FACTORS AFFECTING THE SOCIAL TRANSMISSION OF NOVEL BEHAVIOURS: FROM THE INDIVIDUAL TO THE GROUP

Submitted by Philippa R Laker to the University of Exeter as a thesis for
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I certify that all material in this thesis which is not my own work has been identified and that no material has previously been submitted and approved for the award of a degree by this or any other University.

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Abstract

Social learning allows individuals to acquire beneficial information through observing or interacting with others. A consequence of social learning for group-living animals is that it can facilitate the spread of novel behaviours, individual-to-individual, across the group (social transmission). Following the development of sophisticated statistical techniques numerous studies have shown behaviours to spread via social transmission across numerous species. The speed and pattern of spread appears to be contingent on multiple factors including individual attributes of the model and the learner, the social structure and dynamics of the group and the physical environment that the group inhabits. However, the majority of these studies investigated behavioural spread across single, natural wild groups making it hard to disentangle the relative contributions of each factor. My thesis has taken an experimental, replicated approach to explore how factors of the individual, social environment and environmental conditions can affect social learning and transmission of behaviours. I do so in a way that independently manipulates one aspect of the physical or social environment whilst controlling for other additional factors. I used groups of both pheasant chicks (*Phasianus colchicus*) and domestic fowl chicks (*Gallus gallus domesticus*) to explore the effects of these factors on social learning and behavioural transmission. Firstly, I looked at factors of the individual - I found individuals to vary greatly in social learning performance on a novel foraging task but their sex, mass, dominance-ranking and social position did not explain this individual variation (Chapter 2). I then explored factors of the social environment through manipulating group size (Chapter 3), group structure (Chapter 4) and social foraging dynamics (Chapter 6) to determine their effect on social transmission. Increasing group size during interaction with a novel foraging task did not result in faster behavioural spread as predicted and thus indicates that total numbers of connections to informed individuals may not always best describe the likelihood of social learning (Chapter 3). Similarly, increasing the modularity of a population's network (how clustered it is) did not limit behavioural spread as expected or lead to the establishment of specific behavioural variants within clusters (Chapter 4). These two results indicate that social transmission may follow more complex rules that incorporate proportions of connections to informed individuals, social reinforcement and forgetting rates that influence social learning and transmission of behaviours. By manipulating the social environment, I found scrounging opportunity to greatly facilitate the spread of a novel foraging behaviour (Chapter 5). I reason that this is likely due to the particular social learning mechanism (local/stimulus enhancement) deployed to acquire the behaviour. Lastly, making the group's environment less predictable did not (contrary to predictions) affect how individuals used social information in a separate context (Chapter 6), suggesting that reliance on social information is not generalised across contexts. Taken together this thesis challenges the assumptions and predictions of several current theoretical models about the use of and processes underlying social transmission of behaviours, and clearly reveals a number of factors that appear critical in shaping the use and outcomes of social learning.

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Declaration

Thesis chapters

The five data chapters within this thesis were written in the format of manuscripts for publication and are intended to stand alone. Consequently, information may be repeated across chapters. I (PL) am the primary contributor to all chapters, but significant contributions were made by Joah Madden (JM), William Hoppitt (WH), Michael Weiss (MW), Christine Beardsworth (CB), Ellis Langley (EL), Lucy Capstick (LC), Camille Troisi (CT), Mark Whiteside (MAW) and Jayden van Horik (JvH). See below for detail of each chapter's contributors).

Chapter Two: What makes a good social learner?

PL and JM devised and designed the study, PL collected data and conducted statistical analysis. PL wrote the manuscript with comments provided by JM.

Chapter Three: Does socialising in larger groups result in increased opportunities for social learning and faster information spread?

PL and JM devised and designed the study. PL, CB, EL, JM, LC, CT, MAW, JvH collected the data. PL conducted the statistical analysis with guidance from WH. All contributors provided comments on the manuscript draft.

Chapter Four: The modularity of a social group does not affect the speed of transmission of a novel, socially learned behaviour, or the formation of local traditions.

PL and JM devised and designed the study, PL collected the data. PL conducted statistical analysis with guidance from WH and MW. JM and CB provided comments on the manuscript.

Chapter Five: Scrounging markedly increases the diffusion of a novel foraging behaviour in domestic chicks, *Gallus gallus domesticus*, likely because the behaviour is acquired through local or stimulus enhancement.

PL and JM devised and designed the study, PL collected the data. PL conducted statistical analysis with guidance form WH. JM and MAW provided comments on the manuscript.

Chapter Six: Does changing environment predictability alter general reliance upon social information?

PL and JM devised and designed the study, PL collected the data. PL conducted statistical analysis with guidance form WH. JM and MAW provided comments on the manuscript.

Co-authored papers:

During the course of my PhD I also assisted in collecting data for other lab members, leading to the publication of 8 co-authored papers with several in submission, detailed below:

EJG Langley, G Adams, CE Beardsworth, DA Dawson, **PR Laker**, JO van Horik, MA Whiteside, AJ Wilson and JR Madden (2020). Heritability and correlations among learning and inhibitory control traits. *Behavioural Ecology.* https://doi.org/10.1093/beheco/araa029

KR Griffin, CE Beardsworth, **PR Laker**, JO van Horik, MA Whiteside & JR Madden (2020). The inhibitory control of pheasants (Phasianus colchicus) weakens when previously learned environmental information becomes unpredictable. *Animal cognition*, 23(1), 189-202.

JO van Horik, CE Beardsworth, **PR Laker**, EJG Langley, MA Whiteside & JR Madden (2019) Unpredictable environments enhance inhibitory control in pheasants. *Animal Cognition,* https://doi.org/10.1007/s10071-019-01302-0

JO van Horik, CE Beardsworth, **PR Laker**, MA Whiteside & JR Madden (2020). Response learning confounds assays of inhibitory control on detour tasks. *Animal Cognition*, 23(1), 215-225.

JO van Horik, EJ Langley, MA Whiteside, **PR Laker** & JR Madden (2018). Intra-individual variation in performance on novel variants of similar tasks influences single factor explanations of general cognitive processes. *Royal Society open science*, 5(7), 171919.

JO van Horik, EJG Langley, MA Whiteside, **PR Laker**, CE Beardsworth & JR Madden (2018) Do detour tasks provide accurate assays of inhibitory control? *Proceedings of the Royal Society B: Biological Sciences*, 285: 20180150. https://doi.org/10.1098/rspb.2018.0150

C Meier, RS Pant, JO van Horik, **PR Laker**, EJ Langley, MA Whiteside, F Verbruggen & JR Madden (2017). A novel continuous inhibitory-control task: variation in individual performance by young pheasants (Phasianus colchicus). Animal cognition, 20(6), 1035-1047.

MA Whiteside, JO van Horik, EJG Langley, CE Beardsworth, **PR Laker** & JR Madden (2017) Differences in social preference between the sexes during ontogeny drive segregation in a precocial species. *Behavioral Ecology and Sociobiology*, 71 (7), 103. https://doi.org/10.1007/s00265-017-2332-2

CE Beardsworth, LA Capstick, **PR Laker**, EJG Langley, R Nathan, Y Orchan, S Toledo, JO van Horik, MA Whiteside, JR Madden (2020) Spatial cognitive ability is associated with the development of movement strategies. *In submission*

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Factors affecting social learning and social transmission: from the individual to the group.

Social learning is most broadly defined as ‘learning that is facilitated by observation of, or interaction with, another individual or its products’ (Hoppitt & Laland, 2013; modified from Heyes, 1994). Learning allows individuals to recognise and associate certain environmental stimuli with particular outcomes and so permits individuals to better exploit their environment though using this information to survive and reproduce (Dall, Giraldeau, Olsson, McNamara, & Stephens, 2005). The ability to learn socially from others can provide great benefits in that it allows an individual to obtain valuable information about the environment without paying some of the costs associated with obtaining that information personally. A consequence of social learning for group-living animals is that it allows for novel behaviours to spread individual-to-individual across the group (social transmission). This review aims to briefly summarise the field of social learning before concentrating on the factors that affect the use of social information and how these factors may influence the social transmission of information throughout groups of animals.

1.1 History - Changing themes in the field of social learning

The idea that animals may acquire aspects of their behaviour through the copying of others (social learning) has long been established. While Aristotle commented on the human tendency to imitate, arguing 'mimesis' to be part of human nature, he also observed that birds from different locations produce different songs which could only be acquired when raised by conspecifics (Butcher, 1922). This notion was even practised by early bird merchants and enthusiasts in the 16th century who would expose young songbirds to other species in order for them to incorporate new elements into their own song (Birkhead, 2014). Likewise, Darwin discussed in his field notes how honeybees may imitate the nectar-robbing foraging techniques of bumblebees (Romanes, 1884). Although social learning in non-human animals was observed and recorded by the likes of Aristotle and Darwin, research in this area remained largely human-orientated until the mid-to-late 1900s.

Since formal work into social learning in non-human animals began, research themes have evolved over time. The first waves of research concentrated on demonstrating the occurrence of animals learning from one-another, with many well-known figures (including Thorndike, Morgan and Watson) disputing the ability of animals to learn socially (Galef Jr., 1988). Once the occurrence of social learning was widely accepted, the focus then shifted to identifying the psychological mechanisms behind this copying process (Galef Jr., 1988; Heyes & Galef Jr., 1996). In particular, these early studies aimed to supply evidence of the capability of various species to truly imitate the actions of another, rather than their social learning being based on other arguably more basic mechanisms such as stimulus and location enhancement, response facilitation or emulation (for more information and definitions of these mechanisms see: Heyes, 1994; Heyes & Galef Jr., 1996; Hoppitt & Laland, 2013). However, as evidence of social learning accumulated, the focus shifted again from demonstrating the ability and mechanisms used by animals in learning, to identify circumstances when it may be beneficial for an animal to utilise social information and learn socially as opposed to asocially and thus when social learning might be expected to be evident (in this thesis all instances of social information use describe social learning). This switch in focus from mechanism to circumstance led to a switch in experimental design from largely demonstrator-observer dyads used to identify the presence and mechanism of social learning, to observations and experiments based on more ecologically natural chains and webs of interactions demonstrating social transmission of information and behaviours across groups. This approach has led to the (arguably re)discovery of animal tradition and culture which are seen as the population-level consequences of social transmission (Laland & Janik, 2006; Whiten, Caldwell, & Mesoudi, 2016; Whiten & Mesoudi, 2008). Advances in statistical analyses have complemented these developing research themes allowing for instance the accurate tracking of the spread of novel behaviours throughout groups (Whiten et al., 2016). Current research questions are now focusing on how physical, social and ecological factors can influence spread of behaviour and shape group-behaviours among populations (Cantor & Whitehead, 2013; Firth, 2019; Jones, Aplin, Devost, & Morand-Ferron, 2017; Kulahci & Quinn, 2019).

1.2 Initial innovation

Social transmission is the diffusion of behaviour throughout a group via social learning (Galef, 1988). Formally it is has been defined as occurring "*when the prior acquisition of a behavioural trait T by one individual A, when expressed either directly in the performance of T or in some other behaviour associated with T, exerts a lasting positive casual influence on the rate at which another individual, B, acquires and/or performs T*" (Hoppitt & Laland, 2013). In order for a novel behaviour to spread throughout a group, first one individual needs to acquire this behaviour. Innovative behaviours are new or modified learned behaviours not previously found in the population i.e. they can be a solution to a novel problem or a novel solution to an old problem (Reader & Laland, 2003). One of the most famous documented cases of an innovative behaviour spreading rapidly throughout an animal population was that of blue tits (*Cyanistes caeruleus*) and great tits (*Parus major*) in the early 20th century piercing milk bottle lids in order to gain access to the cream layer inside (Hinde & Fisher, 1951). Although not the focus of this current review, extensive research has investigated which factors correlate with those individuals showing innovative tendencies with most work exploring cognitive factors and personality traits (Greenberg, 2012; Lefebvre & Bolhuis, 2012; Reader, 2003). In short, the majority of studies across many animal taxa document a relationship between innovative propensity and personality, with innovative individuals displaying more explorative and less neophobic personalities, of which these generally tend to be the younger individuals within populations (Day, Coe, Kendal, & Laland, 2003; Greenberg, 2012; Perry, Barrett, & Godoy, 2017; Reader, 2003).

1.3 Individual attributes

Social transmission of a behaviour can be influenced by attributes of individuals within the group. Certain individuals may be more prone to learning socially than others and will preferentially attend to certain others. Factors that affect social learning among dyads will consequently affect paths of transmission across the group. Therefore, an individual's state, attributes and social position within a group, will ultimately shape how behaviour transmits through the group.

1.3.1 Flexibility in social information use by individuals

Population and game theoretic models have shown that in order for social learning to be adaptive, individuals need to be selective in their use of social information (Boyd & Richerson, 1985, 1995; Giraldeau, Valone, & Templeton, 2002; Rogers, 1988). This flexibility in when they prioritise social or asocial learning, has been described as 'social learning strategies' (Laland, 2004). These strategies do not necessarily require conscious decision-making processes of animals, but can have evolved under natural selection to produce rules or contexts under when animals are more prone to utilise social information (Laland, 2004). Social learning strategies in general are divided into 'who to copy' and 'when to copy' strategies (for full reviews of these strategies see: Hoppitt & Laland, 2013; Kendal et al., 2005; Laland, 2004; Rendell et al., 2011).

Firstly, animals may be strategic in which individuals they acquire social information from; the ‘who to copy’ strategies. This strategic copying of certain individuals builds upon the notion of directed learning which was first suggested by Coussi-Korbel and Fragaszy (1995) who emphasised that the likelihood of learning socially can be influenced by the individual attributes of the observer and demonstrator. Certain members of a population are more likely to use social information dependent on their own characteristics such as age (Thornton & Malapert, 2009a), sex (Lonsdorf, Eberly, & Pusey, 2004), genetic makeup (Foucaud, Philippe, Moreno, & Mery, 2013), personality (Dall, Houston, & McNamara, 2004; Morinay, Forsman, Germain, & Doligez, 2020) and asocial cognitive ability (Mesoudi, Chang, Dall, & Thornton, 2016). Additionally, the observer may choose to copy a particular demonstrator because of attributes of that demonstrator. Such attributes may include the demonstrator’s age (Dugatkin & Godin, 1993; Thornton & Malapert, 2009), size (Duffy, Pike, & Laland, 2009), dominance ranking (Nicol & Pope, 1999), prestige (Horner et al., 2010; Kendal et al., 2015), kinship (Schwab et al, 2008), familiarity (Swaney et al., 2001) and sex (van de Waal et al., 2010). Individuals may not simply attend to these fixed characteristics of the demonstrator, but instead track the fitness outcomes that accrue to individuals and then select those demonstrators that derive the greatest benefits from their behaviour. For example selective copying of successful individuals has been shown in the foraging decision of chimps (*Pan troglodytes;* Menzel, 1974), guppies (*Poecilia reticulata;* Lachlan, Crooks, & Laland, 1998) and evening bats (*Nycticeius humeralis;* Wilkinson, 1992). Similarly, copying the nest-site decisions of successful breeders has been demonstrated in pied flycatchers (*Ficedula hypoleuca;* Forsman & Seppänen, 2011; Seppanen et al., 2011) and fruit flies (*Drosophila melanogaster;* Sarin & Dukas, 2009). Finally, the choice of a demonstrator may be frequency dependent. Observers may select a demonstrator after considering the range of behaviours exhibited by all (or a set of) demonstrators in a population and favouring those of either especially common or especially rare behavioural variants. For example, nine-spined sticklebacks (*Pungitius pungitius)* will disproportionately copy foraging decisions more as the number of demonstrators increase (Pike & Laland, 2010). Alternatively, demonstrators of rare behavioural variants may be preferred in order to reduce competition over limited resources. For example, a study looking at the spread of a novel foraging technique in capuchins *(Cebus capucinus)* found these monkeys to pay more attention to rarer techniques (Barrett et al. 2017). These different strategies likely act in concert to govern who an individual will likely copy from.

Animals may also be strategic in when they choose to utilise social information, and this may be dependent on their own state; the 'when to copy' strategies. These social learning strategies include opting to copy when their own established behaviour is unproductive; when asocial learning is costly; when prior information is outdated; and when the observer is uncertain or dissatisfied (Hoppitt & Laland, 2013; Laland, 2004). For example, a study looking at conflicting private and social information during foraging decisions in black garden ants (*Lasius niger)*, showed that inexperienced naïve ants relied more on social information than experienced ants who solely used asocial information (memory) to dictate foraging route decisions (Grüter, Czaczkes, & Ratnieks, 2011). Similar results of inexperienced individuals copying the foraging decisions of demonstrators, more so than experienced conspecifics, have also been shown in Norway rats (*Rattus norvegicus*), sticklebacks (*Pungitius pungitius*) and guppies (Galef, 2009; Kendal, Coolen, & Laland, 2004; van Bergen, Coolen, & Laland, 2004). In these examples, animals were opting to utilise social information when they were uncertain about the payoffs for different foraging strategies. Who-to-copy and when-to-copy strategies are unlikely to operate in isolation but instead likely interact with one another. For example, individuals that are uncertain of the most profitable action in their current environment also tend to be younger, more naïve individuals who then may choose to copy older, more successful individuals.

1.3.2 Stress

The stress experienced by an individual can be a potential influence of social information use. Stress may be affected by environmental influences such as food predictability, predation rates, anthropological disturbance, increased competition, parasite burden and disease level. Rats experiencing increased stress caused by maternal deprivation during rearing are less likely to use social information and show decreased rates of copying demonstrated food preferences from other rats (Lévy et al., 2003; Lindeyer, Meaney, & Reader, 2013; Melo et al., 2006). Stress can also have different effects on social information use, dependent on the developmental stage at which it was experienced (Boogert, Zimmer, & Spencer, 2013). Japanese quail (*Coturnix japonica*) exposed to stress pre-natally (through corticosterone hormone injection into the egg) were more inclined to use social information and copy the foraging decisions of a demonstrator bird than those experiencing stress post-natally (caused through unpredictable food availability; Boogert, Zimmer & Spencer, 2013; Buchanan et al., 2003). Therefore, the level and timing that stress is experienced by an individual can alter their dependence or propensity to utilise social information which will affect the social transmission of information through a group. Many stressors are an inevitable consequence and indirect cost of social living. Group living may affect overall stress levels of the whole group, for example glucocorticoid levels in a wild population of cliff swallows (*Petrochelidon pyrrhonota*) were found to increase with group size (Raouf et al., 2006). Alternatively, group living may affect stress levels of different members of the group unevenly, if for example the group is hierarchically structured and subordinate individuals receive less access to resources and more aggression (Abbott et al., 2003; Sapolsky, 2005).

1.3.3 Social network position

Coussi-Korbel and Fragraszy (1995) first highlighted that social learning would differ between dyads dependent on their relationship and strength of association. These dyads are set within a broader social structure and relationships within a group will influence how information spreads throughout it (Coussi-Korbel & Fragaszy, 1995; Croft et al., 2005; Croft, James, & Krause, 2008). Individuals within a group inevitably will differ in the number and strength of connections and therefore the social position held by individuals. As a result, some individuals will have greater opportunities to receive social information and an increased ability to influence its transmission. For example, certain individuals are often termed ‘gatekeepers’ or ‘keystone individuals’ because of their access to social information and influence over transmission. These individuals may be leaders or dominant individuals that govern access to resources, itinerant individuals that mix with neighbouring groups or socially central individuals that spend increased time with multiple group members (Flack, Girvan, De Waal, & Krakauer, 2006; Lusseau & Newman, 2004; Sih & Watters, 2005; Vital & Martins, 2009).

Social network analysis is a helpful tool in exploring social positions and emergent social structures. This analysis depicts the connections (edges) between individuals (nodes), including their strength of association/relationship (edge weight) within the group (**Figure 1.1**; Croft et al., 2008). Based on this basic principle, many parameters can be calculated for the positions of specific individuals within the group and for the network as a whole. An individual's centrality within the network is highlighted to be important for the acquisition of socially learnt behaviours (Krause, Croft, & James, 2007; Wey, Blumstein, Shen, & Jordán, 2008). Centrality is a measure of how centrally placed within the network an individual is, with more central individuals being important for holding the network together as one unit and can be measured through: degree (number of connections to others), weighted degree (number and strength of connections to others), betweenness (number of shortest pathways through all nodes within the group that pass through that individual), closeness (average path length between an individual to all others in the group), and eigenvector (extended measure of weighted degree that takes into account the centrality of those others an individual is connected to) (**Figure 1.1**; Croft et al., 2008; Newman, 2004; Wey et al., 2008). Individuals more central in the network have more connections to (well-connected) others and so have increased access to social information. Numerous studies have shown that within a network, those individuals with higher centrality are more likely to acquire information via social transmission. For example, in a food-extractive foraging experiment, squirrel monkeys (*Saimiri sciureus*) with higher (eigenvector) centrality were faster in learning how to open the artificial fruit and were more likely to adopt the behavioural variant introduced by the original seeded demonstrator (Claidière, Messer, Hoppitt, & Whiten, 2013). A recent study looked further into the relationship between centrality of social position and learning, through comparing the social networks of a group of ring-tailed lemurs (*Lemur catta*) before and after introducing a novel behaviour

(Kulahci, Ghazanfar, & Rubenstein, 2018b). They found that not only were those more socially central lemurs more likely to learn the novel behaviour but lemurs that did acquire the novel behaviour subsequently become more central within the network through receiving increased affiliation from others. This finding highlighted how the relationship between social network position and learning can be a dynamic process, with each element influencing the other.

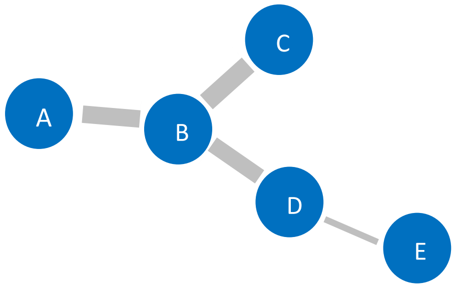


Figure 1.1 A social network diagram, representing individuals (blue nodes) and their connections with others (grey edges) with the strength of those connections indicated by thickness of the edge. Individual A has one connection to another individual and so has a degree of one, while individual B has a higher degree of 3. Individual B has high betweenness, being present in most pathways required to link the other nodes to each other (except for nodes D & E). Individual B also has a higher closeness than A as the average path length connecting it to all others is smaller than the average path length connecting A to all others.

1.4 Social environment

The size, structure and social dynamics of a group can all affect the transmission of behaviour. These factors of the social environment influence the availability of informed demonstrators, pathways of spread between individuals, interactions between individuals and the resulting costs and benefits of using social information.

1.4.1 Group Size

The size of a group that an individual is part of can influence social information use and spread. If individuals can utilise social information effectively and monitor the successes and failures of other group members in terms of foraging, mating and antipredator decisions, then social learning can be a major benefit of group living. Theoretically, the larger the group the greater the chance that any one individual innovates or adopts a novel behaviour. These informed individuals can then become demonstrators for the rest of the group and thus as group size increases, so too do the number of informed demonstrator individuals and therefore opportunities for social learning. An experiment on nine-spined sticklebacks showed that the likelihood of copying the feeder choices of other fish increased with the number of demonstrators present (Pike & Laland, 2010). Therefore, novel behaviours may arise and spread faster within larger groups that hold greater numbers of demonstrators. However, although larger group size may provide greater opportunities for social learning, they also can provide larger numbers of uninformed individuals within the group. These uninformed individuals may reduce the probability of acquiring a behaviour if they act as interference/distraction from informed demonstrator individuals. One study looking at the effect grouping conditions had on solving a food-extractive task in pigeons found that the latency to socially learn the task increased with the number of uninformed individuals and decreased with the number of informed individuals present (Lefebvre & Giraldeau, 1994). Consequently, the ratio of informed to uninformed individuals within the group may be more influential for social transmission of behaviours.

1.4.2 Social structure

Social transmission is not only influenced by group size, but also the structuring of the group. A group's social network structure describes the distribution and strength of associations between individuals (see above) and is likely to be a crucial component in determining the pattern and speed of information transmission throughout the group with information spreading between individuals that are most closely associated (Coussi Korbel & Fragraszy, 1995; Croft et al., 2005; Krause et al., 2015). Indeed recent statistical models identify the presence of social transmission when information spreads along the connections within social network, with those individuals that have more connections to informed individuals being more likely to acquire the information/adopt the novel behaviour (Franz & Nunn, 2009; Hoppitt, Boogert, & Laland, 2010). This assumption is analogous to models of disease transmission (whereby individuals with increased numbers of contacts to infected individuals are more likely to become infected themselves) and is the basis of most research into behavioural transmission (Firth, 2019). However, despite numerous models that test the influence that population structure has on disease transmission, especially within human societies (e.g. Campbell & Salathé, 2013; Salathé & Bonhoeffer, 2008; Salathé & Jones, 2010), models of how social structure can affect information transmission within non-human groups still remain sparse (Cantor & Whitehead, 2013).

The structure of the group can influence the transmission speed, fidelity and robustness of information. More structured social networks generally mean that the degree and strength of the associations between individuals show more variance within the network resulting in average path length being longer (average number of steps the shortest path has between all pairs within a network) (Cantor & Whitehead, 2013). This in turn can affect how information spreads throughout a network. This has been little studied, probably because generating replicated social networks and plotting social transmission on them is not trivial. However, a study investigating information propagation dependent on network structure used a graph-based simulation approach to compare information flow in real life structured networks of primate groups with control networks of reduced structure (Voelkl & Noë, 2010). The control networks that exhibited less structure than the natural ones consisted of: networks with the same edges but all equal weighting; networks with preserved edge weights but shuffled between random individuals; and finally the least structured, being well-mixed random networks with equal edge weightings. Simulations of information diffusion across all these networks showed that information spread faster in the well mixed networks rather than the structured groups and was less prone to extinction during transmission (Voelkl & Noë, 2010). Networks can also become more structured when clusters start to become increasingly separate within a group. This increasing simultaneous fragmentation of the whole population and clumping of subgroups can affect the rate at which behavioural variants are created and maintained within these clusters, and local variation between clusters are argued to be the precursor of behavioural tradition and even distinct cultures (Cantor & Whitehead, 2013).

Increasing the distinctness of clusters within a network increases its modularity (division of a network into modules) which then affects information fidelity and flow within and between these clusters. If culture is defined as socially learnt variants of behaviour that differ between populations, then increasing modularity can give rise to traditions underpinning culture (Cantor & Whitehead 2013; Whitehead & Lusseau 2012). Several studies have investigated how modularity can generate culture by simulating the effect different modularity strengths have on information flow. Models produced by Whitehead & Lusseau (2012) found a threshold modularity coefficient value of 0.3, above which behavioural diversity begins to increase, and so they conclude that in populations where social learning can lead to culture, modularity has to be above this threshold for cultures to emerge. This study simulated information transfer at each interaction between individuals with a certain probability of learning. However, individuals may need multiple interactions with repeated behaviour exposures before information is acquired. When such conditions were imposed, another study found an optimum level of network modularity for information diffusion by using a linear threshold model with social reinforcement where adoption of a behaviour requires several exposures (Nematzadeh et al., 2014). This model showed networks with high modularity (strong clustering) facilitated social reinforcement and promoted local spreading, whereas low modularity (weak clustering) facilitated global spreading, therefore producing an optimum level of modularity for information diffusion. Learning conditions such as social reinforcement might help explain otherwise counterintuitive results of increased network modularity promoting information diffusion (Centola, 2010; Ikeda, Hasegawa, & Nemoto, 2010). This mechanism by which network structure gives rise to culture was extended by Cantor and Whitehead (2013) who highlighted how the relationship may work in reverse, with culture affecting social structure if individuals preferentially interact with others exhibiting similar behaviour. Clearly, network structure can be instrumental in how information spreads throughout the group and can lead to the development of cultural traditions.

1.4.3 Social dynamics

The social dynamics occurring between group members, that is how one individual flexibly responds to the behaviour of other group members, can affect the pay-offs of learning socially and so influence the transmission of behaviour throughout the group in addition to or in conjunction with the size and structure of the group. Social foraging offers an example in which an individual's behaviour is dynamically adjusted according to the behaviour of other group members. During social foraging, individuals can often adopt a scrounging position and acquire food that has been obtained by others, so-called producers. Models exploring the payoffs of adopting scrounging or producing positions have found producing-scrounging tactics to likely be frequency-dependent, with scrounging providing benefits when there are producers in excess (Barnard & Sibly, 1981). If a novel behaviour is introduced into a group (by a producer), scrounging can provide a cost-effective method of obtaining food. However, adopting a scrounging behaviour can affect an individual's likelihood of socially learning the new foraging technique. A series of experiments looking at the social transmission of a novel foraging technique in pigeon flocks showed that those adopting scrounging positions did not socially learn how to obtain the food and instead would only learn the novel behaviour when prevented from scrounging (Giraldeau & Lefebvre, 1986, 1987; Lefebvre & Helder, 1997). Similar studies have found that the opportunity to scrounge is detrimental to social learning during foraging tasks in capuchin monkeys *(Cebus paella*; Fragaszy & Visalberghi, 1989)*,* zebra finches *(Taeniopygia guttata*; Beauchamp & Kacelnik, 1991) and chickens *(Gallus gallus domesticus;* Nicol & Pope, 1994). However the relationship between social learning and scrounging is not entirely clear as several other studies have found scrounging to promote social transmission (Caldwell & Whiten, 2003; Midford, Hailman, & Woolfenden, 2000; Thornton & Malapert, 2009). It is clear from these studies that scrounging opportunity (and perhaps other factors influencing social dynamics) can impact social learning, however what is less clear is which factors determine whether scrounging promotes or retards social learning.

1.5 Physical environment

The occurrence, probability and form of social learning may be influenced by factors beyond the attributes of the observer and demonstrator and the social relationships between them. The environment in which the individual lives is likely to shape the expression of social learning, both independently of, and in conjunction with, the attributes of the individuals involved. Environmental conditions, such as structural complexity or environmental and informational predictability can affect the dependence and use of social transmission of information by animals within a group.

1.5.1 Environment structure

A series of experiments conducted by Day et al. (2001) demonstrated how the physical structure of an environment can affect social transmission of information about food source locations within guppy shoals. Depending on whether barriers dividing up an environment were opaque or transparent, shoal size had different effects on the rate of discovery and transmission of patch locations. These findings were likely a result of different costs being paid depending on whether fish were leaving a small or large shoal to locate and therefore transmit the locations of food patches, with these costs being reduced when the barrier was transparent. A similar result was found in a study looking at how environmental complexity affects social transmission (Webster et al., 2013). Social transmission of information about food patch locations by shoals of three-spine sticklebacks (*Gasterosteus aculeatus*) were compared in either a structurally complex environment or a simple open environment. Structured environments differed from the open tank environment in having a series of barriers gridded throughout the tank and only within this structured environment was food patch location transmitted socially between shoal members. In this example, social transmission of food patch locations was more beneficial in the structured environment where discovering locations asocially was difficult and time consuming. Environments of differing physical structural complexity can therefore affect the ability and propensity of individuals to transmit information socially through altering the costs and benefits of using social information.

1.5.2 Environmental predictability

Another property of environment that may affect the usefulness or validity of using social information is environmental predictability. If an individual is living within an environment that is constantly changing, then they are often likely to be uncertain about information accuracy or reliant on outdated information, and so it may be beneficial to utilise information from others that are informed about the current conditions. A study on European starlings (*Sturnus vulgaris*) investigated the value of social information with varying environmental predictability (Rafacz & Templeton, 2003). Starlings were placed in differing regimes of environmental predictability (changed through the stability of colour cues), after which their propensity to copy the decision made by a demonstrator bird was recorded. They found that birds in an unpredictable environment utilised social information more when it was available to them than did birds in a predictable environment. Similarly, bumblebees (*Bombus terrestris*) also relied more upon social information when foraging on artificial flowers that varied in reward and used asocial learning when in a predictable environment (Smolla, Alem, Chittka, & Shultz, 2016). Theoretical models also support these conclusions, showing social learning to benefit individuals within variable environments (van der Post & Hogeweg, 2009). Therefore, environmental cues and signals may well influence the use of social information and its resultant spread throughout the group.

