA dimension 2 were examined individually, age and sex differences were found for all except for variety of solving actions used. For example, more first-years and males used peck rather than push to solve (Figure 2.6). Both dimension 1 (sidedness) and dimension 2 (micro-technique) significantly varied across the 12 sites (Dim. 1: χ^2 =22.7, df=1, p<0.001; Dim. 2: χ^2 =24.4, df=1, p<0.001; Figure 2.5a) and the 4 subpopulations (Dim. 1: χ^2 =123, df=1, p<0.001; Dim. 2: χ^2 =68.5, df=1, p=0.021; Figure 2.5b).

One of the ways to investigate the effect of social learning on solving behaviour was to examine the relative contribution of personal and social information to the behavioural decision of each individual when solving. I found that the dimensions (sidedness and micro-technique) were significantly explained by both personal and social information, whether the information measures were based on the last or mean solve (all p<0.001; Table 2.8). Personal information had approximately three times the effect of social information on sidedness, and seven times the effect of social information on the micro-techniques that an individual employed (using the mean of previous solves; Table 2.8).

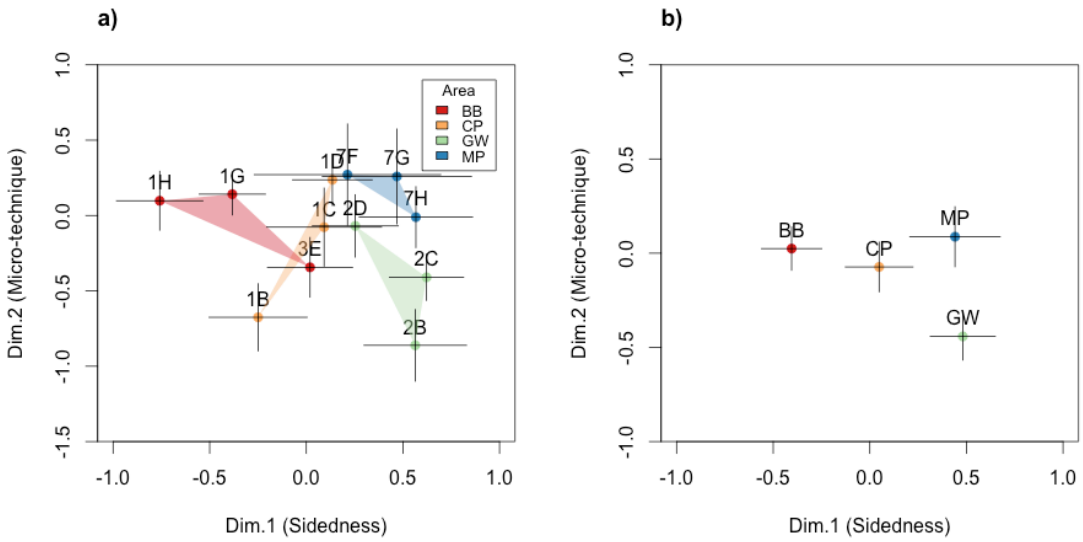

Figure 2.5 Representation of (a) sites and (b) areas according to their mean loadings on the first two multiple factor analysis dimension scores. Dimension 1 represents a cluster of behaviours related to the side preference of the solving attempt, while dimension 2 represents a cluster of behaviours relating to finer-scale body movements. Error bars represent the standard errors of the mean. Sites in (a) are colour-coded according to the subpopulation they are situated in.

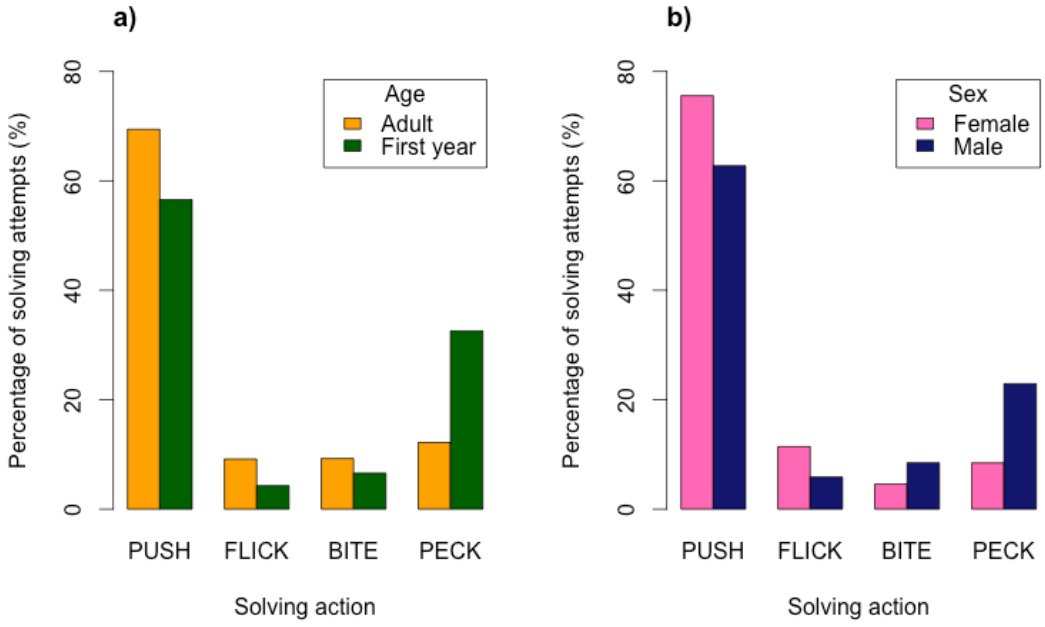

Figure 2.6 Differences in solving action between (a) ages and (b) sexes.

Table 2.8 Relative effects of personal and social information on the individual's values for (a) Multiple Factor Analysis (MFA) dimension 1 (sidedness) and (b) dimension 2 (micro-technique) respectively. Summaries of the fixed effect terms of linear mixed models (LMM) with personal and social information (two measures each, based on previous or mean solves) as fixed effects, and individual and site identities as random effects, to explain each MFA dimension are presented. Likelihood ratio tests were also performed to test for the significance of the fixed effects.

(a) Multiple Factor Analysis dimension 1 (Sidedness)

Linear mixed model			**Likelihood ratio test**		
Fixed effect terms	**Estimate**	**Standard error**	χ^2	**df**	**p-value**
Personal and social information based on: previous solve(s)					
(Intercept)	0.094	0.099			
Personal information	0.293	0.025	1034	1	<0.001
Social information	0.054	0.019	119	1	<0.001
Personal and social information based on: mean solve(s)					
(Intercept)	-0.007	0.084			
Personal information	0.577	0.037	656	1	<0.001
Social information	0.146	0.043	159	1	<0.001

(b) Multiple Factor Analysis dimension 2 (Micro-technique)

Linear mixed model			**Likelihood ratio test**		
Fixed effect terms	**Estimate**	**Standard error**	χ^2	**df**	**p-value**
Personal and social information based on: previous solve(s)					
(Intercept)	-0.188	0.073			
Personal information	0.210	0.026	1158	1	<0.001
Social information	0.007	0.024	131	1	<0.001
Personal and social information based on: mean solve(s)					
(Intercept)	-0.181	0.064			
Personal information	0.372	0.040	659	1	<0.001
Social information	0.099	0.055	184	1	<0.001

2.3.5 Within-individual repeatability

Individuals were significantly repeatable in both dimensions, representing an individual consistency in both their side preference and fine-scale movement used (Dim. 1: R=0.665, CI=0.601-0.716; Dim. 2: R=0.367, CI=0.291-0.430). Relative to previous studies of repeatability in animal behaviour, individuals here showed a very high repeatability in their side preference, and were moderately repeatable in micro-techniques (Bell, Hankison & Laskowski, 2009). They remained repeatable even when controlling for time, site and the particular puzzle-box used (Dim. 1: R=0.667, CI=0.602-0.718; Dim. 2: R=0.370, CI=0.297-0.434). No age (Dim. 1: CI=-0.11-0.17; Dim. 2: CI=-0.03-0.28) and sex (Dim. 1: CI=-0.01-0.27; Dim. 2: CI=-0.10-0.19) differences in conditional repeatability were found in either dimension.

2.3.6 Behavioural assortment in the social network

Individuals were more likely to be socially associated to another individual that had similar sidedness (Dim. 2: r=0.185, se=0.011, p=0.005), and the three solving techniques most associated with sidedness: initial landing position (r=0.011, se=0.005, p=0.006), solving perching position (r=0.055, se=0.005, p<0.001) and side of door contact (r=0.018, se=0.010, p=0.027). Those that tended to use the same positions of door contact when opening the door were also more closely associated to each other (r=0.058, se=0.011, p<0.001). By contrast, individuals were not more connected to others sharing similar micro-

techniques (Dim. 2) and two solving techniques associated with that MFA dimension: solving action and number of door contacts (all p>0.05; Table 2.8).

Table 2.8 Behavioural assortment within the social network of the great tit subpopulations in Wytham Woods. The Newman (2003) assortativity coefficient, r, with weighted network edges was calculated for the two continuous Multiple Factor Analysis (MFA) dimensions, and each solving technique measure (five categorical and two continuous). The p value was calculated using node permutation of the original data stream, controlling for the same date.

Solving technique measure	Newman assortativity coefficient, r	Standard error	p-value
MFA dimension 1 (Sidedness)	0.185	0.011	0.005
MFA dimension 2 (Micro-technique)	0.021	0.009	0.648
Solving action	0.045	0.006	0.848
Initial landing position	0.011	0.005	0.006
Solving perching position	0.055	0.005	<0.001
Position of door contact	0.058	0.011	<0.001
Side of door contact	0.018	0.010	0.027
Number of door contacts	0.0003	0.0045	0.712
Variety of solving actions*	NA	NA	NA

* The model for calculating the assortativity coefficient for the variety of solving actions used failed to converge.

2.4 Discussion

2.4.1 Summary of key results

My study of the spatial and individual variation in an experimentally introduced foraging behaviour in great tits revealed four key results. Firstly, there was considerable variation in the types of fine-scale techniques used within the population when foraging. Secondly, there was spatial and demographic structuring in this variation – site, subpopulation, sex and age all influenced the patterns of variation in the second MFA dimension (micro-technique/fine-scale solving movements). In addition, the value of an individual's MFA dimensions (both side preference and micro-technique) were influenced by personal information from its previous solves, and also by social information from the solving behaviour that it observed in others, with personal information playing a larger role. Also, a substantial proportion of variation was accounted for at the individual level: approximately two-thirds of the largest and one-third of the second largest dimension of variation were attributed to individual identity, and not explained by their sex or age. Finally, individuals were more likely to be associated with others sharing similar side preference and positions of door contact, although this was not the case for micro-technique.

2.4.2 Potential explanations

2.4.2.1 Preferences in fine-scale solving movements

There was reasonable variation in all techniques associated with the introduced foraging behaviour, other than for the side of door contact. This could be a possible explanation why side of door contact did not have as high loadings on dimension 2 of the Multiple Factor Analysis, which rather corresponded to the finer-scale "micro-techniques" used. The result for the side of door contact was expected, as it had been deliberately seeded – the approximately 50:50 ratio observed is consistent with the fact that half of subpopulations were seeded with a blue-side solve, while the other half were seeded with a red-side solve. However despite this variation, across all four sub-populations there were overall preferences for particular techniques: such as a "push" (solving action), door contact at position "2", and perching positions "2" and "4" when solving. Micro-techniques were not controlled in the initial experiment, and it is not known which techniques the trained demonstrators used when they seeded the behaviour in the wild. If all demonstrators used similar micro-techniques, my results would be consistent with the presence of social learning of these main preferences, with local innovation and/or behavioural drift leading to the additional spatial and individual variation. More specifically, this would suggest that social learning mechanisms involving fine-scale local enhancement to the middle door position, fine-scale motor imitation or response facilitation to the solving action could all have been possible. However without knowing the exact micro-techniques used by the original demonstrators, I am unable to rule out alternative explanations based on the observed behavioural variation alone.

The observed patterns of preference could also be a reflection of different efficiencies associated with the use of different micro-techniques. This is especially likely in the case for the position of door contact and solving perching position. Access to the mealworm reward is through a hole concealed behind the door, positioned at the middle of the door (though slightly closer to position 2 height-wise). Thus contacting the door at position 2 should be the most efficient to reach the reward, followed by position 3 – this was reflected in the relative frequencies. For the solving perching position, the two most common positions were 2 and 4 (corresponding to the blue [left] and red [right] side). Indeed, the left/right ratio of 1.15 for solving perching positions was very similar to the blue/red ratio of 1.19 for the side of door contact. Furthermore, solving attempts were generally efficient, with the majority performed within two seconds and requiring three or fewer door contacts (also shown in greater detail in Chapter 3). Hence, it was likely that the resultant preferences for these measures were at least partly a reflection of the efficiencies of different positions.

In addition to the above two potential explanations, individuals may be intrinsically more likely to perform one technique over another (McCarthy & Davison, 1981), with natural foraging behaviours biasing individuals towards certain types of actions (Remsen Jr & Robinson, 1990; Walther & Gosler, 2001). Further study is required to tease apart these possible explanations. In particular, it could be tested whether certain techniques are more efficient than others, by comparing the time taken to solve between different solving techniques. This would be valuable in giving us a glimpse into the possible mechanisms and selective forces acting to shape the patterns observed in these

micro-techniques, and more broadly whether the spatial variation in micro-techniques constitutes cultural differences between areas.

2.4.2.2 Individual repeatability in sidedness and micro-technique

I found that both MFA dimensions were significantly repeatable, but side preferences were more repeatable than preferences in micro-techniques. The high repeatability shows that there was low within-individual variation relative to between-individual variation (Bell, Hankison & Laskowski, 2009). It is not surprising that side preference showed a higher repeatability than micro-technique, as it was experimentally induced and continued to be preferred by the majority in each subpopulation. Between-individual variation and within-individual consistency in micro-techniques, in contrast, either emerged organically, or at least were not controlled in the initial experiment, with possible uncontrolled differences between the initial trained demonstrators. Given its lower repeatability, it is also possible that there is a greater effect of the environment on the micro-technique used or that micro-techniques are less canalised (Bell, Hankison & Laskowski, 2009). Nonetheless, at R=0.67 and R=0.37, both dimensions exhibit an individual repeatability at, or above average to, relative to the repeatabilities observed in other animal behaviours; for example, the personality trait of exploration behaviour in this population of great tits has a repeatability of R = 0.34 (CI: 0.30-0.39) (Dingemanse et al., 2012). Quantifying such within-individual variation allows us to study social traditions, in terms of variation between groups of individuals, accurately and reliably, without violating underlying assumptions (Hayes & Jenkins, 1997).

2.4.2.3 Sex and age differences in micro-technique used

I found evidence for sex and age differences in micro-technique, but not sidedness. It is possible that morphological differences between the sexes in factors such as bill length, bill width and body size (Gosler, 1987) may have played a role in changing the efficiency of different solving actions for each individual (Barluenga, Moreno & Barbosa, 2001). However this cannot explain age differences in preferences; although age differences in foraging behaviour due to morphology in birds have been proposed (Marchetti & Price, 1989), no age differences in morphology in winter are reported in great tits (Gosler, 1987). There were relatively few first-year females in my sample (7 out of 34 first-years with known sex; Table 2.4b). It is possible that this could have skewed the data such that the average first-year micro-technique was more representative of males. Alternatively age differences in micro-technique could potentially be caused by social learning. Most adults would have learnt their behaviour in previous years when the prevalence of each micro-technique in the subpopulations may have been different from the current year, and may have maintained individual-consistency in micro-technique since.