1.6 Informational content

The use and spread of social information may be affected by the type of information or behaviour itself. Individuals may also be expected to selectively deploy social learning depending on the ecological relevance of the task that requires learning. Animals may be genetically predisposed to learn behaviours from others when the stimulus is relevant. For example, monkeys will utilise social information when learning a fear response to snakes but not flowers (Mineka & Cook, 1988). Likewise, blackbirds use social information and exhibit a greater fear response when a stuffed predator, but not a plastic bottle, is accompanied by a conspecific alarm call (Curio, 1988). Similarly, reed warblers (*Acrocephalus* *scirpaceus*) exhibit a stronger defensive response to (biologically relevant) cuckoo predators compared to parrots, after observing conspecifics mobbing both species (Davies & Welbergen, 2009). These experiments highlight that the nature of the information itself can affect whether it is socially learnt and transmitted between individuals.

Individuals are expected to utilise social (as opposed to personal) information when the costs of acquiring information asocially is high. A good example where the cost of acquiring information asocially is high is that of learning about the identity, threats and behaviour of predators which requires direct exposure to the predators and consequently poses a risk to the observing individual (Griffin, 2004). Examples of individuals learning socially when asocial learning is costly include guppies and minnows (*Phoxinus phoxinus*) preferentially utilising social information over asocial learning when experiencing either separation from the shoal or a higher perceived risk of predation (Kendal et al., 2004; Webster & Laland, 2008). Therefore, information may spread faster by social learning when it concerns hazardous or dangerous information.

Finally, whether or not individuals use social learning to attain a new behaviour may depend on the complexity of the behaviour. More complex behaviours are likely costlier to learn *de novo* asocially and so costs can be cut if an experienced demonstrator is chosen and copied, whereas simple novel behaviours may be cheap to learn asocially. Theoretical evolutionary models predict that with increasing task complexity, individuals should rely more heavily on social information (Boyd & Richerson, 1985, 1988; McElreath et al., 2005). These predictions are backed up with empirical evidence of monkeys only utilising social information when learning how to extract food during more difficult complex versions of a food-extraction task (Day et al., 2003; Kendal et al., 2009). Likewise, Byrne and Russon (1998) argue that gorillas (*Gorilla gorilla)* learn socially to handle and process physically and chemically protected plants as the process is too complex to learn asocially. Again, this reliance on social information with complex information can be viewed as following the social learning strategy of using social information when asocial learning is costly in terms of time and effort expended. Therefore, the informational content or form of behaviour itself can affect the reliance on and resulting spread in social information, of which this is independent of any environmental conditions.

1.7 Conclusions and Thesis Overview

Social learning and the resultant social transmission of a novel behaviour throughout a group is dependent upon a multitude of factors from individual to group level influences (see **Figure 1.2** for a schematic representation of some of these effects). Firstly, the type of behaviour or informational content itself may influence the likelihood of it being socially learnt. Then at the basic dyadic level, an individual’s attributes can affect their likelihood of either adopting a social learning strategy or being selected as a demonstrator. The differing patterns of association between individuals within the group will produce a network structure of associations which will subsequently affect the speed and pathways of information spread across the whole group, with payoffs of adopting a novel behaviour influenced by the activities of others. Finally, the physical environment and information content within which the group lives can impact upon the ability of a behaviour to transmit through a group and determine how reliant individuals are on social information.

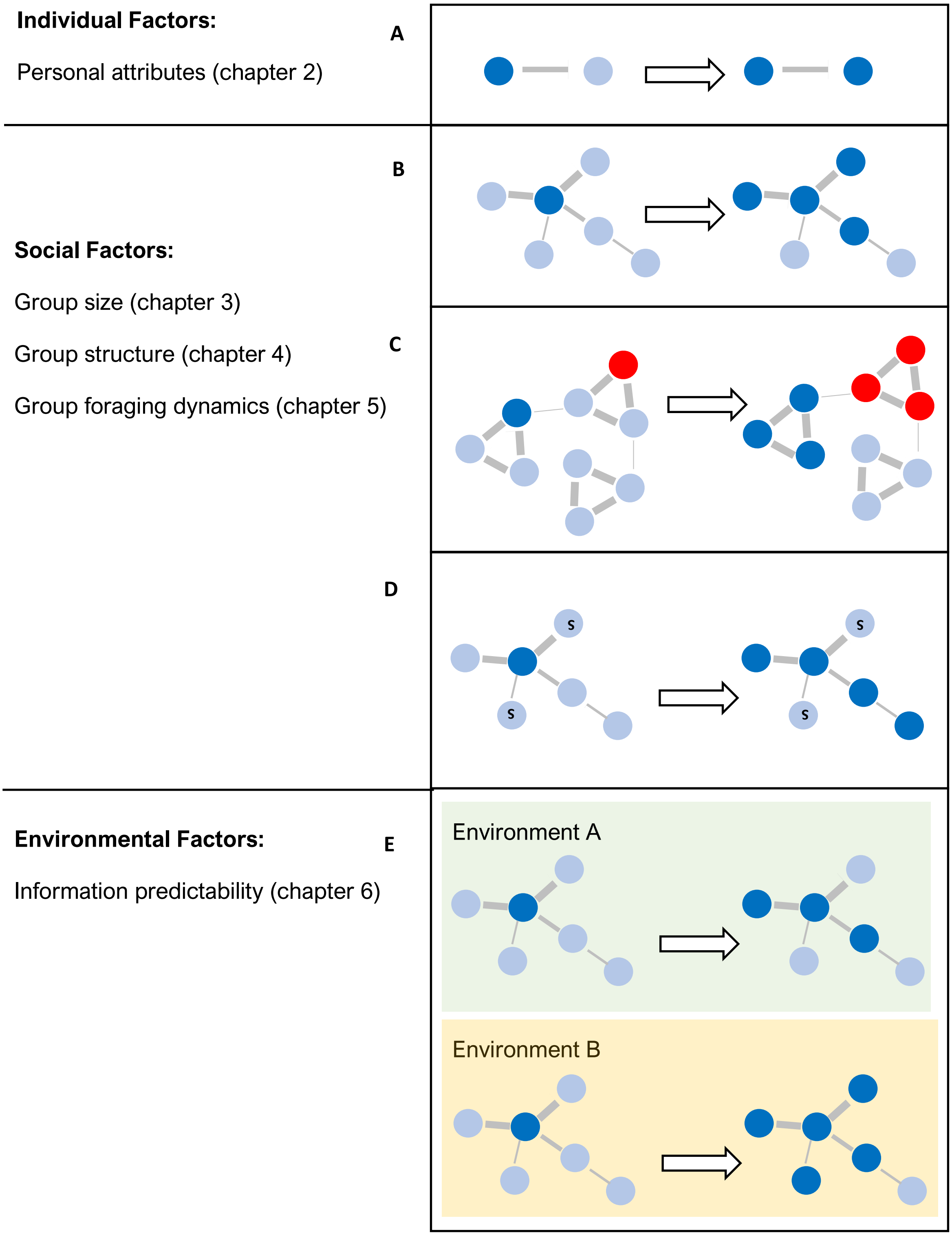


Figure 1.2 Factors affecting social learning and social transmission of information between individuals.

A) Social learning at the dyadic level: an uninformed observer individual (pale blue) learns a new behaviour from an informed demonstrator individual (dark blue). Acquisition of the new behaviour can be influenced by attributes of both the demonstrator and observer and the strength of relationship between them (as indicated by thickness of the grey line).
B) The social transmission of a behaviour will spread throughout a group via social learning starting from the informed individual and reaching those first with the strongest relationship.
C) Group social structure can influence the spread of this behaviour and give rise to traditions if a new behavioural variant (as indicated in red) is restricted within sub-groups.
D) Group social dynamics can influence the spread of this behaviour, for instance adopting a scrounging tactic (s) may prevent learning of the new behaviour.
E) The physical environment may also influence social transmission resulting in an increased or decreased use of social information dependent on conditions.

1.8 Unravelling the contributions of personal, social and environmental factors to the occurrence and use of social learning

As can be seen from **Figure 1.2**, the extent of social learning occurring in a population and the consequences that this has for social transmission is likely to be determined by a combination of the personal attributes of the learner and demonstrator, the size and social structure of the population that they inhabit, and features of the environment in which the population lives. All these features are likely to act in concert with one another. However, the existing body of work that informs our understanding about the causes and consequences of social learning has typically drawn on examples from numerous different modelling approaches and empirical systems. The majority of early work focused on social learning mainly at the dyadic level within laboratories, which although allowing for strict experimental control does not permit consideration of group dynamics representing how information naturally spreads throughout the group. Those later studies that investigate social transmission across wild groups and populations are often unable to do so in controlled and replicated conditions, whereby one aspect of the physical or social environment can be independently manipulated. Mapping information transfer is not trivial and studying multiple groups of multiple individuals, under conditions in which individual access to information, environmental conditions, group composition and group structure can all be experimentally manipulated and accounted for is logistically difficult. However, these individual, social and environmental features are likely to act contingently on one another and therefore such detailed and controlled studies are essential in order to progress the field.

This thesis aims to explore in more detail these influencers of information spread using controlled experimental settings with groups of pheasant chicks (*Phasianus colchicus*) and domestic chicks (*Gallus gallus domesticus*) as study systems. Chickens and pheasants are harem-polygynous species living in hierarchically-structured flocks (Appleby, Mench, & Hughes, 2004; Mench & Keeling, 2001; Robertson, 1997). Importantly, both species are precocial and thus allow for observations and experimental manipulations of the group from hatching without the need for parent birds. Investigating social transmission across young animals allows for strict control over social and environmental conditions experienced from birth thus removing any prior unknown influences. Social learning is also assumed to be important for young animals that are inherently less experienced with their environment than adults and so are more likely to obtain information from others (Biondi, García, Bó, & Vassallo, 2010; Carter, Marshall, Heinsohn, & Cowlishaw, 2014; Dugatkin & Godin, 1993; Franks & Thorogood, 2018; Huffman, 1996; Nicol, 2004). Both pheasants and chickens can be reared in reasonably large groups, enabling larger sample sizes than many other species. They also habituate to human observers quickly, are easily handled and can be individually identifiable through simple fitted leg bands or wing tags. Both species will engage in foraging tasks from hatching and being highly food motivated are also fast to train. Domestic chickens are reared for meat and egg production around the world (with >23 million produced worldwide every year (Food and Agriculture Organization of the United Nations, 2020)) and have been extensively studied in the laboratory, resulting in their behaviours, social system, welfare and management being well known and documented (e.g. Marino, 2017; Nicol, 2015). As a result of farming, chickens are continuously hatched throughout the year and so hold no seasonal constraints in data collection, while pheasants having been under less intense selection than chickens, provide a form of comparative group of a related species, where their individual cognition has also been well-explored (van Horik, Beardsworth, Laker, Whiteside, & Madden, 2019; van Horik, Langley, Whiteside, Laker, & Madden, 2018; van Horik & Madden, 2016). These species therefore make an excellent system for tracking the social transmission of novel foraging behaviours across groups in a controlled laboratory setting, whereby one aspect of the physical or social environment can be independently manipulated.

Group living provides chickens and pheasants access to social information and thus (for chickens) social cognition and social learning has been explored in depth (for reviews see: Marino, 2017; Salva, 2011). Social information is of high importance to young domestic chicks (Nicol, 2004) who, immediately after hatching, will respond to maternal displays of pecking and vocalisations when learning which food items are profitable and which are harmful or less profitable (Nicol & Pope, 1996). These chicks will then start to learn from fellow conspecifics, with experiments showing them to learn the locations of hidden food from others (Gajdon, Mundwiler, & Stauffacher, 2015) and avoiding certain food items after observing another chick display a 'disgust response' (Johnston, Burne, & Rose, 1998). From a few weeks old chicks will begin aggressive behaviours towards each other and start to loosely form dominance hierarchies within their flock which stabilise over time (Nicol, 2015; Rushen, 1982). Importantly, chickens can individually discriminate between and recognise individuals within the flock (Bradshaw, 1991, 1992; D'Eath & Stone, 1999), recall the hierarchical status of others and furthermore infer the position of others based on observations of their interactions (Hogue, Beaugrand, & Laguë, 1996). It has also been shown that chickens will attribute and respond to specific call types of others that provide information on predator types (Evans, Evans, & Marler, 1993) and food locations (Evans & Evans, 1999). In the laboratory, adult hens have been shown to acquire a novel foraging behaviour (key-pecking) after observing an informed bird demonstrating the behaviour, of which the identity and social status (dominance rank) is influential in the likelihood of learning (Nicol & Pope, 1992, 1994, 1999). Social information is therefore important for these birds when learning about food, predators and social positions of others. Given the similar social structure, genetics and ecology to chickens, I presume pheasant's social cognition is similar.

1.9 Chapters Overview

My thesis follows the outline of **Figure 1.2** in order to ask what factors determine the causes and consequences of social learning in groups by considering a suite of likely influential personal, social and environmental factors that can be experimentally manipulated individually. The most basic determinants of whether and how effectively social learning occurs are the attributes and abilities of the individual engaged in learning (**Figure 1.2a**). Since the conception of social learning strategies, research has explored the different factors that dictate the use of social information generating different rules and contexts under which an animal will copy (Hoppitt & Laland, 2013; Laland, 2004). We know from numerous studies that individuals will preferentially copy from others based on certain attributes of these demonstrators and their success outcomes ('who to copy' strategies). Indeed, adult domestic fowl hens have been shown to socially learn a novel foraging behaviour more effectively when the behaviour is demonstrated by a dominant bird (Nicol & Pope, 1999). There has also been considerable attention to how the situational context may lead to individuals becoming more reliant on social information ('when-to-copy' strategies). These strategies include copying 'when dissatisfied', 'when uncertain' and 'when asocial learning is costly' (Hoppitt & Laland, 2013). However, few studies have explored whether certain (physical and quantifiable) attributes of the individual make them more prone and better at using social information. Chapter Two therefore explores how individual attributes, including sex, mass, dominance ranking and social position, may be linked to social information use.

Social learning typically occurs within a broader social context and therefore, understanding how such a context affects social information use is critical. Social learning is dependent on the social environment which can vary in group size and composition, group dynamics and social structure, all of which may influence information spread. Perhaps the most basic variable in social context is the size of group in which an individual operates (**Figure 1.2b**). It has been assumed that associating with more individuals would result in greater opportunities for social learning. However, it is not clear whether simply having more associates will result in increased social learning and faster behavioural transmission or whether other factors such as proportional connections to informed and uninformed associates and natural foraging dynamics will interfere with this relationship. To my knowledge no study has directly tested the effect group size has on the acquisition and diffusion of a socially learnt behaviour, and so I experimentally alter group sizes and map the spread of social learning in artificial groups in Chapter Three.

The size and composition of a group can interact to shape the social structure of a group with consequences for social transmission of behaviours (**Figure 1.2c**). The social structure of a group can influence how information spreads between members; several theoretical models have simulated the effect different structures have on the flow of information and have highlighted modularity as a network property important in the development of traditions and culture (Cantor & Whitehead, 2013; Voelkl & Noë, 2010; Whitehead & Lusseau, 2012). Yet, to my knowledge no studies have empirically tested these assumptions. Chapter Four empirically tests model predictions on social structure through experimentally manipulating network modularity by dictating which chicks associate with each other during a novel foraging task and observing the effects this has on information diffusion speed and fidelity.

One more fine-scale aspect of the social environment that an individual inhabits is the behaviours of others within that group and the opportunities that these group-mate behaviours present for the focal individual (**Figure 1.2d).** Although work has explored the relationship between competitive foraging and social learning, particularly concerning information diffusion in flocks of pigeons (Giraldeau & Lefebvre, 1986, 1987; Lefebvre & Helder, 1997), the relationship that scrounging has with social learning is still unclear. Chapter Five explores the nature of this relationship by manipulating scrounging opportunity via controlled quantities of food reward to measure the impact this has on information spread. Furthermore, this chapter links the relationship scrounging has with the social learning mechanism demonstrated during learning.

The non-social environment that a group occupies may influence the reliance upon social information and thus affect the speed a behaviour transfers through the group (**Figure 1.2e**). The physical structure and complexity of an environment have been shown to alter the payoffs of using social information and resultant rate of social transmission across a group (Day, MacDonald, Brown; Webster et al., 2013). The predictability/variability of the environment also impacts the benefits of using social information, with theoretical models and empirical evidence showing those within an unpredictable environment to rely more on social information (Rafacz & Templeton, 2003; Smolla et al., 2016; van der Post & Hogeweg, 2009). However, it is unknown whether an unpredictable environment *per se* increases the propensity to use social information or whether individuals only pay attention to the predictability of the specific conditions that they may learn about socially. Chapter Six explores this through creating two environments of differing uncertainty and then assessing the reliance on and spread of social information on a novel foraging task by individuals living in those environments.

Finally, I will synthesise these results in Chapter Seven, producing a general discussion and conclusion on the crucial factors influencing social transmission of information within animal groups. My thesis will use carefully controlled experiments to explicitly test predictions, generated from theoretical models and observations of natural groupings, about influences at multiple levels on strategies of social learning. Using controlled experiments, I explore how individual level factors, social structure and group level influences and physical environment can affect social transmission of a novel foraging behaviour across a group.

1.10 Ethical statement

All birds included within this thesis were reared to a standard that exceeded conditions required by the Department for Environment Food and Rural Affairs (DEFRA) and the Animals Scientific Procedures Act (ASPA 1986). All work was approved by the University of Exeter Psychology Ethics Committee and work with the pheasants was conducted under Home Office licence PPL 30/3204.

2

What makes a good social learner?

1.1. Abstract

Animals can gain knowledge about their environment through observing the behaviours of others and learning socially. Individuals vary their reliance on social learning dependent on context and will differentially attend to the behaviours of certain others based on their attributes. However, despite this flexibility in social information use, far less attention has been paid to inter-individual variation in propensity to engage in social learning. This study investigated how an individual's sex, mass, dominance-ranking and social position might affect their use of social information. To obtain individual differences in the propensity or time to utilise social learning I provided domestic chicks with a novel foraging task and measured the level of exposure (number of opportunities) required until an individual first performed the solving behaviour. Importantly I measured dominance and social network position separately from the task and this separated my measures of social attributes from social learning opportunities. I found no relationship between any of the attributes I measured for each individual and their speed to utilise social information, despite a large variation between individuals. My results suggest that previously reported differences in use of social information dependent on these attributes may well reflect differing social learning opportunities and priorities rather than innate dispositions to use social information.

2.1 Introduction

Individuals can acquire information about their environment through personal experience (asocial learning) or through using social information and interacting with or observing the behaviour of others (social learning) (Dall et al., 2005). Individuals can be flexible in their reliance upon social or asocial learning dependent on context; so called ‘when-to-copy’ social learning strategies (Laland, 2004). These strategies describe how the current state of an individual influences their reliance on social information and includes relying upon social learning when uncertain, when prior collected information is likely to be outdated and when asocial learning is costly (Hoppitt & Laland, 2013; Laland, 2004). Individuals can also differ in their likelihood of exhibiting social learning dependent on who they are learning from (Coussi-Korbel & Fragaszy, 1995); so called ‘who-to-copy’ strategies of social learning (Laland, 2004). Thus far individuals have been shown to preferentially learn from others based on a model’s sex (van de Waal et al., 2010), size (Duffy et al., 2009), age (Dugatkin & Godin, 1993; Thornton & Malapert, 2009), dominance rank (Nicol & Pope, 1999), prestige (Horner et al., 2010; Kendal et al., 2015), familiarity (Swaney et al., 2001) and relatedness (Schwab et al, 2008). It is likely that these traits are representative of some indirect measure of success of the model, serving as a cue to the potential benefits available to the observer if they learn from the model. Despite this large body of evidence showing differential likelihoods of social learning dependent on qualities of the model, far less attention has been paid to inter-individual variation in propensity to use social information and engage in social learning and how this variation may be predicted by attributes of the learner, rather than the model. Although certain individual learner attributes may accompany the deployment of ‘when-to-copy’ strategies, it is not clear whether certain attributes mean that an individual is generally more likely to engage in social learning or is a better social learner. To explore this, it is necessary to relate an individual’s attributes to their propensity to use social information or the speed at which they acquire a socially demonstrated novel behaviour.

A small number of studies have explained individual differences in the propensity to use social information by considering an individual's attributes (for a review see Mesoudi, Chang, Dall, & Thornton, 2016). Such attributes have included an individual's age, sex and dominance ranking. Many species, including birds and whales, are said to socially learn vocalisations during a critical period in their youth (Catchpole & Slater, 1995; Whitehead & Rendell, 2014) and empirical studies have found juveniles to be more likely to socially learn a novel behaviour (Aplin, Farine, et al., 2013; Thornton & Malapert, 2009a) and have their food choices influenced (Lupfer, Frieman, & Coonfield, 2003). Younger animals are thought to use social information more as they are naturally naïve in an unknown environment and so reliant upon the behaviours of others for guidance (Galef & Laland, 2005). Sex has also been linked to differences in social information use, with numerous studies consistently finding females to be more likely and faster to socially acquire novel behaviours (Aplin, Farine, et al., 2013; Kappeler, 1987; Lonsdorf et al., 2004; Reader & Laland, 2000; Schnoell & Fichtel, 2012; Watson et al., 2018). Theories explaining this sex difference include greater parental or reproductive investment by females resulting in greater nutritional needs which leads them to prioritise acquisition of beneficial behaviours (Aplin, Farine, et al., 2013; Reader & Laland, 2000). This argument is strengthened by the finding that reproductive state can influence social learning, with pregnant nine-spine sticklebacks, *Pungitius pungitius,* being are more likely to learn socially than non-pregnant individuals (Webster & Laland, 2011). Two studies have found a link between dominance rank and social information use, although with conflicting results. Higher ranking (male) blue tits, *Cyanistes caeruleus*, were found to be less likely to socially learn a novel foraging behaviour (Aplin, Farine, et al., 2013) whereas dominant chickadees, *Poecile atricapillus*, were more likely to socially learn the locations of food patches (Jones et al 2017). What is not clear in both these experiments is whether dominance rank alters the opportunities for learning socially or whether dominance status is linked to differences in propensity or ability to socially learn.

Relating individual attributes to propensity to use social information is difficult. Most previous studies into individual differences in social learning were performed on freely interacting (often wild) groups. Although this is ecologically representative of how information diffuses across natural populations, by default this method allows individuals free choice of partners to learn from. Therefore, it may not be just the individual learner's attributes that are important but also those of the demonstrator and the interaction between them. This makes establishing the effect of a learner's individual attributes difficult. Additionally, the majority of these studies related individual attributes to a binary outcome of whether or not an individual used social information or socially learnt a behaviour (with the exception of Jones et al. (2017) who linked the rate of social transmission with dominance score and Lupfer et al. (2003) who looked at the proportion of diet preference based on observation of a paired demonstrator). By simply recording social learning as being present or absent, more fine-scaled variation in an individual's propensity to socially learn is missed as those individuals that may indeed socially learn in time are counted as non-learners.

One attribute that has not yet been linked to an individual's propensity to socially learn is their social network position. This is particularly surprising given the intrinsic relationship that social learning has with relationships between individuals. Indeed, models of social transmission are based on the assumption that those individuals with more connections (and so more central in their network) have more opportunities to acquire social information and so are more likely to socially learn (Firth, 2019; Hoppitt, 2017). Interestingly the direction of this relationship was recently shown to be dynamic with central individuals not only being more likely to socially learn a novel behaviour, but individuals that learn a novel behaviour subsequently become more central within their group as a result of increased affiliative behaviours directed towards them from group-mates (Kulahci & Quinn, 2019). This finding highlights how social network position can both influence social learning opportunities but also importantly that an individual's social learning ability influences their social position. Individuals have been shown to be consistent in their social network position over time, in their number and strength of connections to others (Aplin, Firth, et al., 2015; Jacoby, Fear, Sims, & Croft, 2014; Krause et al., 2016; Kulahci, Ghazanfar, & Rubenstein, 2018a). It would therefore be plausible to assume that if individuals are inherently more social (having multiple and strong connections to others), then they are perhaps more socially attentive and are therefore more susceptible to using social information and socially learning behaviours from others. The lack of studies into this area is likely due to the difficulty of separating out sociability with increased learning opportunities, because by default more central individuals have more access to social information. The critical question to ask is whether those individuals that are more sociable (having more connections to others) are inherently better at social learning.

Understanding how individual attributes relate to social information use will provide key information on how individuals may differ in their likelihood of acquiring socially learnt behaviours and thus provide further insight in how information transmits through groups which can lead to group-level traditions. While certain physical individual attributes (e.g. sex, mass, age) are an immutable property of the focal individual when recorded, some attributes (such as dominance ranking and social network position) are the product of social interactions and are consequently susceptible to change as the social environment changes which simultaneously alters social learning opportunities. Previous studies have generally been conducted using observation of free-living animals and so it is difficult to separate effects of social attributes from access or opportunity for learning. This means that although we have indications that such attributes are important, such as dominance ranking (Aplin et al., 2013; Jones et al., 2017), there is a risk of conflating attribute and process which makes establishing their role difficult. Therefore, in order to understand how individual attributes relate to social information use, a study system is required that can control for and measure social attributes in a context separate to social learning opportunities.

I explored which attributes correlated with social learning performance using a system that permits precise measures of physical attributes (sex and mass), controls partner choice during learning and disentangles social attributes from opportunity. To obtain individual differences in social learning I provided domestic fowl chicks, *Gallus gallus domesticus,* with a novel foraging task and measured the number of exposures required until an individual socially learnt the solving behaviour. Domestic chicks are easy to rear in the laboratory and importantly will learn foraging behaviours from fellow conspecifics (Nicol, 2004; Chapters 4,5,6). I therefore repeatedly exposed 41 uninformed chicks individually to informed birds demonstrating a novel foraging behaviour and measured how many exposures were required until individuals performed the behaviour themselves. Crucially I controlled pairings of partners to reduce any influence demonstrator attributes would have on social learning. Chicks were therefore exposed to a standardised mixed selection of specific demonstrator individuals during exposures, that were all equally successful in solving the task and so also reducing any influence that cues of demonstrator success (Dawson, Avarguès-Weber, Chittka, & Leadbeater, 2013; Katsnelson, Motro, Feldman, & Lotem, 2008) or demonstrator quality (Coussi-Korbel & Fragaszy, 1995; Laland, 2004) may have on social learning. All 41 chicks were the same age and experienced identical rearing conditions, thus ruling out any age or age-related related effects (such as reproductive state) and effects that might arise from differing rearing conditions. I recorded the sex and mass of individuals to account for any sex or size differences in addition to their dominance ranking and social position. Domestic chicks have been shown to establish dominance hierarchies at a young age, with early levels of aggression predicting future dominance ranking (Guhl, 1958; Nicol, 2015; Rushen, 1982). I therefore inferred emergent dominance rankings from agonistic interactions that occurred outside the context where social learning took place. Social network position was determined from foraging associations during the study period, and these associations were determined separately from the task and so the resultant social network was independent from purely learning opportunities. I then investigated whether these attributes correlated with social learning performance.

2.2 Methods

2.2.1 Subjects and housing

I collected fifty-one day-old domestic chicks, of the Rhode Rock hybrid, from a commercial breeder (Organic Pullets; Hittisleigh) and split them equally between two identical temperature and humidity controlled pens. Chicks of this breed can be sexed from hatching via distinctive feather colouration and so both pens held an almost equal sex ratio. Pens consisted of a main area (in which chicks were restricted for the first week), an extended area (allowing additional living space after week one) and gated access to a testing chamber (where they encountered a novel foraging task) (**Figure 2.1**). I provided chicks with perching material and ad libitum access to chick crumb (1st Poultry CMC; Crediton), water and grit. I weighed all birds at 13 days old (day 13) using a flat digital stand-on scale (Salter, UK; precision = 1g). To identify individuals, I fitted plastic flatbands (Avian ID, Redruth) on day 2 (6.4mm diameter), which were changed for a larger size (8mm diameter) on day 13. At three weeks old I donated chicks to a free-range poultry farm.

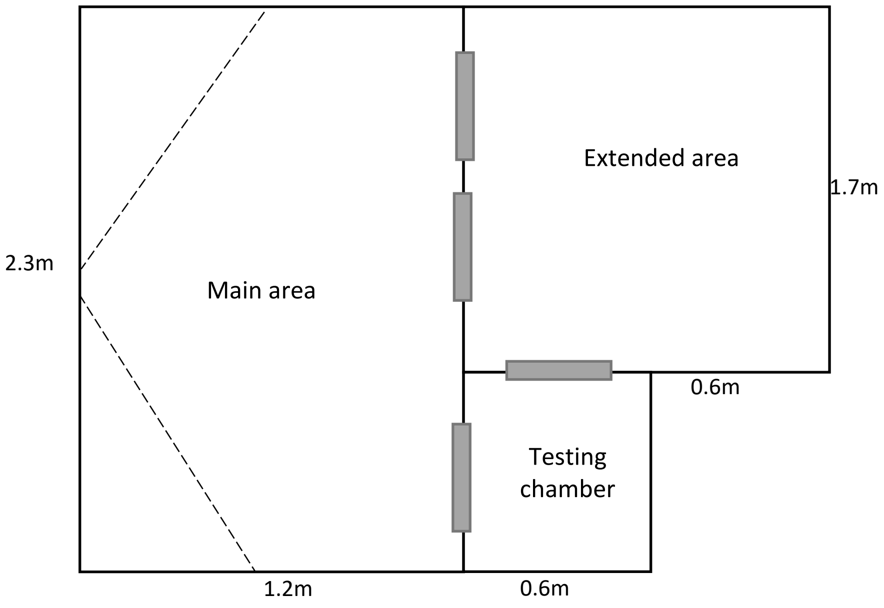


Figure 2.1 Pen layout. Dashed lines indicate perch positions. Grey bars indicate gated doors. During testing chicks cycled through the testing chamber from the main area and out into the extended area.

2.2.2 Establishing dominance ranking

I recorded agonistic interactions between birds, through ad hoc period sampling from day 13-21, conducted randomly throughout daylight hours. Due to the relatively infrequency of events, I was able to monitor a whole pen simultaneously during each sampling period and record any aggressive interactions that occurred between individuals. I recorded the identities of the winner and loser and the type of act performed. Acts were classified as a: ‘Peck’ defined as a bird pecking at another bird in a manner that was not simply obtaining food crumbs from their body; ‘Chase’ whereby one individual would run after another; and ‘Fight’ where two individuals stood tall staring at each other and occasionally pecking or kicking at the other. In a fight the winner was deemed to be the individual that forced their partner to retreat (more often was also the initiator of the interaction too), and I deemed the interaction to be a draw if both birds retreated away at the same time. A total of 208 (Pen A) and 148 (Pen B) aggressive interactions were recorded and used to create emerging dominance hierarchies.

2.2.3 Measuring social position

I created social networks based on foraging associations at the feeders in the main pen area. I collected these associations using a ‘gambit of the group’ approach whereby those birds seen feeding together were all considered to be associated (Croft et al., 2004). I carried out instantaneous point sampling and recorded the identities of chicks seen together at the feeder every two minutes, during ten-minute sampling periods. Chicks were recorded as at the feeder if they had at least one foot in the bowl or were standing at and eating from the bowl. Data were collected from day 4-21, over 188 (Pen A) and 192 (Pen B) ten-minute sampling periods.

2.2.4 Novel foraging task

During the study period, but not during the observation periods, I assessed the speed, specifically the number of opportunities, at which 41 individuals learnt how to solve a foraging task. The task consisted of extracting a food reward from a plain white box (12 x 50cm) that was placed upright and horizontal in the testing chamber (**Figure 2.2**). Ten black lightweight cardboard doors fronted the box and to solve the task, birds had to slide open these doors to the left or right to reveal hidden wells behind containing 3 mini-mealworm rewards. This design was adapted from previous successful studies of social learning in birds (Aplin & Morand-Ferron, 2017; Aplin et al., 2015; Aplin, Sheldon, & McElreath, 2017). The task was only ever presented to birds within the testing chamber, which they could access via a gated door controlled by experimenters.

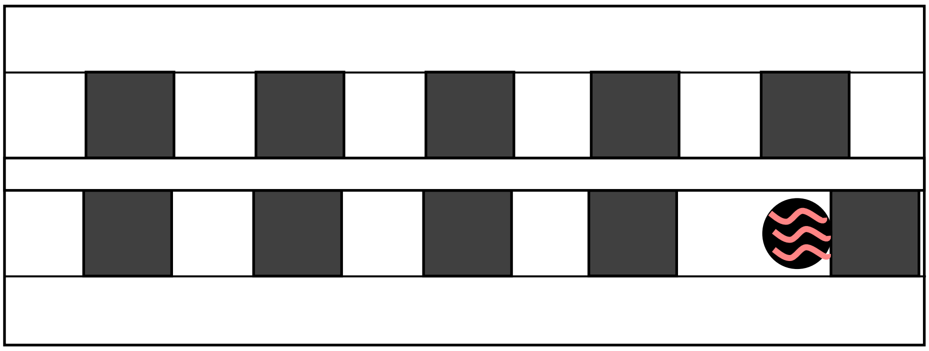


Figure 2.2 Diagram of the novel foraging task apparatus presented in the testing chamber. Bottom right shows a door opened to reveal the hidden well behind, which held mealworm rewards.

2.2.5 Shaping and demonstrator training

During week one, I shaped chicks to voluntarily enter the testing chamber by establishing an association between the chamber and food rewards. This involved scattering mealworms on the floor of the testing chamber and repeatedly cycling all chicks through the testing chamber in groups of gradually decreasing sizes until chicks were comfortable entering the testing chamber alone. During shaping, I placed a plain rectangular white box within the testing chamber in the place where the testing apparatus would later be positioned to reduce any effects of neophobia to the task apparatus.

After this shaping period, from day 7-10, I trained 10 individuals (5 from each pen and comprising 5 males and 5 females overall) as demonstrators to solve a novel foraging task presented to them in the testing chamber. To do this I repeatedly presented these selected individuals with the task in the testing chamber, making the task increasingly hard to solve. Initially the doors on the apparatus were fully open and then gradually I reduced the amount the doors were open until the demonstrator would reliably peck open all the fully closed doors to access mealworm rewards.

2.2.6 Assessing social learning performance

To measure an individual's social learning performance, I recorded how many rounds of demonstrated solving behaviour they had to observe before performing the behaviour themselves (for a schematic of testing procedure see **Figure 2.3).** I assume that I measured social learning performance, rather than asocial learning, in this task for two reasons. Firstly, the likelihood of an individual (of the same age and breed) to solve an almost identical version of this task (the doors were of different colours) has been repeatedly demonstrated to be predicted by their patterns of association as revealed by network based diffusion analysis models (Chapters 4,5,6). Second when this near-identical task was presented to chicks and social learning opportunities were removed (see control condition, Chapter 4), very few birds acquired the solving behaviour.

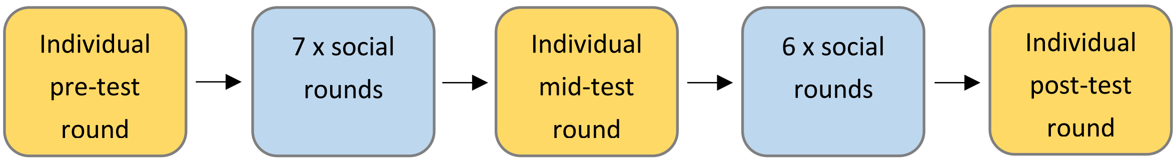


Figure 2.3 Schematic of testing procedure order. All individuals completed all rounds.

First, I assayed all 41 uninformed birds in an individual pre-test round (day 11) to establish whether any could solve the task upon initial contact prior to any demonstrations of solving behaviour **(Figure 2.3**). In this individual round, each bird entered the testing chamber where they then were given one minute to freely interact with the apparatus. The apparatus was baited with one worm/well. After one minute the bird was released, into the extended area of the pen where they were held until all birds in the pen were cycled through the testing chamber. Importantly, no birds solved the task on this first individual pre-test round.

I then conducted 13 social rounds (**Figure 2.3**) where all birds in each pen entered the testing chamber paired with an informed demonstrator bird. Each individual was randomly assigned one of the five demonstrator birds in their pen every round, thus resulting in them having a mixed selection of changing demonstrator birds as social rounds progressed. All demonstrator birds were equally proficient at solving the task – demonstrator birds opened at least 8/10 doors in 98% of the rounds where the observing bird did not open any doors themselves, thus removing any influences in learning that might depend on differing demonstrator performances. Birds were allowed up to three minutes in the testing chamber with the demonstrator, or until all doors had been opened if this happened sooner. After 3 minutes the observed individual was released into the extended area and the demonstrator bird was placed back into the main pen area. I conducted between 2-3 social rounds a day from day 11-15. For every round I recorded whether individuals solved the task.

Approximately halfway through the social rounds (after round 7) and then again upon completion of all social rounds, I carried out an additional mid-test and post-test individual round (**Figure 2.3**). This was to determine if any birds had acquired the behaviour but were unwilling to perform it in the presence of the demonstrator bird. These rounds were identical to the first individual pre-test round, where each bird was allowed one minute to interact with the apparatus. Again, I recorded which individuals solved the task within these individual rounds.

Therefore, for every individual I obtained a social learning score being the round they had first performed the novel solving behaviour (1-15). Those individuals that never performed the solving behaviour were given a capped score of 16.

2.2.7 Statistical analysis

Creating a dominance hierarchy

I built a dominance hierarchy based on the observed aggressive interactions. I calculated Elo ratings for all individuals within each pen using the ‘elo’ package (Heinzen, 2019) in R v.3.5.3 (R Core Team, 2016). Elo ratings were developed as a way of ranking chess players and are created from data documenting the sequential outcomes between interactions (Elo, 1978; Albers & De Vries, 2001). Each individual is represented by a value that increases with wins and decreases with losses, but importantly the increase/decrease takes into account the probabilities of each outcome dependent on the individuals involved (Albers & De Vries, 2001). Therefore, I inputted the order and outcomes of aggressive interactions recorded between the chicks to derive their Elo rating which represents their dominance position at this stage in life.

Extracting social position from foraging association networks

I created social networks from the foraging associations observed at feeders within each of the main pens. To do this I use the group by individual function within the ‘asnipe’ package (Farine, 2018) in R. This function produces a social network of association indices which describe how often pairs of birds were seen together at the feeder in relation to how often they were seen at the feeder overall. I then tested whether these social networks differed from random and were therefore meaningful, before extracting eigenvector centrality scores for each individual to represent their social position within the group. Centrality is a measure of how centrally placed an individual is within the network with more central individuals holding increased connections to multiple others (Croft et al., 2008). Eigenvector centrality produces a value representing the number and strength of connections an individual has to others while also taking into account the centrality of those connected others (Newman, 2004). This measure is frequently used in behavioural diffusion studies and is argued to be the best measure in reflecting an individual’s position within the entire network (Claidière et al., 2013).

Firstly, to test whether associations differ from random I compared my real observed network with random networks created from permutations of the data stream (Whitehead, 2008). Using the ‘asnipe’ package (Farine, 2013), I permuted the foraging associations data to generate 10,000 random networks with 10 swaps per permutation; swaps were constrained within ten-minute time periods to control for the possibility that individuals within ten minute sampling periods were more likely to associate together. I then extracted the Standard Deviation of Association Indexes from those permuted networks. If individuals are associating non-randomly in the long term (between sampling periods) I would expect to see a larger standard deviation of my real observed networks compared to those standard deviations obtained from permuted random networks (Whitehead, 2008). P values are therefore the proportion of Standard Deviations from the permuted networks that were greater than or equal to the observed network statistic (Whitehead, 2008).

The Standard Deviation of Association Indexes from my real observed networks were significantly different from those obtained from permuted networks in both Pen A (10,000 permutations, P value < 0.0001) and Pen B (10,000 permutations, P value < 0.0001); **Figure 2.4**). This indicates that networks created from foraging associations were non-random and so extracting centrality within those networks provides a meaningful score of social preferences and association patterns.

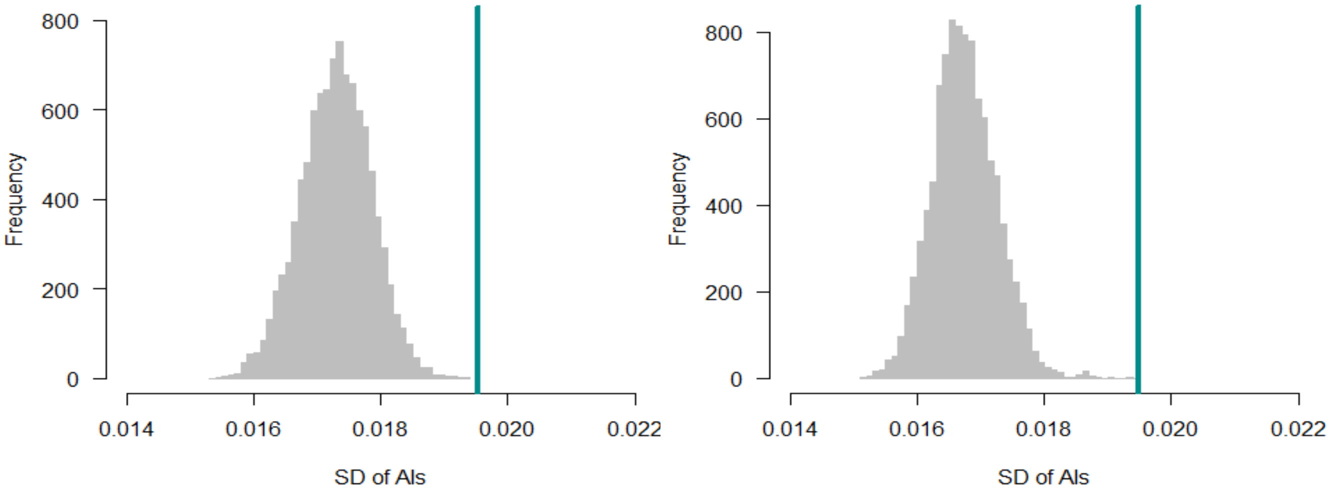


Figure 2.4 The standard deviation of association indexes (SD of AIs) of the observed network (green), compared to those obtained through permuting the data (grey) for both pens.

Relating individual attributes to social learning performance

To test whether an individual's social learning score (round they first performed the task-solving behaviour) was predicted by individual attributes I fitted a Generalised Linear Mixed Model (GLMM) with a poisson error distribution and log link function using the 'lme4' package (Bates, Maechler, Bolker, & Walker, 2015) in R. My global model included an individual's social learning score as the response variable with sex, mass, Elo rating and eigenvector score as fixed factors and pen ID as a random factor. I standardised my global model (scaling variables so that their mean is zero and standard deviation is 0.5, thus making them directly comparable to each other) using the 'arm' package (Gelman & Su, 2018) and then used an information theoretic approach to compare all possible nested models and selected the top models by AICc value. Top models were those that had an AICc difference <2 (Burham & Anderson, 2002). Using the MuMIn package (Barton, 2019), I then averaged across my top models weighted by AICc to produce parameter estimates and confidence intervals.

2.2.8 Ethics

All work was approved by the University of Exeter Psychology Ethics Committee. Birds were reared under conditions that exceeded those recommended by the Department for Environment Food and Rural Affairs (DEFRA) and the Animals Scientific Procedures Act (ASPA 1986). To reduce stress, I habituated birds to human observation from one day old and trained then to voluntarily enter the testing chamber through shaping procedures with food rewards.

2.3 Results

2.3.1 Which individual attributes affect social learning performance?

Thirty-six birds had acquired the novel solving behaviour by the end of the experiment, with a wide range in social learning scores (**Figure 2.5**). Despite this variation I found little support that my measured individual attributes influenced social learning performance. My best fitting model, as indicated by AICc score was the null model (with no individual attributes included as explanatory factors of learning performance), however several others had an AICc score difference of less than two that included an effect of mass sex or elo rating (**Table 2.1**). Upon averaging across these top models however I found coefficient estimates of these factors to be very small with standard errors that overlapped zero (**Table 2.2**).

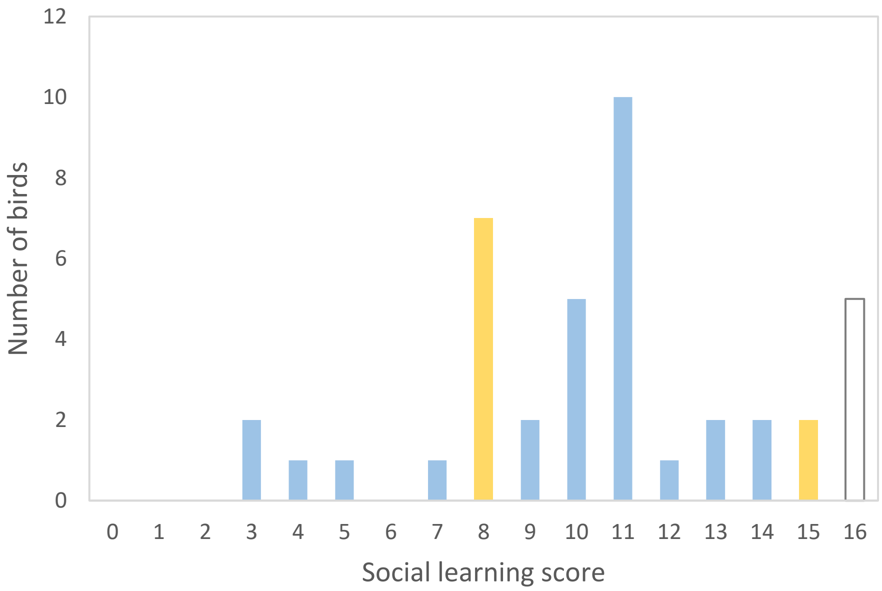


Figure 2.5 Frequency of social learning score achieved by all birds. This is the first round in which a bird exhibited the novel behaviour. Yellow bars indicate individual rounds, blue bars social rounds and the unfilled final bar those birds that did not learn.

Table 2.1 Top ranked models as indicated by an ∆AICc of less than 2. The attributes included within the model (* indicates a 2-way interaction between attributes), corresponding AICc, ∆AICc and model weighting shown.

Attributes included	AICc	∆AICc	Weight
None (Null Model)	223.9	0	0.148
Mass	225.0	1.10	0.085
Sex*Elo	225.0	1.13	0.084
Elo	225.4	1.45	0.070
Mass, Sex*Elo	225.7	1.84	0.060

Table 2.2 Coefficient estimates of each factor on social learning score produced from averaged weighted top models. Standard Error (SE), Z value and P value of averaged model coefficient shown.

	Coefficient*	SE	Z value	*P value*
Intercept	*2.33*	*0.07*	*33.80*	*<0.001*
Mass	0.04	0.09	0.48	0.63
Sex+	0.02	0.07	0.32	0.75
Elo	-0.07	0.17	0.39	0.70
Sex:Elo	0.16	0.26	0.60	0.55

*Effect sizes have been standardized on two SD following Gelman (2008). +Male was the reference sex

2.4 Discussion

I found substantial variation in social learning by domestic chicks on this novel foraging task, with individuals acquiring the solving behaviour from the third demonstration of solving behaviour all the way to the last, fifteenth demonstration, with a small proportion of individuals (12%) never learning to solve the task. Despite this variation, social learning performance (the round in which individuals acquired the behaviour) was not predicted by the sex, mass, dominance ranking or social position (centrality score) of the individual.

Previous work has simply considered whether an individual did or did not make use of social information and thus succeeded or failed to acquire a socially learnt behaviour (e.g. Aplin, Sheldon, & Morand-Ferron, 2013; Kappeler, 1987; Lonsdorf et al., 2004; Schnoell & Fichtel, 2012; Watson et al., 2018). If I had followed this approach, then I would have simply compared the five birds that never solved the task with the 37 birds that did. In doing so, I would have lost much information about individual differences in the use of social information. Instead, I discriminated between individuals at a finer scale by looking at the amount of exposure to trained demonstrators it took for them to exhibit the novel behaviour. I found a wide range in required exposures, with some acquiring the behaviour after only 2 exposures while others took 13. The distribution of social learning scores is approximately normal (excluding those five individuals that did not learn the behaviour and so were capped at 16) with the majority of individuals learning between 7-10 exposures of demonstrators. Notably I see a peak of individuals performing the novel behaviour during the individual-round conducted in the middle of social rounds. This suggests that some individuals were more likely to perform the novel behaviour in the absence of the demonstrator. This is possibly due to opportunities to practice alternative foraging techniques (such as scrounging food from wells opened by the demonstrator bird) being absent in individual rounds and therefore to gain the food reward birds had to perform the behaviour themselves. This spike in behaviour acquisition highlights the importance of considering individual trials when assessing learning. Out of the 41 birds tested, 46 birds (88%) had performed the novel behaviour by the final round.

Many other studies report lower levels of individuals having acquired a novel behaviour (e.g. 53% (Aplin et al., 2013), 44% (Kappeler, 1987), 50% (Schnoell & Fitchell, 2012). My results suggest that these previous studies may not have allowed some individuals sufficient opportunities to acquire and exhibit the novel behaviour. By simply categorising individuals into those that socially learn and those that do not, such approaches are potentially missing out on individuals that can learn given more time. By grading the speed of social learning, I could gain a more subtle understanding of how individual attributes relate to social learning.

I found no effect of sex on an individuals' speed of social learning. Despite several studies finding females to be more inclined to use social information and faster at socially learning (Aplin, Farine, et al., 2013; Kappeler, 1987; Lonsdorf et al., 2004; Reader & Laland, 2000; Schnoell & Fichtel, 2012; Watson et al., 2018), I found no evidence of this for domestic chicks on my task. This could be due to a difference in species, the type of task presented, or it could be a result of the young age I tested birds at. Those studies finding a sex difference were conducted on adults and so if sex differences in social learning are a result of differential reproduction or parental investment priorities (Aplin, Farine, et al., 2013; Reader & Laland, 2000), then these factors would not be present at the young age of my tested chicks. My results suggest that female chicks are not born better social learners. It would therefore be interesting to conduct this test on older individuals (of the same species and task) to establish whether females do indeed become faster social learners with time and therefore demonstrate this difference to be a result of experience and/or need rather than innate disposition.

Neither an individual's mass nor their dominance ranking (as indicated by their Elo rating) were significant predictors of social learning performance. Mass and dominance may be linked as larger stronger individuals often tend to be the more dominant individuals (Chase & Seitz, 2011; Chase, Tovey, Spangler-Martin, & Manfredonia, 2002; Perlman, Borries, & Koenig, 2016). Previous studies in other bird species have found conflicting results with more dominant (male) blue tits using social information more (Aplin, Sheldon, et al., 2013) while more dominant chickadees used it less (Jones et al., 2017). I did not find dominance ranking to influence social learning in either direction; more dominant individuals were no faster or slower at socially learning the novel behaviour. As chicks were tested within artificially induced pairings in an isolated chamber away from the group, dominance ranking may have played less of a role in influencing social learning opportunities in my setup than in natural settings where it has been previously suggested to explain differences in social information use (Kappeler, 1987; Langen, 1996). For example, subordinate individuals that may normally have access to new resources restricted within a group setting (as it gets monopolised by dominant individuals), would be more able to gain closer access to the task apparatus and observe demonstrated behaviour in my controlled setting. Additionally, being paired with several differing demonstrator birds between rounds would limit any effect that a particular dominant or subordinate demonstrator bird may have on learning opportunity. Constraining social interactions (and therefore levelling social learning opportunities) may well explain why I find dominance ranking to hold no influence on social learning in my setting. It is also possible that, as with sex differences, variation in social learning may develop with dominance ranking over time as rankings solidify and strengthen, differentiating more with age. I also found no relationship between mass and social learning score. This might reflect the lack of a role for dominance in these settings (with body size being related to dominance rank) or it could be due to the small variation in mass between chicks at this young age and potentially as they grow and variance in mass increases, an effect becomes visible.

I found foraging associations between chicks to be non-random - chicks consistently foraged with certain individuals over others when in their main pen area. This indicates that they have preferred and/or avoided partners and differ in their position within the social network based on these foraging associations. Individuals that are more central within a group have been repeatedly shown to have a higher likelihood of socially learning a behaviour (e.g. Aplin, Farine, Morand-Ferron, & Sheldon, 2012; Claidière et al., 2013; Kulahci et al., 2016; Schakner et al., 2017). This is explained by more central individuals having increased access to information and thus being more likely to socially learn - a basic assumption to diffusion models (Firth, 2019; Hoppitt, 2017). Following a prior study that demonstrated how centrality can subsequently change after an individual learnt a novel behaviour (Kulahci et al., 2018) I aimed to further investigate the relationship between social position (centrality) and social learning outside the context of social learning opportunities. However, an individual's eigenvector centrality score extracted from foraging networks did not predict their social learning performance. Those individuals that were more central within networks of foraging associations (and so had more connections to well-connected others) were no more likely to use social information and learn faster from demonstrator individuals in a separate set of enforced associations than less central individuals. Although I found no relationship with centrality and social learning it is still possible that centrality based on other interactions may relate to social learning performance and is an avenue for future research. For example, Kulahci et al (2018) constructed networks based on affiliative behaviours (approaching individuals and grooming) rather than foraging associations. To my knowledge my study is the first study to separate centrality with social learning opportunity (as all birds interacted with the novel foraging task in a separate chamber in standardised dyads) and therefore makes a crucial step in investigating effects of social positions.

Although this study considered the influence of an individual's sex, mass, social ranking and social position on social learning performance, it is possible that other unmeasured attributes may have also played a role. Both personality and general cognitive ability, which are both likely determined at least in part by genetic make-up, have also been linked to how an individual uses social information. An individual's personality, defined as consistent individual difference in behaviour and often measured on a bold-shy spectrum (Dall et al., 2004; Sih, Bell, & Johnson, 2004), has been linked to how an individual uses social information. Some studies find bolder more exploratory individuals to be less prone to using social information (Kurvers et al., 2010; Rosa, Nguyen, & Dubois, 2012), while others find the opposite of bolder individuals being more prone to using social information (Carter, Marshall, Heinsohn, & Cowlishaw, 2014a; Marchetti & Drent, 2000; Nomakuchi, Park, & Bell, 2009). Additionally, general cognitive ability may also dictate an individual's likelihood of socially learning. Again, there is conflicting evidence into the direction of this relationship. Several studies have found a positive relationship between social information use and asocial learning ability or innovation tendency (Aplin, Sheldon, & Morand-Ferron, 2013; Bouchard, Goodyer, & Lefebvre, 2007) which indicates a common underlying cognitive mechanism. Conversely, others have found a negative relationship (Burkart, Strasser, & Foglia, 2009; Katsnelson, Motro, Feldman, & Lotem, 2011), which is suggestive of some form of trade-off between asocial and social learning. Thus far only one study on fruit flies, *Drosophila melanogaster,* has explicitly linked the use of social information to the presence of a specific allele (Foucaud et al., 2013). While I was unable to assay individual learning speed and personality within the study period, these attributes may better predict individual differences in social learning and are worth further investigation.

I found large inter-individual variation in social learning performance by domestic chicks on a novel foraging task. I investigated how four attributes (sex, mass, dominance ranking and social position) may relate to their performance using a system that simultaneously controlled partner choice during learning, measured and controlled physical attributes and separated social attributes from opportunity. I found social learning performance (in the time taken to socially learn a novel behaviour) to be unrelated to all these measured traits. I therefore conclude that either other individual attributes may better predict social learning performance or that the decision to use social information is much more plastic and dependent on an individual's current state. I suggest that previously reported attributes that predict likelihood of social information use (such as sex and dominance ranking) may well be a consequence of social learning opportunities or differing priorities rather than innate ability. Inter-individual variation in social learning is a relatively unexplored area and I hope my results help further understanding into inter-individual differences in social learning.

3

Does socialising in larger groups result in increased opportunities for social learning and faster information spread?

3.1 Abstract

A major benefit of group living is the opportunity it provides individuals to acquire beneficial information from others, such as socially learning a novel foraging behaviour. A larger group with greater numbers of individuals provide more sources available to acquire information from and so more opportunities for social learning. Consequently, interacting with multiple individuals in larger groups may be expected to result in increased spread of novel behaviours. However, interacting within larger groups may also provide increased distraction away from learning and offer alternative foraging tactics which decrease social learning and behavioural spread. I investigated the relationship between the size of group an individual is interacting within and social transmission of novel behaviours. To do this I presented young pheasants, *Phasianus colchicus,* with a novel foraging task and monitored the spread of solving behaviour across four populations that were repeatedly exposed to an identical task in controlled group sizes. In two populations, pheasants interacted with the task in small groups (3 individuals), while in two other populations interactions occurred in larger groups (6 individuals). I then tracked the spread of behaviour within each population using a Network Based Diffusion Analysis (NBDA), while simultaneously recording alternative foraging tactics. I found that the novel foraging behaviour spread at the same rate throughout all four populations, regardless of grouping condition. While I found that the novel foraging behaviour spread socially across

populations, I found equal support for NBDA models where social learning was dependent on the total number of connections to informed individual and when it was dependent on the proportion of informed connections, suggesting that both these factors may have played a role for pheasants socially learning this behaviour. I also found, in concord with previous work, the foraging tactic of scrounging (obtaining food from another individual without exhibiting the novel behaviour) was more prevalent in larger groups, however this did not have a detrimental effect on learning and overall spread.

3.2 Introduction

Individuals can acquire information through personal interaction with their environment (asocial learning) and through interacting with or observing the behaviour of others (social learning) (Dall et al., 2005). One assumed benefit of group-living is the opportunity for individuals to observe the behaviour of group mates and so socially learn advantageous behaviours (Clark & Mangel, 1984, 1986; Galef & Giraldeau, 2001; Heyes & Galef Jr., 1996; Zentall & Galef, 1988). As the size of a group increases, probabilistically more individuals will acquire information (such as a new adaptive behaviour) through asocial means (Liker & Bókony, 2009; Morand-Ferron & Quinn, 2011), and so potentially providing others with new social learning opportunities. Indeed, the foraging efficiency of fish has been found to increase with increasing shoal size, a result presumed to be due to information transfer of foraging locations (Day et al., 2001b; Morgan, 1988; Pitcher, Magurran, & Winfield, 1982; Ryer & Olla, 1991, 1992). Similarly, a novel foraging behaviour both arose and spread faster within larger groups of Australian magpies, *Cracticus tibicen dorsalis*, which was assumed to be a result of social transmission (Ashton, Thornton, & Ridley, 2019). While overall group size might provide greater opportunities for social learning of novel behaviours, the consequences of associating with increasing numbers of individuals in larger (sub)group sizes may not directly result to increased use of social information and social learning.

Firstly, associating with more individuals may indeed provide an environment conducive to socially learning. In addition to overall group size resulting in an increased likelihood of a new behaviour arising, increasing the number of demonstrators performing that behaviour can change an individual’s likelihood of acquiring/adopting it. Studies on fish and rats have shown that the probability of an individual socially learning a behaviour increases with the number of individuals demonstrating that behaviour (Beck & Galef, 1989; Chou & Richerson, 1992; Laland & Williams, 1997; Sugita, 1980). Thus, as an individual associates with an increasing number of others that are performing a behaviour, the more likely they are to socially learn that behaviour. Consequently, associating with multiple individuals that are demonstrating a certain behaviour may result in a faster adoption of that behaviour by individuals as they become more likely to socially learn it. Second, associating with multiple individuals provides a wider array of individuals with differing attributes that may make them especially attractive to learn from. Individuals do not necessarily copy others equally, instead showing preferential attention to particular demonstrators dependent on their characteristics; 'who to copy strategies' (Coussi-Korbel & Fragaszy, 1995c; Hoppitt & Laland, 2013; Laland, 2004; Rendell et al., 2011). These characteristics can be attributes of the demonstrator such as size, sex and dominance ranking, or direct measures of success attained by the demonstrator (Hoppitt & Laland, 2013). Consequently, associating with a greater and more diverse array of individuals to copy from could result in individuals being more selective in whom they choose to copy from and as a result, might choose to use social information more often.

Alternatively, associating with multiple others within larger groups may not present an environment of increased learning opportunities. Although a larger group is likely to hold more informed individuals, it will also contain higher numbers of uninformed individuals which may distract attention away from informed demonstrators. Many studies showing social learning of a behaviour to increase with the number of informed individuals (Beck & Galef, 1989; Chou & Richerson, 1992; Laland & Williams, 1997; Sugita, 1980), generally assessed individuals on the likelihood of socially learning from one or multiple informed demonstrators and did not provide additional uninformed osbervers who may distract from or interfere with the learning process. A food extractive task in pigeons (*Columba livia*), revealed that birds were slower to socially learn the task when accompanied by an increasing numbers of bystanders (uninformed individuals) and faster when accompanied by increasing numbers of informed demonstrator birds (Lefebvre & Giraldeau, 1994). Thus it has been suggested that rather than total number of connections to informed indivuals, the ratio of informed to uninformed connections may be more influential whether an individual adopts a behaviour by social learning (Firth, 2019).

Finally, associating within larger groups may actively impede social learning. Within larger groups there often exists greater competition among individuals over food which may, in turn, lead to defensive behaviour and thus distraction away from learning (Nicol & Pope, 1994). Larger groups may also permit individuals to exhibit alternative foraging strategies. The opportunity to scrounge food from other informed individuals, rather than learning how to extract food independently, can inhibit social learning of novel foraging behaviours. When given the option of scrounging, pigeons did not socially learn how to solve a novel food extraction task, instead they adopted a scrounging tactic and would only learn this task when prevented from scrounging (Giraldeau & Lefebvre, 1986, 1987b; Lefebvre & Helder, 1997). Likewise, an increased scrounging opportunity has also been shown to inhibit social learning in capuchin monkeys Cebus apella (Fragaszy & Visalberghi, 1989), zebra finches Taeniopygia guttata (Beauchamp & Kacelnik, 1991) and chickens Gallus gallus domesticus (Nicol & Pope, 1994). If an individual is successful at scrounging, they do not to learn the foraging behaviour themselves. Provided that both game-theoretic models (Afshar & Giraldeau, 2014; Beauchamp, 2001; Caraco & Giraldea, 1991; Vickery, Giraldeau, Templeton, Kramer, & Chapman, 1991) and empirical studies (Aplin & Morand-Ferron, 2017; Coolen, 2002; Dumke, Herberstein, & Schneider, 2016) show a disproportionate increase in scroungers with increasing group size, associating within larger group sizes may therefore retard social learning.

As individuals socially learn a behaviour through observing others, the size of group an animal associates with is likely an obvious influencer. What is yet unclear is whether associating with others in larger group sizes results in more demonstrations of behaviours from multiple individuals and so more opportunities for social learning and an increased likelihood of acquiring those behaviours, which ultimately results in faster behavioural spread across the whole population or, whether larger groups can act to distract from or impede social learning and even provide alternative foraging opportunities (e.g. scrounging), resulting in overall slower behavioural spread. Thus, group size may influence learning differently dependent on several factors. If the likelihood of social learning is influenced by the total number of connections an individual has to informed others, then interacting as part of larger groups would offer an advantage. Alternatively, if an individual's attention is split across all members of a group then the proportions of connections to informed over uninformed individuals may be more important than group size. Finally, if group size alters foraging dynamics this may also influence the likelihood of social learning. I therefore investigated the effect of group size on social learning, specifically exploring differing models of social transmission and foraging strategies used and how these affect the spread of behaviour across the wider population.

I experimentally manipulated the size of group in which an individual encountered a novel foraging task and determined the effect this had on social learning and behavioural transmissions across the wider population. To do this I presented young pheasants, *Phasianus colchicus,* with a novel foraging task and monitored the spread of solving behaviour across four populations in which individuals were repeatedly exposed to an identical task in controlled group sizes. Importantly, the overall size of the four populations did not differ, but only the size of groups interacting with the task during each exposure. I maintained a semi-natural setting where individuals could interact freely (and exhibit natural foraging strategies) while maintaining strict experimental control over the size of groupings and time exposed to the task. In two populations I allowed individuals to repeatedly interact with the task in small groups (3 individuals), while in the other two populations I allowed individuals to interact with the task in larger groups (6 individuals). I recorded the group compositions during repeated exposures to the task, the order in which individuals acquired the novel solving behaviour and the identity of individuals exhibiting an alternative foraging strategy, obtaining the reward via scrounging food from other group members. I used a dynamic network-based diffusion analysis (NBDA) to assess whether group members acquired the behaviour through asocial or social learning and whether the rate of social transmission (likelihood of socially learning from an informed individual) differed with grouping condition. I considered two differing hypotheses for this analysis: the first assumed the likelihood of social learning was related to the total number of connections to informed individuals and the second assumed this was relative to the proportion of connection to informed individuals. This then allowed me to see how group size may affect social learning and social foraging strategies used and how this affects behavioural transmission across the wider population.