2.4.3 Implications for social learning and underlying mechanisms

2.4.3.1 Spatial variation in behaviour and the role of social learning

Consistent behavioural variation was found in foraging behaviour at the puzzle-box between individuals, sites and subpopulations. As for all behavioural differences, this variation could be due to a combination of genetic, environmental, social and personal factors. My study aims to partition this variation, in order to establish the contribution of social learning to this variation and gain insights into possible social learning mechanisms. Thus, in the design of my study, I have attempted to minimise the effect of possible genetic and ecological factors, so that any differences in behavioural repertoire observed would more likely be due to a social effect. My study was conducted on a wild population, but coupled field observations with an identical experimental set-up across the different sites that controlled for the local foraging environment, hence reducing ecological influences. Puzzle-boxes were further rotated amongst sites, controlling for any differences between boxes. Furthermore, the study was focused on a single population of birds within a relatively small geographical area, and thus genetic variation was unlikely to be significant. Although there is some kin assortment within foraging flocks (Silk et al., 2014), the dispersal distance in this population of great tits is two to three times greater than the distance between sites (Szulkin & Sheldon, 2008), so genetic effects are very unlikely to be the main force driving behavioural differences. By maintaining experimental control over some variables, I could thus undertake the study in a relatively naturalistic context while overcoming the usual restraint of field observations. Hence, I expected that if spatial variation in behaviour was found,

and especially if it were influenced by the behaviour of near associates, it would be likely that social learning had a relatively significant role in the formation of those behavioural differences.

My results suggest that there was spatial variation at both site and subpopulation level in both behavioural dimensions, with sites generally being clustered within subpopulations in both 'sidedness' and 'micro-techniques'. Additionally, while individuals relied more on personal information, they also significantly incorporated social information on the solving behaviour of their conspecifics for both sidedness and micro-technique. However, while individuals were more closely associated with others of similar sidedness, they were not so with others of similar micro-technique. In side choice, these observed spatial variation, influence of solving information by others, and assortment, are all consistent with the social foraging traditions reported in Aplin et al. (2015). There half of the subpopulations were seeded with demonstrators solving on the blue side, and the other half on the red side, and the information spread by social learning. Social conformity to the side of door contact, combined with non-random movements between subpopulations over three generations, could result in different sites (nested within subpopulations) developing distinct side preferences. Conformist bias is a social phenomenon (Boyd & Richerson, 1985), and thus incorporation of social information and assortment based on sidedness would be expected if it were the case – which was shown in our analysis.

While the micro-technique was not controlled for in the original demonstrators, I still observed variation between sites and subpopulations. It seems unlikely that such local differences in micro-technique would be due to genetic or ecological factors (see above). Yet given this is a wild population, we

are unable to completely rule out these explanations. The puzzle-box controlled the immediate local foraging environment, but other ecological variables such as the level of competition or density of local habitat varied across sites, and those could have influenced the micro-technique used. For example, sites with more competitors could pressure individuals to use fewer door contacts, and the relative position of the puzzle-box door to nearby bushes could influence the initial landing position, all of which affect the micro-technique. However, my results suggested that social learning played at least a partial role in the fine-scale behaviours used during solving - from the locations of landing and solving position, to the body movements used when opening the door.

The results suggested that social learning was involved in forming individual preferences for particular micro-techniques. However social network analysis found no link between the patterning of social interactions and the distribution of micro-techniques across the population (social network assortment). Caution should be applied to the social network assortment results, as assortment can only imply correlation, not causation. That is, there could be other factors making it less beneficial for individuals to associate with others of similar micro-technique. Alternatively, social learning may operate on these traits at too fine a temporal scale to be detected by over-winter networks (i.e. it may be a fleeting effect at feeding events rather than indicating ongoing preferential attention to social associates). It was thus useful to use three different ways of measuring the potential contribution of social learning to the observed behavioural variation, as a combination of methods allows a more multi-faceted and more reliable picture. On the whole, my results indicate the presence of social influences on micro-technique, but at a weaker level than for

sidedness. This may indicate an overall lower tendency or investment in the social learning of fine-scale behaviours, as compared to more coarse-scale behaviours like side preference. However, because there was a significant association between individuals using similar positions of door contact to solve (a relatively fine-scale behaviour not considered under "micro-technique"), it may be that investment in social learning of fine-scale behaviours is selective. This may more broadly reflect the ecological significance of social learning in this species.

2.4.3.2 Possible social learning mechanisms

While this study is unable to definitively identify the social learning mechanisms used by foraging great tits, it can provide some helpful insights, and form a base for further investigation. Already, stimulus and local enhancement (Krebs, MacRoberts & Cullen, 1972; Slagsvold & Wiebe, 2011) have been proposed to be main social learning mechanisms in great tits. Previous work on the same behaviour in this population have additionally deduced observational learning as another possible social learning mechanism underlying the spread of the behaviour (Aplin et al., 2015), with evidence from both network-based diffusion analysis (Franz & Nunn, 2009) and using the bidirectional control procedure (Dawson & Foss, 1965). A limitation of the bidirectional control procedure is its inability to distinguish between several potential social learning mechanisms, including fine-scale local enhancement (attraction to the exact spatial point on the door), emulation (surmising the goals of the puzzle) and imitation (replication of the body actions of the demonstrator).

My results showed that individuals were assorted based on their door contact position, which hinted at the possibility of fine-scale local enhancement as one of the underlying social learning mechanisms. It could be fine-scale local enhancement, rather than imitation or emulation, which could have explained the side conformity found in Aplin et al. (2015). If so, this has great implications on our understanding of mechanisms that underlie the development of culture and conformity, and supports recent studies finding that imitation is not necessary for the formation of traditions (Franz & Matthews, 2010; van der Post & Hogeweg, 2008). The most definite way to prove this would be for future work to focus on developing a different experimental task that provides alternative solutions for a puzzle-box that shares the same point of contact to control for fine-scale local enhancement.

2.4.4 Conclusion

In summary, this study shows that behaviours associated with an experimentally induced foraging tradition (sliding a door to obtain food) are repeatable within individuals and vary spatially across sites and subpopulations. This was found to be the case for both a coarse-scale (side preference) and a finer-scale measure (solving movements) of the behaviour. However my study also revealed that the role of social learning in the formation of this behavioural tradition largely operated at three associated levels – in the choice of door side, position on the perch when landing and solving, and position of bill contact at the door. Taken together, this suggests that fine-scale local enhancement could largely explain the apparent observational learning in great tits, lending support

to the theory that non-imitative processes can result in persistent social traditions and cultures. This study provides an alternative approach to more traditional ethnographic methods, by examining variation within a population at multiple levels and using a mix of ethnographic and model-fitting approaches. Investigating the role of social learning in the formation of traditions at different scales is perhaps the next step forward in providing an insight into the level of homology between mechanisms of tradition formation between different taxa.

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CHAPTER 3

Social learning and foraging efficiency in wild great tits (*Parus major*)

Chapter 3: Social learning and foraging efficiency in wild great tits (*Parus major*)

Abstract

Learning from others does not only help individuals gain new foraging techniques, but may also enable them to improve their foraging efficiency. However, few studies have examined the relationship between social learning and foraging efficiency, even though it is another way by which social learning can influence fitness. In this paper, I examine the relationship between social learning and the efficiency of solving an artificial foraging task in free-living great tits (*Parus major*). My study suggests that both individual and social factors influencing foraging efficiency in great tits. In particular, social learning likely contributed to individual improvement over time, but this effect was potentially masked by competition at a local scale. Finally, I also found further support for a potential role of social learning in generating population patterns of behaviour, as population prevalence of solving behaviour could not be explained by differences in efficiencies of solving techniques. This study highlights the need for future work on social learning not to just focus on its influence on spatial variation in behaviour, but also examine how social learning impacts temporal patterns of behaviour.

Keywords: bidirectional control procedure, foraging efficiency, great tits, social learning, temporal patterns.

3.1 Introduction

Social learning, where individuals alter their behaviour in response to observations of others' behaviours or their products (Heyes, 1994), is an important aspect of the foraging ecology of many species (e.g. Laland & Hoppitt, 2003; Lefebvre & Bouchard, 2003). Individuals can learn from others where to forage, what is edible, and when the optimal time is for feeding (Galef & Giraldeau, 2001). Importantly, social learning can thus enable individuals to better adapt to temporal and spatial variation in the environment, increasing their chances of survival and reproduction (Hoppitt & Laland, 2008; but see Giraldeau, Valone & Templeton, 2002).

Social learning is often framed in terms of the acquisition of a new skill, but investigating social impacts on how individuals learn to be more efficient in performing a skill is also important as that, too, has significant fitness consequences (Eliassen et al., 2009; Raine & Chittka, 2008). Individuals that have learnt to be more efficient in foraging are able to gain more energy in the same amount of time, which could increase their chances of survival and reproduction (Lemon, 1991).

Foraging efficiency has often been defined as the net rate of energy intake, calculated by the energy gained divided by the energy expended while foraging (Weathers & Sullivan, 1991; Pyke, Pulliam & Charnov, 1977). Most studies on foraging efficiency have attempted to test one of optimal foraging theory's assumptions: that natural selection would select for individuals that are more efficient at foraging (Pyke, 1984). Thus, it would be expected that individuals would preferentially employ more efficient foraging behaviour. Individuals can

become more efficient in foraging by a number of ways, including learning to use more efficient foraging techniques or through repetitive practice (Evans & Raine, 2014; Berridge, 2000).

In social foraging species, foraging efficiency can be affected by both individual factors such as age (Marchetti & Price, 1989), and social processes such as social facilitation, where an individual's behaviour changes as a result of the presence of others (Zajonc, 1965). In particular, species that utilise social learning when acquiring new foraging skills might also employ it to improve their skills over time. However, only a handful of studies have investigated how social learning influences the improvement in performance over time in animals (e.g. Laland & Plotkin, 1990; Pongrácz et al., 2003; Zajonc, 1965), despite extensive research investigating social learning in the context of novel skill acquisition (see Zentall & Galef, 2013). One possible reason for this relative lack of research focus is that change in performance over time may also be attributed to factors other than learning, such as motivation (Lieberman, 2000). However, a recent study has suggested that tracking changes in performance over time can still be a valuable proxy for learning, with learning having a significant contribution to foraging performance and reproductive success in the field (Dukas, 2008). More generally, the way through which learning affects fitness is via its effect on performance (Raine & Chittka, 2008).

In this paper, I study the foraging efficiency of free-living great tits (*Parus major*), and used it to investigate learning in terms of the improvement of a foraging skill. In particular, I examine the role of social learning in influencing improvements in foraging efficiency and in explaining population patterns in variation in foraging techniques. Great tits are well known for their ability to

prise open milk bottle caps to feed on cream (Fisher & Hinde, 1949), a skill that was at least partly acquired through social learning (Lefebvre, 1995). They are also well known for being opportunistic foragers, with flexible foraging behaviours (e.g. predating on hibernating bats in winter; Estók, Zsebők & Siemers, 2009), which is associated with greater likelihood of using social learning (Reader, 2003). Furthermore, they form social foraging flocks in winter (Hinde, 1952), providing ample opportunities for social learning. Thus, they are a great model species to investigate not just how social learning influences the acquisition of novel foraging behaviour, but also whether or how social learning is also involved in the improvement in foraging efficiency over time.

I conducted a field experiment with an artificial foraging task where individuals could obtain a mealworm reward by sliding open a bidirectional door of a puzzle-box. Using an artificial foraging task to study foraging efficiency is useful in several ways. First, the puzzle-box automatically recorded all visits and solves by individuals that had been tagged with passive integrated transponders (PIT). This allowed all successful foraging attempts to be recorded, enabling a more accurate and complete tracking of foraging efficiency over time. Secondly, solving the puzzle-box yielded one mealworm per solve, as it reset after each solve. This standardises the energy gain per solve, with variation in efficiency due to the energy expended while foraging, which is proportional to the time taken to solve. Hence, in this study, foraging efficiency could be easily estimated by solving efficiency, which is the rate of solving (inverse of time taken to solve).

I first tested whether the initial time taken to solve or change in the time taken to solve across the experimental period were influenced by individual and social factors. Second, I examined whether there were differences in the

efficiency of techniques used to solve the puzzle-box and subsequently investigated (i) whether changes in solving efficiency over time were due to changes in the choice of techniques used, and (ii) whether population patterns in the variation of solving techniques could be explained by changes in solving efficiency. If population preferences in solving behaviour could not be attributed to solving efficiency, one of the alternative factors driving those patterns instead could be social learning (Reader, 2004).

3.2 Methods

3.2.1 Study system

This work was performed on the free-living population of great tits in Wytham Woods, Oxfordshire (51°46'N, 1°20'W) - an area spanning 385ha that has been the focus of a long-term breeding survey. An estimated 90% of the individuals in this population had been caught previously with the use of mist-nets in winter, or in the nest-box during the spring (Aplin et al., 2013). These birds are uniquely identifiable, as upon capture they are fitted with a British Trust for Ornithology (BTO) metal leg ring and plastic leg band containing passive integrated transponder (PIT) tags. In addition, all individuals are aged as first year or adults (second year or older) and sexed (male or female) according to plumage colour (Svensson, 1994). All work had been subjected to review by the Department of Zoology ethical committee, University of Oxford.

3.2.2 Data collection

This study was carried out in the winter between 24th November 2014 and 9th January 2015, across 4 subpopulations within Wytham Woods (see Chapter 2; Figure 2.1) – Great Wood (GW), Common Piece (CP), Brogden's Belt (BB) and Marley Plantation (MP). Among these 4 sub-populations, Brogden's Belt has the highest number of uniquely identifiable individuals, at 167 individuals, while Marley Plantation has the least, at 87 individuals, and is completely isolated from all the others (Chapter 2; Table 2.1). Three sites within each subpopulation were selected for the study (Chapter 2; Figure 2.1). A puzzle-

box that could be 'solved' by sliding a bi-directional door to obtain a mealworm reward was placed at each site over a four-week period (20 days of data collection). Mealworms are a highly preferred and relatively nutritious food source for this species (Aplin et al., 2015). Each puzzle-box contained a perch with an RFID (radio-frequency identification) antenna that could read PIT tags, as well as internal hardware and software that monitored duration and behaviour when at the puzzle-box. Thus, for tagged individuals, both the solving attempt and the time taken to solve could be recorded throughout the experimental period. A tag was present and recorded for 55.4%* of all attempts by great tits at the puzzle-box.

In addition to this data, I obtained visual data from each site by the use of small CamOne Infinity cameras to film the activity at each puzzle box (approximately 47.5h of footage in total). Data from the footages only represent a subset of the full dataset from the puzzle-box data. All sites had at least one filming session (each lasting about an hour), and one site from each subpopulation was additionally filmed twice a week over the four weeks of study. I processed the footage using iMovie (vers. 10.0.3, Apple Inc. 2014), and recorded the time taken to solve (from landing to when the mealworm reward was accessible), as well as seven fine-scale solving techniques used (initial landing position, solving perching position, position of door contact, side of door contact, number of door contacts, solving action and number of the types of solving actions used). A fuller description of the data collection methodology for this study can be found in Chapter 2.

* This percentage was calculated from video-processed data, as opposed to the complete puzzle-box data, as the species of untagged individuals cannot be determined using the puzzle-box data.

3.2.3 Statistical analyses

As the data analysed in this study was longitudinal, I used linear mixed models (LMMs) for the analyses to account for repeated measures. Linear mixed models assume a normal error distribution, which would be violated if efficiency were fitted as the response variable, as efficiency is bounded by 0 and 1. Hence, I used a transformed efficiency measure, log-transformed time taken to solve, as the response variable instead in all analyses, but reported my results by what it meant in terms of efficiency. I only included uniquely identifiable great tits and successful solves in the analyses, so that I could track individuals across time and the efficiency of their solves. Although not including the birds that are unable to be uniquely identifiable may be a confounding factor, it may not be as crucial since it is likely that most birds that learnt to solve would have been sampled. This is because over 90% of individuals were estimated to have been tagged in this population (Aplin et al., 2013; Farine et al., 2015), thus it is likely that occasional antennae malfunctioning could have resulted in more unidentifiable individuals than expected, as opposed to having a sizeable number of untagged birds. Hence, the overall trend of efficiency change over time in most individuals is likely to have been captured by the data used for this study, even if some data points were missing due to the exclusion of unidentifiable individuals.

I performed all the data analysis using R version 3.1.1 (R Development Core Team, 2014), and fit LMMs using the lme4 package in R (Bates et al., 2014).