3.3 Methods

3.3.1 Subjects and housing

I hatched one hundred and ninety two pheasant chicks between the 24th and 25th May 2017 and housed them in four identical temperature-controlled enclosures in populations of 48 individuals for 3 weeks. Enclosures consisted of a main area, an extended area and gated access to a testing chamber where birds entered to interact with a task (**Figure 3.1**). Birds were confined to the main area for the first week and this main area was then expanded by lifting a barrier to include the extended area from week two. I provided birds with commercial chick crumb and water *ad lib* and habituated to human observers from day one. All birds were individually identified by small, numbered wing tags fitted at ten days old.

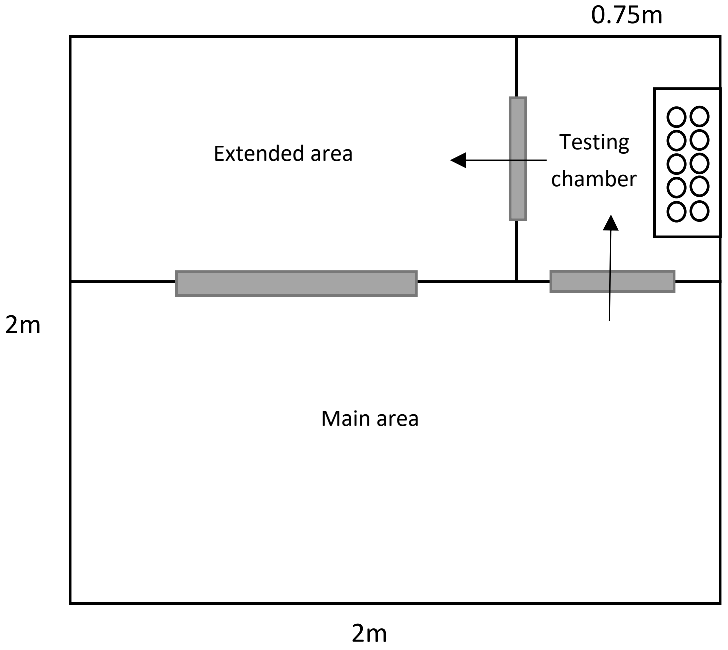


Figure 3.1 Enclosure layout. During testing birds were cycled through from the main area into the testing chamber where they interacted with the task (position of task shown) before exiting into the extended area. Grey bars indicate gated doors.

3.3.2 Training and Task apparatus

Before the experiment began, I shaped birds to voluntarily and individually enter the testing chamber (29/05/17 - 02/06/17). This shaping comprised scattering mealworms on the floor of the testing chamber and repeatedly cycling groups of birds through the testing chamber where they obtained food rewards. Group size was gradually decreased until all birds voluntarily entered the chamber individually.

The birds faced a novel extractive foraging task within the testing chamber. To solve the task birds had to peck through a sheet of tissue paper in order to obtain a concealed mealworm reward – an experimental protocol that has proven successful in several bird species (Blue tits, *Cyanistes caerueus,* Aplin et al. 2013; Starlings, *Sturnus vulgaris*, Boogert et al. 2008; New Zealand robins, *Petroica longipes*, Shaw et al. 2015; Pheasants, *Phasianus colchicus,* van Horik et al. 2016). The apparatus consisted of a white box with two rows of five wells (2cm diameter, 1.9cm deep) each containing three mealworms and covered by a taut sheet of white tissue paper. To encourage birds to peck through the tissue paper (and speed up overall spread of solving behaviour throughout the group), four of the wells always had a hole punctured through the paper and so exposing the mealworm rewards underneath.

To ensure a starting point to the spread of this novel foraging behaviour, I trained one bird per population to become a demonstrator (03/06/17 – 04/06/17). I repeatedly exposed this individual to the task apparatus until they consistently solved the task (through performing the novel pecking through paper behaviour). Initially the task was presented to demonstrator individuals with tissue paper on all wells fully punctured open. The size of holes on the wells was then gradually reduced until demonstrator birds could peck open fully covered wells.

3.3.3 Experimental procedures

I conducted three stages of testing. First, a pre-test allowed me to determine if any individuals could solve the task independently before having experienced a demonstration (03/06/17); Second, 12 social rounds in which birds interacted with the task in groups (05/06/17- 09/06/17); Third, a post-test to ascertain final numbers of individuals solving the task when tested alone (09/06/17). All birds therefore completed 14 rounds (the individual pre- and post- test round plus 12 social rounds).

3.3.3.1 Pre-test and demonstrator selection

During pre-testing, birds could engage with the test apparatus for one minute whilst alone. Two birds (of 192) solved the task in this initial test and so these two individuals plus another two were selected to become demonstrators, resulting in one demonstrator per population. All four demonstrator birds were trained until they consistently solved the task (see above for details).

3.3.3.2 Social rounds

All 48 birds in each population (including the one demonstrator bird) passed through the testing chamber once in each of the 12 social rounds. In two populations, birds were allowed to enter the testing chamber, and hence encounter the task apparatus, in groups of three individuals (small group). In the other two populations birds were allowed to encounter the task apparatus in groups of six individuals (large group). On every round, each group spent three minutes in the testing chamber before being released into the extended area. Birds entered the testing chamber of their own volition and I made no attempt to control associations or group composition. For the first five rounds, birds were given one box of 10 wells to interact with for the three minutes, however from round six onwards, as more individuals learnt to solve the task and so exhausted the number of available sealed wells, birds were presented with a second 10 well box after 90 seconds to permit more learning opportunities. For each round I recorded the identities of birds in each group, the state of each bird being informed (1) or uninformed (0) depending on if they had performed the solving behaviour, and lastly if they obtained food by scrounging from wells opened by another bird.

3.3.3.3 Post test

After the 12 social rounds, I tested all birds individually again to assay whether they were able to solve the task. This test was presented to identify any birds that had learnt the behaviour but had not performed it in the presence of peers. As with the pre-test (see above) each bird spent one minute in the testing chamber alone with the apparatus.

3.3.4 Statistical analysis

3.3.4.1 Does group size affect the likelihood of learning to solve the task?

To investigate whether group size influenced the number of rounds an individual took to solve the task (the overall rate of behavioural acquisition), I fitted a Cox proportional hazards mixed effect model with grouping condition as a categorical predictor variable and population as a random effect using the using the ‘survival’ and ‘coxme’ packages (Therneau, 2015, 2018; Therneau & Grambsch, 2000) in R v.3.3.1 (R Core Team, 2016). The round each bird learnt the solving behaviour was the dependent variable with birds that did not learn treated as censored observations capped at the last post-test round. This survival analysis modelled the cumulative probability that an individual had of acquiring the solving behaviour in each round (through both social and asocial learning). Cox survival analysis will generate a hazard ratio for the grouping conditions with an estimated hazard ratio of 1 indicating no difference in the likelihood of acquiring the solving behaviour between group size condition, with values significantly lower or higher indicating a difference.

3.3.4.2 Do pheasants use social information to solve the task and does this vary with grouping condition?

I tested whether the task solving behaviour was learnt socially using a Network Based Diffusion Analysis (NBDA; (Franz & Nunn, 2009). Specifically, I conducted a dynamic variant of Order of Acquisition Diffusion Analysis using the ‘NBDA’ package (Hoppitt, Photopoulou, Hasenjaer, & Leadbeater, 2020) in R on all four diffusions across the four populations. NBDA allows us to evaluate the evidence for whether the solving behaviour was at least sometimes learnt socially, as opposed to purely asocially and provides an estimate of the strength of social transmission relative to asocial learning. NBDA is an extension of the Cox model which assumes the hazard rate of an individual learning the solving behaviour by social learning is proportional to their strength of connections to informed individuals, thus if the solving behaviour follows the connections within the population's social network social transmission is inferred. A dynamic variant of NBDA allows for the network to change over time such that the networks represent social learning opportunities as they developed across the experiment.

The dynamic social networks were created from the group compositions observed in each social round when small or large groups of birds interacted with the task and the informed status of the birds. I assumed that, for each round, social learning of the task solving behaviour could potentially occur between any individual that was informed at the start of the round and any individual that was in the same group and uninformed at the start of the round. Additionally, I assumed that birds could learn the behaviour and transmit it within the same round to another uniformed individual. Finally I also expected that birds may have their learning influenced by observation of or exposure to informed birds in earlier rounds and that social learning might latently occur in one round but not be manifested in behaviour until a later round. Therefore, I firstly created cumulative networks for each round which represented a cumulative sum of associations formed with the current and all prior rounds. These cumulative networks were then multiplied with the state of each individual (informed=1 or uninformed=0) every round to provide cumulative networks of learning potential. i.e., the connection from bird B to bird A at round X represents the number of rounds A and B have been together prior to and including round X during which A has been informed. These dynamic networks of learning potential were then related to the order in which chicks first learnt the solving behaviour.

I considered two differing hypotheses of social transmission within the NBDA. Our first hypothesis assumed the likelihood of social learning to be relative to the total number of connections to informed individuals (H1). Our second hypothesis assumed social learning to be relative to the proportion of informed connections (H2). We therefore ran the NBDA analysis either with untransformed dynamic networks of learning potential (H1) or with transformed networks (H2). To transform the networks for H2 we divided the networks of learning potential by the group size minus one (5 for the large grouping condition and 2 for the small, thus representing how an individual’s attention was split among fellow group members).

The dynamic networks (untransformed and transformed) were then related to the order in which chicks first learnt the solving behaviour, with those that learnt in the testing chamber together in same round counted as being tied (using the ‘true tie’ function which allows for all possible orders in which the birds may have learnt from one-another). Sex was included as an individual level variable that may affect the asocial and/or social learning rate because pheasants are sexually dimorphic in body size at a young age (Whiteside et al., 2017) and because other species show differing cognitive performance dependent on sex (e.g. 51,52). NBDA will provide a social transmission rate (*s* parameter) which estimates the increased rate of learning per unit connection (either based on total (H1) or proportional (H2) connections to informed individuals). I considered models where the social transmission rate was constrained to be the same across all four populations (if social transmission was just as likely between grouping conditions), different between conditions (as might be expected if birds were more likely to socially learn in larger groups that comprise a larger range of available demonstrators), and lastly where social transmission rates differed between all four populations. I used an unconstrained modelling approach to fit all possible models of differing social transmission rates, asocial learning rates and the effect the individual level factor of sex has on these, and adopted an information theoretic approach to compare and select the best model using the Akaike Information Criteria corrected for small sample size (AICc) (52,53).

3.3.4.3 Do scrounging rates differ with group size?

I tested whether the number of individuals scrounging was affected by grouping condition and whether this changed with progressing rounds by fitting a generalised linear mixed model (GLMM) with a poisson error distribution and sqrt link function using the ‘lme4’ package (Bates et al., 2015). The total number of birds scrounging per population per round was the response variable with round number and grouping condition (small/large) as explanatory fixed factors and enclosure ID as a random factor. To assess whether the number of birds scrounging within each round differed depending on grouping condition I included an interaction term between round and grouping condition. The best model was selected using an information theoretic approach comparing models through AICc values.

3.3.5 Ethics

All work was conducted under Home Office licence PPL 30/3204 held by JRM and approved by the University of Exeter Psychology Ethics Committee.

3.4 Results

3.4.1 Does group size affect the likelihood of learning to solve the task?

The number of birds able to peck through paper and obtain food rewards increased as the testing rounds progressed until approximately half of the population could solve the task by the final round (**Figure 3.2**). This rate of increase was similar between populations regardless of grouping condition. We found no evidence for a difference in the speed of learning between birds in the small and large grouping conditions (Hazard ratio large/small = 1.13, 95% C.I.= 0.73 – 1.74, Z =0.56, events (e) = 90, p = 0.58; **Figure 3.2**).

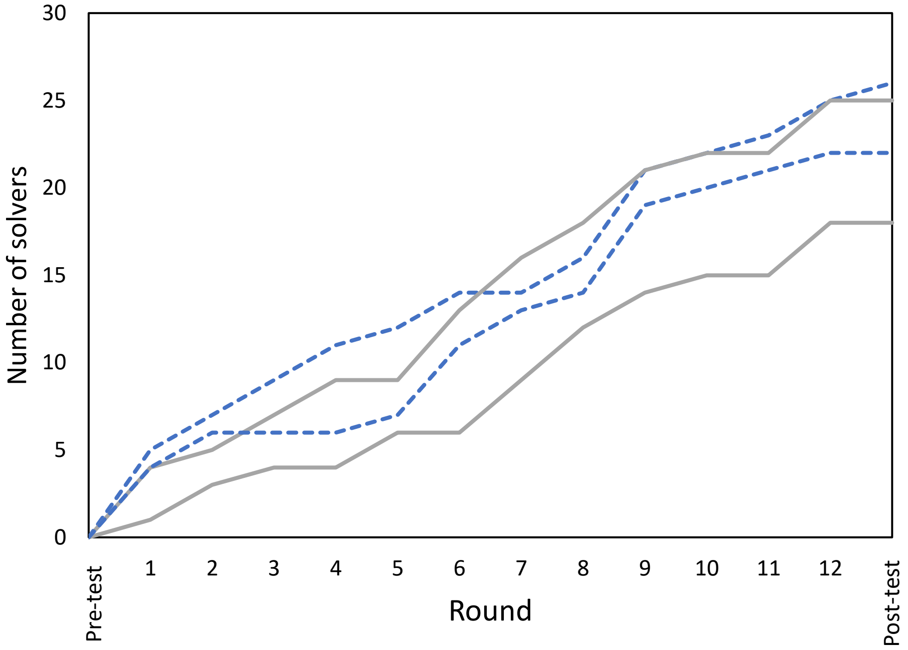


Figure 3.2 The cumulative number of individuals able to solve the task by pecking through the tissue paper. Dashed blue lines indicate the two enclosures in the small grouping condition and solid grey lines indicates the two enclosures in the large grouping condition.

3.4.2 Do pheasants use social information to solve the task and does this vary with grouping condition?

Using an AIC model averaging approach across all candidate models we found support for the social transmission of solving behaviour. Although fewer models represented pure asocial learning within all the candidate models of both hypotheses, support for models of social transmission was greater, even when asocial support was multiplied to the equivalent number of models (**Table 3.1**). Across both hypotheses, there was similar support for social transmission rates being equal across all four enclosures or differing within enclosure but minimal support for this difference depending on grouping condition (**Table 3.1**). There was also little support for an effect of sex on either the asocial or social learning rate in either hypothesis, the support being less than 50% for models that included sex indicating that these effects are unlikely to be in the best predictive models (**Table 3.2**). For the first hypothesis where social transmission is estimated based on the total number of connections to informed individuals, the top model included an equal social transmission rate (*s)* across populations of small and large grouping conditions, with *s* estimated at 0.38 [95% CI: 0 - 1.81; 90% CI: 0.02 - 5.00] times greater than the asocial learning hazard rate per informed connection, with no influential effect of sex on learning rate. For the second hypothesis, where social transmission is estimated based on the proportion of connections an individual has to informed individuals, the top model again included an equal social transmission rate (*s)* across populations of small and large grouping conditions, with *s* estimated at 1.11 [95% CI: 0 – 5.12; 90% CI: 0.06 – 5.00] times greater than the asocial learning hazard per proportional unit of connection, with no influential effect of sex on learning rate. As zero was only just included in the 95% confidence intervals of *s* and not included within the 90% confidence intervals for models of both hypotheses, this strongly indicates that social transmission of behaviour was at least partially responsible for the spread of behaviour between individuals across populations. Overall, it was estimated that nearly half of all learning events occurred by social transmission (H1 = 45% of learning events [95% CI: 0-67]; H2 = 44% [95% CI: 0-66]). The AICc scores for the top models of either hypothesis however were very similar; 611.32 for H1 and

611.29 for H2, thus providing no distinguishable support for one hypothesis over the other.

Table 3.1 Support shown for models of differing social transmission rates (number of models for each type shown) after model averaging across all candidate models for both H1 and H2 hypotheses .

Model	Number of models	Weightings (H1)	Weightings (H2)
No social transmission (purely asocial learning)	2	0.13	0.13
Social transmission rate equal for all enclosures	4	0.37	0.39
Social transmission rate dependent on grouping condition	4	0.13	0.13
Social transmission rate different for all enclosures	4	0.36	0.35

Table 3.2 Support for models that include an effect of sex on either the asocial or social learning rate after model averaging across all candidate models for both hypotheses.

	Sex on asocial learning rate	Sex on social learning rate
H1: Social transmission proportional to total number of informed connections	0.44	0.34
H2: Social transmission proportional to relative number of informed connections	0.46	0.35

1) *Do scrounging rates differ with group size?*

The total number of birds scrounging in each enclosure increased with each progressing round, with higher rates of increase in large groups compared to small groups (**Table 3.3**; **Figure 3.3**). The best model included an interaction term between the fixed effects of round and grouping condition, accounting for 95% of model weightings (**Table 3.3**).

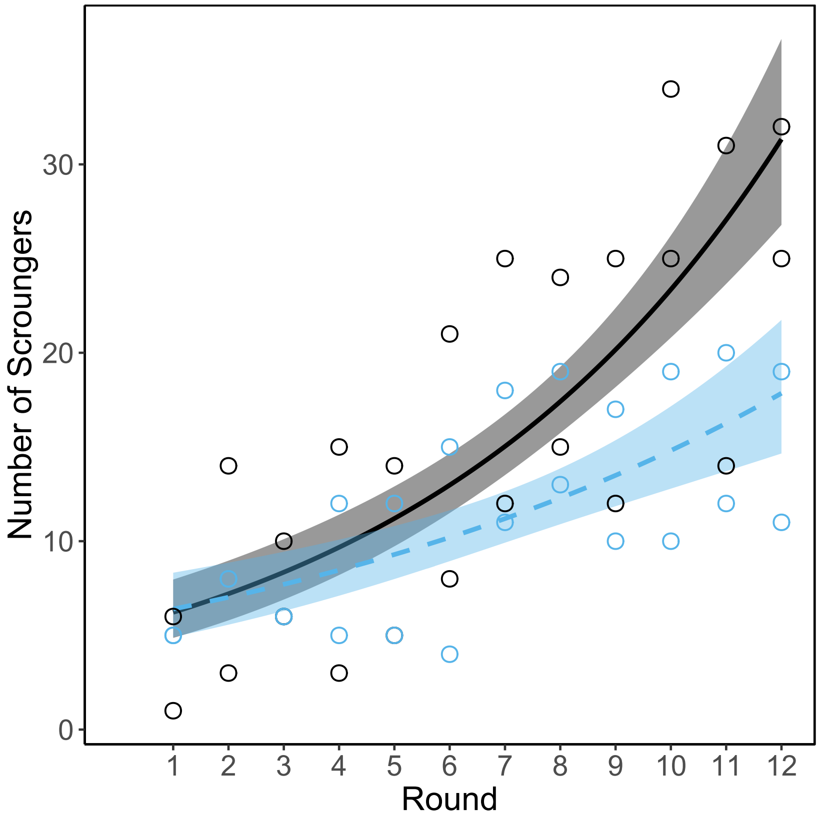


Figure 3.3 The total number of scroungers within each enclosure in the small (dashed blue) and large (solid grey) grouping condition for each progressing round, with predicted lines fitted and 95% confidence intervals shown.

Table 3.3 Models ranked in order by AICc values with included explanatory factors; enclosure was included as a random effect in all models. Change in AIC value (ΔAICc), degrees of freedom (df) and model weighting shown.

Included explanatory factors	**ΔAICc**	**df**	**Weight**
Round + Grouping condition + Round-Grouping condition Interaction	0.0	5	0.97
Round	7.7	3	0.02
Round + Grouping condition	9.1	4	0.01
Null model *(only random effect of enclosure)*	123.2	2	<0.001
Grouping condition	124.0	3	<0.001

3.5 Discussion

I found evidence that social transmission was at least in part responsible for the spread of a novel foraging behaviour across populations of pheasants. However, neither the overall uptake of the behaviour, nor the rate at which pheasants were likely to socially learn, was affected by the size of group individuals associated in when interacting with the task. I also found, in concord with theoretical models and previous studies (Afshar & Giraldeau, 2014; Aplin & Morand-Ferron, 2017; Beauchamp, 2001; Caraco & Giraldea, 1991; Coolen, 2002; Dumke et al., 2016; Vickery et al., 1991), populations interacting with the task in large groups did contain a proportionately higher number of individuals that obtained food through scrounging tactics; however this did not detrimentally affect social transmission of behaviour.

Conducting a dynamic NBDA indicated that pheasant chicks likely utilised social information when learning to solve a novel foraging task. I considered two differing hypotheses of social transmission in the NBDA; the first where the likelihood of social learning was directly related to the total number of connections an individual had to informed individuals, and the second where this was related to the proportion of informed connections. Models within both these hypotheses provided support for the diffusion of solving behaviour following social networks created from associations within the testing chamber. While the top model of these differing hypotheses provided different social transmission rates (*s* parameters) due to their differing units, they both estimated that just under half of all learning events occurred through social learning. Averaging across model sets of both hypotheses however did not show social transmission rates (that is the likelihood of socially learning from informed individuals) to be greatly influenced by grouping condition. Thus, despite the larger grouping condition providing a greater array of individuals during task interaction, birds were not more likely to socially learn from informed individuals than those within in the small grouping condition. Although sex has been shown to influence learning within other species (Jones et al., 2003; Lonsdorf et al., 2004), again averaging across models of either hypothesis showed no support for sex affecting either the social or asocial learning rate within pheasants at this young age. It is possible that as birds age and sexual dimorphism increases, an effect of sex on learning would emerge. Thus for pheasant chicks at this age, social learning played a key role in the acquisition of the novel foraging behaviour but neither a bird’s sex nor the group size they interacted with the task in affected their likelihood of social learning from informed others.

Equivalent numbers of birds acquired the novel foraging behaviour within each round across populations and grouping conditions, with similar numbers of individuals having learnt the solving behaviour by the end of the experiment. Thus, birds that were in populations of the large grouping condition did not appear to gain any benefits of increased social learning due to multiple demonstrators and were overall no faster at acquiring the novel foraging behaviour across progressing rounds than birds in the small grouping condition populations. If the likelihood of socially learning the novel behaviour increased with the total number of connections to informed individuals then encountering the task in a larger group would have been expected to increase social learning by individuals, resulting in faster behaviour spread across the wider population. However, I found no such apparent advantage for those in larger groups, suggesting that social learning and resultant transmission does not necessarily directly increase with increasing numbers of demonstrating individuals and additional complex factors may also be at play.

I found equal support for models of social transmission that assumed the likelihood of social learning to be proportional to the total number and the relative number of connections to informed individuals. The majority of studies investigating behavioural diffusions within animal populations follow the assumption that social learning by an individual will increase with their number of connections to informed demonstrators (Firth, 2020). However, evidence from the human literature along with several animal studies has led to the suggestion that social transmission may follow more complex rules that include aspects such as the proportion of informed and uninformed associates (Centola, 2018; Firth, 2020;

Guilbeault, Becker, & Centola, 2018; Rosenthal, Twomey, Hartnett, Wu, & Couzin, 2015). For example, the behavioural escape response of fish has been found to follow a fractional contagion based on the proportion of fish around them also displaying the evasive behaviour (Rosenthal et al., 2015). Comparing the AICc values of the top models from either hypothesis were indistinguishable, suggesting that, for pheasants in this task, social learning may have been influenced by both the total number of connections to informed individuals and the relative proportions of connections to informed over uninformed individuals. This may have arisen because the benefit of more potential informed demonstrators is offset by the distraction offered by an increasing number of uninformed individuals. To separate these two hypotheses further, it would be worth experimentally constructing groups that differed in two separated dimensions: total size, altering the number of potential connections available; and the proportion of informed vs. uniformed individuals with either many or few informed individuals. Nevertheless, this study highlights the need for continued investigating into more complex factors of social transmission, as more basic assumed rules of social transmission may not always lead to predicted results.

Although the spread of solving behaviour did not differ between conditions, group size did influence foraging strategy. In general, as rounds progressed and more birds learnt to peck through paper, the number of birds scrounging from opened wells increased. Crucially, the increase in scroungers was much greater with progressing rounds in the large grouping condition compared to the small. This result matches game-theoretic models of social foraging tactics (Afshar & Giraldeau, 2014; Beauchamp, 2001; Caraco & Giraldea, 1991; Vickery et al., 1991) and matches empirical finings of other studies that report an increase in scrounging with increasing group size (Aplin & Morand-Ferron, 2017; Coolen, 2002; Dumke et al., 2016). Scrounging has been shown to influence social learning, with many studies reporting an inhibition of learning with increasing scrounging (Beauchamp & Kacelnik, 1991; Fragaszy & Visalberghi, 1989; Giraldeau & Lefebvre, 1986, 1987; Lefebvre & Helder, 1997; Nicol & Pope, 1994). Therefore, I might have expected that, if larger groups offer more opportunities for scrounging and thus providing an alternative means of acquiring the reward, then social transmission would have been decreased under these conditions. However, I found no evidence of social transmission rates differing between conditions and so find no evidence of scrounging opportunity either inhibiting or promoting learning in this case. I suspect that increased scrounging rates in larger groups provided an additional foraging tactic but this did not hinder social learning as might be expected in this task, because either the act of scrounging a worm from an opened well was fast and did not detract attention away from learning the task or perhaps because scrounging did not provide sufficient benefits to drive individuals to solely adopt this foraging tactic.

One confound of the experiment was that although the reward value per successful forage was consistent across treatments, with three mealworms in each well, this inevitably meant that overall there was less food available in the larger grouping condition. This variation in reward availability could have altered competition levels across the conditions which may, in turn, have affected learning rates. Studies on Australian magpies (*Gymnorhina tibicen*) and pheasants have shown a positive relationship between an individual's (asocial) learning performance on cognitive tasks and the size of the group in which they associate (Ashton, Ridley, Edwards, & Thornton, 2018; Langley, van Horik, Whiteside, & Madden, 2018). One explanation of those previous results is that increased competition increases food motivation prompting greater investment in learning about (novel) foraging methods (Smulders, 2018). Therefore, increased competition for food could have promoted either asocial or social learning. However, I found no difference in social transmission rates between conditions and the overall probability of individuals acquiring the behaviour was equal across conditions indicating that asocial learning was also not affected. Therefore, I conclude that the difference in overall food reward did not result in a noticeable difference in acquisition of solving behaviour due to this increased competition.

In summary, I show that for young pheasants interacting with a novel foraging task in either large (6 individuals) or small (3 individuals) sized groups, resulted in no noticeable difference on the rate at which the solving behaviours spread across populations. While I found evidence, from conducting a dynamic NBDA, that the behaviours spread socially between individuals, the rate of social transmission (that is the likelihood of learning from informed individuals) also did not differ with group size. I found equal support for two differing hypotheses within the NBDA; one where social learning was relative to the total number of connections has to informed individuals and one where this was relative to the proportion of informed connections, thus suggesting that for this task in pheasants, both factors may have played a role and highlighting the need for future studies to investigate additional factors of social transmission. I also found, in agreement with previous work, that the foraging tactic of scrounging disproportionately increased with group size, however this did not negatively impact social learning and behavioural spread disputing the notion that scrounging behaviour is inherently detrimental to social transmission .

4

The modularity of a social group does not affect the speed of transmission of a novel, socially learned behaviour, or the formation of local traditions

4.1 Abstract

The social structure of a group describes the distribution and strength of associations between individuals and is crucial in determining how a socially learnt behaviour will spread. Despite predictions from theoretical models on how specific parameters of social structure will influence social transmission, empirical manipulations remain scarce. Modularity is one such property that is predicted to affect overall behavioural spread and be vital for the establishment of behavioural variants/traditions (Cantor & Whitehead 2013; Whitehead & Lusseau 2012). I therefore experimentally manipulated the modularity of populations of domestic fowl chicks, *Gallus gallus domesticus,* to see the effect on social transmission of a novel foraging behaviour. I compared the spread of behaviour in populations that held a network of high or low modularity against a control population that prevented social learning. I found the novel foraging behaviour to spread socially between individuals when social transmission was permitted, however, modularity did not increase the speed of behavioural spread nor lead to the initial establishments of such traditions. This result is perhaps suggestive that additional factors in the social transmission process may influence and dictate behavioural spread leading to conflicting results.

4.2 Introduction

Social learning enables information (such as novel foraging behaviours) to spread throughout a group of animals (Hoppitt & Laland, 2013). This spread is determined by both the attributes of individuals and the social connections between those individuals within the group (Krause, James, Franks, & Croft, 2015). Coussi-Korbel and Fragaszy (1995) first highlighted the importance social connections has for social learning opportunities with the likelihood of learning depending on the associations and relationships individuals have with one another. They introduced the notion of 'directed social learning' whereby attributes of individuals can affect the likelihood of learning; since then evidence has accrued of kinship, sex, age, dominance, size and familiarity all being significant factors (for reviews see Laland, 2004; Rendell et al., 2011). Such dyadic affiliations are set within a broader social structure or network of polyadic connections between multiple individuals and consequently how a group is structured will influence how information spreads throughout; those individuals that are closely associated or affiliated are more likely to learn from one-another (Coussi-Korbel & Fragaszy, 1995; Croft et al., 2005; Croft, James, & Krause, 2008). Group structure can be described and quantified using metrics derived from Social Network Analysis through depicting the connections (edges) between individuals (nodes) including the strength of relationship between them (edge weights) (Croft et al., 2008). Using this approach, it has been demonstrated that particular network structures do indeed correlate with information flow and facilitate behavioural traditions and culture (Allen, Weinrich, Hoppitt, & Rendell, 2013; Aplin, Farine, et al., 2015; Aplin et al., 2012; Atton, Hoppitt, Webster, Galef, & Laland, 2012; Cantor & Whitehead, 2013; Claidière et al., 2013; Farine, Aplin, Sheldon, & Hoppitt, 2015; Firth & Sheldon, 2015; Firth et al., 2016; Hobaiter, Poisot, Zuberbühler, Hoppitt, & Gruber, 2014; Jones et al., 2017; Kulahci et al., 2016, 2018b; Schakner et al., 2017). These studies recorded information flow across established, natural networks (but see Aplin et al 2015; Firth & Sheldon, 2015; Firth et al., 2016), typically only considering one or two networks per study. Consequently, isolating or identifying specific aspects of the network structure that are important determinants of information transmission is difficult because they are commonly bound up with other network properties and likely highly dependent on the composition and history of the group. However, there are a few theoretical models which test the influence that different social structures have on information transmission within non-human societies (Cantor & Whitehead, 2013; Nunn, Thrall, Bartz, Dasgupta, & Boesch, 2009; Voelkl & Noë, 2010; Whitehead & Lusseau, 2012). Yet experimental manipulations of social structure to test the resulting effects are lacking.

A small number of studies have experimentally altered social structure to see the effect that this has on information transmission. One study found that manipulating the physical environment of sticklebacks (*Gasterosteus aculeatus*) caused a change in both shoal structure and information flow (Webster et al., 2013). When in more complex environments fish formed smaller groupings with more varied connection strengths, and only under these conditions, as opposed to simple open environments, did the shoal's association network predict information flow. Similarly, Morrell et al. (2008) compared foraging behaviour of naturally-formed shoals of guppies (*Poecilia reticulata*) with those they had artificially created (comprising of random shoal members). Natural shoals were found to be more structured (comprising of individuals with associations of differing strengths) than artificial shoals and while they did not test information transmission directly they found that naturally formed shoals performed better on a foraging task which was likely facilitated by social learning and information flow. Lastly, the social structure of wild songbirds has been manipulated through restricting access individuals have to automated feeders and therefore altering social foraging partnerships (Firth & Sheldon, 2015; Firth et al., 2016). Changing foraging associations subsequently altered pathways of information transmission in the discovery of new food patch locations (Firth et al., 2016) and even had consequences for contexts outside of foraging including changing associations at nesting sites (Firth & Sheldon, 2015). These studies show that modifying the social structure of natural groupings, either directly or as a result of habitat alteration, will change how information spreads throughout the group. These approaches can seldom be applied to change a particular network metric of interest, but instead unpredicted network structures emerge from the experimental manipulations of environment or association, which are then linked to efficacy of information transmission.