In summary, I first assessed whether the time taken to solve from the puzzle-box data was accurate enough to be used as a proxy for the supposedly more accurate video-processed data using regression analysis. Next I modelled

the change in efficiency over time using a LMM. Following that, I excluded birds that had learnt how to solve in previous years to remove it as a confounding effect, and investigated individual and social factors affecting this by adding additional fixed effects. I then examined the efficiency of different solving techniques using LMMs, investigated whether individuals change their behaviour over time using two different methods depending on the type of variable, and explored whether efficiency explained population behavioural patterns using correlation analysis. I will elaborate on these methods in the following subsections.

3.2.3.1 Comparison of time taken to solve from puzzle-box and video-processed data

The time taken to solve recorded manually from video-processed data was assumed to be more accurate than times recorded automatically at the puzzle-box data, as there could be recording errors from the puzzle-box. For example, birds landing on certain positions of the perch may not have their PIT tags read immediately when they land, resulting in an under-estimation of the solving time. However, because the sample size available for the puzzle-box data was many times larger for previously naïve individuals (puzzle-box: number of solves=57622, number of individuals=217; video-processed data: number of solves=705, number of individuals=74), the raw puzzle-box data may allow more extensive analyses than that collected by video alone.

To test whether data collected automatically at puzzle-boxes were a good proxy for video-processed data, I performed regression analysis by fitting a random intercept LMM with log-transformed video-processed time taken to

solve as the response variable, puzzle-box time taken to solve as the fixed effect and individual identity as the random effect. Video-processed time taken to solve was log-transformed to prevent violations of LMM assumptions. Then, to test for significance of the fixed term, I performed a likelihood ratio test (LRT) with another LMM without a fixed effect using maximum likelihood estimators (Pinheiro & Bates, 2000).

3.2.3.2 Changes in efficiency over time

Learning curves often follow a power law (Newell & Rosenbloom, 1981; Ritter & Schooler, 2001), and thus I would expect the time taken to solve to decrease over time according to a power function. To test this hypothesis, I first compared the Akaike information criterion (AIC) values for three random slope LMMs: no transformation of variables (linear), log-transformation of the response variable (exponential) and log-transformation of both response and explanatory variables (power), to examine which model best fit the data. I used the time taken to solve as the response variable, observation number (the n^{th} time an individual has solved in the focal winter) as the predictor variable, and used individual identity as a random effect. To test whether there was a significant change in efficiency over time, I performed a likelihood ratio test between the best-fitting model of those described above and a model where there was no predictor variable.

3.2.3.3 Factors affecting solving efficiency

This is the second (areas BB and MP) or third year (areas CP and GW) that puzzle-boxes have been introduced into Wytham Woods. Hence, there would have been individuals (estimated at around 40% of the population in those areas) that have learnt how to solve the puzzle-box in experiments from previous winters. I first examined whether there were overall differences in mean solving efficiency and changes in solving efficiency over time between individuals that had solved in previous experiments ('previously knowledgeable') and those only observed in this experimental period ('previously naïve'). If so, to prevent the confounding effect of prior knowledge, I subsequently only included previously naive individuals in all remaining analyses. The only exception to this was when calculating the overall efficiency of solving techniques, where individuals that solved in previous years were also included. This inclusion is justified as: (1) this analysis was not focused on tracking individual learning over time and thus previous solving knowledge was less of a confounding effect, and (2) this analysis required the use of video-processed data. Given 50% of individuals (making up 61% of solving events) from the video-processed data were previously knowledgeable, including these individuals resulted in much greater power.

Following this, I examined the factors underlying differences in initial solving efficiency between individuals and their change of efficiency over time. These include individual factors such as age and sex, but also social factors such as local density and the overall proportion of knowledgeable individuals in the population. I estimated local density by using the number of solves performed by

other individuals within a 245s time window in the same site prior to each solve. The time window was set at 245s as this was the average duration a group would be foraging around the puzzle-box (Aplin et al., 2015). The date an individual first solved was considered a proxy for the second factor, as the number of knowledgeable and efficient birds increased over time.

To investigate which of these factors significantly influenced the change in efficiency, I fitted each factor separately as an additional fixed effect to the best-fitting random slope LMM in Section 3.2.3.2. Then, I tested the significance of each additional fixed effect and its interaction with log-transformed observation number by using likelihood ratio tests with maximum likelihood estimators.

3.2.3.4 Efficiency of solving techniques

The choice of solving technique used could also influence the change in solving efficiency over time, if solving techniques varied in efficiency. Thus I examined whether certain solving techniques were more efficient than others. For this analysis, I ran each solving technique measure as a fixed effect in a separate LMM model, fitting individual identity as a random effect. As individuals were able to use more than one option for several technique measures within an attempt, I used two variations of solving technique measures, fitted in separate models: (i) each technique combination, and (ii) a subset of attempts using only a single technique option. The former solving technique measure investigates if certain technique combinations were more efficient than others, while the latter solving technique measure investigates the efficiency of each individual solving

technique option. I then performed a likelihood ratio test using maximum likelihood estimators with each of these models and a random-intercept model where the technique measure was removed as a fixed effect, to examine whether the technique measure significantly explained solving efficiency. If there were a significant difference in efficiency found between single options of a technique measure but a visual inspection of the data suggested that it could be due to a single relatively inefficient option, then I repeated the method with the removal of the 'outlier' option.

I also looked at whether there were age differences in the three solving technique measures with the greatest variability in efficiency amongst options. If the solving technique measure is categorical, I used a chi-squared test. If it is continuous, I used a random intercept LMM, with individual identity as the random effect to control for pseudo-replication.

To examine whether changes in efficiency over time were due to changes in the choice of option over time, I used two methods. For categorical technique measures (e.g. solving action), I examined differences in the timing of usage between the most efficient and least efficient option, within individuals found to use both options. To standardise across individuals, I first divided all the observation numbers of each individual by their own maximum observation number. Then I weighted the most efficient and least efficient option for each individual by the mean standardised observation number for each option, and calculated the difference between the options. Differences were deemed to be significant if the 95% confidence internal did not overlap zero. For ordinal technique measures (e.g. number of door contacts), I fitted a random slope LMM with the technique measure as the response to observation number, and

individual identity as a random effect. I then used a likelihood ratio test to test whether observation number significantly explained the technique measure.

Finally, I investigated whether there was an association between the frequency and efficiency of each technique option in the population using Pearson's correlation test in all options except for side (left or right). Across the combined sub-populations, there were no differences in frequency between the sides of door contact, thus no association was assumed between frequency and efficiency. This analysis extends the results in Chapter 2, by examining whether the variation in techniques in the population could be explained by the efficiencies of the different options.

3.3 Results

3.3.1 Measuring time taken to solve using the puzzle-box data

The results suggested that puzzle-box data could reasonably be used in place of video-processed time taken to solve (R^2=0.506; LRT: χ^2=252, df=1, p<0.001). This did not decrease drastically even after the removal of an outlier (R^2=0.483; LRT: χ^2=173, df=1, p<0.001; Figure 3.1). Furthermore, using the puzzle-box data potentially provided much greater statistical power to observe changes over time as the mean (±S.E.) number of observations per individual is 229.8±0.7, compared to 12.3±0.3 for the video data. Thus, in this paper, I used the time taken to solve from the puzzle-box automated data collection to calculate foraging efficiency. The only exception was when examining the foraging efficiency of solving techniques, as solving techniques could only be examined using video-processed data.

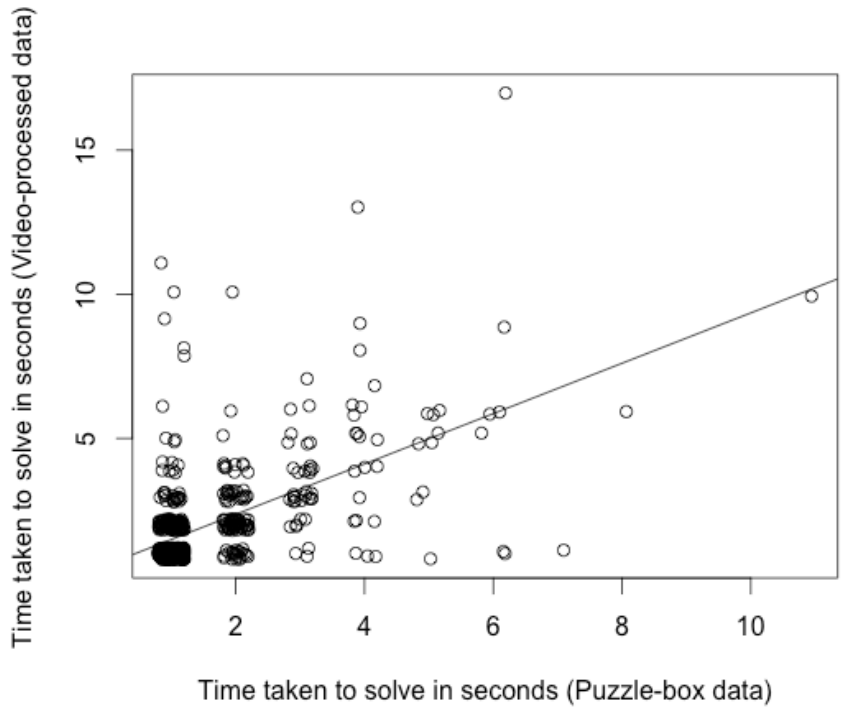

Figure 3.1 Relationship between the time taken to solve an artificial foraging task from data obtained through automatic recording by the software within the puzzle-box, and data obtained through manual processing of video footage, represented by a straight line and after the removal of an outlier,.

3.3.2 Differences between knowledgeable and naïve individuals

Birds that had solved in previous experiments accounted for 42.9% of all individuals observed in this study, and for 59.2% of solving events at the puzzle-boxes. As the preceding experiments were conducted in previous winter seasons, the remainder of individuals largely consisted of birds in their first year and immigrants. Previously knowledgeable individuals were initially more efficient in solving (LMM: est=-0.528, se=0.067; LRT: χ^2=9.45, df=1, p=0.002), with a mean initial solving time of 1.77s as opposed to previously naïve individuals that had a mean of 3.15s. However, previously knowledgeable individuals had a smaller increase in efficiency over time (LMM: est=0.090, se=0.013; LRT:

χ^2=44.0, df=1, p<0.001). Thus, to prevent the confounding factor of previous knowledge, all subsequent results are that of birds seen for the first time in the winter of this study.

3.3.3 Changes in efficiency over time

Temporal changes in the time taken to solve the puzzle-box obeyed a power function. The power model (log-transformation of both response and explanatory variables) had by far the lowest AIC value (power: ΔAIC = 0, exponential: ΔAIC = 848, linear: ΔAIC = 62876) and thus was used to model all further changes in efficiency over time. Solving efficiency increased over time (LMM: est=-0.144, se=0.011; LRT: χ^2=115, df=1, p<0.001; Figure 3.2), with a mean initial solving time of 3.25 seconds (calculated by the mean predicted response variable for the first solve of each individual). This decreases to 1.65 seconds after 50 solves, then to 1.49 seconds after 100 solves and 1.36 seconds after 250 solves. Much of the variance in the data (49%) could be explained by differences in initial solving efficiency between individuals.

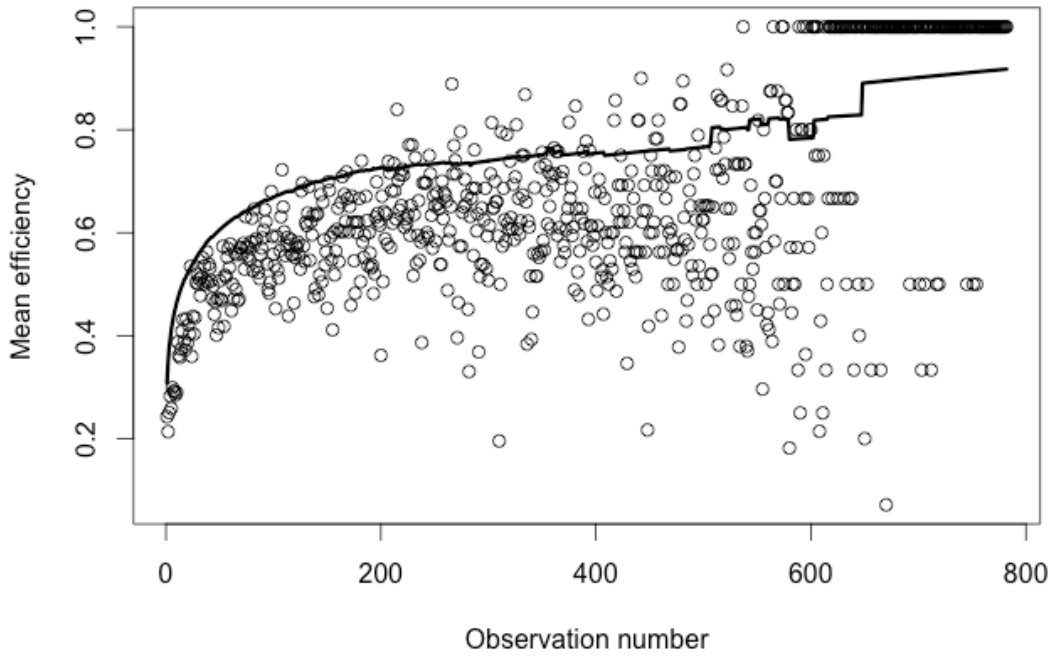

Figure 3.2 Increase in mean solving efficiency over observation numbers (n^{th} time an individual solved in the focal winter). Each point represents the mean efficiency across individuals at each observation number. The power curve is based on the mean predicted solving efficiencies over observation numbers using a random slope linear mixed model, with log-transformed time taken to solve from the puzzle-box data as a response to log-transformed observation number, and individual identity as a random effect.

3.3.4 Factors influencing solving efficiency and its change over time

3.3.4.1 Individual factors: age and sex

Age (first year or adult) was known for 96.0% tagged individuals (68 first years, 51 adults); sex was known for 69.4% of individuals (54 males, 32 females). 92.2% of previously-naïve adults were not immigrants, but had been ringed as nestlings. There was no effect of sex on either initial solving efficiency or the change in efficiency over time (Table 3.1). By contrast, there was a significant influence of age on both initial solving efficiency and the change in solving efficiency over time. First years had a lower initial solving efficiency (LMM: est=0.465, se=0.102; LRT: χ^2= 11.0, df=1, p<0.001) but a larger increase in solving efficiency (LMM: est=-0.075, se=0.022; LRT: χ^2= 11.6, df=1, p<0.001).

Table 3.1 No effect of sex on initial solving efficiency and the change of efficiency over time. Likelihood ratio tests with maximum likelihood estimators were performed to test the significance of the interaction between sex and log-transformed observation number, or sex as an additional fixed effect. The chi-squared statistic (χ^2), degrees of freedom (df) and p-values are presented, with significant p-values (p<0.05) marked by an asterisk (*).

Model 1 fixed effects	Model 2 fixed effects	χ^2	df	p-value
Log(observation number)+sex	Log(observation number)	1.78	1	0.182
Log(observation number)*sex	Log(observation number)+sex	0.46	1	0.498

3.3.4.2 Social factors: local density and number of knowledgeable individuals

Local density (estimated as the number of solves by others within a 245s window before the focal individual) had a significant influence on both initial solving efficiency and the change in solving efficiency over time. Higher densities were correlated with greater initial solving efficiency (LMM: est=-0.010, se=0.003; LRT: χ^2=4.05, df=1, p=0.044), but a smaller increase in efficiency over time (LMM: est=0.002, se=0.001; LRT: χ^2=19.5, df=1, p<0.001).

The date when individuals first solved did not have a significant effect on the initial solving efficiency (LRT: χ^2=0.032, df=1, p=0.859). However those that first learnt to solve later in the experimental period had a greater increase in efficiency over time (LMM: est=-0.006, se=0.002; LRT: χ^2=6.91, df=1, p=0.009). There was no significant interaction between social density and the date that individuals first solved (LRT: χ^2=0.820, df=1, p=0.365), nor any significant three-way interaction between log-transformed observation number, social density and the date that individuals first solved (LRT: χ^2=3.61, df=1, p=0.057).

3.3.5 Comparing the relative efficiency of solving techniques

Variation was found in six out of seven fine-scale aspects of solving behaviour: initial landing position, solving perching position, position of door contact, number of door contacts, solving action, and variety of solving actions used (see Chapter 2). There were significant differences in efficiency between combinations of solving technique options for all solving technique measures that could have had more than one option per solve (Table 3.2a; all $p<0.05$). When each single technique option was examined, there were still significant differences in efficiency between all solving behaviours, other than solving perching position (Figure 3.3, Table 3.2b). The position of door contact and initial landing position had obvious outlier options that appeared to be much less efficient than others - contacting the front of the door and landing on a non-perch position respectively (Figure 3.3). When these options were excluded, only initial landing position showed significant differences between solving technique options (Table 3.2c).

Table 3.2 Efficiency of solving techniques. The difference in efficiency of (a) combinations of solving technique options, (b) single solving technique options, and (c) single solving technique options after removing outlier options. Differences were investigated using a likelihood ratio test between linear mixed models with and without the solving technique measures (a-c) as fixed effects. The chi-squared statistic (χ^2), degrees of freedom (df) and p-values are presented, with significant p-values ($p<0.05$) marked by an asterisk (*).

(a) Combinations of solving technique options

Solving technique measure	Number of combinations	χ^2	df	p-value
Side of door contact	4	47.8	3	<0.001*
Solving perching position	37	107	36	<0.001*
Solving action	17	117	16	<0.001*
Door contact position	21	143	20	<0.001*

(b) Single technique options

Solving technique measure	Number of options	χ^2	df	p-value
Side of door contact	2	12.7	1	<0.001*
Initial landing position	11	22.2	10	0.014*
Solving perching position	11	11.4	10	0.330
Solving action	4#	13.7	3	0.003*
Variety of solving actions used	4	37.1	1	<0.001*
Door contact position	5	12.2	4	0.016*
No. of door contacts	15	348	1	<0.001*

There are 5 technique options for solving action, but the "foot" option was always performed in combination with other techniques and never performed as a single option.

(c) Single technique options after removing outliers

Solving technique measure	Number of options	Outlier removed	χ^2	df	p-value
Initial landing position	10	Non-perch positions	20.7	9	0.014*
Door position	4	Door front	5.15	3	0.160

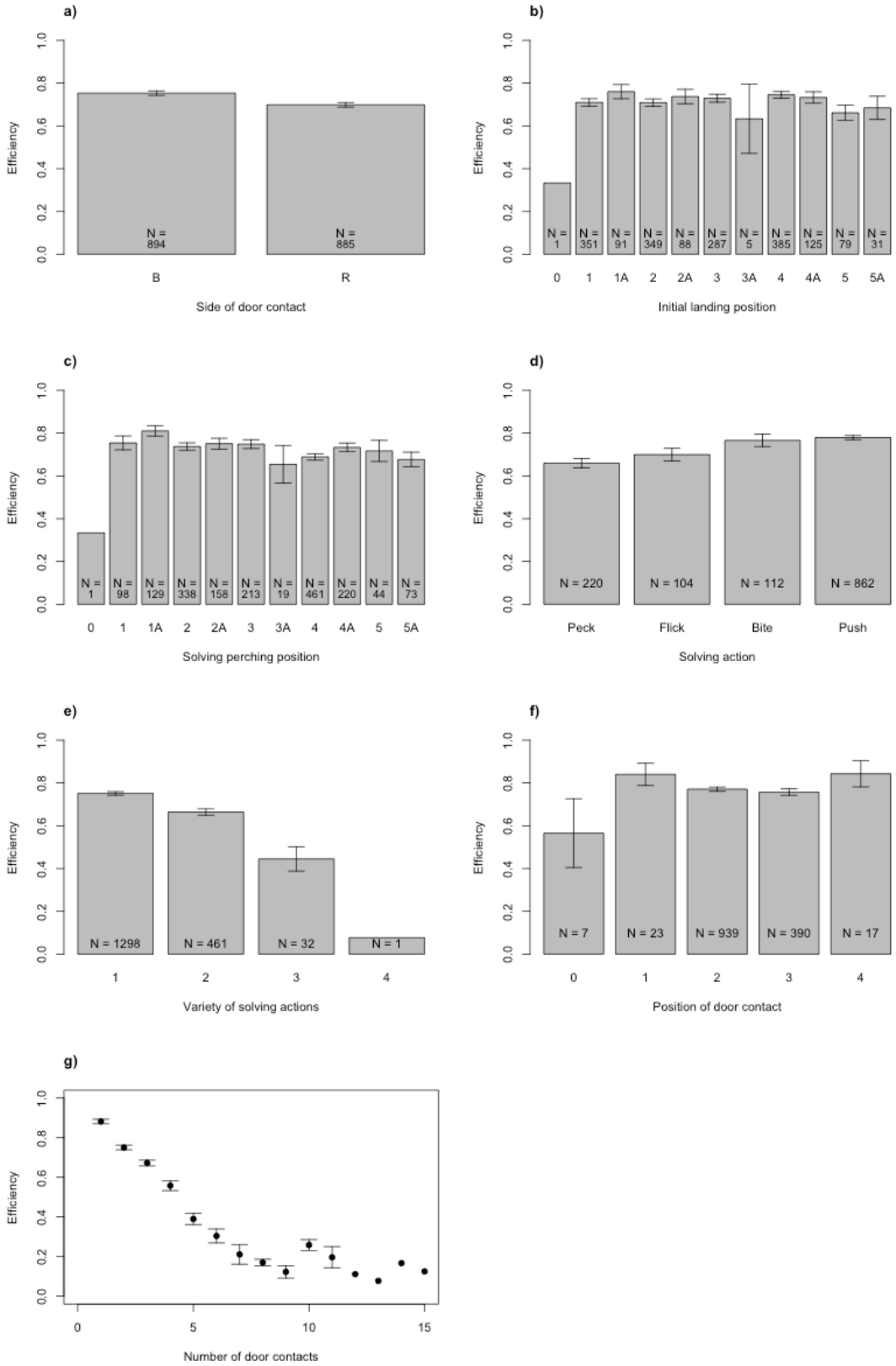

Figure 3.3 Mean efficiencies of single solving technique options for 7 solving technique measures (error bars indicating the standard error of the mean, and 'N' indicating sample size).

However, except for the type of solving action, variety of solving action and number of door contacts, the differences between the options (excluding outliers) were relatively small (Figure 3.3). Biting and pushing were the most efficient solving actions, while pecking was the least efficient (Figure 3.3d). Solving events were less efficient when multiple types of solving action were used (LMM: est=0.165, se=0.027; LRT: χ^2=37.1, df=1, p<0.001; Figure 3.3e). Finally, a larger number of door contacts were correlated with less efficient solving times (LMM: est=0.181, se=0.009; LRT: χ^2=348, df=1, p<0.001; Table 3.2b).

Adults generally used more efficient solving techniques than first-years. They performed more pushes and fewer pecks (Chi-squared test: χ^2=71.7, df=3, p<0.001; Figure 3.4a), and used fewer door contacts to solve (LMM: est=0.590, se=0.171; LRT: χ^2=11.6, df=1, p<0.001; Figure 3.4b), even though there was no age difference in the variety of solving actions used (LMM: est=0.065, se=0.055; LRT: χ^2=1.41, df=1, p=0.235).

Despite differences in efficiency, individuals did not change their techniques to more efficient techniques over time, except for the variety of solving actions used (Table 3.3). Over time, individuals tended to use fewer solving actions in a solving event (LMM: est=-0.005, se=0.002; LRT: χ^2=5.61, df=1, p=0.018). I also found no association between the overall frequency in the population of fine-scale solving behaviours and their efficiency, other than the number of door contacts (Table 3.4).

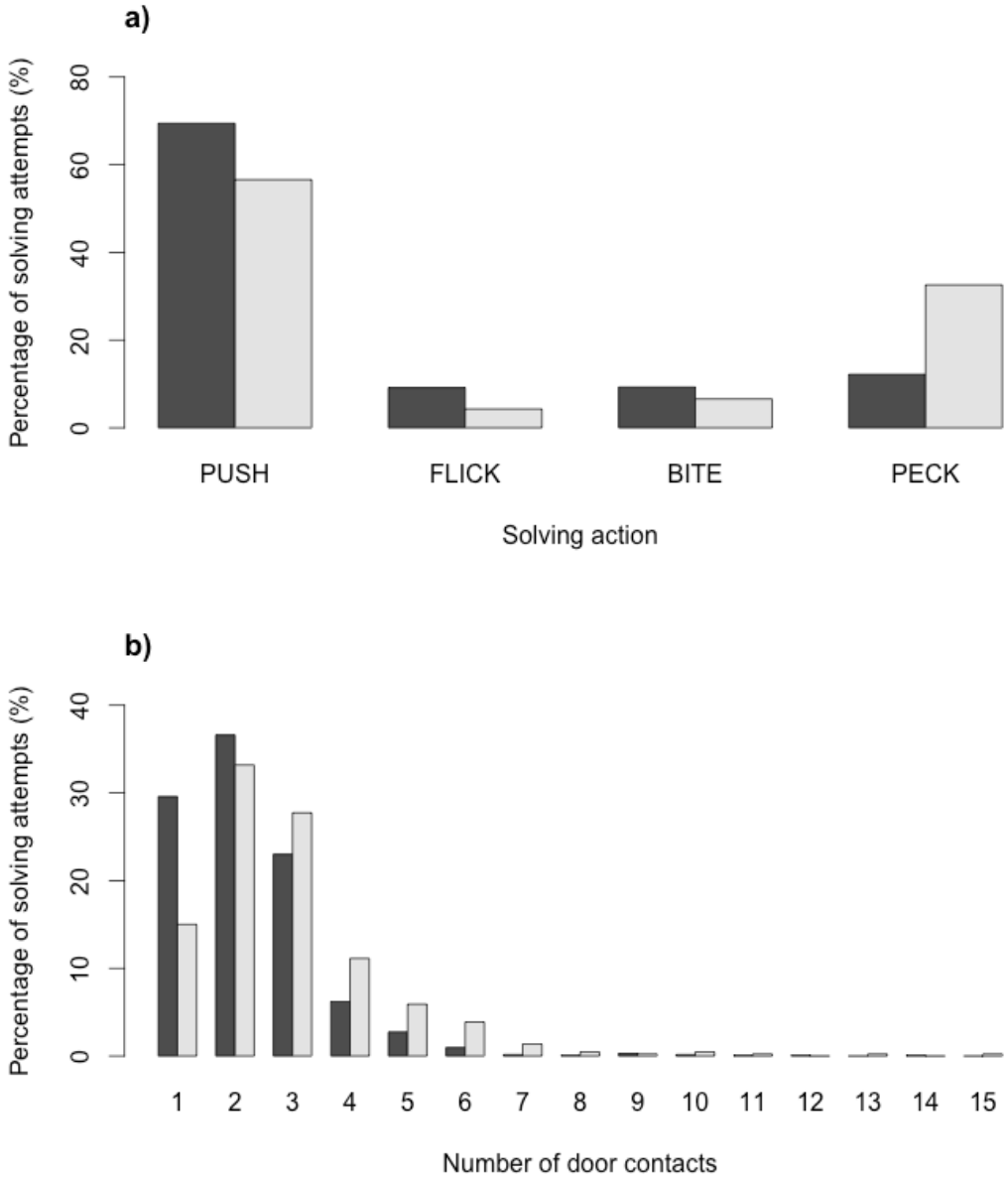

Figure 3.4 Age differences in (a) solving actions, and (b) number of door contacts used. Adults (second year or older) are represented in dark grey, while first-years are in light grey.

Table 3.3 Changes in the solving technique option choice by individuals over time, for solving technique measures with differences between non-outlier options. (a) Categorical solving technique measures: The difference in standardised observation number between the least and most efficient technique option of each measure with 95% confidence intervals (CI). (b) Ordinal solving technique measures: Results of a likelihood ratio test between random slope linear mixed models with and without observation number as a fixed effect, and with individual identity as the random effect. The chi-squared statistic (χ^2), degrees of freedom (df) and p-values are presented, with significant p-values ($p<0.05$) marked by an asterisk (*).

(a) Categorical solving technique measures

Solving technique measure	Mean difference	95% CI
Side of door contact	-0.330	-4.86, 0.72
Initial landing position	0.024	-1.02, 1.04
Solving action	-0.292	-2.45, 0.695

(b) Ordinal solving technique measures

Solving technique measure	χ^2	df	p-value
Variety of solving actions	5.61	1	0.018*
Number of door contacts	0.69	1	0.407

Table 3.4 Association between frequency and efficiency of each single technique option within the solving technique measures, using Pearson's correlation test. Significant p-values ($p<0.05$) are marked by an asterisk (*).

Solving technique measure	R	t	df	p-value
Initial landing position	0.470	1.60	9	0.145
Solving perching position	0.368	1.19	9	0.265
Solving action	0.539	0.90	2	0.464
Variety of solving actions	0.795	1.79	2	0.215
Position of door contact	0.095	0.17	3	0.879
Number of door contacts	0.912	8.03	13	<0.001*

3.4 Discussion

3.4.1 Summary of key results

In this paper, I used automated monitoring of great tits solving an artificial foraging task to investigate the relationship between social learning and foraging efficiency. For the individuals observed for the first time in this experiment, their initial solving efficiency and change of efficiency over time were likely influenced by both individual and social factors. In addition, there were differences in efficiency between most solving technique measures, but changes in an individual's solving efficiency were largely not explained by a change in technique. Rather, it appeared that individuals were both reducing variability in their solving actions and improving their preferred techniques. Population patterns in solving behaviour were also not explained by efficiency, except for the number of door contacts.

3.4.2 Potential explanation of results

3.4.2.1 Individual effects on foraging efficiency

Age was the only individual factor examined in this thesis that had an effect on foraging efficiency. Age differences in foraging in birds have been posited to be due to developmental constraints in juveniles (Marchetti & Price, 1989), such that adults could have been stronger and so used more efficient solving actions. Alternatively, as majority of previously naïve adults were residents in my study, it could be that they had observed from a distance in previous years without approaching the puzzle-box. That could have given them

a head start in solving the puzzle-box over the first-years which would definitely only have seen this task for the first time. By contrast, it was expected that sex did not affect foraging efficiency or learning curves, as my experiment was performed outside of the breeding season (Galea, Kavaliers & Ossenkopp, 1996).

3.4.2.2 Social effects on foraging efficiency

My results suggested a positive influence of local density, but no effect of date of initial solve, on initial solving efficiency. By contrast, both local density and the date of initial solve had a significant impact on the change in solving efficiency over time. However, their effects seemed contradictory, as higher local density (possibly resulting in greater opportunities to observe efficient solutions performed by others) but an earlier date of initial solve (which likely meant fewer efficient and knowledgeable individuals) resulted in a lower change in efficiency over time. Yet, no interaction effects were found between the two.

A possible explanation for the differences and apparent contradiction between the social effects on initial solving efficiency and change in efficiency over time respectively, could be due to the effects acting at different scales. The date of initial solve was a rough proxy for the number of knowledgeable individuals, but the actual number would vary with each flock, measured by local density. In addition, there is a trade-off between the cost of competition and benefits from being in groups, such as social learning or group defence (Seppänen et al., 2007; Beauchamp & Fernández-Juricic, 2005), thus local density could be a better reflection of competition than social learning in this experiment. A greater effect of competition than social learning could be a

reason why local density, but not date of initial solve, had an influence on initial solving efficiency. Individuals that do not solve fast enough may be displaced under high competition, hence the first time an individual solved successfully may have to be relatively fast. Alternatively, at higher local densities, there could be a lower need for vigilance and so individuals are able to solver faster initially.