An alternative approach to understanding how network structure influences information flow in groups has been to use theoretical models. Nunn, Thrall, Bartz, Dasgupta, & Boesch (2009) simulated information flow across artificial populations to look at the effect different social parameters have on transmission. Of the parameters that changed social structure, they found that increasing the size of subgroupings within a population enhanced the spread of behaviour across the population and reduced the chance of the behaviour going extinct. Using a similar approach, Voelkl & Noë (2010) simulated information propagation across networks constructed from real-life data collected from primate groups. By comparing information flow across the real networks against networks that had various aspects of their structure manipulated, they also showed that information was spread faster in well-mixed networks and was less prone to extinction during transmission compared to the real-life structured networks (Voelkl & Noë, 2010). Thus, these models predict that the more structured a network becomes, the slower that information is predicted to transmit across the group.

One network property that has been explicitly proposed to be influential on information flow and influence the formation and maintenance of local behavioural traditions and culture is modularity (Cantor & Whitehead, 2013). Modularity is a structural property indicating the amount that a network is divided into distinct clusters and is represented by a coefficient value between 0 (completely mixed networks) and 1 (a highly structured network divided into perfect clusters) (Newman, 2004). Consequently, the modularity of a network will affect how likely information will transmit both within and between clusters, and so as modularity increases and clusters become more distinct, information spreads rapidly within a cluster but fails to extend to other, neighbouring clusters. Culture, defined as socially learnt group-specific behaviours (Laland & Hoppitt, 2003), therefore only arises in networks with sufficient modularity so that certain behaviours arise and are constrained within clusters (Cantor & Whitehead, 2013; Whitehead & Lusseau, 2012). Theoretical models simulating social transmission on networks have shown a threshold modularity coefficient value of 0.3. Above this value, as modularity increases so too did distinct behavioural variants arising within clusters in the network (Whitehead & Lusseau, 2012). Consequently, we expect that in groups of low modularity (well mixed, with few distinct clusters), information will spread rapidly and evenly to produce a homogenous expression across the population. In contrast, in groups of high modularity (being highly structured with distinct, weakly linked clusters), we expect that information may spread more slowly, getting stuck within particular clusters, but that within these clusters of well-connected individuals, we might see a conformity of behaviour that may differ from that of other clusters, resulting in several different behavioural traditions within the population. Despite these theoretical predictions, no study has experimentally manipulated the modularity of a group's network (or indeed any other specific network measure) and then observed how this subsequently affected the spread of information or behaviours on the network.

I empirically tested how the modularity of a population's network structure effects the spread of a novel behaviour within domestic fowl chicks, *Gallus gallus domesticus*. Domestic chicks are gregarious, easy to rear in the laboratory and will socially learn about foraging behaviours in early life (Nicol, 2004). I manipulated the groupings of chicks as they encountered a novel foraging task to produce populations that held networks of high or low modularity. To confirm that the solving behaviour of the foraging task spread socially between chicks, I compared the rate of learning in populations of chicks that could learn the novel foraging behaviour socially from others (those in both the high and low modularity populations), with populations in which chicks could only learn the task asocially. Providing an asocial learning control allowed me to determine the baseline rate at which individuals simultaneously acquire the novel foraging behaviour without any effects of social learning. Within the populations where social learning of the behaviour was permitted, I compared the overall rate of spread and the rate of social transmission between populations with high and low network modularity. I predicted, in accordance with theoretical models, that (if socially learnt) the novel foraging behaviour would spread faster in the less-structured populations of low modularity. I also predicted that a difference in social transmission rates between social conditions might arise in that by manipulating modularity by default familiarity between certain individuals during task interaction is altered which has been shown to influence the likelihood of learning. I included sex and mass as variables that may affect the social or asocial learning rates, given that these factors have been shown to influence learning in previous studies (e.g. Jones, Braithwaite, & Healy, 2003; Lonsdorf, Eberly, & Pusey, 2004; Shaw, 2017). Finally, I expected to find that within the populations of high network modularity, solving techniques of the novel foraging behaviour would be contained within clusters and so lead to the formation of distinct local traditions, suggested to underpin cultures (Cantor & Whitehead, 2013).

4.3 Methods

4.3.1 Subjects and housing

One hundred and fifty-four domestic chicks (*Gallus gallus domesticus,* of the Rhode Rock hybrid), split across three batches, were collected as day-olds from a commercial breeder (Organic Pullets, Hittisleigh). Each batch was split into two populations, and each population was housed in a replicated (temperature and humidity controlled) pen, giving a total of six populations overall. The first batch comprised of 27 birds in each population (11 male: 16 female), the second of 24 (12 male: 12 female) and the third of 26 (13 male: 13 female). This breed of domestic chick allows sexing from hatching by feather colouration. Each pen consisted of a 2.3m x 1.2m main enclosure where the birds were housed for the first week, after which they had access to an additional 1.2m x 1.7m enclosure for the remaining two weeks (**Figure 4.1**). Chicks were provided with commercial chick crumb (1st Poultry, Crediton Milling Company), water and grit *ad lib,* in addition to perching materials*.* Coloured plastic flat bands (Avian ID, Cornwall) were fitted to identify individuals on day three and changed for a larger size at two weeks old. I weighed chicks when they were 2 weeks old, using a stand-on flat digital scale (Salter, UK; precision = 1 g). During the study period chicks interacted with a novel foraging task which involved birds voluntarily entering a 0.60m x 0.50m testing chamber adjoining their main enclosure (via a filtering chamber) to interact with the task. At three weeks old chicks were donated to a local free-range poultry farm.

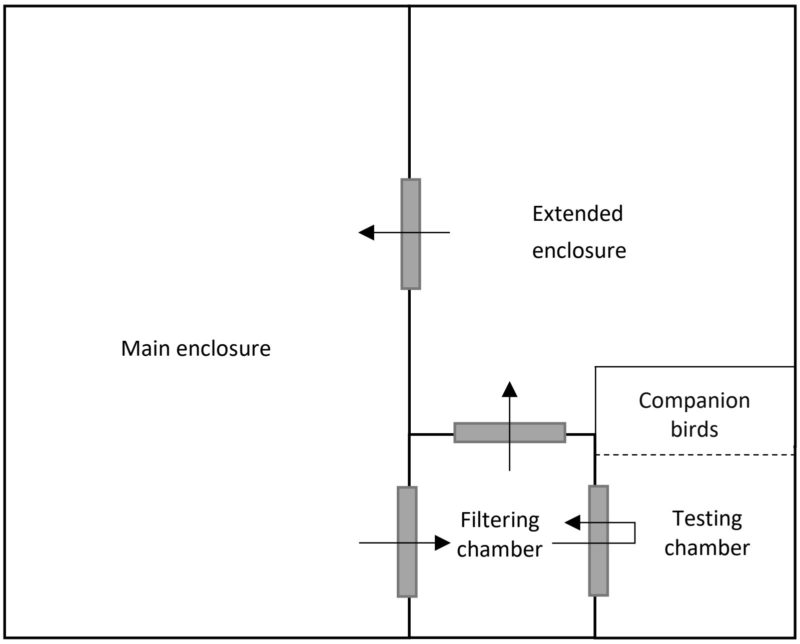


Figure 4.1 Pen enclosure layout. During the experiment chicks were cycled from the main enclosure through the filtering chamber and into the testing chamber where they interacted with the task before exiting into the extended enclosure after testing (see arrows). Grey bars indicate gated doors. Dashed line indicates mesh partition of companion birds for Batch 3 (asocial condition).

4.3.2 Experimental procedures

I presented chicks with a novel foraging task and looked at the rate birds acquired the solving behaviour in populations upon which I had imposed different learning conditions (**Table 4.1**). Birds within populations in Batch 1 and 2 were tested under conditions which allowed them to socially learn the solving behaviour from one-another and in which I manipulated the modularity of the group structure to produce two populations of high network modularity and two populations of low network modularity (**Table 4.1**). Birds within populations in Batch 3 were restricted to asocial learning only (**Table 4.1)**, which allowed me to determine the rate at which the solving behaviour would be acquired asocially without any social transmission.

Table 4.1 Experimental conditions and dates for each of the six populations within the three batches.

Batch	Population	Number of birds	Condition
1	1	27	Social – High Modularity network
(03/11/17 - 25/11/17)	2	27	Social – Low Modularity network
2	3	24	Social – High Modularity network
(26/01/18 - 17/02/18)	4	24	Social – Low Modularity network
3	5	26	Asocial control
(31/10/18 – 22/11/18)	6	26	Asocial control

4.3.2.1 Novel foraging task:

The novel foraging task presented to the birds consisted of a white box with 10 lightweight cardboard doors that could be slid horizontally open to reveal hidden wells containing mealworm rewards (**Figure 4.2**). The apparatus was adapted from previous studies of social learning in birds (Aplin, Farine, et al., 2015; Aplin & Morand-Ferron, 2017; Aplin et al., 2017). The 10 wells (2 rows of 5 wells, 2cm diamter, 1.9cm deep), were concealed by cardboard doors that were painted half-red half-blue. Birds could solve the task by two different techniques; they could push the red side to the right or the blue side to the left to access the well behind and obtain the mealworm rewards.

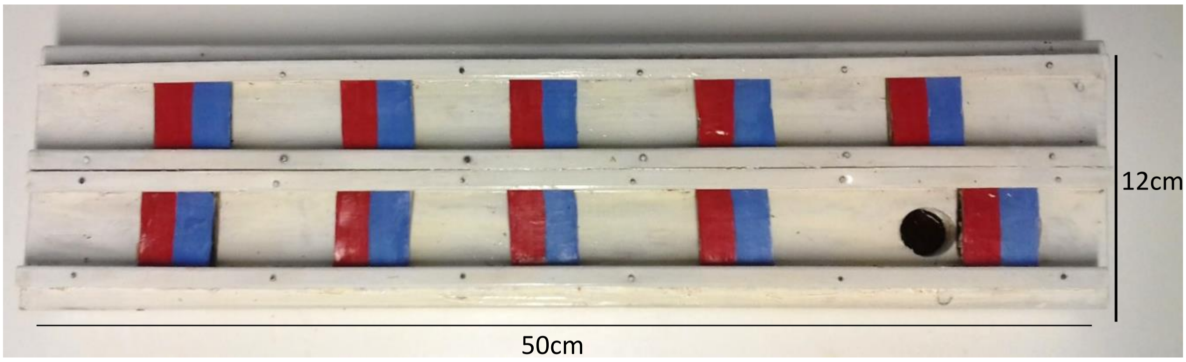


Figure 4.2 Foraging task apparatus. The novel foraging behaviour required to solve the task involved birds pecking at either the blue or red side to slide the door open in order to access the hidden well behind and obtain mealworm rewards. Bottom right door opened to reveal well.

4.3.2.2 Experiment structure

Birds in all three batches received the same experimental structure comprising of three stages; a pre-test round (presented when birds were 7 days old - day 7), 13 grouped rounds (days 13-19) and finally a post-test round (day 20). The pre-test and post-test round consisted of all birds in each population interacting with the task apparatus individually for one minute to a) confirm that none could solve the task prior to the experiment and b) provide final numbers and identities of those able to solve the task at the end of the experiment. The 13 grouped rounds differed slightly between the conditions. For populations in the social conditions, where social learning of solving behaviour was permitted, birds interacted with the task in pre-determined groups of 3 for 3 minutes where all birds could freely interact with the task and each other. Three mini-mealworms were available in each of the 10 wells of the apparatus in these grouped rounds. Populations in the asocial condition could only asocially learn the solving behaviour and so during the 13 grouped rounds birds interacted with the task individually, but two companion birds were present in the testing chamber to keep the social environment consistent within conditions but these birds were prevented from accessing the task apparatus by a mesh barrier (**Figure 4.1**). These two companion birds (one male, one female) were the same for the whole population and never interacted with the task themselves. Only one standard sized mealworm was available behind each of the ten wells in the asocial condition to ensure the mean reward was the same as the social conditions (3 mini-mealworms is an average equivalent weight to 1 standard mealworm). For all conditions, during each round I recorded which individuals solved the task (they opened a well, took and ate a mealworm) and the technique used to do so (whether they pushed red to the right or blue to the left).

Birds only ever interacted with the task in the testing chamber which allowed me to strictly control the time spent with the apparatus and the group compositions (for social conditions). In order for birds to be comfortable with testing conditions, during the first week (before the start of the experiment), I shaped the birds to associate the testing chamber with live mini-mealworm rewards and habituated them to handling by the experimenter. For populations in the social condition I selected one male to be a seeded demonstrator bird and prior to the start of the grouped rounds I trained this individual to successfully solve the task. The purpose of the demonstrator individual was to ensure an initial starting point to the diffusion of solving behaviour by providing one bird that could solve the task that others could learn from. I elected to use the same demonstrator bird for both populations (within a batch) to reduce any effects of directed learning bias that might depend on individual attributes of the demonstrator (Hoppitt & Laland, 2013; Rendell et al., 2011). Within each population, the demonstrator passed through the testing chamber once every round (as did all other birds) and when outside of the testing chamber, he was housed equally between the two populations to ensure equal familiarity with birds in both populations.

4.3.2.3 Manipulation of social structure

Birds within populations in the social conditions (batch 1 and 2) were permitted to learn socially from one-another and so entered the testing chamber in groups of three individuals. I pre-determined the composition of groupings in order to create social networks with specific modularities of my choosing. The networks were created as a summed association of all the testing chamber groupings across rounds and so each population's network represents how often birds were associated together during task interaction. In each batch I created one population with a network structure of high modularity and one population with a network structure of low modularity (**Figure 4.4**). Populations of high network modularity had groups of the same three individuals consistently entering the testing chamber together more often than not over the 13 grouped rounds. This gave highly structured networks with modularity coefficient values of 0.73 (Batch 1) and 0.63 (Batch 2). In contrast, the populations of low network modularity saw much more varied combinations of the three individuals every round and so created much more random well-mixed networks with modularity coefficients of 0.15 (Batch 1) and 0.18 (Batch 2).

4.3.3 Statistical analysis

4.3.3.1 Does social learning and network modularity affect the likelihood of acquiring the solving behaviour?

To investigate whether condition (social of high modularity, social of low modularity and asocial control) influenced the time to acquire the solving behaviour I fitted a Cox proportional Hazards mixed effect model with condition as a categorical explanatory variable and population as a random effect using the 'survival' and 'coxme' packages (Therneau, 2015, 2018; Therneau & Grambsch, 2000) in R v.3.3.1 (R Core Team, 2016) using the R studio wrapper (RStudio Team, 2016). This survival analysis modelled the probability a bird had of acquiring the solving behaviour and obtaining the reward with each progressing round, with round to solve the task treated as a censored observation capped at the last post-test round. Survival analysis generates hazard ratios for each condition with a score >1 showing increased likelihood of acquiring the solving behaviour and a score of <1 a decreased likelihood of acquiring the behaviour.

4.3.3.2 Does the solving behaviour spread socially throughout the populations and do rates differ between social network structures?

To determine whether the behaviour performed to solve each task was learnt socially or asocially I conducted a Network Based Diffusion Analysis (NBDA) (Franz & Nunn, 2009; Hoppitt et al., 2010), specifically a dynamic (time-dependent) Order of Acquisition Diffusion Analysis (OADA) using the 'NBDA' package (Hoppitt et al., 2020) in R. NBDA's have been successfully used on a range of taxa to show the spread of a socially learnt behaviour through a group and in calculating the strength of social transmission occurring (Hoppitt & Laland, 2013). This analysis assumes that the probability of an individual solving the task is proportional to their strength of connections to informed individuals. If the task is socially learnt, then the spread of solving behaviour will essentially follow the links in the group's social network. If the solving behaviour is learnt asocially (say through trial and error) then the order in which individuals solve the task will be independent of the social network. A dynamic NBDA allows for the network to change over time and so directly tracks the spread of behaviour to changing associations (Hoppitt, 2017).

I created a dynamic network based on the changing testing chamber associations and therefore potential social learning opportunities. I used a cumulative network based on associations formed in the testing chamber which for each round represented the current and previous testing chamber associations up to that time period. At every round, the state of each individual was recorded as either informed (1) if they had solved the task at least once, or uninformed (0) if they had never solved the task. I multiplied the state of the individual with the cumulative networks to provide a dynamic network of developing learning opportunities (such that birds could only learn from informed birds they entered the testing chamber with). This cumulative network of learning opportunities was then related to the order in which chicks first learnt the solving behaviour, with those that learnt in the testing chamber together in same round counted as being tied (using the 'true tie' function which models all scenarios of possible orders in which birds learnt). This approach fulfils the ideal criterion of an NBDA where the researcher knows exactly when a behaviour has been performed, by whom and who observed each performance (Hoppitt, 2017).

I used a stratified OADA where I assumed that the baseline rate of asocial learning was equal across all the populations. This baseline rate of asocial learning was derived from the rate at which birds acquired the solving behaviour in the asocial control condition populations in Batch 3. To determine whether social network structure affected the rate of social transmission (how likely birds were to socially learn the behaviour from an informed individual) I compared models of differing social transmission rates. Social transmission rates may vary if social dynamics affected by social structure (such as familiarity with certain individuals) influence social learning. I therefore compared models where transmission rates were assumed to be either the same for diffusions occurring within the same modularity condition, or different depending on modularity condition, or different for all four diffusions regardless of modularity condition. The social transmission rate was set at zero for the asocial learning condition populations. Sex and mass of each bird were included as individual-level variables that may affect the asocial and/or social learning rate. All possible models of differing social transmission rates and individual level variables were fitted and the Akaike Information Criteria corrected for small sample size (AICc) utilised for model averaging and in selecting the best predictive model (Burnham & Anderson, 2002)

4.3.3.3 Does social structure influence the adoption of different solving techniques by the birds?

To investigate whether birds were using a solving technique that matched those of individuals that they are most closely associated with, I tested for assortment based on technique bias of individuals in the number of red and blue solves performed, using the ‘assortnet’ package (Farine, 2014) in R. A network of testing chamber associations was created for birds in the high modularity condition populations and those in the low modularity condition populations. Those birds that never solved the task were removed from the network so as not to influence the calculated assortment coefficient. As not all birds performed the same number of solves, I accounted for uncertainty in individual’s technique bias using beta distributions describing the probability of choosing red and running 10,000 Monte Carlo simulations. For each Monte Carlo simulation of estimated true bias, I measured the weighted continuous assortment metric. I report the mean estimate (with 95% confidence intervals) of assortment from these simulations. I predicted that if birds were learning the exact technique to solve the task or conforming to other’s decisions then I would see positive assortment of individuals solving techniques within the social network. Further, I expected that this assortment would be seen most strongly in the highly modular networks where I would expect conformity within a cluster.

4.3.4 Ethics

All work was approved by the University of Exeter Psychology Ethics Committee and birds were reared at a high standard, exceeding the requirements provided by the Department for Environment Food and Rural Affairs (DEFRA) and the Animals Scientific Procedures Act (ASPA 1986).

4.4 Results

4.4.1 Does social learning and network modularity affect the likelihood of acquiring the solving behaviour?

Birds in the social condition populations were much more likely to learn the solving behaviour with each progressing round compared to birds in the asocial condition populations (high modularity condition: Haz = 13.25 ± 0.44 (SE), Coxph, Z=5.89, events (e)= 87, p=<0.001; low modularity condition: Haz=10.53 ± 0.44, Coxph, Z=5.34, events (e)= 87, p=<0.001 **(Figure 4.3**)). However, there was no difference in the likelihood of learning the solving behaviour between birds in the high and low modularity condition (Haz=0.80 ± 0.22, Coxph, Z=-1.03, events (e)= 87, p=0.30 (**Figure 4.3**)).

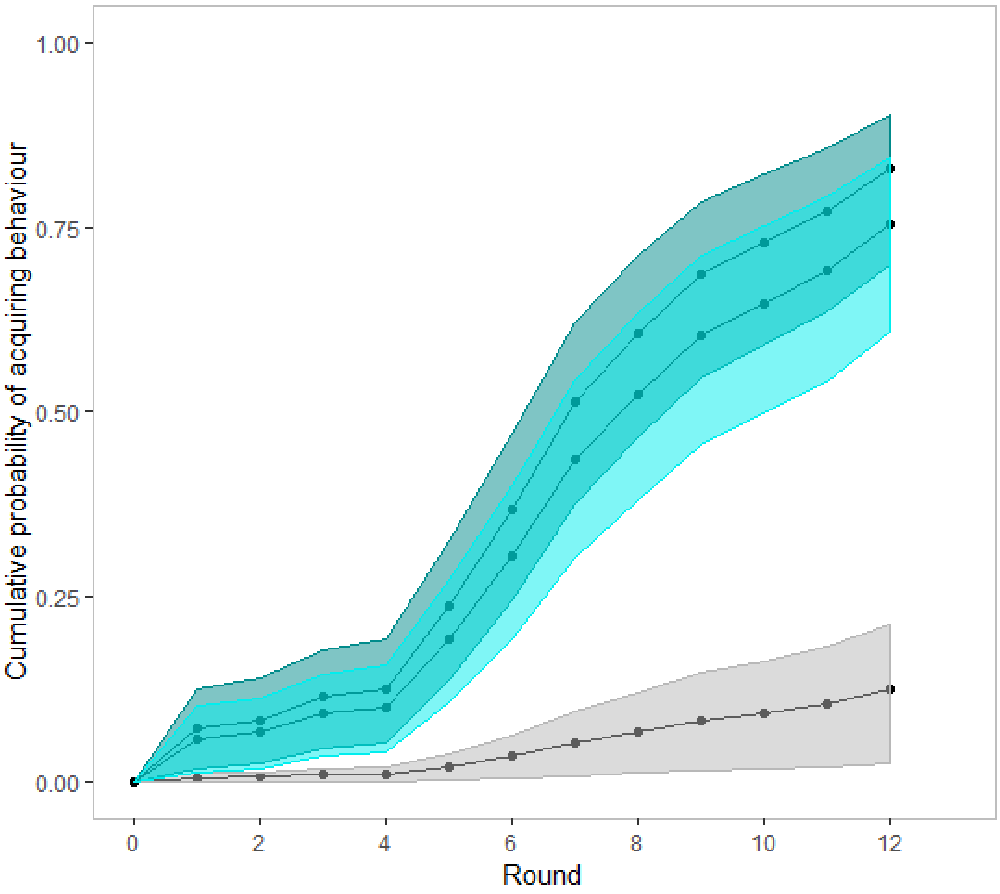


Figure 4.3 The cumulative probability a bird has of acquiring the solving behaviour in each round when from populations of the high modularity social condition (dark green), low modularity social condition (light green) and asocial control condition (grey). 95% confidence intervals shown by coloured bands.

4.4.2 Does the solving behaviour spread socially throughout the populations and do rates differ between social network structures?

Fitting stratified OADA models showed that the solving behaviour spread socially throughout the populations where social learning was permitted. To obtain support for differing social transmission rates I averaged across all candidate models weighting relative to their AICc value. This approach showed no support for models of pure asocial learning in all the diffusions ($\sum w<0.001$) with the most support for social transmission of equal rates for both high and low modularity conditions ($\sum w=0.544$), and less support to rates differing dependent on population or modularity condition (**Table 4.2**). Although candidate models included fewer models of asocial learning compared to ones that included social transmission, the support given to social transmission models far outweighed asocial learning even when asocial support is multiplied up to the equivalent number of models. Using model averaging I also obtained support for the inclusion of the variables sex and mass to evaluate their importance on either the asocial or social learning rate. I obtained support of less than 50% ($\sum w=0.5$) for either variable influencing the asocial or social learning rate (**Table 4.3**) and this indicated that they are better not included in the final model. The final top model therefore included an equal social transmission rate across populations of high and low modularity, an estimated 1.53 (95% CI: 1.20-2.16) times greater than the asocial learning rate with no influential effect of sex or mass on learning rate.

Table 4.2 Support shown for differing hypothesis after model averaging across all candidate models.

Model	Support
Pure asocial learning in all diffusions	<0.01
Equal rates of social transmission for both high and low modularity	0.54
Different rates of social transmission depending on network modularity	0.17
Different rates of social transmission depending on population	0.28

Table 4.3 Support for the variables sex and mass influencing the social or asocial learning rate.

Learning rate effected	Variable included	Support
Asocial	Sex	0.23
Asocial	Mass	0.21
Social	Sex	0.32
Social	Mass	0.29

4.4.3 Does social structure influence the adoption of different solving techniques by the birds?

I found no evidence of local ‘cultures’ of solving techniques. The mean assortativity coefficient (calculated from distributions of estimated true bias), describing how similar social neighbours were to one another in their solving technique, for the high modularity networks was -0.10 [95% CI: -0.25 – 0.07] and for the low modularity networks the mean was -0.003 [95% CI: -0.14 – 0.19]. Therefore, birds did not match their solving technique to those they were most closely connected to in the networks in either the high or low modularity condition (**Figure 4.4**).

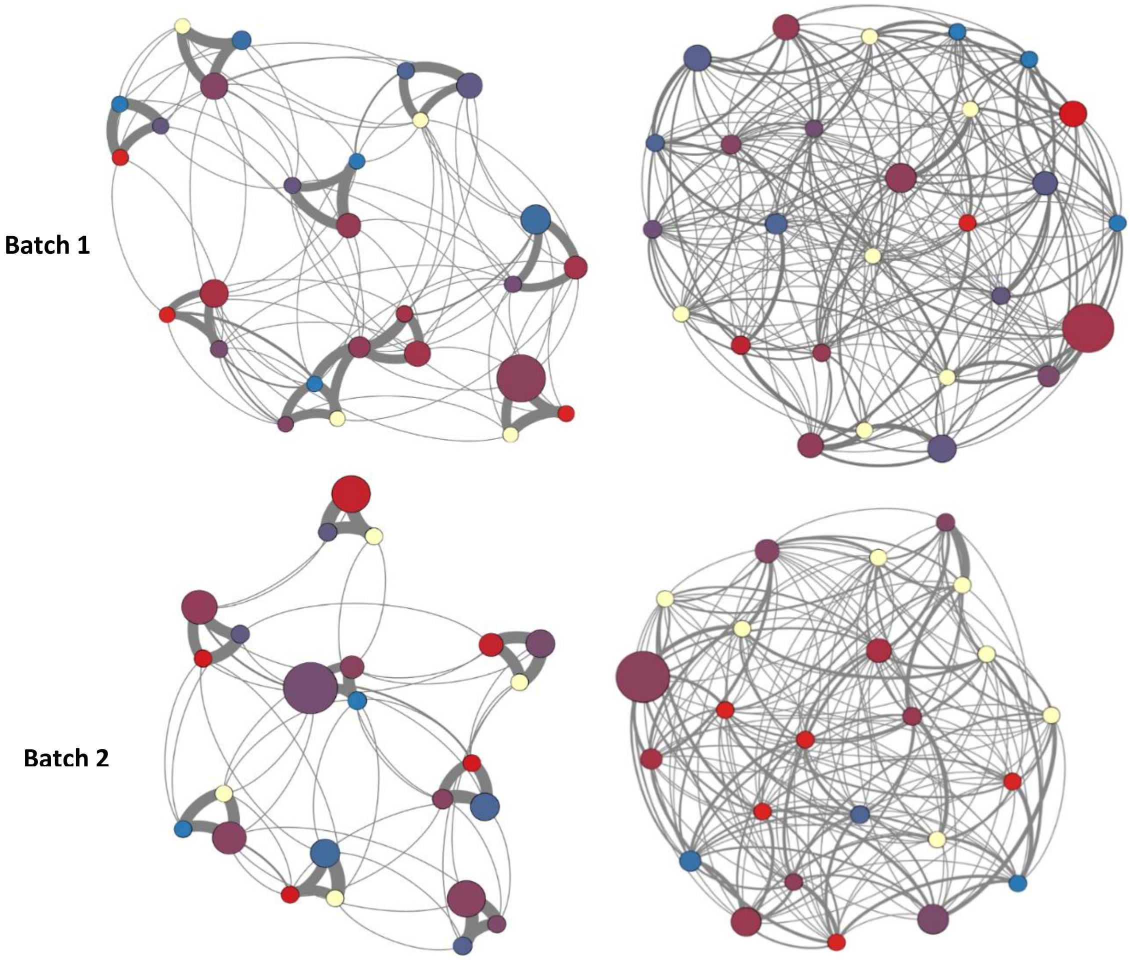


Figure 4.4 Social networks of the high (left) and low (right) modularity populations. Node colours represent an individual's bias in solving technique through a gradient of red (all solves performed were pushing red) to blue (all solves performed were blue), yellow nodes indicate birds that never performed the solving behaviour. Node size is proportional to the total number of solves performed by each bird.

4.5 Discussion

Social learning was essential for enabling a novel foraging behaviour to spread throughout populations of domestic chicks. When social learning was restricted and birds could only learn through asocial means, they were far less likely to acquire the solving behaviour compared to those populations which permitted social learning to occur. However, contrary to my predictions, manipulating the social structure, specifically the modularity of the network which varied from high (a population comprising several distinct small clusters of birds that repeatedly encountered the foraging task together) to low (a population that was well mixed such that there were no distinct clusters of birds repeatedly encountering the task together), did not affect the rate of behavioural spread throughout the population nor lead to the establishment of shared forms of solving techniques within clusters.

The novel foraging behaviour (solving the task through sliding open doors to access mealworm rewards) spread rapidly throughout the populations where social learning was permitted. Individuals in both the high and low modularity conditions (where social learning could occur) were over ten times more likely to acquire the solving behaviour with progressing rounds compared to individuals in the asocial learning populations, resulting in far more birds having acquired the solving behaviour by the end of rounds compared to the asocial populations. Conducting a NBDA provided strong support for social transmission in populations where opportunities for social learning were permitted, with almost zero support for asocial learning alone accounting for this spread. This result highlights simply how instrumental social learning can be for the acquisition and spread of novel behaviours throughout animal groups, demonstrating that purely time opportunity alone does not lead to the adoption of novel behaviours. The NBDA showed no strong influence of sex or mass on the social or asocial learning rate. This may be because these factors do not have a significant effect on social transmission when chicks are young and before they are fully developed and sexually dimorphic.

The rate of social transmission (how likely an individual will socially learn from another upon demonstration) did not appear to vary significantly between populations where group network structure was experimentally manipulated to be of high or low modularity. Given that familiarity has been shown to influence the likelihood of social learning (Swaney et al., 2001), I expected that individuals within the high modularity population who were repeatedly interacting together in the testing chamber (and consequently were more familiar with one-another) may be more likely to learn from one another and so have a higher rate of social transmission. However, I found no evidence of rates differing dependent on modularity condition, with the strongest support given to models assuming an equal transmission rate across treatments. Thus, when birds were able to observe the behaviour of an informed individual they were not more or less likely to socially learn it within the high or low modularity condition. Given that I artificially selected and enforced group composition and social structure, it may be that familiarity influences the likelihood of social learning (as reported by Swaney et al., 2001) only when it is result of natural partner preferences.

I predicted, based on theoretical models (Voelkl & Noë, 2010), that the novel behaviour would spread faster within less structured populations of low modularity. Within the populations of low modularity, individuals were well mixed and associated with many others during task interaction, crucially including those informed individuals demonstrating the novel behaviour. Therefore (provided transmission rates did not differ between conditions) I expected the novel behaviour to spread rapidly as rounds progressed and informed individuals associated with many different naive individuals. However, I found no difference in the overall rate of acquisition across populations in the high and low modularity social conditions; birds were just as likely to adopt the novel behaviour throughout rounds regardless of the modularity condition. I offer several suggestions to explain this somewhat surprising result that focus on an increased complexity of behavioural transmission.