Later in the experiment, there would be a larger number of more efficient solvers, which could provide more opportunities to not just observe more solutions, but to observe more efficient solutions (Griffin & Guez, 2015). Thus, birds that solved later should better be able to become more efficient. However, it is probably only under lower local densities that slower solvers would be more likely to solve successfully without being displaced and practise what they had observed during instances with higher local densities. This 'room for improvement' of the slower solves captured during lower local density instances could then have led to the observation of a higher population-level change in efficiency over time.

However, it is important to note that local density effects and the effect of the date of initial solve could be explained by other factors than social learning. For example, as mentioned previously, local density could be more a proxy of the level of competition or vigilance, and the date of initial solve could reflect the body condition of individuals. Thus, while this study suggests that social learning is likely to be important in influencing foraging efficiency, it is also important to examine this more closely in future using more direct measures of social learning.

3.4.2.3 Role of technique choice on learning curve

The initial solving efficiency varied between individuals, and almost half of the variation in the data could be explained by individual identity. A possible reason could be due to individual preferences for certain techniques over others, as individuals were repeatable in the solving techniques they used (see Chapter 2), combined with reasonable differences in efficiency among some of the solving technique options. These efficiency differences between techniques were expected, as different motor actions often vary in efficiency in solving a task, as seen in keas (Werdenich & Huber, 2006) and New Caledonian crows (Auersperg et al., 2011). I would also expect individuals to be more efficient with a lower number of door contacts and types of actions used, as it takes time to perform each contact and action; this was found to be the case.

As several of the solving technique measures had differences in efficiencies between options, the improvement in efficiency over time in individuals could be due to individuals choosing more efficient techniques over time. I did not find evidence for this, however, except for a small effect in the variety of solving actions used. Thus, individuals were becoming more efficient over time by becoming more efficient and specialised in their preferred techniques, rather than by choosing more efficient techniques over time. This is consistent with results in Chapter 2 where I found that solving techniques were repeatable within individuals, and suggests some level of conservatism in behaviour (Hrubesch, Preuschoft & van Schaik, 2009).

Great tits could have based their choice of solving action for each solve on a factor, other than efficiency, that did not vary with time. With each subsequent

solve, they may have become more sure of matching their actions to that unknown factor, and so become more specialised during each solve. This could be an individual-level factor like bill size or body condition, but could also be a social factor such as the technique of the birds that solved before it, suggesting social learning. Another explanation could be that most of the solving technique measures only had slight differences in efficiency, thus it might have been more beneficial for individuals to improve in the technique they first used to solve through practice, than to try other techniques and spend time learning about the efficiencies of solving techniques.

3.4.3 Implications of results

3.4.3.1 Social learning impacts on improvement in foraging over time

My results suggested not only an influence of age, but also social influences such as local density on solving efficiency, a proxy for foraging efficiency, and its improvement over time. This meant that social processes probably do not just have an important role to play in the acquisition of the task, as shown in in Chapter 2 of this thesis (also see Aplin et al., 2015), but may also play a role in the improvement of individuals' ability to solve the task thereafter. Being a faster solver is important to the fitness of an individual as it reduces the likelihood of being displaced, but also enables a greater rate of food intake.

My results suggest a possibility that having more efficient examples in the population in general, but lower competition at a local scale, could help individuals improve faster in solving. It is thus likely that there was an involvement of social learning in the improvement of foraging over time, though

future work should examine this further by using more direct measures of social learning such as examining the efficiency of other individuals observed to solve prior to each attempt.

3.4.3.2 Social learning impacts on population patterns

The observed patterns of preference for certain techniques over others observed in Chapter 2 could not be explained by differences in the efficiency of solving techniques. This could imply that population preferences of solving techniques are either a reflection of the solving techniques used by initial demonstrators, suggesting an effect of social learning, or due to inherent preferences in great tits. However, because the frequency of techniques varies across sites (see Chapter 2), social learning seems a more likely explanation. Thus, my findings give additional support to the suggestion made in Chapter 2 that observational learning is the potential mechanism behind the initial learning of techniques to solve the puzzle-box.

3.4.3.3 Implications for optimal foraging theory

Optimal foraging theory states that the foraging strategy that results in maximum fitness would be favoured by natural selection and thus be advantageous for individuals to adopt (for reviews, see Krebs, Stephens & Sutherland, 1983; Pyke, 1984). The classical view of this theory predicts, in our case, that individuals would choose the solving technique that is the most efficient, to maximise the benefit-to-cost ratio, so as to maximise fitness. For each

solving attempt, the benefit is constant (energy given by one mealworm), whereas the cost varies depending on the time taken to solve. However, I found no association between the frequency and efficiency of most solving technique measures, and individuals were generally improving their solving efficiency by being more efficient in the use of their preferred techniques, instead of learning to use more efficient techniques to improve their solving efficiency.

My result thus contradicts the initial prediction based on optimal foraging theory, and thus has implications on how we understand and apply this theory in practice. It may be too simplistic to solely use the rate of energy gain to determine which technique is optimal. Other factors such as body condition could influence foraging decisions (Houston & McNamara, 2014). My results also suggest an impact of social learning, and social effects may have had an effect on foraging efficiency (e.g. Kao et al., 2014). In addition, my results found that differences in efficiency between options for most solving technique measures were small, which meant that there could be less emphasis on optimisation of foraging techniques. This should be considered in studies looking at optimal foraging theory by investigating more deeply the relationship between the choice of foraging techniques and foraging efficiency.

3.4.4 Limitations and future work

There are several limitations to the approach used in this study. First, my study found no population-level association between preference and efficiency of solving techniques were observed, but this does not imply the lack of an association at the individual level. The efficiency of each technique could differ

with individuals, as found in a previous study (Partridge, 1976). There may also be individual differences in cognition enabling certain individuals to be more efficient initially or improve their efficiency more over time (Cole, Cram & Quinn, 2011). Furthermore, there may be partial preferences in foraging, such that the optimal technique may not always be chosen (McNamara & Houston, 1987), as behaviour is stochastic and not deterministic.

Also, here I used observation number (the n^{th} time an individual solves) as a measure of time for each individual. I did so as individuals often improve with practice, or by watching others, which would only occur if the individual were present at the puzzle-box, and thus observation number is likely to be the best measure of time. Yet the actual time interval between consecutive observation numbers varied between and/or within individuals, and time taken between consecutive solves may have influenced the solving efficiency as well. For example the memory of spatial positions in tits is reduced over time (Healy & Krebs, 1992). It would thus be useful for future work to investigate how the interval between solves affects solving efficiency, to obtain a clearer idea of how solving efficiency changes over time.

Furthermore, not all solving attempts were successful, but only successful solves were used as a measure of solving performance in this study. Another measure of solving performance could be the proportion of solving attempts that were successful, as opposed to the efficiency of successful solves. The individual and social factors investigated in this study could have affected the success of solves in ways which could be different from the efficiency of solves. However, it would be unlikely since being able to solve faster would probably increase the chances of a successful solve, by reducing the likelihood of being displaced

halfway during an attempt. Nonetheless, it would be valuable to investigate the effect of different factors on the probability of success of solves, and whether there is a relationship between both measures.

Despite these limitations and the need to address these in future research, my study opens up the importance of a new area of social learning – its role in the temporal variation in foraging performance. Thus, future social learning research should also focus on this area when examining the impact of social learning on the evolution and ecology of different species. A comparative approach may also be useful, to test the hypothesis that species that do not forage socially would be more reliant on individual factors to improve their foraging efficiency over time.

Future work could also focus on the scale by which social learning could affect foraging efficiency at a deeper level, as my results had suggested the possibility of a greater importance of local social effects. Besides, my study used rough proxies for social learning, which suggested that social learning is likely to impact improvements in foraging efficiency, but future studies should aim to study this using more direct measures of social learning such as examining the efficiency of other individuals that solved recently prior to each attempt.

3.4.5 Conclusions

In summary, I found that social learning likely had an impact on the improvement in foraging efficiency over time in great tits. This probably through improvements in each individual's preferred foraging technique rather than choosing more efficient techniques over time. I also found additional support for

social learning shaping the spatial patterns in foraging behaviour at the population level, as efficiency was ruled out as a cause. Both the acquisition new skills and improvement of existing skills could potentially have significant impacts on fitness. By finding social influences at both these stages, this study demonstrates the need for future work on social learning to not just to be solely focused on its effect on skill acquisition, but also on the improvement of skills over time.

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CHAPTER 4

Mechanisms and processes underlying social learning in great tits (*Parus major*)

Chapter 4: Mechanisms and processes underlying social learning in great tits (*Parus major*)

Abstract

Social learning is a potential process by which animals acquire adaptive behaviours. Despite the widespread use of social learning in great tits (*Parus major*), few studies have examined its underlying mechanisms and processes in this species, although this may be informative of the evolution of social learning. I conducted an open-diffusion experiment to investigate social learning mechanisms and processes in great tits, through the use of a two-action foraging task. I found support for the possibility of fine-scale local enhancement or emulation, on top of local and stimulus enhancement, as the mechanisms underlying social learning of foraging in great tits. I also found that social learning propensity is associated with the activity of demonstrator individuals. Although my results remain inconclusive due to low sample size, it is useful as a methodological exploration of using an open diffusion experiment with a two-action task to investigate social learning mechanisms in great tits, and fits in well with the ecology of great tits. Finding that fine-scale local enhancement is partially responsible for social learning of foraging in great tits, implicates our understanding of formation of traditions and the presence of conformity.

Keywords: great tits, open diffusion, *Parus major*, social learning mechanisms, two-action method.

4.1 Introduction

Social learning, where individuals modify their behaviour after observing or interacting with others or their products (Heyes, 1994), has been a topic of great interest in wide-ranging fields for decades. In particular, the past couple of decades have seen multiple studies attempting to investigate the processes behind social learning, especially for social learning mechanisms such as imitation (Akins, Klein & Zentall, 2002; Fawcett, Skinner & Goldsmith, 2002; Kis, Huber & Wilkinson, 2015). Studying the mechanisms underlying social learning not only allow us a glimpse into animal cognition (for example, imitation is often thought of as a more 'complex' mechanism due to the need of solving the correspondence problem of translating visual input into motor output; Heyes, 1993), but also allow us to understand the mechanisms that could lead to the development of traditions and culture (Franz & Matthews, 2010). Furthermore, it gives us a better understanding of how adaptations to the environment via social learning could have evolved in different species (Webster & Laland, 2013).

The bulk of social learning studies have been done on captive individuals, but this has been criticised for the lack of ecological validity (Kendal, Galef & van Schaik, 2010). For example, keas have been found to learn socially in captivity (Huber, Rechberger & Taborsky, 2001) but not in the wild (Gajdon, Fijn & Huber, 2004). Although more studies have now focused on studying social learning in the wild (Galef, 2004; Thornton & Malapert, 2009), it has remained difficult to distinguish between social learning mechanisms in wild populations, due to the lack of experimental control. One way to mitigate this difficulty is to move away from dyadic captive experiments to more naturalistic open-diffusion captive

experiments (e.g. Whiten & Flynn, 2010; Aplin, Sheldon & Morand-Ferron, 2013), but this is still restricted to captive individuals. Another way is through field experiments coupled with modelling, such as the stochastic mechanism-fitting model approach used by Hoppitt et al. (2012). Yet another way that might be useful is to combine both field and captive approaches, to investigate social learning mechanisms in a repeatable yet ecologically relevant manner.

One way to distinguish between social learning mechanisms employed in field and captive experiments is the two-action method by Dawson & Foss (1965), which allows social facilitation and local and stimulus enhancement to be controlled for (Galef, Manzig & Field, 1986). This method uses a task with two possible solutions, with two treatment groups each with a demonstrator trained to solve the task using one of the solutions, and a control group with no demonstrator. Social learning can be inferred if there are differences in solving by naïve individuals in the treatment groups compared to the control group, and imitation inferred if naïve individuals are more likely to perform the same solution as their demonstrators. However, this method has been criticised, as the apparent 'imitation' could be a result of individuals learning about the affordances of the task's manipulandum instead of direct copying of the demonstrator's action (Zentall, 2001), and the two actions could differ in the ease of performance (Hopper et al., 2007). Thus, a bidirectional procedure was developed, which was able to control for social facilitation and coarse-scale local and stimulus enhancement while allowing both solutions to be performed by the same action, just in different directions (Heyes & Dawson, 1990). However this procedure also has limitations, as it cannot rule out fine-scale local and stimulus enhancement to the different contact points (Aplin et al., 2015; Hoppitt & Laland,

2013). To overcome these limitations and reliably identify imitation, an experiment needs to be designed such that individuals are able to solve both in the same direction and same action as their demonstrators in the bidirectional and two-action task respectively.

In addition to studying social learning mechanisms, there is also value in studying factors that influence the process of social learning (Coussi-Korbel & Fragaszy, 1995). Understanding both aspects would provide a fuller understanding of how culture could have evolved, and the role of social learning in the acquisition of adaptive behaviours. For example, as certain social learning mechanisms may involve an element of asocial learning (indirect social learning), and some argue that similar mechanisms may underlie both types of learning (Heyes, 1994; Heyes, 2012), there may be a correlation between an individual's innovative and social learning ability. Yet, trade-offs between the two have also been purported in the literature (Kendal et al., 2005; Burkart, Strasser & Foglia, 2009). Examining this relationship may reveal insights as to whether the underlying mechanism for both types of learning are the same, with implications for our understanding of the evolution of animal cognition and culture (Reader, 2003; Heyes, 2012). However, only a few studies have looked at the intra-specific relationship between individual innovative abilities (or innovation) and social learning capabilities, for example in pigeons (Bouchard, Goodyer & Lefebvre, 2007), common marmosets (Burkart, Strasser & Foglia, 2009) and blue tits (Aplin, Sheldon & Morand-Ferron, 2013). In addition to innovative ability, there could be other factors influencing the process of social learning. Often, studies have focused on other individual factors such as age, sex and personality (Smith, King & West, 2002; Choleris & Kavaliers, 1999; Marchetti

& Price, 1989). Fewer have examined social influences, such as producer-scrounger games (but see Caldwell & Whiten, 2003; Giraldeau & Lefebvre, 1987; Fritz & Kotrschal, 1999), even though social factors are key in affecting social learning (Coussi-Korbel & Fragaszy, 1995).

Social factors might particularly influence social learning propensity in species that live in social groups, such as great tits (*Parus major*) in winter, which form fission-fusion foraging flocks. Great tits have been found to use social learning in a number of different contexts: such as foraging (Aplin et al., 2015; Krebs, MacRoberts & Cullen, 1972) and song learning (Fayet et al., 2014). Despite this, there has been a paucity of studies examining the mechanisms underlying social learning in great tits. The main form of social learning mechanism thought to be at work in such species that forage socially is that of local enhancement (Krebs, MacRoberts & Cullen, 1972; Pöysä, 1992). Great tits can employ stimulus enhancement, as wild-caught great tits taught to solve a puzzle-box to yield a reward were able to solve identical puzzle-boxes placed in the wild when released from captivity much faster than their naïve counterparts (Aplin et al., 2015). However there could be more complex mechanisms at work as well. For example, observational learning had been suggested as a possible mechanism in captivity (Sasvári, 1979), and also in the wild (Aplin et al., 2015).

Here, I performed an open-diffusion captive experiment using a two-action task, to investigate (i) the social learning mechanisms underlying foraging and (ii) factors affecting social learning propensity in great tits. Previously, field experiments using a bidirectional task, which could be solved by sliding a door either left or right to obtain a mealworm reward, indicated conformity in the direction of solving and suggested the presence of observational learning in wild

great tits (Aplin et al., 2015). However, this could also be due to fine-scale local enhancement to the side of door contact, as suggested by my field experiment looking at fine-scale details using the same task, which found positive assortment of the social network based on the position of door contact (see Chapter 2). However, as the fine-scale body movements of the original demonstrators were not controlled for in either field experiment, no conclusive evidence could be drawn from this study. In this paper, I complement the field experiment approaches that used a bidirectional control procedure by using a captive two-action experiment, to obtain greater control to distinguish between different mechanisms, while reducing limitations of the bidirectional control procedure.