Currently, most theoretical models of behavioural/social transmission follow the assumption that individuals with more connections to others are more likely to acquire and pass on behaviours (Firth, 2019). This underlying principle accurately represents instances of disease transmission and is the basis to NBDA (Franz & Nunn, 2009; Hoppitt, Boogert, & Laland, 2010). However, if behaviours follow more complex contagion rules then differing population structures, including modularity, might generate differing results. The proportion of informed to uninformed individuals may be more influential in behavioural acquisition than simply the total number of connections to informed individuals (Firth, 2019). Indeed, group evasion response in fish has been shown to be more effectively modelled by fractional contagion (Rosenthal et al., 2015). Modularity will by default influence these relative proportions and so even though birds within the low modularity populations hold more total connections to informed individuals, the proportion of these informed connections may have been lower than in high modularity populations. Additionally, factors such as social reinforcement and forgetting rates may also change how modularity influences behavioural transmission. If birds required greater social reinforcement (several separate exposures of the demonstrated behaviour) in order to learn, then lower modularity may not lead to faster transmission because each pairing might only occur once or a few times, so impeding social reinforcement. Only if the behaviour was learnt quickly (say after a single exposure) would low modularity lead to the rapid spread of behaviour throughout the group. Whereas, if social reinforcement was required then birds in the high modularity population may have had higher learning rates as they were consistently entering the testing chamber with the same (potentially informed) individuals each round. Indeed social reinforcement is thought to be the main driver in studies which found somewhat counterintuitive results of increased modularity promoting information diffusion (Centola, 2010; Nematzadeh et al., 2014). Similarly, forgetting rates (the likelihood that an informed individual ceases to exhibit a learned behaviour) may have also played a role in the spread of solving behaviour. This may be exaggerated if the forgetting rate is also dependent on social reinforcement such that individuals are more likely to ‘forget’ or cease continuing to exhibit a learned behaviour if they are interacting with novel partners. Depending on the forgetting rate, social structures have been shown to have different effects on information transmission including the likelihood of behavioural extinction (Voelkl & Noë, 2008). If the forgetting rate is high, then birds that have acquired the behaviour may well go on to forget it and subsequently do not act as a demonstrator to other informed individuals. Therefore, as with learning rates, increased modularity may facilitate spread as it retains clusters of familiar individuals that are likely to keep demonstrating the behaviour to one-another. If we consider a complex model of social transmission, which includes social reinforcement and forgetting rates, then an optimum level of modularity may exist whereby local spreading is promoted and acts as an incubator facilitating global spreading across the whole network provided there is a sufficient level of connectivity (Nematzadeh et al., 2014). By looking at two extremes conditions of modularity (0.73-0.63 vs 0.15-0.18), I may have examined two equally (sub)optimal conditions for behavioural spread where birds in the low modularity condition may be overall more likely to encounter informed individuals but depending on the time interval between subsequent demonstrations may well not adopt the behaviour or even forget it, whereas birds in the high modularity condition were overall less likely to encounter informed individuals but those that did so experienced repeated demonstrations in short succession. Future work should therefore investigate intermediate modularity values to see if there is a non-linear relationship between modularity and information flow and if such an optimal level does exist.

Although I found strong evidence that the opportunity for social learning increased the acquisition of the novel foraging behaviour, I found no evidence that individuals adopted the specific technique of obtaining the reward from their social partners. Birds did not match their solving technique (preferring to peck open the red or blue side of the door) to others closest to them in the network. I predicted that if birds were to match their behaviour to others then I would see the emergence of arbitrary traditions/culture within clusters in the high modularity populations. However, I did not detect such clusters of conformers, implying that the technique used to solve the task by a bird was not affected by the techniques used by others who they associated with the most when in the testing chamber.

This result is contrary to other studies which found individuals matched their behaviour to the specific variant they observed others performing the most frequently (Aplin et al., 2015; Claidière et al., 2013). One possibility why I found no evidence of assortment or difference between modularity networks was that the birds were using a different social learning mechanism to those in other studies. Within a diffusion experiment, observational learning mechanisms of either emulation or imitation were suggested to explain how social network position predicted the behavioural variant acquired by squirrel monkeys, *Saimiri boliviensi* (Claidière et al., 2013). In a similar experiment which showed that sub-populations of wild British songbirds established local traditions of a specific foraging technique, although the social learning mechanisms responsible were not discussed, the mechanism of local enhancement was ruled out (Aplin et al., 2015). My results, however, may have arisen due to other forms of social learning mechanisms such as local or stimulus enhancement. Instead of paying attention to the exact action, individuals might have had their attention to the apparatus increased but they paid little attention to the precise action of others (which direction they opened the door or colour that they pecked at). A second explanation for my results is the timescale that the experiment operated over. I was recording the solving techniques used during first acquisition of the task and gave them only 15 opportunities to exhibit a successful food retrieval. It may be that birds would match and conform to the technique of their predominant social partners over a longer time, resulting in group-specific behaviours in the high modularity condition. A conformity effect over time was found in the sub-populations of songbirds (Aplin et al., 2015), however an erosion of group differences over time was found within groups of squirrel monkeys (Claidière et al., 2013). Future work should continue exploring the stability of behavioural variants to gain a better understanding of the emergence of behavioural tradition and culture (Claidière et al., 2013).

My experimental manipulations show that the modularity of a social network did not affect either the speed of transmission of a novel behaviour (the acquisition of which I confirmed to be almost entirely dependent on social learning), nor did it enhance or retard the formation of local traditions of solving techniques of the novel behaviour. I reason that factors such as proportional connection to informed individuals, social reinforcement and forgetting rates may be important components that can obscure effects of social structure in the transmission of information across groups and so future theoretical models should take this into account. To my knowledge this is the first study to deliberately manipulate a specific property of social structure and empirically test the effect this has on information flow. I hope this study stimulates others to similarly test the assumptions predicted by theoretical models of social structure for information transmission, crucial for the understanding of behaviour spread and culture.

5

Scrounging markedly increases the diffusion of a novel foraging behaviour in domestic chicks, *Gallus gallus domesticus*, likely because the behaviour is acquired through local or stimulus enhancement.

5.1 Abstract

Foraging within a group can allow for individuals to adopt a scrounging strategy and obtain food that has been procured by others (producers). In adopting a scrounging strategy, the social learning of novel foraging behaviours can be affected. Some studies have found it to restrict learning of behaviours while others find it to promote learning. I investigated this relationship further by linking the effect of scrounging with the social learning mechanism used. I recorded the spread of a novel foraging behaviour across four populations of domestic fowl chicks, *Gallus gallus domesticus,* that experienced differing scrounging opportunities. In populations that had the opportunity to scrounge during task interaction, individuals were around five times more likely to acquire the novel foraging behaviour. Scrounging therefore appeared to greatly increase social transmission of novel behaviour throughout the population. I found no evidence that individuals were socially learning the precise technique of novel foraging behaviour that they observed others doing, thus indicating that individuals were deploying a social learning mechanism that does not require close observation of exact actions, such as stimulus or local enhancement. I reason that scrounging may influence the use of social learning differently depending on the social learning mechanism used.

5.2 Introduction

A benefit of group living is the opportunity it provides for the social transmission of advantageous behaviours. Through social learning, animals foraging within a group can transfer profitable information about discovered food patches, novel food items and foraging techniques (Clark & Mangel, 1986; Giraldeau & Beauchamp, 1999; Giraldeau & Caraco, 2000). However, when a novel foraging behaviour is introduced into the group, some group members, described as scroungers, do not exhibit the foraging behaviour themselves, but instead benefit through taking food that has been obtained by others, referred to as producers (Aplin & Morand-Ferron, 2017; Barnard & Sibly, 1981; Giraldeau & Lefebvre, 1986, 1987). Acquiring food through scrounging can range from sharing in discovered food patches (Giraldeau, 1984; Giraldeau & Dubois, 2008) to outright stealing of food from others (Brockman & Barnard, 1979; Morand-Ferron, Sol, & Lefebvre, 2007). Although by adopting this alternative frequency dependent strategy (Aplin & Morand-Ferron, 2017; Barnard & Sibly 1981), the scrounging individual may benefit immediately from the food, it may fail to learn a novel foraging technique because it is not observing the producer's actions or it may cause the producer to stop exhibiting the novel technique when in its presence to avoid food being lost. Consequently, the presence of scroungers may retard the spread of information, specifically the adoption of a novel foraging technique, within a group.

The assumption that social learning of new foraging behaviours is inhibited by the opportunity to scrounge food is commonly stated. For example, when a novel foraging behaviour is introduced into a flock of pigeons, *Columbia livia,* the spread of this behaviour is limited to only a few individuals acting as producers with the rest scrounging food from these individuals (Giraldeau & Lefebvre, 1986, 1987). When these producers are later removed from the flock, the behaviour is still not demonstrated by the remaining individuals, suggesting that scrounging inhibited the social learning of this behaviour. Likewise, field experiments of introduced novel foraging tasks in primates found that those individuals scrounging food failed to learn the demonstrated tool-using behaviour (Fragaszy & Visalberghi, 1989, 1990; Stammbach, 1988). Varying explanations as to why scrounging inhibits social learning include the presence of other scrounging individuals distracting, confusing and physically obstructing observation of a behaviour, or the reinforcement of scrounging behaviour overshadowing the new foraging behaviour (Beauchamp & Kacelnik, 1991; Lefebvre & Helder, 1997). The inhibiting effect that scrounging has on learning has been prevented by adding a transparent screen or barrier during experiments which prevents scrounging while maintaining observation of the demonstrated behaviour, as shown in zebra finches *Taeniopygia guttata* (Beauchamp & Kacelnik, 1991), domestic fowl *Gallus gallus domesticus* (Nicol & Pope, 1994) and pigeons (Lefebvre & Helder, 1997). Therefore, in contrast to wild conditions, social learning may be more commonly observed in laboratory systems where scrounging can be experimentally restricted.

The extent to which the opportunity to scrounge inhibits the social learning of a novel foraging behaviour may be influenced by other mediating factors which affect both whether an individual learns the behaviour and whether they choose to perform it. The value of the reward gained from scrounging can influence how scrounging affects learning. For example, during the diffusion of a novel foraging behaviour in pigeons, increasing the quantity of reward obtained by the informed demonstrator bird increased the likelihood of the observer learning the behaviour, while increasing the reward obtained by the observer through scrounging decreased their likelihood of learning (Giraldeau & Templeton, 1991). The transmission of a foraging behaviour in common ravens, *Corvus corax,* persisted in the presence of scrounging, possibly because the quantity of food available to scrounge was low meaning that scrounging was possible but unprofitable (Fritz & Kotrschal, 1999). Thus, instead of scrounging preventing the learning of a technique, individuals may choose to adopt a scrounging role when it is more profitable than producing (Broom & Ruxton, 1998). The effect of scrounging on social learning may also be influenced by the number of other group members exhibiting scrounging tactics. Pigeons exposed to a pre-trained demonstrator bird either singly or in groups of three all scrounged food from the demonstrator individual; however only those exposed singly showed that they had learnt the demonstrated behaviour during a post-exposure assay, possibly due to reduced confusion during task observation (Lefebvre & Helder, 1997). This study also highlighted the difference between learning and performing a behaviour, demonstrating the importance of a post-test assay. When exposed singly to a demonstrator bird, pigeons adopted a scrounging position, however these same birds performed the learnt behaviour when later tested individually in a post-test assay, and so showing that absence of behaviour does not necessarily demonstrate an absence of learning (Lefebvre & Helder, 1997).

Conversely, scrounging may be conducive to social learning. Scrounging induces close physical contact and social interaction between individuals which are necessary for social learning (Coussi-Korbel & Fragaszy, 1995; Fragaszy & Visalberghi, 1990). Field experiments on wild populations of Florida scrub-jays, *Aphelocoma coerulescens,* and meerkats, *Suricata suricatta,* both found that scrounging food during foraging increased the likelihood of an individual learning a new behaviour (Midford et al., 2000; Thornton & Malapert, 2009a). Indeed, the spread and adoption of a specific technique during a novel food acquisition task in meerkats appeared to be very much driven by scrounging behaviour; with individuals being more likely to learn and solve the task if they had previously scrounged from a successful solver (Thornton & Malapert, 2009a). Florida scrub-jays socially learned the position of new food patches (as indicated by an encircled ring) in a scrounging enabled condition but did not learn food patch locations when scrounging was restricted (Midford et al., 2000). Similarly, common marmosets, *Callithrix jacchus*, better learnt a novel foraging behaviour when they could scrounge than when they could only observe tutors extracting food (Caldwell & Whiten, 2003).

Therefore, although the relationship between scrounging and learning has been investigated both in the laboratory and in the wild, the relationship remains unclear. The majority of early studies suggest that scrounging inhibits social learning whereas later studies show evidence that scrounging facilitates learning. These differing results may be due to several factors. Firstly, those studies showing scrounging to facilitate social learning may have been conducted on species that tolerate others in close physical proximity and so, while scrounging, they can also observe closely the performed behaviour. However mixed results of scrounging both inhibiting and facilitating learning are found across a wide array of different social group-living species which are all likely to be accepting of close contact by other group members. Another contributing factor is the social setting which individuals experienced during learning. Some studies physically separated the demonstrator and observer individuals (Beauchamp & Kacelnik, 1991; Caldwell & Whiten, 2003; Lefebvre & Helder, 1997; Nicol & Pope, 1994) while others let them interact naturally in a more open diffusion setting (Fragaszy & Visalberghi, 1989, 1990, Giraldeau & Lefebvre, 1986, 1987; Midford et al., 2000; Stammbach, 1988; Thornton & Malapert, 2009a). However, no clear correlation is seen between these different environments and whether scrounging hindered or promoted learning. Finally, the mechanisms used during learning may influence the relationship scrounging has with learning. When learning through mechanisms such as local or stimulus enhancement, an individual's attention is drawn to either the location or the object of interest (for more details of definitions see: Heyes, 1994; Hoppitt & Laland, 2013). When learning through observational mechanisms, (such as observational R-S learning, imitation or emulation), an associative link is formed and either the exact actions are copied or an individual performs actions required to achieve the same end (Heyes, 1994; Hoppitt & Laland, 2013). The distinction between these mechanisms of learning within studies may be important as it is plausible that scrounging may interact differently with these different mechanisms of learning. For example, scrounging may enhance learning reliant on stimulus or local enhancement through increasing attention to the area/stimulus. Alternatively, if learning occurs by more observational mechanisms then increasing the opportunity to scrounge may add distraction/confusion and thus negatively influence learning by preventing individuals from closely watching the exact actions constituting the behaviour. To my knowledge, no study has investigated the relationship between scrounging and social learning while making an explicit link to the social learning mechanism used.

I used controlled laboratory conditions to investigate the effect scrounging has on the spread of a socially learnt novel foraging behaviour while simultaneously exploring the mechanism used to facilitate learning, across populations of domestic fowl chicks, *Gallus gallus domesticus*. Domestic fowl are a gregarious species that will socially learn about foraging behaviours, particularly early on in life (Nicol, 2004), and so make an ideal system for investigating social transmission of behaviour. I introduced an extractive foraging task to populations of domestic chicks and manipulated scrounging opportunity by varying the divisibility of the reward while keeping the social setting constant between conditions but still permitting individuals to interact freely during the task. In the high scrounging condition, solving the foraging task provided a food reward consisting of multiple pieces and so allowing the potential for birds to scrounge when others solved the task. The low scrounging condition provided only one single food reward when the task was solved and so restricted scrounging opportunity when an individual solved the task. I investigated the rate at which the novel behaviour spread through the population in these differing scrounging conditions. I predict that the behaviour will spread socially throughout populations, and that scrounging conditions would influence this spread either positively or negatively. To disentangle the social learning mechanism used to solve the task, and thus potentially explain the relationship scrounging has with social learning, I designed the apparatus so that it could be solved in two ways (pushing the red side of the door to the right or the blue side to the left). If individuals adopt the solving technique based on what they have observed others do and populations are thus biased in a particular solving technique, this would indicate imitation or emulation. However, if an individual's solving technique is not biased by what they have observed and is not conserved across the population, this would indicate stimulus or location enhancement.

5.3 Methods

5.3.1 Subjects and Apparatus

5.3.1.1 Enclosure and rearing conditions

Two batches (Batch 1: 16th March - 3rd April 2018; Batch 2: 8th March - 29th March 2019), each of 48 'Rhode Rock' domestic chicks were purchased from a dealer (Organic Pullets, UK) when one day old (day 1). For each batch, birds were randomly allocated to one of two identical temperature and humidity-controlled enclosures (**Figure 5.1**), thus giving a total of four populations overall. Each population of 24 birds had an equal sex ratio; birds of this breed can be sexed from hatching through feather colouration. I provided commercial chick crumb, water and bird grit *ad libitum* and provided perches in the main enclosure. I kept the birds within the main enclosure area during the first week and from week two onwards allowed them further free access to the extended enclosure area. Birds were individually identified through coloured plastic leg bands (Avian ID, UK) fitted on day 2, which I changed for a larger size on day 14. Birds were also weighed on day 14, using a flat stand-on digital scale (Salter, precision = 1 g).

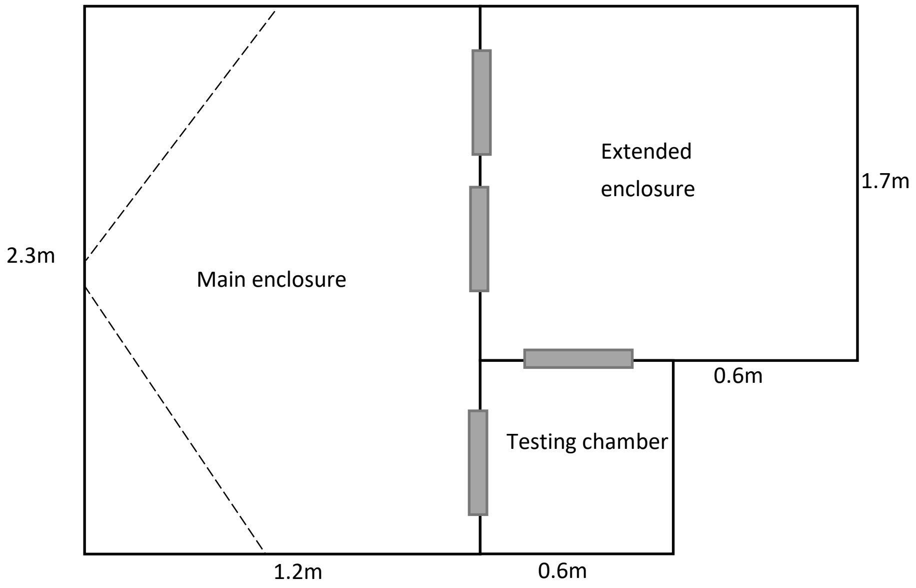


Figure 5.1 Enclosure layout. Dashed lines show perches and grey bars indicate doors between different enclosure sections. During experiments doors were controlled so that all birds were cycled from the main enclosure through the testing chamber and out into the extended enclosure. The second enclosure was symmetrically identical.

5.3.1.2 Task apparatus

The novel foraging behaviour comprised of extracting food from a task apparatus; a design adapted from that developed by Aplin et al. (2015). The task apparatus consisted of an upright box (12 x 50 x 4 cm) with ten lightweight cardboard doors painted half-red half-blue, each covering a well (2 cm diameter) holding mealworm rewards (**Figure 5.2**). To solve the task, birds were required to slide open a door to either the right (red) or left (blue) to reveal the hidden worms behind.

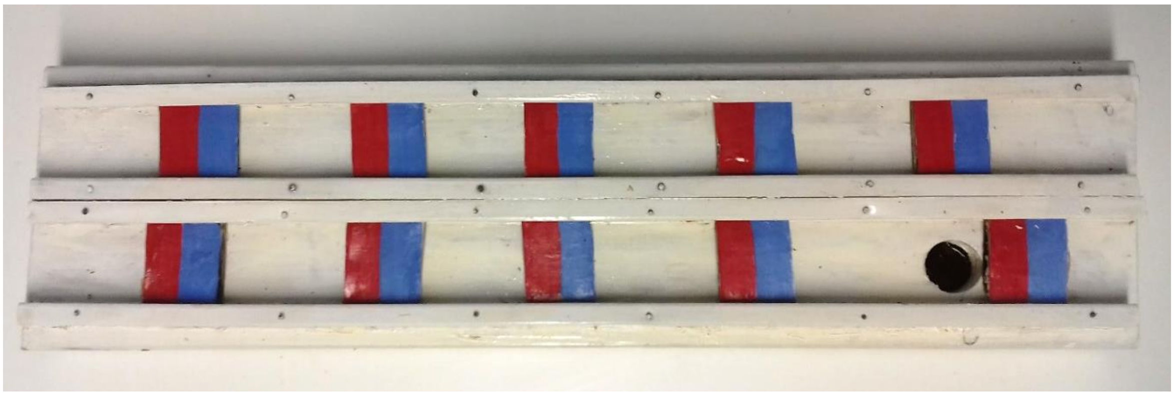


Figure 5.2 Novel foraging task. Bottom right shows an opened door revealing the hidden well behind where mealworm rewards would be placed.

5.3.2 Procedure

5.3.2.1 Training and general testing procedure

I tracked the spread of solving behaviour across all four populations. The task was always presented within the testing chamber and so during the first week I shaped birds to voluntarily enter the testing chamber (day 4-6). This consisted of scattering mealworms across the floor of the testing chamber and repeatedly allowing groups of birds into the testing chamber and out into the extended enclosure. Group size gradually decreased until all birds were comfortable entering the chamber individually.

In order to initiate the diffusion of solving behaviour, in each batch, I trained one male bird to open the doors using a technique (pushing blue or red) so that they could serve as a seeded demonstrator for both populations. The demonstrator bird was trained to solve the task by pushing the red side to the right for pens in batch one and the blue side to the left for pens in batch two. Training involved repeatedly exposing the demonstrator bird to the task apparatus (day 7-11). Initially doors were fully open, allowing free access to mealworms in wells, and then gradually doors were increasingly closed until all the bird could open fully shut doors. In this training process doors were prevented from being opened in one direction dependent on the batch condition. Throughout the duration of the experiment the seeded demonstrator split their time equally between the two populations. By having the same demonstrator bird in each population starting the information diffusion for each batch, I controlled for any initial preferences in directed learning that might arise from different demonstrator birds (Coussi-Korbel & Fragaszy, 1995; Hoppitt & Laland, 2013).

First, I presented all birds with a pre-test round (day 6) where they entered the testing chamber individually and were given one minute to interact with the apparatus; this allowed me to determine if any individuals could solve the task prior to experiencing social demonstration. None did so. Birds were then cycled through the testing chamber in naturally formed groups of three for a total of 13 rounds over the period of the week (day 12 – 18). During each round, lasting three minutes, I recorded the identity of the individuals in each group, which birds solved the task, and for those that solved the task, I noted their technique through the direction of their push (red/blue). The demonstrator bird cycled through the testing chamber with the rest of the birds once each round. Lastly, after completing the 13 rounds in groups, each bird was tested individually again in a post-test round (day 18) for one minute to determine whether an individual could solve the task when alone. Therefore, all birds completed an individual pre-test round, 13 grouped rounds and a final individual post-test round.

5.3.2.2 Experimental conditions

In batch one I wanted to investigate how scrounging opportunity influenced spread of solving behaviour and so I experimentally altered scrounging opportunities in the populations by manipulating the divisibility of the food reward in the task (**Table 5.1**). I established a low scrounging opportunity condition in one population by providing a single standard sized mealworm in each well. This was not divisible among the three birds in the chamber. I established a high scrounging opportunity in the other population by providing four mini-mealworms (equivalent in mass to the larger single worm) in each well. This permitted each bird in the chamber the opportunity to eat a worm once the well had been opened.

To investigate which social learning mechanism was likely being used to learn the solving behaviour I looked at whether an individual solved the task using the technique most frequently observed and so whether the solving technique was conserved across the population. Therefore, whereas the two populations in batch one had a demonstrator bird that had learnt to solve the task by pushing the red side to the right, the two pens in batch two had a demonstrator bird that had learnt to solve the task by pushing the blue side to the left. As data from batch 2 was also being used to address a different set of questions (Chapter 6), both pens in this batch experienced high scrounging opportunities (4 mini-mealworms in each well).

Table 5.1 Conditions presented in each population of birds.

Batch	Population	N	Scrounging Condition	Demonstrator trained colour
One	1	24	High	Red
	2	24	Low	Red
Two	3	24	High	Blue
	4	24	High	Blue

5.3.2.3 Ethics

All birds were reared to a standard that exceeded conditions required by the Department for Environment Food and Rural Affairs (DEFRA) and the Animals Scientific Procedures Act (ASPA 1986). All work was approved by the University of Exeter Psychology Ethics Committee.

5.3.3 Analysis

Is the behaviour transmitted socially between individuals?

To test whether the behaviour was spread socially between individuals within a population I conducted a Network Based Diffusion Analysis (NBDA; Franz & Nunn, 2009; Hoppitt, Boogert, & Laland, 2010), specifically a dynamic Order of Acquisition Diffusion Analysis (OADA) using the 'NBDA' package v.0.8.2 (Hoppitt et al., 2020) in R v.3.3.1 (R Core Team, 2016). A NBDA infers social learning if the order in which individuals acquire a behaviour relates to their social network. The assumption within the analysis is that those individuals with more/stronger connections to informed individuals are more likely to socially learn the behaviour. However, if the task is asocially learnt, say through trial and error, then the order individuals acquire the behaviour will not relate to their social network. The dynamic version of this analysis allows for the social network to change over time and so allows for the behaviour spread to be more accurately tracked to changing associations.

The dynamic network represented potential social learning opportunities based on the changing testing chamber associations. Based on the groupings of three birds entering the testing chamber I created cumulative networks for every round that represented the current groupings for that round plus the previous groupings in prior rounds. Given that birds could only learn from other informed individuals, the state of every individual at each round, recorded as either informed (1) or uninformed (0), was then multiplied with the cumulative networks to provide networks of developing learning opportunities. The order birds learnt was then related to these dynamic networks of learning opportunities.

I included sex and (standardised) mass of each bird as individual-level variables that may affect the asocial and/or social learning rate, based on prior studies suggesting these factors to be influential (Jones et al., 2003; Lonsdorf et al., 2004; Shaw, 2017). I then used a model selection approach to compare all possible models that included or excluded social transmission and with differing effects of individuals level variables (sex and mass) on social and/or asocial learning, using Akaike Information Criteria corrected for small sample size (AICC) for model averaging and obtaining hypothesis support (Burnham & Anderson, 2002).

Does scrounging opportunity affect the likelihood of acquiring the behaviour?

I fitted a Cox proportional hazards (coxph) model to analyse the likelihood an individual will have acquired the behaviour at each given round with scrounging condition as a categorical explanatory variable and the 4 populations as a random effect, using the ‘survival’ and ‘cox.me’ package (Therneau, 2015; Therneau & Grambsch, 2000) in R. This survival analysis modelled the likelihood that an individual in either scrounging condition will have acquired the solving behaviour at each given round. As round was capped for all individuals at the last post-test round this was treated as a censored observation. Coxph models provides an estimated hazard ratio (Haz) of which above 1 indicates an increased chance of acquiring the behaviour and below 1 indicates a decreased chance.

Which social learning mechanism are birds using to solve the task?

To determine if the specific technique first adopted to solve the task was transmitted socially, and therefore provide evidence for the social learning mechanisms used, I fitted a Generalised Linear Mixed Model (GLMM) with a binomial error distribution and a logit link function using the ‘lme4’ package (Bates et al., 2015) in R. The full model included a bird’s first solving technique (red/blue) as the dependent variable with a fixed effect of the technique that their initial demonstrator was trained on and an interaction term between the number of red and blue solves the focal bird had observed and I included population as a random factor. The full model was standardised using the ‘arm’ package (Gelman et al., 2018) and I used an information theoretic approach, selecting the best model based on AICc values (Burnham & Anderson; 2004). If the best model included a fixed effect of population, this would indicate a group-level bias within the population dependent on the colour the initial seeded demonstrator was trained on. If the interaction term (between the number of red and blue solves observed) was included in the best model, this would indicate an individual level bias based on the number of red and blue solves observed.

5.4 Results

5.4.1 Is the behaviour transmitted socially between individuals?

Fitting dynamic OADA models showed strong evidence that the novel foraging behaviour spread socially between individuals in all four populations. After model averaging across all candidate models, those that included social transmission received 83% of the model weightings, while models based on asocial learning alone received 17% support (**Table 5.2**). Although there were fewer models of asocial learning compared to ones that included social transmission, the support given to social transmission models far outweighed asocial learning (even when asocial support is multiplied up to the equivalent number of models) (**Table 5.2**), and so providing strong evidence for social transmission of solving behaviour. Thus, when averaging across all models based on model weightings, behaviour was estimated to be transmitted with an increase on the asocial learning rate of 1.40 (± 0.22 SE) per unit connection to an informed individual. Using model averaging, I was also able to obtain support for the inclusion of the variables sex and mass and model averaged estimates in order to evaluate their importance on the asocial and social learning rate. I obtained support of far less than 50% for either sex or mass influencing the asocial or social learning (thus indicating it is best not included in the final mode) (**Table 5.3**).

Table 5.2 Support given through model averaging to models that included social transmission and those that were based purely on asocial learning.

	Number of Models	Support
Asocial Learning	3	0.17
Social transmission	10	0.83

Table 5.3 Support given through model averaging to models that included sex and mass affecting either the asocial or social learning rate.

Variable	Learning rate	Support
Sex	Asocial	0.30
	Social	0.24
Mass	Asocial	0.41
	Social	0.31

5.4.2 Does scrounging opportunity affect the likelihood of acquiring the behaviour?

The likelihood that birds would have acquired the novel foraging behaviour within rounds differed between the two scrounging conditions. By the final post-test round, in batch one in the high scrounging condition 83% (20/24) of birds had acquired the novel behaviour compared to 17% (4/24) in the low scrounging condition. In batch two, both populations were of the high scrounging condition and by the final post-test round 67% (16/24) and 58% (14/24) had acquired the behaviour. Overall, birds that were in the high scrounging condition populations had a much greater chance of becoming informed than those in the low scrounging condition population (Haz. = 4.91 ± 0.47; Coxph, $Z = 3.38$, events (e) = 55, $p < 0.001$; **Figure 5.3**).

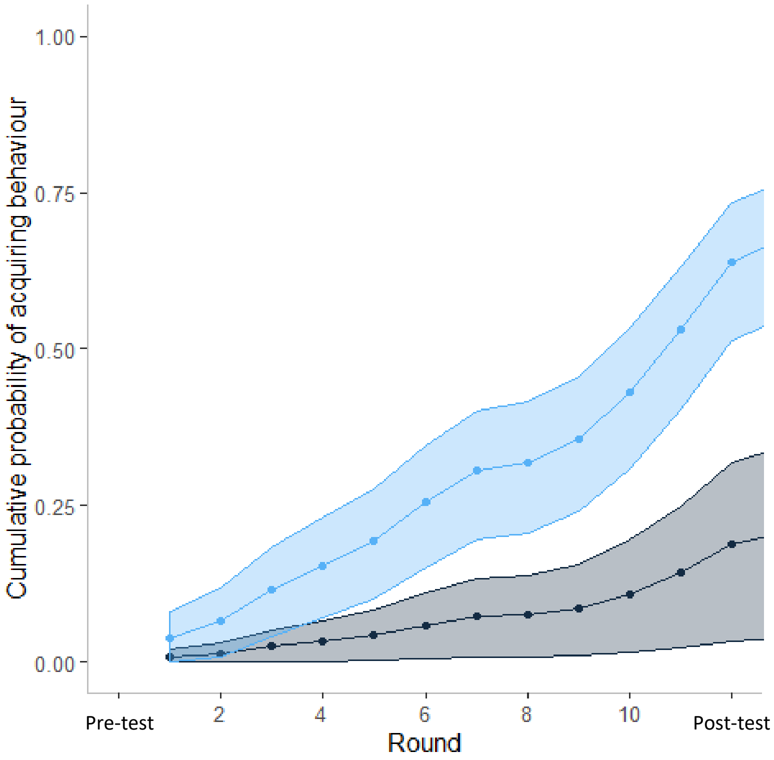


Figure 5.3 Coxph model predictions showing the cumulative probability that an individual has acquired the behaviour with each progressing round in the high scrounging (blue) and the low scrounging (grey) condition. Shaded regions indicate 95% CI.