4.2 Methods

4.2.1 Subjects

24 wild-caught great tits were used in this experiment. They were caught using mist-nets from three different sites within Oxfordshire: John Krebs Field Station, Bagley Woods and Wytham Woods, between 4th and 21st February 2015. Upon capture, they were fitted with a British Trust for Ornithology (BTO) metal leg ring, a plastic leg band with a Passive Integrated Transponder (PIT) tag, and a unique colour ring for easy visual identification. They were also aged and sexed according to plumage characteristics (Svensson, 1994). There were equal numbers of males and females caught, and a total of 10 adults and 14 juveniles.

The great tits were caught in three groups of eight, and each group was housed in eight separate indoor cages in the same room within 1.5h of capture. Each 45 x 45 x 68 cm wire-mesh cage had an attaching roost box, and contained a bowl of water and a bowl with a mix of peanut granules, sunflower seeds and live mealworms. The lights in the room were set to gradually turn on and off at 7.30am and 5.30pm to mimic natural light regime. Subjects were housed overnight before being transferred into a 5 x 5 x 3m outdoor group aviary the next morning. The outdoor aviary contained 10 nest-boxes, tree branches, two large bowls of water, a bowl of live mealworms, and a freely-accessible feeder containing peanut granules and sunflower seeds. The subjects were allowed to settle in the aviary for a full day before the social learning experiment was conducted on the third and fourth days of captivity. During experimental days, there were no live mealworms provided. On the fourth day after the completion of the experiment, the subjects were caught in the nest-boxes after dark, and

transferred back into their indoor cages. The light regime of the housing room was set to gradually turn off 1h after the birds were transferred, to allow the birds to settle. They were subsequently released the following morning after removing their colour rings.

4.2.2 Experimental procedure

4.2.2.1 Demonstrator training

Two of the three groups were allocated to a treatment each: 'swing' and 'slide', and the last group served as a control. The control group contained eight naïve individuals, while the 'swing' and 'slide' groups had seven naïve individuals and one demonstrator each. To reduce the number of confounding factors, I held the age and sex of demonstrators constant; both were adult females. I specifically chose birds that had previously learnt how to solve a puzzle-box, which had a bidirectional sliding door that could be slid to obtain a mealworm reward. This reduced the amount of training required as I expected that they would (i) not be as neophobic towards the puzzle-box, and (ii) be motivated to approach and solve the puzzle by prior experience of food reward. This puzzle-box was opaque and cuboid-shaped, and contained an internal circuit board to record the identity of individuals that had landed and/or solved, as the PIT tags of the individuals would be detected by radio-frequency identification (RFID) antenna within the perch attached below the door. A fuller description of this puzzle-box could be found in Aplin et al. (2015) and Chapter 2 (Section 2.2.2) of this thesis.

For this particular study, I modified the puzzle-box so that it was a two-action task rather than a bidirectional task. I replaced the bidirectional door with

a door that could be opened by either sliding to the left, or swinging outwards, supported by a hinge attached to the left side of the door (Figure 4.1). For both actions, the location of contact is the same (on the right side of the door), to control for fine-scale local or stimulus enhancement during learning.

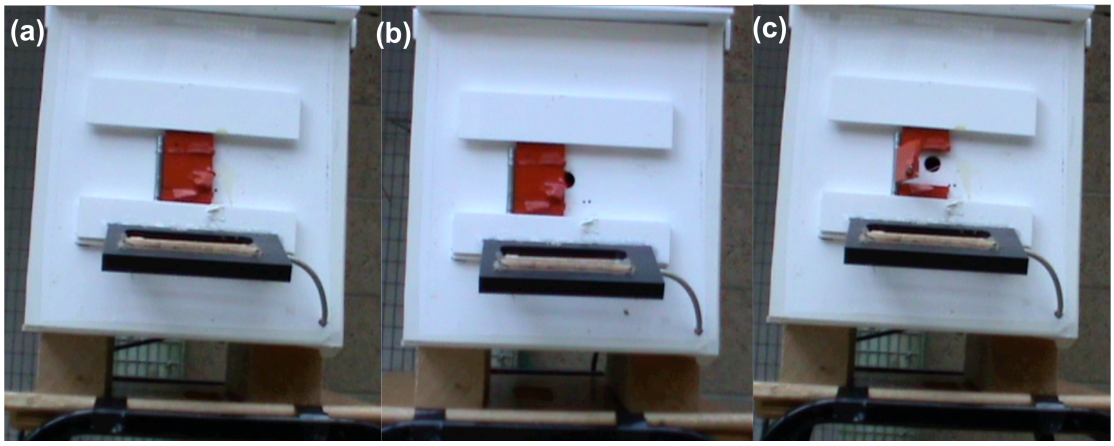

Figure 4.1 Various positions of the door of the puzzle-box: (a) original (unsolved), (b) after solving by sliding, and (c) after solving by swinging.

Due to the modification, the demonstrators had to be trained to solve the modified puzzle-box. Both demonstrators were food-deprived for up to an hour before training. They were then transferred into a large indoor training room where the two-action puzzle-box has been placed. The demonstrators, which had solved the bidirectional puzzle-box previously, were expected to slide the door when presented with the two-action puzzle-box. Thus, it was easier to train the 'slide' demonstrator than the 'swing' demonstrator. For the 'swing' demonstrator, I used tape to block the door from being slid. I then employed a stepwise progressive training approach by first leaving the door swung fully

open and reward fully accessible, then gradually leaving a smaller gap between the door and frame, until the demonstrator learnt to swing the door open. Afterwards, I removed the tape so that the door could potentially be slid, and observed the demonstrator's solves to ensure that it would solve by swinging instead of sliding. I considered the demonstrator trained after it had solved by swinging for three times consecutively. For the 'slide' demonstrator, it was easier to train as it had previously learnt to slide the door to obtain a reward, and had solved using the same side as in this experiment. I observed its solves to ensure that it would solve by sliding, and considered it trained after it had solved by sliding for three times consecutively. During the subsequent experiments, both demonstrators were observed to be fully consistent in the solving technique used. Training took no more than a day, and I performed the training on the day of capture after the individuals have had 2h to settle in their indoor cages.

4.2.2.2 Innovative ability

To quantify an individual's ability to innovate, I presented each individual with a novel lever-pulling task, as characterised in Cole, Cram & Quinn (2011). I used a transparent plastic tube containing a platform supported by a toothpick lever in this task, with two live waxworms on top of the platform and a plastic dish directly below the tube to catch those waxworms when the task was solved. I also placed a waxworm in the dish at the beginning of the task to attract the individual to the tube and reduce neophobia. To solve the task, individuals had to pull and remove the lever so that the platform and waxworms dropped onto the dish below. All individuals except the two demonstrators were presented with

the task 1h before darkness on the evening of capture, and for 2h after light the following morning, to reduce disturbance. All individuals ate the free waxworm, and 54.5% of individuals managed to solve the task. This proportion was comparable to the results found in Cole, Cram & Quinn (2011), which involved the same task on great tits from the same study population and found 99% of individuals eating the free waxworm and 44% of individuals successfully solving the task.

4.2.2.3 Social-learning mechanisms

To investigate social learning mechanisms in great tits, I placed a two-action puzzle-box on a wooden stool in the outdoor aviary for each group between 0755 and 0810 in the morning on the third and fourth days of captivity. About 3m from the puzzle-box, I also positioned a Sony camcorder, containing a 32GB micro SD card, facing the box front on another wooden stool. The puzzle-box was left in the aviary for approximately 7h each day, resulting in a total of 43.8h of video footage across all 6 days of experiments. The identity of all individuals that had landed on the puzzle-box perch, scrounged or solved, were recorded by the puzzle-box, and the individuals were visually identified in the video footages by their unique colour bands. The technique used for each solve (either slide or swing) was recorded by video analysis using iMovie (vers. 10.0.3, Apple Inc. 2014), and matched to the data stream from the puzzle-box.

4.2.3 Data analyses

To investigate whether there was an effect of social learning, I compared the proportion of individuals that learnt to solve in the control and treatment groups. To test the hypothesis that great tits learn by imitation, I observed the proportion of solvers that used the same technique as the demonstrator of their group, but also observed the solve prior to initial solve of naïve individuals, to get a rough measure of who an individual has learnt from. I also investigated whether there were differences in the number of solves and rate of solving (calculated by total number of solves divided by the difference in timing between the final and initial solves) between the demonstrators for the treatment groups.

To compare the means of the latency to initial contact (proxy for task awareness) and scrounging of the puzzle-box between the two treatment groups, I used the Wilcoxon rank-sum test. All latencies were calculated from the time the first demonstrator solved (ranging between 1.4min and 11min from the introduction of the puzzle-box), and individuals that did not contact the puzzle-box were given a maximum latency of 54360s which was the longest period of time the puzzle-boxes were available across two days.

To compare whether different groups had significantly different numbers of individuals contacting or scrounging from the puzzle-box, or different innovative abilities, I used Fisher's exact test. I also used Fisher's exact test to examine whether there was an association between scrounging and solving. Finally, to examine whether there was a significant correlation between the latency to initial solve and the latency to initial contact and initial scrounge, I used Spearman's correlation test. I excluded individuals in the control group

when examining scrounging in all analyses, as there were no solvers in the group and hence no opportunity to scrounge.

I carried out all analyses in R version 3.1.1 (R Development Core Team, 2014). I did not perform any Bonferroni corrections, following recommendations by Nakagawa (2004) on the likely low statistical power in this study.

4.2.4 Ethical statement

This work was performed under Natural England licenses 20123075 and 20131205, and has been reviewed by the Department of Zoology ethical committee, University of Oxford. All birds were brought into captivity using BTO-standard cloth bags within 1h from the time of capture. They were also regularly monitored when in captivity and given free access to food, water and roost boxes except during the training for demonstrators (see above). To reduce the stress involved when transferring birds from their indoor cages to the outdoor aviary and vice versa, birds were caught in the dark. Disturbance was kept to a minimum during experimentation through the use of a video camera.

4.3 Results

4.3.1 Group differences in learning to solve the puzzle-box

There was a significant difference between the numbers of individuals that learnt to solve between groups (Fisher's exact test: p=0.045). None of the naïve individuals solved in either the control or 'swing' groups, but 42.9% of the naïve individuals solved in the 'slide' group. However, all 3 individuals that learnt to solve in the 'slide' group did not use the same technique as the original demonstrator of the group, but instead swung the door to solve. All individuals were consistent in the technique they used to solve the puzzle-box, except for individual Y837891, the first naïve individual to learn to solve, which slid the door during its first attempt, then used the swing solution for all of its subsequent solves.

Of the 3 individuals that learnt to solve, the initial solve of the first and last naïve individual to solve were performed after a solve by the demonstrator, while the initial solve of the second naïve individual to solve followed a 'swing' solve by Y837891 (the first naïve individual to solve). The number of solves by other individuals prior to each of these individuals' first solves ranged from between 136 and 168. Two of the solvers were juvenile females while one was an adult male, and all had managed to solve the lever-pulling task. However, innovative ability did not differ significantly between solvers and non-solvers (Fisher's exact test: p=0.221).

While none of the individuals landed on the puzzle-box in the control, 78.6% (11/14) of naïve individuals in treatment groups did (Figure 4.2). While all naïve individuals in the 'slide' group scrounged, only one naïve individual

scrounged in the 'swing' group (Fisher's exact test: p=0.005; Figure 4.2). In addition, all naïve individuals that solved had also scrounged previously. However, solving was not significantly associated with scrounging (Fisher's exact test: p=0.209).

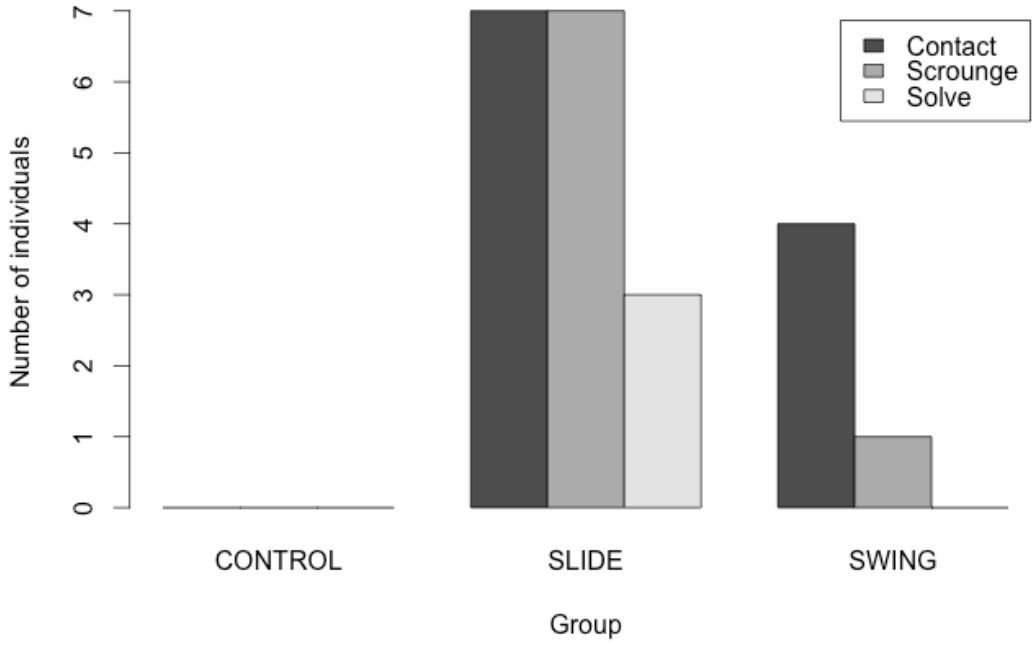

Figure 4.2 Number of individuals in control and 'slide' and 'swing' demonstrator treatment groups that contacted, scrounged from, or solved the puzzle-box.

4.3.2 Solving by demonstrators

There was a difference in solving between the treatment demonstrators. The 'slide' demonstrator performed almost twice the number of solves and solved twice as often as the 'swing' demonstrator (Table 4.1; Figure 4.3). The rate of solving was also generally constant for both demonstrators (largely linear relationship between the cumulative latency of each solve from the first solve and the number of solves; Figure 4.3).

Table 4.1 The number of solves over two days of experiments and rate of solving by the demonstrators in the 'slide' and 'swing' treatment groups.

Treatment	Number of solves	Rate of solving (solves/min)
Slide	264	0.304
Swing	112	0.140

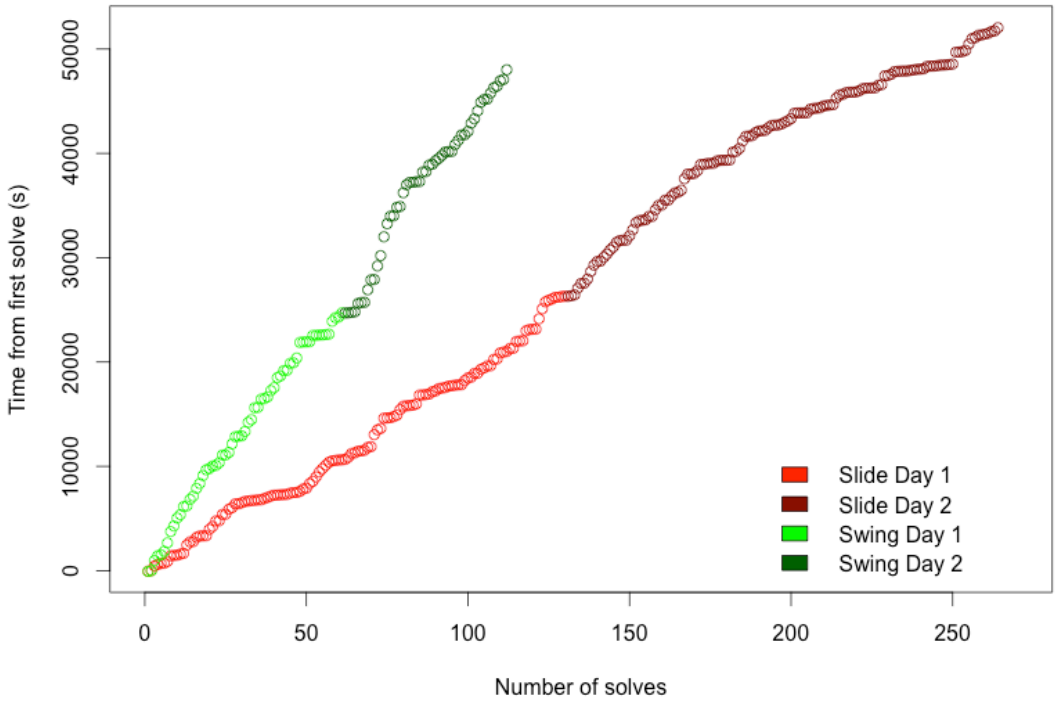

Figure 4.3 The cumulative time taken to solve calculated from the first solve by 'slide' (red) and 'swing' (green) demonstrators across two days of experiments.

4.3.3 Latency to first actions between treatment groups

The mean latency of puzzle-box contact was significantly shorter for the 'slide' group compared to the 'swing' group (Wilcoxon rank-sum test: W=3, p=0.007; Figure 4.4). This same pattern was observed for the mean latency of scrounging from the puzzle-box (Wilcoxon rank-sum test: W=1, p=0.002; Figure 4.4). In addition, the latency to first solve had no significant correlation with the latency to initial contact (r_s=0.385, p=0.077), and the latency to initial scrounge (r_s =0.277, p=0.338).

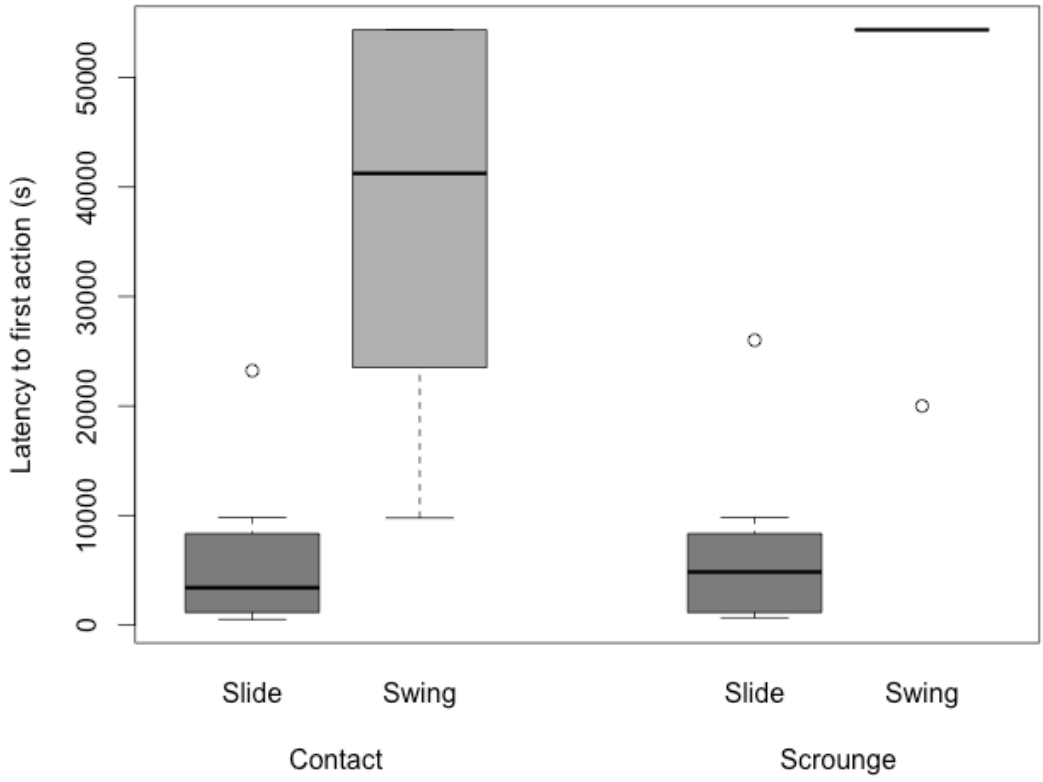

Figure 4.4 Latency to initial contact of and scrounging from the puzzle-box in 'slide' and 'swing' demonstrator treatment groups in a novel foraging task. Individuals that did not contact, scrounge from and/or solve the puzzle-box were given a maximum latency of 54360s.

4.4 Discussion

4.4.1 Summary of key results

Overall, individuals with a demonstrator were more likely to approach and solve the puzzle-box than those without. Naïve individuals that learnt to solve all came from the 'slide' group, where the demonstrator solved twice as fast and as many times as that in the 'swing' group, but all adopted the 'swing' technique to solve. They also all solved the innovation task, and scrounged before solving. However, there was no association of solving with the ability to innovate, or with scrounging, both terms of the presence of and latency to each action.

4.4.2 Social learning mechanisms

Having controlled for fine-scale local and stimulus enhancement, as individuals have to contact the same part of the manipulandum in either solution, my results supported the presence of coarse-scale local and stimulus enhancement, and the possibility of emulation. However, there was no conclusive evidence for the presence of imitation, response facilitation or simple social facilitation.

There was a likely presence of stimulus enhancement as the 'slide' demonstrator was able to solve the puzzle-box in the training room soon after being introduced to it, even though it had previously first learnt to solve it in the wild. As none of the individuals in the control group, but the majority of those in the treatment groups, approached the puzzle-box, it was likely that there was

coarse-scale local enhancement involved, as the solving by the demonstrators may have attracted the other individuals towards the puzzle-box. Social facilitation was unlikely to be a social learning mechanism behind the learning of this foraging task since none of the individuals in the control group learnt despite being in a group with other conspecifics.

My findings provided insufficient support for imitation and response facilitation. Although the initial solve for two of the three non-demonstrator solvers matched that of the individual that solved before it, one of these solvers subsequently changed to another solving action for all following solves. Also, none of these solvers matched the action of their group's original demonstrator, despite the original demonstrator performing the highest number of solves during the experiment.

Hence, it is likely that emulation, or trial-and-error learning following coarse-scale local and stimulus enhancement, could be the main mechanism behind learning of this foraging task. All non-demonstrator solvers had previously scrounged, which likely implied knowledge of the resulting reward associated with solving the puzzle-box. It is unlikely that the individuals had formed an association between the demonstrator and reward instead, rather than the puzzle-box with reward, as that association alone is unlikely to result in learning how to solve the task subsequently by themselves. This supports emulation as a possible social learning mechanism, as emulation is where individuals achieve the same result or goal without necessarily copying the same action as the demonstrator. Even though it was possible that non-scroungers could have observed the demonstrator from a distance obtaining a reward by solving, this could not be measured. This is unlike scrounging, which could better

quantify an individual's knowledge of a reward from the puzzle-box. However, trial-and-error learning after being attracted to the puzzle-box by coarse-scale local and/or stimulus enhancement could be an alternative explanation. Since one of the individuals first solved by sliding then switched over to swinging for all subsequent solves, this hinted at the possibility that the individual could have attempted to solve by trial and error during the first couple of times and subsequently chose the method that was the easiest (whether it was to remember or to perform).

On top of these two potential mechanisms, fine-scale local enhancement could be possible as well. It is not possible to deduce this solely using the two-action task in this experiment, as the point of contact to solve is the same for both solutions. However it can potentially be inferred when results from this two-action task is compared to that from a bidirectional control procedure where the point of contact differs between solutions. A previous experiment in wild great tits that used a bidirectional control procedure suggested that social learning mechanisms involved were likely to be more than just local or stimulus enhancement (Aplin et al., 2015). Instead, observational learning was inferred to be present, as individuals tended to solve using the same solution as other individuals. However, their results could be alternatively be explained by fine-scale local enhancement to the side of the bidirectional sliding door, or point of contact on the door side (Chapter 2). Since there was insufficient evidence for observational learning once fine-scale local enhancement was controlled for in my study, it is possible that the conformity observed in Aplin et al. (2015) could be due to fine-scale local enhancement instead (but see later Section 4.4.4 for limitations).

The results of this study are supported by several others that found an involvement of local and stimulus enhancement in bird foraging (Krebs, MacRoberts & Cullen, 1972; Sherry & Galef, 1990; Fryday & Greig-Smith, 1994). Imitation has been found in certain bird species such as pigeons, quails or budgerigars (Akins & Zentall, 1996; Akins, Klein & Zentall, 2002; Heyes & Saggerson, 2002), but these have been the exceptions. Most studies often find that apparently imitative social learning could be explained by 'simpler' mechanisms (Sherry & Galef, 1990; Fritz & Kotrschal, 1999), and there has been a lack of evidence showing imitation in the wild (Galef & Giraldeau, 2001; Slagsvold & Wiebe, 2011). Particularly in tits and chickadees, local enhancement has been the main social learning mechanism identified (Krebs, MacRoberts & Cullen, 1972; Sherry & Galef, 1990), which is not surprising as these species forage in groups. Furthermore, it has been proposed that even local enhancement can lead to the formation of traditions (Franz & Matthews, 2010); hence my results are consistent with the observation of stable traditions in great tits (Aplin et al., 2015).

My findings also suggested a possibility of emulation, on top of local and stimulus enhancement. Few studies have conclusively deduced emulation in bird foraging (e.g. Klein & Zentall, 2003; Auersperg et al., 2014), and none, to my knowledge, shown in the wild. To more conclusively deduce whether great tits use emulation (as opposed to just local or stimulus enhancement), future work could employ a ghost or end-state control to observe if individuals were able to learn just by seeing the affordances or solved state of the manipulandum (Hopper, 2010). It would be interesting if emulation were found to be a mechanism used by great tits to learn to forage, as it might imply that, in

particular, for great tits that generally feed on nuts, observing how a nut cracks open is also important – not just observing the location where other birds are feeding.

4.4.3 Factors affecting social learning propensity

This study suggested that social factors may affect social learning propensity more than individual factors. Naïve individuals that learnt to solve the puzzle-box were of mixed ages and sexes, which did not suggest an age or sex effect. Although all of them had previously succeeded in solving the lever-pulling task, I still found a lack of significant association between social learning and innovative ability. This is surprising as an association between innovation and social learning has been shown in several other species (Aplin, Sheldon & Morand-Ferron, 2013; Bouchard, Goodyer & Lefebvre, 2007), although some studies have also found a trade-off between the two (e.g. Burkart, Strasser & Foglia, 2009). Besides, social learning of foraging in great tits has often been attributed to 'simpler' mechanisms such as local and stimulus enhancement (e.g. Krebs, MacRoberts & Cullen, 1972), where individuals may be attracted to a location or stimulus by other individuals but rely on their individual innovative abilities to obtain the food reward. A possible explanation for the lack of association between asocial and social learning could be due to low statistical power as a result of small sample size (see Section 4.4.4 for limitations). It may also be because other factors are more important in influencing social learning propensity, such as social factors (see below). Nonetheless, unless more

replicates are performed, caution should be taken when examining the implications of this result.

By contrast, my results suggested a significant influence of social factors on social learning propensity, though this is largely through the level of activity by demonstrators, rather than scrounging. Although social dynamics could affect the opportunity to scrounge (Coussi-Korbel & Fragaszy 1995), I found that the presence and latency to scrounge was not significantly associated with the presence and latency to solve respectively. Thus, this suggests that scrounging does not increase the likelihood of social learning. However, as all naïve individuals that learnt to solve also scrounged in my experiment, I cannot conclude that scrounging has an inhibitory effect on social learning either, unlike a study on pigeons finding that scroungers never learnt to solve (Giraldeau & Lefebvre, 1987). Likely, my results are due to a lack of statistical power because of the low sample size, such that any relationship between scrounging and solving may not be detected statistically, not unlike that for innovative ability discussed above.

There are several reasons that could explain why all naïve individuals that learnt to solve also scrounged initially, a phenomenon also found in common ravens, marmosets and meerkats (Fritz & Kotrschal, 1999; Caldwell & Whiten, 2003; Thornton & Malapert, 2009). First, scrounging potentially indicates knowledge of a food reward by naïve individuals, which had been found to predict social learning propensity (Palameta & Lefebvre, 1985). Second, scrounging could only occur if an individual landed immediately following a solving event, thus scroungers would most likely have observed the solve, increasing the chances of social learning (Caldwell & Whiten, 2003). My results

may have differed from that in a study on pigeons (Giraldeau & Lefebvre, 1987), because of differences in the relative trade-off between producing (or solving) and scrounging (Fritz & Kotrschal, 1999). It was relatively more difficult to scrounge in my experiment, as the puzzle-box would reset after each solve, limiting the time for scrounging, and only one bird could scrounge at any time. This is unlike the experiment on pigeons, where the food reward was available for multiple scroungers and indefinitely until it is completely consumed. However, unless more replicates are performed, my results remain inconclusive.

By contrast, my results suggested that another social factor, the level of activity of demonstrators, was important in influencing social learning propensity, though this has not been an aspect that has been explored actively in the literature previously. Naïve individuals only managed to learn in the 'slide' group, whose demonstrator solved twice as often and as much as that in the 'swing' group. In fact, the number of solves by the 'swing' demonstrator across both days of experiments was less than the minimum number of solves by other individuals prior to naïve individuals' first solve. Thus, the lack of naïve individuals learning to solve in the 'swing' condition could be due to their demonstrator not performing enough solves or solves frequently enough.

Prior to this study, I had conducted ten dyadic social learning experiments using video demonstrators, as the using videos allow for the standardisation of the exact motor action of the demonstrator and have been successfully used in other bird species (D'eath, 1998; Evans & Marler, 1991), but all naive individuals failed to learn. Postulating that perhaps great tits were unable to learn to forage from videos, I then performed six dyadic social learning experiments, but again, none of the individuals learnt after multiple testing

sessions within a day. Hypothesising that it could be due to a dyadic system being unnatural thus hindering social learning, especially for great tits that forage in flocks during winter, I then conducted three one-day open-diffusion social learning experiments. Again, no learning was observed. Since all naïve individuals in the current study learnt on the second day of experimentation, it could be that for all these previous experiments, the lack of social learning observed might be due to insufficient number of observations of demonstrators solving. Thus, the possibility of great tits learning to solve from videos, or in dyads, should not be ruled out completely. In fact, it was shown to be possible to deduce social learning in great tits from a dyadic design (Sasvári, 1979).

Overall, my study could potentially have important implications for social learning studies. The lack of evidence for social learning may not necessarily imply that those species do not use social learning, rather there may be an observational threshold that was not reached. The more often and more times a demonstrator solves, the greater the amount of attention given by naïve individuals, and the more likely naïve individuals would learn to solve (Range & Huber, 2007). Furthermore, the more a demonstrator solves, the greater the amount of opportunity for scrounging, which could aid social learning.

4.4.4 Limitations and future work

A major limitation of this study was the small sample size used. There was only one replicate for each group, and a small number of subjects (22 naïve individuals and 2 demonstrators). This allowed only descriptive statistics to be used and correlations, but not causation, to be drawn. This had also severely

limited the conclusive power of my results, as only 3 naïve individuals managed to learn to solve the puzzle-box. Thus, this study could only give an indication of potential patterns, and future work should include a greater number of replicates, to be able to obtain greater statistical power to draw firmer conclusions. Due to this limitation, this study better serves as a methodological exploration, being, to my knowledge, the first two-action method and open-diffusion experiment performed on great tits. This study has furthermore shown that employing a mix of methods to distinguish between social learning mechanisms could be a useful way forward. The results of the bidirectional approach previously employed in Aplin et al. (2015) was better able to give insights on the underlying social learning mechanisms when taken in light with the results from the two-action method used in this study.

Finally, while open diffusion experiments allow social learning experiments to be conducted in a more naturalistic setting, they provide less control and thus makes it harder to distinguish between mechanisms with great certainty. For example, in this study, each naïve individual's first solve was compared to the preceding solve to determine whether there was imitation. However, that naïve individual may not actually have observed the preceding solve, but rather, it would more likely have observed the solves from which it had scrounged. Future work could also make use of social network analyses to predict which individual each bird would most likely have observed and learnt from, based on the individual it was most closely associated with.