5.4.3 Which social learning mechanism are birds using to solve the task?

The best model, providing nearly 60% of weighting, was one that did not include an interaction between the number of red and blue doors observed opened or a fixed effect of the colour the demonstrator bird was trained on (**Table 5.4**). Therefore, the technique (pushing at the red or blue side of the door) used in a birds first solve was not influenced by the amount of red or blue solve techniques they had observed, nor the colour the demonstrator was initially trained on to solve the task.

Table 5.4 Comparison of models of differing structures ranked by AICc difference and subsequent weightings. The technique an individual used in their first solve was investigated by models including fixed effects of the colour the demonstrator was initially trained on to solve the task and an interaction between the number of red and blue doors the individual observed solved. All models include a random effect of population.

Fixed effects included:	df	ΔAICc	Weight
None	2	0	0.57
Reds: Blues Observed	3	2.17	0.19
Demonstrator Colour	3	2.23	0.19
Demonstrator Colour + Reds: Blues Observed	4	4.5	0.06

5.5 Discussion

An introduced novel foraging behaviour spread rapidly via social transmission within populations of domestic chicks. Crucially, scrounging appears to greatly accelerate this social transmission process. Individuals in populations that had the opportunity to scrounge during task interaction were around five times more likely to acquire the novel skill during experimental rounds. Consequently, in populations where scrounging was possible, far more birds had learnt the novel behaviour at the end of the experiment (20, 16 and 14 out of 24 compared to only 4 in the low scrounging condition). My result matches those studies that showed scrounging to have a positive effect on social learning (Caldwell & Whiten, 2003; Midford et al., 2000; Thornton & Malapert, 2009a).

The novel foraging behaviour was transmitted socially between birds, with the order in which birds learnt the sliding behaviour being predicted by their associations during task interaction. The NBDA provided substantial support for social transmission of this behaviour, with an estimated rate of social transmission 1.40 times the asocial learning rate per informed connection. I assume that asocial learning rates did not differ greatly between populations of differing batches as conditions were kept almost identical. Furthermore I assume scrounging condition would not affect asocial learning rates because all birds were recorded as being informed (having learnt the task) upon their first solve, and this means that asocial learning would not have been affected by multiple behaviour-reward associations (provided in the increased number of mini-mealworms) in the high scrounging condition. Therefore, given that so few birds acquired the novel foraging behaviour in the low scrounging condition, I can conclude that the increased scrounging opportunity was responsible for enabling the behaviour to spread socially. At an individual level, I found no significant effect of sex or mass on the asocial or social learning rate.

I recognise conclusions drawn from this study on scrounging and social transmission should be taken cautiously given the small sample size. As with many network studies, I was unable to manipulate and observe numerous populations - I had a single population for the low scrounging condition and 3 populations of the high scrounging condition. However, given the gross difference in extent of behaviour spread between scrounging conditions and the strong support for social transmission in all models, I believe that this provides sufficient evidence of scrounging affecting social transmission. This conclusion is strengthened because I was able to tightly control other potential influential factors. Firstly, the behaviour required to solve the task did not vary with scrounging conditions (an issue that has previously been highlighted (Midford et al., 2000)); the sliding door action was the same regardless of whether birds were in the low scrounging condition (received a singular mealworm reward) or the high scrounging condition (receiving multiple mealworms). Secondly, I used the same seeded demonstrator to initiate social transmission within each batch and so did not bias transmission based on the initial demonstrator's attributes. Lastly, the time exposed and social environment was kept identical for all birds in either condition.

I reason that scrounging greatly increased behavioural transmission in this experiment due to the social learning mechanism deployed. I found no evidence that the technique in which an individual first solved the task was influenced by the proportion of solving techniques they had observed. Nor was the technique the seeded demonstrator was initially trained on conserved across the population. This indicates a form of social learning mechanism in operation that does not require close observation of exact actions, such as stimulus or local enhancement. I propose that the social learning mechanism used may be crucial to how scrounging affects learning. In this experiment scrounging enhanced social learning that is dependent on stimulus or local enhancement likely through increasing general attention and interest to the area/apparatus. It is possible that previous studies finding scrounging to facilitate learning were also looking at behaviours acquired through stimulus or local enhancement. Indeed, of those studies finding scrounging to enhance learning, Midford et al (2002) discuss area and object copying (which I term as local and stimulus enhancement respectively) as the mechanism responsible for jays learning to dig for food in an encircled area, and, while Thornton & Malapert (2009) did not try to identify the learning mechanism used when meerkats acquired foraging behaviours, they did emphasise that the task provided could be learnt through local or stimulus enhancement rather than more complex mechanisms. However, and perhaps providing an example to counter my argument, Caldwell and Whiten (2003) suggested that scrounging facilitated learning in common marmosets as close physical contact allowed the observer to obtain more ‘task-relevant information’. Although they did not explicitly discuss specific social learning mechanisms this does suggest that more observational learning mechanisms were used, however learning by stimulus and local enhancement was not ruled out. Conversely, studies that found a negative effect of scrounging included tasks given to primates that involved manipulating levers and using tools (Fragaszy & Visalberghi, 1989, 1990; Stammbach, 1988) and tasks given to birds involving breaking through tissue paper, pecking at levers/keys and pushing/pulling flaps (Beauchamp & Kacelnik, 1991; Giraldeau & Lefebvre, 1986, 1987; Lefebvre & Helder, 1997; Nicol & Pope, 1994). It could be that the latter studies involved more complex behaviours and learning mechanisms which required greater attention to fine-scale actions, such as imitation and emulation, which were disrupted by scrounging. Future work should thus take into account the possibility scrounging interacts differently with social learning dependent on how a behaviour is acquired.

I suggest that scrounging influences social learning differently dependent on mechanism (with scrounging enhancing learning by stimulus/local enhancement), however this relationship may well be dynamic with the opportunity to scrounge in turn affecting the mechanism used. An individual’s decision to adopt a scrounging tactic is commonly flexible and contingent on both the opportunity and the profitability of the action and the behaviour of others (Broom & Ruxton, 1998; Fritz & Kotrschal, 1999; Giraldeau & Templeton, 1991; Lefebvre & Helder, 1997). This could then in turn determine the mechanisms by which an individual could learn the behaviour. For example the exact method of opening artificial fruit was found to be copied in squirrel monkeys *Saimiri boliviensi,* indicating imitation or emulation (Claidière et al., 2013). In that study, they trained up an alpha male to be the demonstrator individual and so likely reducing the chance that individuals would scrounge from him; therefore perhaps allowing them to pay close attention to the method demonstrated by the informed individual (Claidière et al., 2013). Similarly, wild songbirds adopt the technique most frequently performed by others in their network when solving a novel foraging task (Aplin et al., 2015). Again, scrounging opportunity was reduced in that study by restricting access to the food for one second after a solving bird had left the apparatus. Perhaps by restricting scrounging in these experiments, individuals had the opportunity to closely observe the actions of others and imitate/emulate them rather than immediately attending to the reward associated with the location or apparatus. I did not test the same birds in both high and low scrounging conditions and observe whether they were consistent in their learning mechanism, however this would be an interesting avenue for future research to investigate.

I demonstrate that, under conditions in which the group size and composition are held constant (controlling the social environment) and the tracked behaviour remains consistent across conditions, increased scrounging opportunity greatly facilitates social transmission of a novel foraging behaviour across groups of birds. Although such scrounging may be expected to perturb social conditions and so reduce opportunities for shared attention to the novel task, or even provide an alternative foraging strategy, I found that this did not retard rates of learning and resultant social transmission. I believe that, in this situation, this is because the learning mechanism did not require the naïve individual to pay close attention to the specific actions of the demonstrator to facilitate imitation or emulation, but instead they learned through an enhancement of the area facilitated by the actions or perhaps simply the presence of the demonstrator there, associated with the presence of a reward to scrounge in that location. Therefore, I can conclude that the spread of information within a group may be assisted by opportunities for naïve individuals to scrounge rewards from informed demonstrators, perhaps strengthening their attention to salient features of the environment necessary to acquire the new skill, without requiring that they accurately imitate or emulate specific actions.

6

Does changing environment predictability alter general reliance upon social information?

6.1 Abstract

Animals can gain information about their environment through personal interaction (asocial learning) or through observing others (social learning). The type of environment can influence how an individual learns, with both theoretical and empirical studies showing animals to rely more on social information and prioritise learning from others when in an unpredictable or variable environment. However, it is unknown whether this increased reliance upon social information is solely restricted to when learning about aspects of the environment that vary or whether unpredictability per se creates a general increased reliance upon social information that extends across contexts. I reared domestic fowl chicks under two environmental conditions of differing predictability (of feeder location) and subsequently tested their reliance upon social information within the original varied environment and on a separate novel foraging task. I found some evidence for an increased reliance upon social information in an unpredictable environment, however there was no transference of this reliance to a different context in which the environment had not been varied.

6.2 Introduction

Animals can collect information about their environment through personal experience (asocial learning) or through attending to social information (social learning) (Dall et al., 2005; Danchin, Giraldeau, Valone, & Wagner, 2004). Individuals are flexible in when they prioritise asocial or social information depending on conditions and context; this flexibility can be described as social learning strategies (Laland, 2004). Such flexibility may be especially important when an individual is living within a variable environment which may result in animals differentially prioritising social and asocial information when learning new behaviours.

Socially learning 'when uncertain' and 'when prior information is outdated' are known strategies that are likely to be deployed in an environment that is unpredictable due to temporal or spatial variation. Several studies have provided evidence of animals following a 'copy when uncertain' strategy and preferentially using social information when information is unknown and/or unreliable (Dunlap, Nielsen, Dornhaus, & Papaj, 2016; Galef, Dudley, & Whiskin, 2008; Kendal et al., 2015; Stroeymeyt, Giurfa, & Franks, 2017). For instance, when deciding on new nest site options, informed ants *Temnothorax albipennis,* that have completed multiple visits to potential nests and so have a greater certainty of their private (asocial) information will rely less on the behaviour of others (social information), and *vice versa* when they have less experience of the potential options (Stroeymeyt et al., 2017). More generally, younger individuals are especially prone to using social information perhaps because they are inherently more uncertain having not had as much experience with the environment (Biondi et al., 2010; Carter et al., 2014; Dugatkin & Godin, 1993; Franks & Thorogood, 2018; Huffman, 1996; Nicol, 2004). The strategy of socially learning when prior information is outdated is demonstrated through an experiment that looked at feeder choice in nine-spined sticklebacks, *Pungitius pungitius*, after fish personally interacted with differentially rewarded feeders and then observed others at the same feeders (van Bergen et al., 2004). They showed that as time increased since fish last interacted with the feeders themselves, reliance on their asocially acquired information diminished as it became increasingly outdated and instead fish became more reliant on social information provided by where other fish appeared to be feeding. These strategies may be especially important and thus likely to be deployed within an environment that is unpredictable such that individuals may be unsure as to which behaviour is beneficial at that time with previously acquired information becoming outdated or irrelevant quickly.

Theoretical models have explored how environmental variability should influence social information use. Initial models indicated social learning to provide no net increase in fitness within a variable environment and to only offer benefits within a relatively stable predictable environment (Boyd & Richerson, 1985, 1988; Feldman, Aoki, & Kumm, 1996; Laland & Kendal, 2003; Rogers, 1988). However, since these early models, the notion that individuals can be flexible in their use of social information (following various social learning strategies such as those previously described) allows social learning to increase the mean fitness of a population (Laland, 2004; Laland & Kendal, 2003). Indeed, when the benefits of social versus asocial information use are modelled under conditions where outdated preferences cannot be inherited and environmental change affects both asocial and social information equally (in terms of which becomes outdated quicker) then social learning can benefit individuals experiencing high levels of environmental variability, increasing the rate of adaptation to the local environment (van der Post & Hogeweg, 2009). A high proportion of social learners within a population arises when virtual individuals are modelled foraging in environments where resources are highly variable in quality (Smolla et al., 2016). A recent extension to this model has also shown that social learning phenotypes will diverge under these conditions, with some individuals relying more on social learning that others (Gilman, Johnson, & Smolla, 2020). In support of these general predictions, individual-based spatially explicit models of foraging *Gyps* vultures under different management programmes found that when resources were modelled to be unpredictable (no provisioning of supplementary food), individuals using social information were more successful than those using asocial information and *vice versa* in predictable settings (Deygout, Gault, Duriez, Sarrazin, & Bessa-Gomes, 2010).

Conclusions from theoretical models are supported by empirical studies also finding increased environmental variation causing a greater reliance on social information. A study tracking the social transmission of novel food patches in black capped chickadees, *Poecile atricapillus,* found transmission rates to be greater in rural as opposed to urban habitats (Jones et al. 2017). Rural habitats were assumed to be more unpredictable because they were not so well supplied with reliable artificial bird feeder stations (unlike the urban environment) and this was presumed to lead to greater reliance on social information as birds attended to sites where others were feeding. An experiment directly manipulating the variability of floral reward within an array of artificial flowers, showed that when bumblebees, *Bombus terrestris,* were foraging in a variable environment, they used social information (presence of other bees foraging) as opposed to asocial information (associating floral colour with reward) which they used in a predictable environment (Smolla et al., 2016). Likewise, an experiment manipulating the reliability of feeders, through changing which feeder was most rewarding, also resulted in nine-spined sticklebacks relying more on social information when feeders were less predictable (van Bergen et al., 2004). Similarly, a novel experiment on European starlings, *Sturnus vulgaris*, tested the value of social information under differing environmental conditions. Environmental variability was manipulated through the use of available visual cues within a foraging task (Rafacz & Templeton, 2003). They showed starlings relied on social information and copied a demonstrator's decisions in an unpredictable environment (when cues did not reliably indicate reward) and benefitted from this when they could do so. Environmental unpredictability may have long term consequences for an individual's use of social learning. Japanese quail, *Coturnix japonica*, raised in either an unpredictable or predictable environment (through timing of food availability) both used social information during a food choice task administered later in life but in different ways (Boogert et al., 2013). Those birds raised in the unpredictable food condition avoided the choice of the demonstrator while those raised in predictable food condition selected the same choice as the demonstrator bird. These experiments provide compelling evidence of individuals paying close attention to cues given by others, and thus exhibiting social learning, when making subsequent choices in a more variable environment.

To my knowledge, all current evidence of increased reliance upon social information arising from a variable environment has come from studies that considered the use of social information in a context that was directly related to the aspect of the environment for which the reliability was varied. For example, when the reliability of floral colour cues was manipulated it led bees to look to where others were foraging on these same flowers (Smolla et al., 2016). Likewise, when the location of rewarding feeders varied, it led fish to become more reliant on observations of the feeding behaviour of others to indicate which feeder they should approach (van Bergen et al., 2004). Thus we know that individuals pay close attention to the predictability of particular aspects of their environment when deciding whether to use social information or not, but it is not clear whether unpredictability *per se* creates a general increased reliance upon social information, as indicated by changes in social information use in an unrelated context. If so, this would suggest that the individual follows more general strategic rules, for example increasing reliance upon social information in multiple contexts when the general environment is unpredictable rather than deploying social learning to solve specific problems.

I aimed to extend previous work by assessing whether a greater reliance on social information generated from increased environmental variation will also affect reliance on social information in a separate context, as expected if social learning strategies are generalised. Therefore, I reared two populations of domestic chicks, *Gallus gallus domesticus,* under environmental conditions of differing predictability (of feeder location) and subsequently tested their reliance upon social information on a separate novel foraging task. Domestic chicks are easy to rear under standardised controlled conditions and importantly will learn socially from one another (Nicol, 2004; Chapters 4, 5). For my unpredictable environment, I manipulated the location of food sources in their living environment by switching twice daily which two of eight feeders were rewarding. For the predictable (control) environment the same two feeders out of the eight remained consistently rewarding for the duration of the study. I analysed feeder associations to see if birds within an unpredictable environment relied more upon the social cue of others feeding and as a result grouped together more at feeders. I presented birds with a separate foraging task (previously ascertained to be socially learnt) in an adjoining chamber and recorded the social transmission rate of solving behaviour throughout each population to assess their general reliance on social information. I was able to control for any effect that sex and/or mass may have on the learning rate of solving behaviour. I predicted that firstly, those birds reared in an unpredictable environment would adopt a strategy of increased reliance on social information relevant to the particular unpredictable aspect of their environment, indicated by their attending to cues of other birds foraging at the perturbed feeders, and so resulting in increased group sizes at the feeders. Second, I expected this increased reliance on social information to be generalised and therefore transferred across to a separate context (learning a novel foraging technique) which was not itself unpredictable.

6.3 Methods

6.3.1 Subjects and housing

Two identical pens, that differed only in environmental predictability, each held a population of 25 domestic fowl chicks of the 'Rhode Rock' variety. This breed allows sexing from hatching due to feather colouration. Birds were collected as day-olds from a commercial dealer (Organic Pullets, Hittisleigh) on the 8th March 2019, were sexed and then randomly assigned to either pen while maintaining an equal sex ratio. Pens were temperature and humidity controlled and included perching. I provided birds with water, food and grit *ad libitum*. Birds were kept within the main enclosure area of the pen for the first week and from week two onwards had access to the extended area (**Figure 6.1a**). A testing chamber adjoined their pen, in which birds were presented with a novel foraging task. To allow identification of individual birds, at three days old, I fitted them with unique combinations of coloured plastic flatbands (Avian ID, Redruth), which I changed for a larger size at two weeks old. I weighed birds when they were 13 days old, using a flat digital scale (Salter, UK; precision=1g) that they stood on. At the end of the three-week study period, I donated all birds to a local free-range poultry farm.

6.3.2 Environment manipulation

I created two differing conditions of environmental predictability. When birds reached three days old (day 3), I positioned eight feeders in the main area of each pen, of which two were rewarded while the other six were identical but empty of food (**Figure 6.1a**). In the predictable environment, the two rewarded feeder positions were the same throughout the whole study period, whereas in the unpredictable environment, the location of the two rewarding feeders changed twice daily. Feeders were pyramid in shape with a tray at the bottom where food collects (Omlet, UK). I added a black collar around the feeder to prevent birds from seeing whether a feeder was empty or rewarding from a distance and so forcing them to either approach the feeder and look under the collar or use social information and look to where other birds were feeding (**Figure 6.1b**). Critically, this created an environment in which birds were unaware which feeders were rewarded without exploring the area or using social cues (where other birds were feeding).

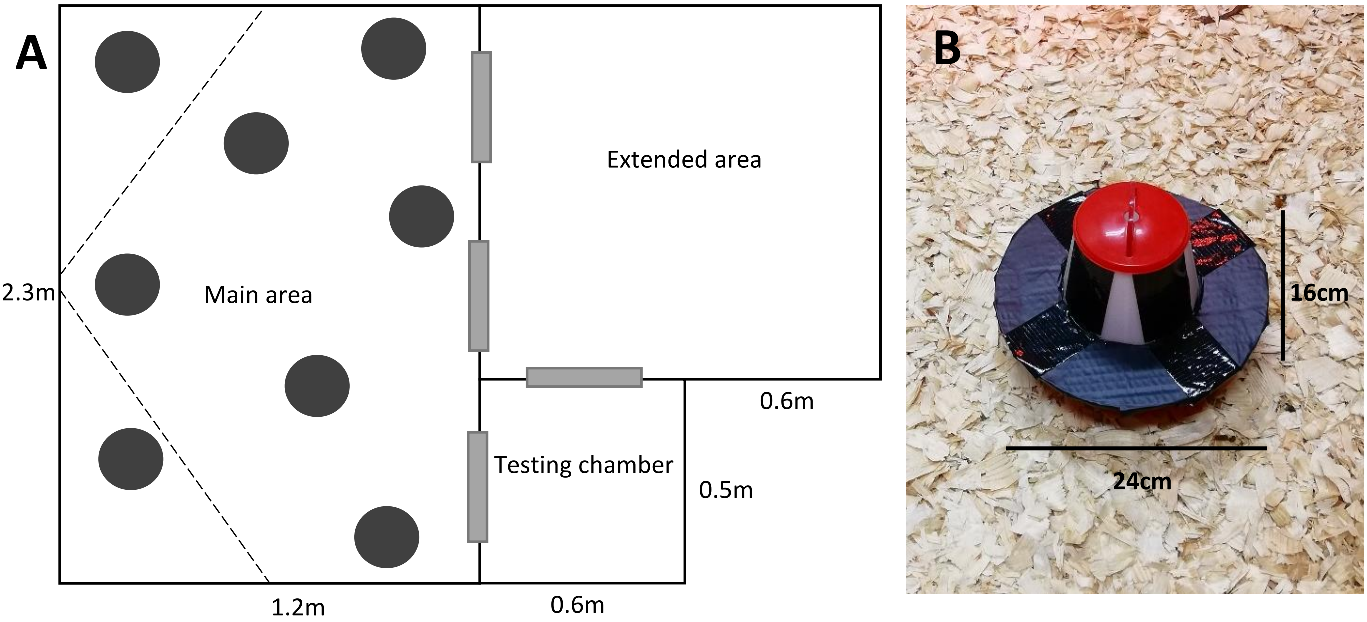


Figure 6.1 Pen set-up to create different variable environmental conditions. A) shows the locations of the 8 feeders within the main pen area, of which two would be rewarding. Grey bars indicate gated doors and dashed lines show the location of perches. B) shows the design of feeder.

6.3.3 Feeder associations

I recorded the number of birds foraging together at the rewarding feeders within the main pen area. I carried out instantaneously point sampling across both pens recording group size of foraging individuals every two minutes, in ten-minute sampling periods. A bird was considered foraging if their head was positioned under the black collar of the feeder. Feeder associations were collected from day 4 to day 20 (11/03/19 - 27/03/19) during 148 (Unpredictable environment) and 134 (Predictable environment) ten-minute sampling periods.

6.3.4 Testing reliance upon social information in a separate context

I repeatedly presented birds with a separate novel foraging task when in the testing chamber, in a location adjacent to, but separate and distinct from, their main feeding and living environment where environmental predictability was manipulated. I assessed their reliance upon social information in this task through recording the spread of solving behaviour across all individuals in each population.

6.3.4.1 Novel foraging task

The task required birds to slide open lightweight cardboard doors in order to access hidden mealworms in wells behind (**Figure 6.2**). The apparatus comprised a wooden box, 12 x 50cm, within which were 10 wells (arranged as two rows of five), each covered by doors, painted half red half blue. The wells were filled with mini-mealworms and the box was presented upright (12cm vertical) in the testing chamber. The task apparatus was adapted from previous studies of social transmission in birds (Aplin & Morand-Ferron, 2017; Aplin et al., 2015; Aplin, Sheldon, & McElreath, 2017).

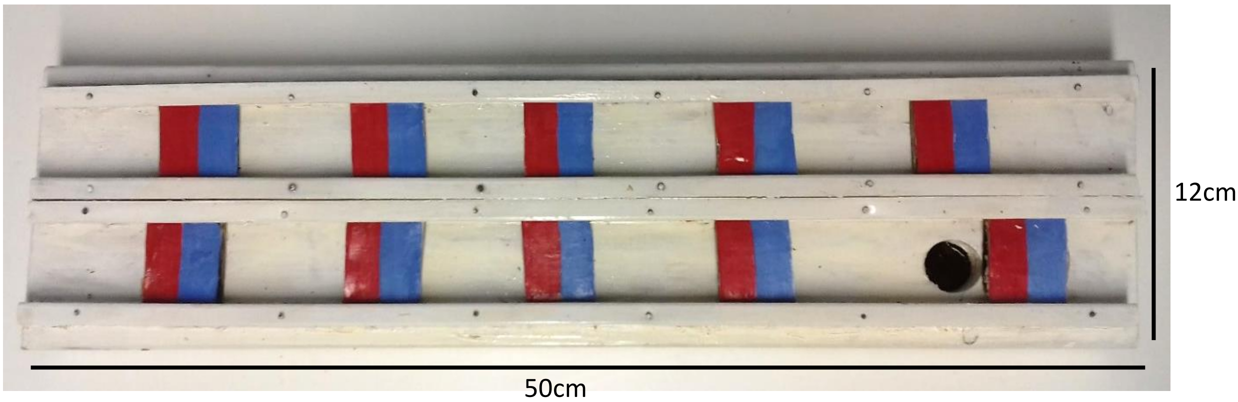


Figure 6.2 Novel foraging task apparatus. Bottom right shows door opened to the right exposing the hidden well behind which would hold mealworm rewards.

6.3.4.2 Shaping and demonstrator training

I shaped the birds to associate the chamber with mealworm rewards (day 4 to 6) before I started testing so that they would enter the testing chamber and engage with the apparatus without interference from experimenters. To do this I scattered mealworms all over the floor of the testing chamber and on a plain white box where the task apparatus would later be positioned and repeatedly allowed birds to enter, explore and pass through the chamber in gradually decreasing group sizes, until all birds were comfortable entering alone.

To provide a starting point to social transmission and to ensure that birds would be able to socially learn the solving behaviour, I trained one male bird to become an informed demonstrator. I shaped this demonstrator bird (days 7-10) by exposing them to the task with the doors initially fully opened allowing unobstructed access to the mealworm rewards and then gradually decreasing the amount the door was opened until the bird could solve the task by sliding open fully closed doors. I chose to have the same demonstrator bird for both populations, in order to remove any bias that could arise from having differing demonstrators with differing attributes (Coussi-Korbel & Fragaszy, 1995; Laland, 2004). This demonstrator bird split their time outside the testing period equally between the two populations to ensure equal familiarity with birds in both populations.

6.3.4.3 Testing

All birds in both populations completed a pre-test round (day 7), 13 social rounds (days 11-17) and a post-test round (day 18). The pre-test round was to ensure that no birds could initially solve the task and involved each bird entering the testing chamber for one minute where they could interact with the baited apparatus (1 mealworm/well) in isolation before being released into the extended area. None did so. The 13 social rounds involved groups of three birds entering the chamber to interact with the task for three minutes, before being released into the extended area. I did not control the group compositions within these rounds, rather birds entered the chamber with others at will and I recorded the group compositions and whether an individual solved the task. A bird was considered to have successfully solved the task (classified as informed) if they slid open any door obtaining a mealworm from the well behind. Birds that had not yet solved the task were classified as uninformed. In these rounds, the apparatus was baited with 4 mealworms per well. The demonstrator bird cycled through the testing chamber once in each of the social rounds like all the other birds. Birds were cycled through the testing chamber for 13 social rounds, completing 2 rounds a day, one in the morning, one in the afternoon. The post-test round was identical to the pre-test and enabled me to determine which birds could solve the task when in isolation.

6.3.5 Ethics

All birds were reared to a standard that exceeded conditions required by the Department for Environment Food and Rural Affairs (DEFRA) and the Animals Scientific Procedures Act (ASPA 1986). All work was approved by the University of Exeter Psychology Ethics Committee.

6.3.6 Analysis

6.3.6.1 Do feeder associations differ depending one environmental predictability?

Firstly, to determine if the size of groups foraging together at rewarding feeders within the main pen differed between my two populations experiencing differing environmental conditions, I carried out a Mann-Whitney test in R v3.5.3 (R Core Team, 2016). Second, to determine if the variance differed between the two populations (potentially as a result of birds being more clumped at feeders at given times) I conducted a modified robust Brown-Forsythe Levene-type test based on the absolute deviations from the median in R using the ‘lawstat’ package v3.3 (Gastwirth et al., 2019).

6.3.6.2 Does the acquisition of solving behaviour differ between pens of differing environmental predictability?

In order to test whether environmental predictability affected the acquisition rate of solving behaviour, I carried out a ‘time to event’ analysis to investigate whether birds within the unpredictable environment differed in their likelihood of acquiring the solving behaviour each round compared to the predictable environment. I fitted a cox proportional hazards model using the ‘survival’ package (Therneau, 2015; Therneau & Grambsch, 2000) in R. The round the solving behaviour was first acquired was the response variable with environmental condition as a categorical fixed factor. Round was a censored observation capped at the last post-test round. This analysis modelled the likelihood that an individual in either condition had acquired the solving behaviour at each given round. Coxph models provide an estimated hazard ratio (Haz) which indicates whether there is an increased (>1) or decreased chance (<1) of acquiring the behaviour.

6.3.6.3 Is the solving behaviour socially transmitted across the pen and do social transmission rates differ between pens of differing environmental predictability?

I used a Network Based Diffusion Analysis (NBDA; Franz and Nunn 2009; Hoppitt, Boogert, and Laland 2010) to determine if the solving behaviour spread via social learning throughout the populations. A NBDA will infer social learning if the order in which individuals acquire the solving behaviour is related to a relevant social network. I used a dynamic variant of NBDA (specifically an Order of Acquisition Diffusion Analysis) where the social network is allowed to change over time, using the 'NBDA' package v.0.8.2 (Hoppitt et al. 2020) in R. The social networks used in this analysis were created from the testing chamber groupings of birds in each social round and thus represent who could have possibly learnt from whom. Cumulative networks of these testing chamber associations were created and so provided time-ordered networks representing the current and previous testing chamber associations for each round. Individuals were classified as informed or uninformed for each round. Informed birds were able to solve the task as indicated by their having done so in previous rounds. Uninformed birds had never solved the task. An individual's classification was combined with the cumulative networks of associations to provide time-ordered networks of potential social learning opportunities for each round - individuals could only learn from informed individuals. I included sex and mass as potential individual level factors influencing the asocial and/or social learning rate as previous evidence shows these traits can affect social learning (Aplin, Farine, et al., 2013; Duffy et al., 2009; Lonsdorf et al., 2004; Reader & Laland, 2000; Schnoell & Fichtel, 2012; van de Waal et al., 2010; Watson et al., 2018), asocial learning performances and motivation (Jones, Braithwaite, & Healy, 2003; Rowe & Healy, 2014; van Horik &

Madden, 2016). To investigate the factors influencing the order of behavioural acquisition I adopted an unconstrained modelling approach (Hoppitt & Laland, 2013) and fitted all possible combinations of social and asocial models with differing combinations of individual level variables. I then averaged across all candidate models to provide support for differing model types and variables based on Akaike information criterion corrected for sample size (AICc) (Burnham & Anderson, 2004).

6.4 Results

6.4.1 Do feeder associations differ depending on environmental predictability?

There was no difference in the median size of groups of birds feeding together at feeders in the main pen area between the unpredictable and predictable environment (W=329810, N=148,134, p=0.95; **Figure 6.3**). A median of three birds fed together at a time at the feeders in both environmental conditions. Post-hoc analysis showed that groups in the unpredictable environment had greater variance in size, driven by some especially larger clusters ($F_{1,1623}$=12.76, p<.001; **Figure 6.3**).