4.4.5 Conclusion

Overall, this study found support for coarse-scale local and stimulus enhancement, together with emulation, as the most likely mechanisms behind the social learning of foraging behaviour in captive flocks of great tits. When results were compared to those from an experiment using a bidirectional control procedure, there was also support for fine-scale local enhancement as an underlying social learning mechanism. Additionally, social factors such as the number and rate of demonstrations may play a greater role in determining the likelihood of social learning, compared to individual factors such as the ability to innovate. Although greater sample size and more replication is needed to obtain more definite evidence, my inferences generally fit in well with the ecology of great tits. Great tits form foraging flocks in winter and are good innovators (Morand-Ferron et al., 2011), which are characteristics that support the use of local and stimulus enhancement as adaptive strategies. This is because these mechanisms, often considered 'simpler' than imitation, rely on individuals using trial and error learning after having been attracted to the location or stimulus by others (Boyd & Richerson, 1996). Developing greater cognition or ability for imitation may not confer that much more of an selective advantage for great tits, if local and stimulus enhancement alone are sufficient for most social learning (Slagsvold & Wiebe, 2011; Heyes, 1993). By contrast, local enhancement may be very advantageous for a species like the great tit whose winter food supply often varies spatiotemporally (Aplin et al., 2012).

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CHAPTER 5

General Discussion

Chapter 5: General Discussion

This concluding chapter focuses on assessing the contribution of the present study towards addressing the specific aims of this thesis. Here, I discuss its implications for our understanding of social learning and future work in this area.

5.1 Thesis aims

The overall aim of this thesis was to further our understanding of social learning and its formative role in the expression of adaptive behaviours. Social learning can influence the distribution of behaviours across space, leading to the formation of group- or population-specific traditions (Laland & Janik, 2006). Yet little is known about the scale of behaviour for which spatial differences can be observed. Such an understanding is not only informative of the processes and ecology of animal cultures, but can also be suggestive of underlying social learning mechanisms (Levin, 1992). Social learning can also affect behaviour at the temporal level, helping animals to become more proficient or efficient (e.g. Laland & Plotkin, 1990). However very few studies have investigated how social learning impacts behaviour throughout the learning process, hampering our ability to develop a more complete understanding of the impact of social learning on fitness.

In general, the mechanisms by which social learning acts to generate individual and population-level behaviour can be informative, not just of the underlying cognition required (Heyes, 1993), but also of the ecology of social

information use (Webster & Laland, 2013). Even though there has been much work done examining social learning mechanisms in numerous species, almost all of the existing work has been based on captive work alone, reducing the ecological validity of the results (Kendal, Galef & van Schaik, 2010; Hoppitt et al., 2012). This thesis thus aimed to address gaps in the literature, using a combination of field and captive approaches to examine the role of social learning in generating group-level behavioural patterns, and the mechanisms and processes by which these behaviours arise.

5.2 Key findings and implications

5.2.1 Role of social learning in spatial patterns of foraging behaviour

In Chapter 2 of this thesis, I found that social learning likely explained the spatial distribution of a range of foraging techniques used by free-living great tits at an artificial task. This was observed not just in side preference in a bidirectional control procedure task, as found in Aplin et al. (2015), but also at a finer scale – such as in the body movements used to solve task. Within the population, the prevalence of these multiple scales of behaviour could not be explained by the efficiency of each technique, supporting the hypothesis that social learning could be responsible instead (Chapter 3). In addition, although individuals mostly relied on personal information in their decision-making, there was a significant additional contribution of social learning towards the choice of foraging technique (Chapter 2). Upon closer inspection however, I found that individuals tended to associate by side preference (side of door contact and positions on the perch) and position of the door that was contacted (Chapter 2).

This suggested that even though social learning contributed to the spatial distribution of behaviour at multiple scales, its impact at these different scales varied. An effect of social learning for 'coarse-scale' foraging was therefore well supported, but at a finer scale, social learning was more location-based than action-based.

This thesis highlights how important it is for social learning studies to investigate learnt behaviour at multiple different scales. This can reveal the scale of the ecological significance of social learning – for example, it seems likely that great tits do observe others at a finer scale, but are less focused on the actions compared to the location. The scale at which animals take in information from their environment can also influence the establishment and maintenance of traditions by affecting the scale of behaviour that is "passed" from an individual to another within a population.

5.2.2 Influence of social learning on foraging efficiency

I showed that temporal patterns in foraging behaviour are manifested more probably in terms of changes in foraging efficiency than in foraging techniques. Over time, individuals became more efficient in solving (a proxy for foraging efficiency), but it was generally not due to the use of more efficient techniques (Chapter 3). In fact, I found that individuals were repeatable in their choice of foraging technique, at levels that were equivalent or even higher than the repeatability of other behaviours, such as personality, observed in the same population (Dingemanse et al., 2012; Chapter 2). This could be suggestive of

some degree of conservatism or 'habit formation' in individuals' ongoing choice of foraging technique (Pesendorfer et al., 2009).

Individual practice and experience is often attributed as the main reason behind changes in foraging efficiency over time (Berridge, 2000). However, in Chapter 3, my results suggested that both the initial foraging efficiency and the subsequent improvements in foraging efficiency in great tits were influenced by a range of factors. This included factors such as age or prior solving experience, but also social factors such as local density and date of initial solve, which I used as rough proxies for social learning. Greater local density may imply both greater competition and greater opportunities for social learning, although there is often a trade-off between these two (Seppänen et al., 2007). On the other hand, a later date of initial solve could mean that there are greater numbers of efficient solvers to learn from, and so may serve as a more direct proxy of social learning (Griffin & Guez, 2015). I found that local density but not the date of initial solve affected the initial foraging efficiency, suggesting that competition may have had a greater impact than social learning on the initial time taken to solve. However, both factors influenced the improvement of foraging efficiency over time, although in a seemingly contradictory manner – a lower rate of improvement was associated with greater local density and an earlier date of initial solve. This could be due to scaling effects. The date of initial solve could be a proxy for the level of experience in the population as a whole, while local density may be a proxy for effects that occur at a more local spatial scale. Thus, at the population level, my results suggested that social learning may influence improvements in foraging efficiency, but also that this may be masked by competition when examined at a more local scale.

This chapter highlighted the importance of investigating the effect of social learning not just on skill acquisition, but also on the improvements in skills after acquisition. In particular, I found that after the initial acquisition of a novel foraging technique, there may still be the effect of social learning on improvements in foraging efficiency. This effect could potentially be mediated by an additional social effect of competition. The results from Chapter 3 also supported the need to measure social learning at different scales, as it suggested that the effect of social learning may be masked at a local scale due to competition.

5.2.3 Social learning mechanisms in great tits

My findings in this thesis suggested that fine-scale local enhancement or emulation, in addition to coarse-scale local enhancement and stimulus enhancement, are most likely the mechanisms by which great tits socially learn foraging traditions. Local enhancement has been suggested as the main social learning mechanism in great tits (Krebs, MacRoberts & Cullen, 1972; Slagsvold & Wiebe, 2011), and can transmit information with sufficient fidelity to result in the formation of traditions (Franz & Matthews, 2010). However, observational learning (referring to more complex mechanisms such as imitation or emulation) has been also been purported to be responsible for social learning in parids (Aplin, Sheldon & Morand-Ferron, 2013). For example, great tits tended to solve a bidirectional control procedure task using the same side as that which was most commonly performed by others (Aplin et al., 2015). My findings do not conflict with the suggestion by Aplin et al. (2015) that observational learning

was involved, as my study supported possible effect of emulation, though not imitation. However, my findings suggested that these results could also be explained by an even simpler mechanism – that of local enhancement at a fine scale.

In Chapter 2, I found that social network associations predicted the distribution of side preferences, and of position of door contact. The link between social interactions and these foraging behaviours illustrated that the scale at which social learning operates at is mainly the specific location of door contact – both the side of, and exact spot on, the door. This suggests that on top of any coarse-scale local enhancement (attraction to the location of the puzzle-box), there is a fine-scale local enhancement to the side of the door and the exact spot of door contact. In Chapter 4, I tested this hypothesis further by using captive experiments, which enable greater control and experimental rigour. My results, while inconclusive, suggested that individuals would not adopt the same action as that performed by others when exposed to a two-action method that controlled for fine-scale local enhancement. Thus imitation is unlikely to be the mechanism underlying social learning in great tits; instead, either emulation (observing the affordances of the task) or fine-scale local enhancement (copying the point of contact on the task) is more likely to be responsible. Future work is needed to distinguish between these two possibilities – in particular, a 'ghost' control could be employed where the manipulandum moves automatically without being contacted by any individual (Hopper, 2010). This would reveal whether great tits can learn by observing the affordances of the manipulandum, without requiring the presence of a demonstrator individual.

The main winter food types that great tits feed on are nuts like beechmast, which are patchy and clumped (Gibb, 1954). Hence it may be adaptive to rely on local enhancement (both coarse and fine-scale) when searching for food. Krebs, MacRoberts & Cullen (1972) found evidence for such local enhancement, observing that great tits were attracted not only to the tree, but also to the particular branch that it had seen others forage on. Provided that great tits use the same mechanism while foraging for natural resources as they do in the experimentally introduced foraging task, my study could potentially extends that of Krebs, MacRoberts & Cullen (1972) by suggesting that great tits may be attracted to the location of food at an even finer scale – possibly to a specific location on the branch. My study is also consistent with Fisher & Hinde's (1949) proposition that great tits were not using 'complex' social learning mechanisms when learning to prise open milk bottles in the wild. I additionally propose that great tits probably learnt to prise open the milk bottles by having their attention targeted towards the foil caps rather than just the milk bottle itself.

This result may also implicate our understanding of learning mechanisms that underlie conformity and the formation of traditions, as well as the interpretation of results when using the bidirectional control procedure to identify imitation. A conformist bias, where individuals prefer to adopt the behavioural variants that are most frequent (Boyd & Richerson, 1985), can be a vital factor in the formation and persistence of group traditions (Aplin et al., 2015). An assumption underlying observations of conformity is that individuals must be able to recognise different behavioural variants, and because of that, imitation has been assumed to be necessary (Henrich & Boyd, 1998). However,

my results suggested that fine-scale local enhancement could support conformist learning. This also reflects recent studies that found that mechanisms other than imitation could lead to established traditions (Franz & Matthews, 2010; van der Post & Hogeweg, 2008; Caldwell & Millen, 2009). Finally, my findings suggest that bidirectional control procedure developed by (Heyes & Dawson, 1990) alone is insufficient to identify imitation, as individuals adopting the same solution that they observed others perform could be a result of emulation or fine-scale local enhancement. Ideally, experiments should involve a suitable two-action task, such as the method used in this thesis, to rule out fine-scale local enhancement. This should also be complemented with a 'ghost' control, such as the design used by Akins, Klein & Zentall (2002), to rule out emulation.

5.3 Limitations

There are a few key limitations of the work contained within this thesis that need to be considered, as they have repercussions on the reliability and interpretation of my results. First, although the combination of field and captive experiments in this thesis is an approach that integrates results that are ecologically valid and obtained through tight control (Morand-Ferron et al., 2015), it is still limited. The results from the captive experiments still may not necessarily be valid in the field – for example, I found that the propensity for social learning was apparently reduced in captivity (Discussion section in Chapter 4). However, because certain information can only be obtained through captive assays, there cannot be a sole focus on field experiments alone. Captive

experiments thus need to be designed in a manner to increase their ecological relevance without losing too much experimental control.

Second, although both my field and captive studies supported fine-scale local enhancement as a mechanism underlying social learning in great tits, they lack strong conclusive power. In particular, I deduced an operation of fine-scale local enhancement in Chapter 2 due to significant assortment of the social network by the side and position of door contacted. This assumed that the behavioural assortment resulted from individuals adopting similar techniques to those they had most observed and interacted with. Instead, it may have been due to a third factor that affected both association rates and foraging behaviour. For example the orientation of puzzle-boxes may have been important, with individuals using a particular puzzle-box more likely to land on one side of the perch. Network randomisations with these possible site effects in mind were performed, however there could still be other unknown factors not controlled for.

The field experiment was complemented by a captive study in Chapter 4. However, the captive experiment suffered from a small sample size. Using a dyadic design instead of an open diffusion may have been more able conclusively distinguish social learning mechanisms, albeit with less ecological validity (Kendal, Galef & van Schaik, 2010). I chose to adopt an open diffusion approach in Chapter 4 (Whiten & Mesoudi, 2008) partly because of a failure to observe social learning when trials were performed using a dyadic design. This is in contrast to the widespread use of social learning in this same foraging task in the wild (Aplin et al., 2015; Chapter 2). Increased stress in an artificial environment (Mendl, 1999), and a deprived social environment lacking the complex social

dynamics of great tit foraging flocks (Coussi-Korbel & Fragaszy, 1995), may have been why great tits were less likely to use social learning in captivity. However, even using an open diffusion approach in outdoor aviaries, only 3 out of 22 naïve individuals learnt to solve, greatly limiting the statistical power needed to determine underlying learning mechanisms. Thus, Chapter 4 is more useful as a methodological exploration and the findings should not be assumed to be robust. Rather, the study presented in Chapter 4 showed the usefulness of using a two-action method to complement the bidirectional approach, in order to control for the possibility of fine-scale local enhancement. It also highlighted need for caution when relating captive experiments to wild ecology, by demonstrating that great tits are much less likely to learn in captivity than in the wild.

5.4 Future directions

This thesis inevitably raises several further questions and areas that would be useful for future work to investigate. First, this work calls for a deeper examination of how the ecology of each species affects the scale at which social learning is used, by extending this work to other taxa. Observing whether species with similar ecology obtain information at similar scales, or use similar social learning mechanisms, can reveal how much underlying social learning mechanisms are a reflection of the level of environmental detail that is ecologically relevant to each species. This can thus increase our understanding of the evolution of social learning.

Second, for a better understanding of the influence of social learning on temporal behavioural patterns, the study in Chapter 3 should be extended by

investigating the apparent discrepancy between the effects of social learning and direct competition further. Previous studies have suggested a trade-off between the two in relation to group size (Seppänen et al., 2007), but in a species like the great tit with a winter fission-fusion flock structure, the relationship between the two social effects could be more nuanced. For example, when there is high social density, individuals may not get to feed as much unless they are extremely fast (unless they are dominant), but they have more opportunities to good quality information, influencing their overall foraging efficiency. This hypothesis requires further testing, by looking at the effect of dominance, which is a more direct measure for competition than social density, on patterns of foraging efficiency and social learning.

Finally, it was intriguing to find that prevalence of each foraging technique within the population was not a reflection of their relative efficiencies (Chapter 3). To better understand its implications for social learning and optimal foraging theory, future work should focus on uncovering the reason behind this phenomenon. It could be due to the relatively short 4-week window for learning and gathering information (such that individuals may not have reached their optimal foraging behaviour yet). Alternatively, habit formation may have lead individuals to become efficient in using certain techniques, rather than switching to seemingly more efficient techniques. If there is a cost in switching, this may be the most optimal behaviour when the difference in efficiency between different techniques is small (Figure 3.2). This would provide a clearer picture of the strategies employed in decision-making, and allow a better understanding of why individuals appear to be mainly using social learning to refine their foraging techniques, rather than to switch techniques.

5.5 Conclusion

Overall, this thesis has revealed that social learning of a foraging task at a finer-scale is more location-based than action-based, and that individuals likely do not only use social learning to aid in their acquisition of a novel skill, but also when improving their foraging efficiency over time. Furthermore, it has suggested that social learning of foraging in great tits is based on a combination of local enhancement at both coarse and fine scales, stimulus enhancement, and possibly emulation. The work in this thesis hence highlights the need for future work in the field of social learning to be broadened to include its impacts on temporal variation in behaviour, and to be examined at different scales. It is important for scale to be more widely considered in this field, as the reliance of social learning on the observation of patterns of behaviour renders it particularly sensitive to scaling effects (Levin, 1992). Widening the areas of research of the impacts of social learning on animal behaviour will also enable a greater understanding of the adaptive value of social learning, and its role in the foraging niche.

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