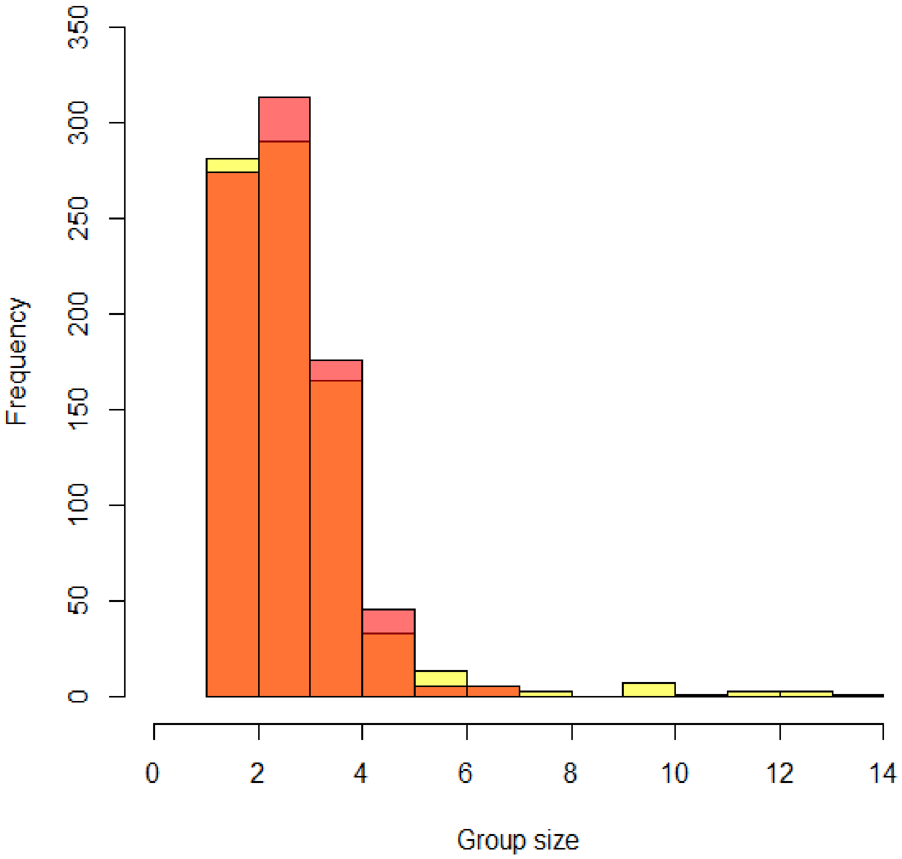


Figure 6.3 Frequency distribution of the group sizes of birds seen feeding together in the unpredictable (yellow) and predictable (red) environment, overlap of ranges is shown in orange.

6.4.2 Does the acquisition of solving behaviour differ between pens of differing environmental predictability?

Birds in both populations were increasingly likely to acquire the solving behaviour as rounds progressed. However, I found no evidence that the rate of overall learning differed between treatments, with birds in either environmental condition being just as likely to acquire the solving behaviour in each round (Haz. = 1.13 ± 0.36; Coxph, $Z = 0.36$, events (e) = 31, p =0.72; **Figure 6.4**). A total of 13 birds in the variable condition and 15 in the predictable condition had acquired the solving behaviour by the final round.

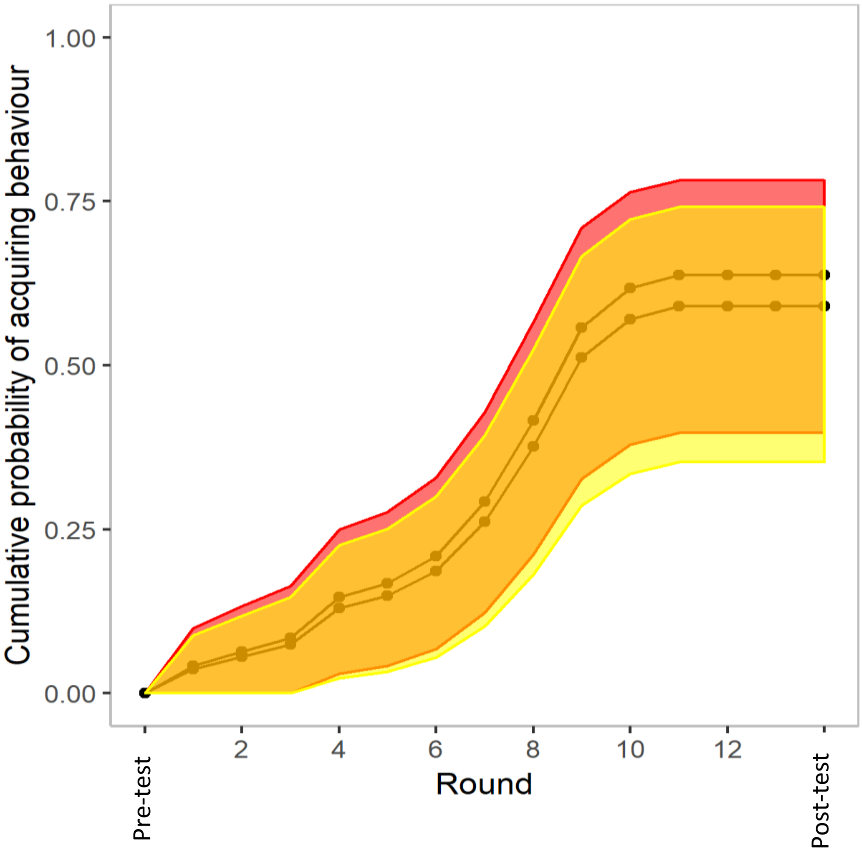


Figure 6.4 The predictive cumulative probability of an individual acquiring the solving behaviour with each round dependent on condition (red= predictable, yellow= unpredictable, orange indicates overlap in range). 95% confidence interval bands shown.

6.4.3 Is the solving behaviour socially transmitted across the pen and do social transmission rates differ between pens of differing environmental predictability?

Fitting time-dependent NBDA models showed that that the novel behaviour required to solve the task spread socially throughout the populations, with birds learning the solving behaviour from others that were exhibiting it in the testing chamber. Using an information theoretic approach and averaging across all candidate models weighted by their AIC value showed that the most support was given to models that included social transmission of behaviour with equal rates across both populations ($\sum w=0.48$), and much less support provided for models of purely asocial learning ($\sum w=0.24$; **Table 6.1**). Although there were fewer models of asocial learning compared to ones that included social transmission, the support given to social transmission models ($\sum w=0.76$) outweighed asocial learning (even when asocial support is multiplied up to the equivalent number of models). Averaging across all weighted models that included equal social transmission gave an estimated rate of social transmission rate of 1.37 (SE ± 0.37) times greater than the asocial learning rate per connection to informed others. Again, averaging across all weighted candidate models showed no evidence for an effect of mass or sex on the asocial or social learning rate with support of under 50% indicating the variables are better not included in the best predictive model than there are included (**Table 6.2**).

Table 6.1 Support provided, based on AIC values, to asocial and social models with equal or different rates of social transmission.

Model	*Number of models*	*Support*
Asocial model	3	0.24
Social model - Equal transmission rates	10	0.48
Social model - Different transmission rates	10	0.28

Table 6.2 Averaged support for each variable on the asocial and social transmission rate.

Variable	Model averaged support
Mass	
on asocial learning rate	0.14
on social learning rate	0.39
Sex	
on asocial learning rate	0.18
on social learning rate	0.48

6.5 Discussion

I found limited evidence of chicks increasing their reliance on social information when reared in an unpredictable environment, and no evidence of a reliance upon social information being generalised when learning a novel foraging task. I searched for such evidence in two contexts. First, I expected the size of foraging groups in unpredictable environments to be larger as all individuals fed simultaneously, using the cues of others to indicate whether a location, in this case a feeder, was profitable or not. This would indicate a specific response to unpredictability with individuals adjusting their social information use strategy to the immediate context in which they found themselves. Although I found no difference in the average number of birds associating together at a feeder at any one time, I did find a greater variance in group size in the unpredictable environment, with larger groups more often seen feeding together compared to the control predictable environment. Second, I expected that individuals living in an unpredictable environment would make more use of social information in a novel context, specifically showing stronger effects of social learning in the acquisition of a novel foraging method. This would indicate that they exhibited a general change in social learning strategy that went beyond the specific aspect of their environment that was predictable or not. However, although the novel foraging task was learnt socially and spread throughout the populations, I found no difference in the reliance upon social information when learning to solve it between the chicks living in predictable or unpredictable environments.

I found no difference in the average (median) number of chicks foraging together at the rewarded feeders in the main living area but did observe a difference in the variance of group sizes. Group size may have not been influenced greatly by the environment manipulation due to small costs of individually searching for and locating rewarding feeders owing to the small size of the test arena and ease of travel around it. There is substantial evidence of individuals following a strategy of using social information only when ‘asocial learning is costly’ with costs comprising time and/or energy (Day et al. 2003; Kendal et al. 2009; Kendal, Coolen, and Laland 2004; Laland and Kendal 2009; McElreath et al. 2005;

Webster and Laland 2008). Therefore, if searching for and locating the feeders was simply insufficiently costly then they might not have used social information (where other birds were feeding). Additionally, the unpredictability of feeders (changing locations two times a day) may not have been high enough to warrant a noticeable switch to social cues. Other studies that varied the environment did so through removing food at random periods within the day (Boogert et al., 2013), randomly allocating which one in three wells was rewarded every trial (Rafacz & Templeton, 2003) and randomly selecting 2/12 flowers to be rewarding during training (Smolla et al., 2016). These manipulations were perhaps more unpredictable than changing the positions of rewarding feeders twice daily. If the rewarding feeder locations were varied even more then birds may have relied more on social information. It is also possible that birds were using social information to locate rewarding feeders but just did not group together more at feeders within the unpredictable pen because they were fed in excess and so could use social information to locate rewarding feeders and visit them at a later time when required. This may have allowed them to escape competition or interference at the feeders. However, the unpredictable environment had a greater variance of group sizes with larger groups more often seen feeding together compared to the predictable environment indicating a greater reliance upon social cues. It is possible that when rewarding feeders are first discovered in the unpredictable environment more birds initially gathered together at these feeders for a short while until normal numbers of individuals resume foraging together until feeder location is next changed. This brief occurrence of large groups then could have increased the variance but did not affect the median number feeding together. Given the difference in variance, the lack of difference between median group sizes at a feeder does not necessarily mean that those birds within an unpredictable environment were not relying on social information and future work should investigate whether social information use increases proportionally with unpredictability.

Despite this suggestion that birds were using social information in the immediate situation where the environment was unpredictable, I found no evidence of birds facing such unpredictability being more likely to generally rely more upon social learning. Although I determined that social learning was critical to facilitate the spread of solution to the novel foraging task, the rate of transmission did not vary between conditions and therefore the likelihood of birds acquiring the novel foraging behaviour with increasing rounds did not differ between environments of differing predictability. I predicted that birds raised in an unpredictable environment would, as a result of enhanced use of social cues when attending to the feeding behaviour of others in the main pen, transfer this reliance on social information when presented with a novel foraging task in another context and therefore increase the rate of social transmission. Despite theoretical models (Deygout et al., 2010; Smolla et al., 2016; van der Post & Hogeweg, 2009) and empirical work (Jones et al., 2017; Rafacz & Templeton, 2003; Smolla et al., 2016; van Bergen et al., 2004) suggesting an increase in social information use when in a variable environment, I did not find such an increased reliance on the task accompanying a more unpredictable environment. The equal rates of social transmission may be a result of social cues in general not being relied upon more in the unpredictable environment, as suggested by the lack of difference in foraging group sizes (discussed above), and therefore individuals also did not increase use of social information within the task. Alternatively, even if social cues were relied upon more when locating rewarding feeders in an unpredictable environment, this was not transferred to another context and individuals fine-tune their use of social information strictly according to context. Previous studies that found an increased reliance on social information all varied the reliability of reward or associated cues and tested animals within that same context (Rafacz & Templeton, 2003; Smolla et al., 2016; van Bergen et al., 2004).

It is also possible that other factors may have masked or prevented birds from increasing their use of social information during the novel foraging task. For instance, social information use is predicted to increase with behavioural complexity (Day et al., 2003; Kendal et al., 2009; McElreath et al., 2005) and perhaps this task was simply too easy to solve with minimal social information required to attract their attention. If I had provided a harder task in the testing chamber that required closer observation of more complicated actions to obtain the reward then maybe I would have seen a difference between populations with those in the variable environment being more used to closely observing the behaviour of others. Alternatively, the level of social learning could have already been at a ‘ceiling’ level in the predictable environment with birds being totally reliant upon social information for the behaviour to spread. This would then mask any increased reliance I may see in the unpredictable environment because social learning was already at a very high level. Finally, rather than social information use at a group level increasing, some individuals may have relied upon social information more so than others depending on individual differences. When virtual foragers are modelled in spatially and temporally variable environments, a divergence of social leaning phenotypes has recently been shown to emerge, with some individuals using social learning more so than others (Gilman et al., 2020).

I find no evidence for sex or mass influencing asocial or social learning during this task. This may be due to the individual level factors in general having no substantial effect for domestic chickens learning this task or it could be as result of the young age I tested the birds at. I may not find an effect of sex or mass when birds are a few weeks old as they show little sexual dimorphism and their mass is still similar. Indeed, studies find learning rates to differ between the sexes were conducted on adult individuals (Aplin, Farine, et al., 2013; Lonsdorf et al., 2004; Reader & Laland, 2000; Schnoell & Fichtel, 2012; van de Waal et al., 2010; Watson et al., 2018). Likewise those studies looking at mass were again on older individuals that likely varied more in mass and/or had correlated mass-related factors such as dominance influencing learning or motivation (Duffy, Pike, Laland, 2009; Jones, Braithwaite & Healy, 2003l Rowe & Healy, 2014, van Horik & Madden, 2016). It may be that as birds develop, sex and mass have effect learning rate more.

I explicitly tested whether an unpredictable environment would lead to a general predisposition to use social information. I found no evidence of individuals transferring a preference for social information use to another context as indicated by their reliance upon social information when learning a novel foraging task. In accordance with theoretical models and previous empirical work, I found some evidence for an increased reliance upon social information in a foraging task performed within the immediate unpredictable environment with a greater variance in group size of birds foraging together at the feeders. However, there was no transference of this reliance to a different context in which the environment had not been varied; birds reared in the unpredictable environment did not rely on social information more when learning a separate novel task. Future work should continue to investigate the factors affecting individual differences in social information use alongside the conditions under when social information is favoured and whether social information use generally can be shaped by environmental conditions or whether individuals are highly selective in the circumstances in their use of social information.

7

General Discussion

7.1 Abstract

Social learning enables novel behaviours to spread rapidly throughout groups and is essential for the establishment of group level traditions that underpin culture. The social transmission of novel behaviours is widely reported across many species; from potato washing in Japanese macaques to milk bottle opening in great tits and blue tits, nut cracking in chimpanzees and lobtail feeding in humpback whales. However, individuals are not all equal in their use of social learning from one-another and their reliance upon social information during learning varies both between individuals and within individuals as environmental and social conditions vary. Social transmission of novel behaviours is therefore the emerging product of a multitude of individual, social and environmental factors that all influence and dictate spread. My thesis has explored this range of factors, extending from individual attributes to the properties of the group and the environment in which the group lives. This has allowed me to determine the importance that differing aspects of the social and physical environment have for the social transmission of behaviours. Consequently, I can suggest how each contribute in isolation and conjunction with one another to explain the occurrence and influence of social learning. Whilst I have used a single, fairly tightly controlled model system (domestic and pheasant chicks) to explore these factors, the principles that I have revealed and reported may be applied more generally in future studies of social learning and the spread of novel information within groups. I will briefly summarise the findings of those chapters before then moving on to discuss implications and future research directions.

7.2 Summary of findings

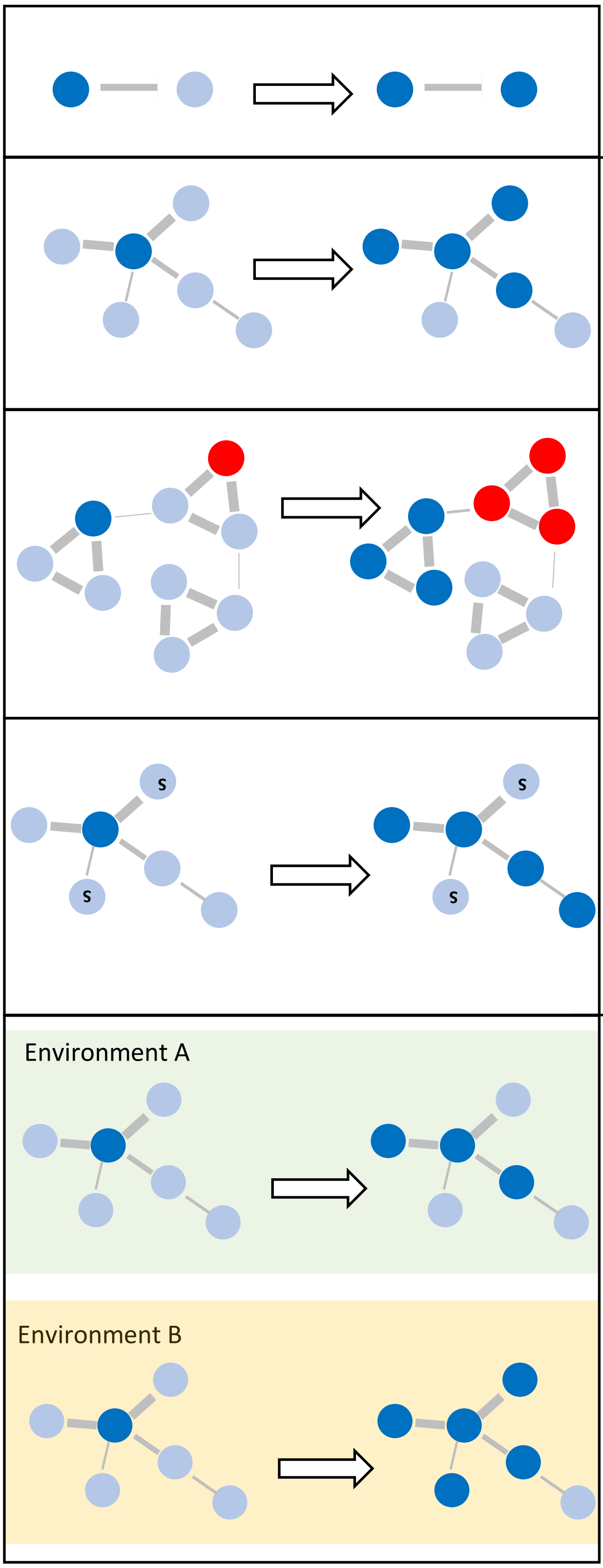
This thesis explored factors that influence social learning and the transmission of novel behaviours throughout groups (**Figure 7.1**). The experiments conducted used both traditional dyadic testing and natural diffusion style approaches, while manipulating aspects of the physical and social environment in order to assess their impact on behavioural spread. I started by exploring how individual factors (personal attributes) may influence the likelihood of using social information when learning a novel behaviour (Chapter 2). I then progressed on to explore how differing social factors affect behavioural transmission through investigating the effects of group size (Chapter 3), group structure (Chapter 4) and foraging dynamics (Chapter 5). Finally, I studied the influence the environment can have for social information use and thus social transmission (Chapter 6).

Throughout the thesis I used a newly developed variant of Network Based Diffusion Analysis (NBDA) to identify social learning and this repeatedly revealed the novel foraging behaviours studied to be socially transmitted across the groups of pheasant and domestic chicks. In total I presented 16 different groups of pheasant and domestic chicks (totalling 492 birds) with a novel foraging task and tracked the spread of behaviour via NBDA. NBDA is a sophisticated statistical technique that identifies socially transmitted behaviours and determines the strength of social transmission. The analysis infers social transmission if the order in which individuals acquire a novel behaviour within a group matches the group's social structure. Importantly, the new version of NBDA allows the group's social network to change over time, rather than requiring group associations to be represented in a single static network. This allowed me to more precisely map the developing social learning opportunities, as groups of pheasant and domestic chicks interacted with the task in progressing rounds. In all analyses I found the solving behaviour to the novel foraging tasks presented (Pecking through paper task – Chapter 3; Sliding door task - Chapters 4, 5, & 6) to be socially transmitted across all populations. Thus, I can confidently say pheasant and domestic chicks deployed social learning when acquiring these novel foraging behaviours, and so my experimental paradigms, despite being highly controlled and artificial, provide a solid framework to explore how differing factors influence social transmission.

Individual Factors:

Personal attributes (Chapter 2)

Sex, mass, dominance-ranking and social position of an individual did not correlate with the speed at which young chicks socially learnt a novel foraging behaviour. Suggesting that relationships detected with these attributes may better reflect social learning opportunities and differential needs rather than innate differences in social learning.



Social Factors:

Group size (Chapter 3)

Interacting in a larger group size did not lead to overall faster behavioural spread. Thus, demonstrating that rather than the total number of connections to informed individuals, the proportion of informed to uninformed connections can also influence the adoption of a socially learnt behaviour.

Group structure (Chapter 4)

A novel foraging behaviour did not spread faster across groups that held a more modular network structure. Additional factors such as behavioural reinforcement and forgetting rates may therefore play an important role in social transmission, suggestive of more complex transmission processes.

Group foraging dynamics (Chapter 5)

The opportunity to scrounge food during a novel foraging task was essential in allowing the solving behaviour to spread across the group. Evidence of local/stimulus enhancement during learning may be responsible for differing results found in how scrounging influences social learning.

Environmental Factors:

Information predictability (Chapter 6)

Birds reared in an environment unpredictable in food location did not transfer over an increased reliance on social information when presented with a separate foraging task. Therefore, even if reliance upon social information use is increased by environmental conditions, this does not affect general use of social information in differing contexts.

Figure 7.1 Individual, Social and Environmental factors that may influence social learning and social transmission, explored within the thesis. Summary of key findings given for each chapter.

7.2.1 Individual Factors

In Chapter 2, I investigated whether individual attributes related to performance on a socially learnt novel foraging task. This chapter explored social transmission at the most basic level - between dyads of individuals. Although work has explored how individuals can be flexible in information use dependent on context (Hoppitt & Laland, 2013; Laland, 2004) and has shown animals to preferentially copy from certain individuals dependent on characteristics (Coussi-Korbel & Fragaszy, 1995; Laland, 2004), much less attention has been shown to individual differences in propensity to socially learn (Mesoudi et al., 2016). I therefore repeatedly exposed domestic chicks to demonstrations of task-solving behaviour by informed demonstrator individuals (the model) and recorded their social learning performance, through the number of repeated exposures required before they learnt how to solve the task themselves. By standardising dyads during exposures, I was able to control for and limit effects of preferential learning based on model attributes and instead concentrate on the differing attributes of the learner. For this task, I found that individual learner attributes of mass, sex, dominance ranking and social position (based on foraging associations) of domestic chicks provided no indication as to how quickly an individual learnt the solving behaviour. Birds were tested at a relatively early age and it is possible that as they develop, these attributes become more distinct and later influence social learning performance. The results of Chapter 2 therefore suggest that, for this task, social learning performance is not dependent on these individual attributes of the learner and if a relationship further develops with age, this is likely a resultant effect of differing opportunities and/or need associated with those attributes.

7.2.2 Social factors

Group Size and Number of Associates

In Chapter 3, I progressed on to looking at how the crude scale of the social environment can influence behaviour spread. This chapter investigated how the number of associates an individual has, influenced the likelihood of socially learning a novel foraging behaviour and subsequent spread of that behaviour throughout the wider population. I presented pheasant chicks with a novel foraging task which they interacted with in either small or large groups. Based on transmission models that assume an individual is more likely to socially learn a behaviour when accompanied by an increasing number of informed associates (Firth, 2019; Hoppitt, 2017), I predicted that birds interacting in the larger groupings would be more likely to acquire the novel foraging behaviour and so facilitate faster overall behaviour spread. However contrary to predictions, increasing the number of associates present during learning did not increase the rate of social learning or result in a faster spread of behaviour across the wider population, indicating additional factors may be at play during social learning. Consequently, I found equal support for models where social transmission was dependent on the total number and proportion of connection to informed individuals suggesting that both these factors may be important for social learning of certain behaviours.

Group Structure

Chapter 4 further explored social structure and social transmission through investigating the effect that network modularity has for behavioural spread. Many theoretical models discuss the importance of modularity for behavioural transmission, with assumptions that increasing modularity decreases overall behavioural spread and increases the likelihood of behavioural variants within clusters (Cantor & Whitehead 2013; Whitehead & Lusseau 2012). However, I found that modularity did not affect the speed of behavioural transmission nor lead to the initial establishments of such traditions. The spread of a novel behaviour did not travel faster through populations of domestic chicks that were experimentally induced to exhibit a social network structure of low modularity compared to groups of higher modularity. Nor did specific variants of solving technique form within distinct clusters in the highly modular networks. Again, this result is perhaps suggestive of additional factors in the social transmission process that are important such as social reinforcement and forgetting rates, and thus suggesting a more complex transmission process.

Social Dynamics within the Network

Chapter 5 moved from looking at social structure to how dynamic social interactions influence transmission. This chapter focused on social foraging dynamics and the impact that scrounging has for learning and behavioural transmission. Scrounging food obtained by others has been shown to influence social learning, both in the laboratory and in the wild (Beauchamp & Kacelnik, 1991; Caldwell & Whiten, 2003; Fragaszy & Visalberghi, 1989; Giraldeau & Lefebvre, 1986, 1987; Lefebvre & Helder, 1997; Midford et al., 2000; Nicol & Pope, 1994; Thornton & Malapert, 2009a). However, there have been conflicting results as to the direction of this relationship, with studies showing it to both retard and promote social learning. Therefore, I manipulated scrounging opportunity during a natural diffusion experiment on domestic chicks and explored the effect it had on social learning and transmission throughout the wider population. I obtained evidence for the type of social learning deployed by birds in order to link the impact scrounging has with learning mechanism. Scrounging was found to be highly important for the facilitation of social transmission, with the behaviour hardly spreading at all when scrounging opportunity was restricted. I conclude that the social learning mechanisms deployed by birds in my experiments were likely to rely on stimulus or local enhancement and argue that these mechanisms may positively co-vary with scrounging because opportunities for scrounging simply enhance attention to the task apparatus.

7.2.3 Environmental Factors

Finally, Chapter 6 looked at how the physical environment may affect social information use and behavioural transmission, particularly the effect of unpredictability of information that I manipulated by making resource locations predictable or unpredictable. Evidence from both theoretical models and empirical studies have previously shown animals to increase their use of social information when learning about resources that are unreliable and variable (Rafacz & Templeton, 2003; Smolla et al., 2016; van der Post & Hogeweg, 2009). I explored this further by investigating whether an increase in social information use is a general response to unpredictability or whether this is a specific focused response only when learning about those variable resources. Environmental predictability was manipulated within groups of domestic chicks by experimentally changing the locations of rewarded feeders in their main living area. I determined firstly whether birds were more reliant upon social information when locating rewarded feeders and second whether this increased reliance would be transferred so a separate context - a novel foraging task presented in a separate testing chamber. I found some evidence of an increased reliance upon social information when locating feeders within the pen. However, birds did not appear to generalise this reliance and increase use of social information during a separate foraging task and subsequently the resultant spread of solving behaviour did not change across manipulated predictability conditions.

7.3 Key findings and possible implications

7.3.1 Individual differences in social learning

This thesis explored how a set of individual attributes may influence variation in social learning both in isolation and in a group setting. Chapter 2 tested 41 domestic chicks in a traditional dyadic paradigm to explicitly investigate how different measured attributes of an individual may influence social learning performance. These measured attributes included: sex, mass, dominance ranking and social network position. I also considered the effect of a subset of individual attributes in the diffusion models in Chapters 3, 4, 5 & 6 which tracked the spread of behaviour across 16 groups (totalling 492 pheasant and domestic chicks) when I included (where possible) an individual’s sex and mass in the models to further evaluate their influence on social transmission when in a group setting. These attributes were selected based upon previous studies either showing them to influence social learning rate or suggesting them to have a possible effect. They also constituted a range of both relatively stable, fixed-in-time traits (sex and mass) and traits which are more flexible, potentially changing over time and with social environment (dominance ranking and social network position).

I found dominance rank, social position, sex and mass of an individual did not explain significant differences in social learning of a novel foraging task when tested in isolated pairings (Chapter 2). Likewise, sex and mass also exerted no influence on social transmission of behaviour when tested within a group setting (Chapters 3, 4, 5, & 6). My results differ from previous studies who have found both a sex difference (Aplin, Sheldon, et al., 2013; Kappeler, 1987; Lonsdorf et al., 2004; Reader & Laland, 2000; Schnoell & Fichtel, 2012; Watson et al., 2018), and an influence of dominance rank in how individuals use social information (Aplin et al., 2013; Jones, Aplin, Devost, & Morand-Ferron, 2017). Although not explicitly tested by others, I anticipated mass may influence task performance as it is likely linked to dominance rank and strength of an individual. Following a recent suggestion that social learning ability subsequently influences social relations within a group (Kulahci et al., 2018b), I also predicted social position might predict performance on a socially learnt task.

I suggest several explanations as to why my results differ from other studies finding a relationship with these attributes. These include a difference in the species being tested and the age at testing. Firstly, it is possible that these attributes simply do not influence social learning for domestic and pheasant chicks. However, given that studies on other species that have similar social structures (sexually dimorphic, group-living, with dominance hierarchies) have observed these differences, it seems less likely to be a species difference and potentially a consequence of age tested instead. Those studies finding females to use social information more and socially learn novel behaviours faster were all conducted on older individuals (Aplin, Sheldon, et al., 2013; Kappeler, 1987; Lonsdorf et al., 2004; Reader & Laland, 2000; Schnoell & Fichtel, 2012; Watson et al., 2018). Through testing pheasant and domestic chicks at a young age (2-3 weeks) I found that sex difference in social learning propensity or ability are not evident from birth. Therefore, observed differences in social learning may be an effect that is established over time as a result of associated opportunity or need. For instance, females may become more inclined to acquire novel behaviours and thus quicker to socially learn to meet energetic demands due to increased reproductive need (Aplin, Farine, et al., 2013; Reader & Laland, 2000). Alternatively, opportunities in social learning may differ if the species has sex-specific social organisation or if a certain sex is allowed closer proximity to others and can therefore more easily observe their behaviour (Marcoux, Whitehead, & Rendell, 2006; Mesoudi et al., 2016). Similarly, differing social learning opportunities may also explain previously observed effects of dominance rank. Through standardising pairings between dyads of individuals in Chapter 2, I was able to limit any effects dominance may have on learning opportunities (such as subordinate individuals having restricted access to task apparatus) and thus evaluate if dominance ranking influences social learning outside of opportunity. I found it did not; a higher dominance ranking in chicks did not result in an increase or decrease in how quickly they socially learnt a novel foraging behaviour. This may explain the previous conflicting results if dominance is representing a difference in opportunity under natural, unmanipulated patterns of association, which may consequently alter social learning of novel behaviours if for instance dominant individuals are able to observe behaviours more closely, monopolise areas or even scrounge food. I also consistently found that an individual's mass had no effect on social learning when they were tested in isolation (Chapter 2) or within a group setting (Chapters 4,5 & 6). Again, this absence of effect may be a result of birds being tested when very young when variance in mass is not large and so its effects are perhaps not yet visible and/or a result of imposed equal social learning opportunity which mass might effect when in a group setting. Thus, rather than these attributes directly influencing an individual's ability or propensity to socially learn, overall my results suggest that observed differences in social information use based on these attributes may be a reflection upon differing associated needs or opportunities of social learning.

Separating out opportunities from propensity to socially learn is difficult to do in natural group settings, but valuable for further understanding causes of individual differences in social learning. To my knowledge only one other study has explored how an individual's social learning performance affects their social position, finding that after lemurs acquired a new foraging skill they became more central within their group's social network as a result of increased affiliative behaviours received from others (Kulahci et al., 2018b). Through observing social interactions in a context separate to learning of the task I was able to investigate whether social position (network centrality) related to an individual's speed of social learning, that was not a consequence of learning opportunities (Chapter 2). I found that individuals with higher network centrality were not intrinsically more likely to use social information or become faster at socially learning new behaviours. Therefore, my result supports the underlying assumption of transmission models that more socially central individuals are faster to socially learn new behaviours simply due to increased access to social information rather than being inherently better at using this information (Firth, 2019; Hoppitt, 2017;

Kurvers, Krause, Croft, Wilson, & Wolf, 2014). However, I only explored social structure through measuring centrality of foraging associations, and it is possible that other measures (such as affiliative interactions and proximity data) might still explain differences in social information use. Research should therefore continue to investigate the potential for a dynamic relationship between social learning and social position.

It is possible that additional attributes, unmeasured in this thesis, may better predict individual differences in social learning. For instance, asocial learning ability and innovative tendencies have also been linked to the propensity to use social information, although with differing results dependent on study. Some studies have found a positive link between asocial learning and social learning performances (Aplin, Sheldon, & Morand-Ferron, 2013; Bouchard, Goodyer, & Lefebvre, 2007), which is suggestive of a general cognitive ability that influences all learning. However, other studies have found a negative link (Burkart et al., 2009; Katsnelson et al., 2011) which is more indicative of a trade-off between these two types of learning and thus individuals may have specific abilities for different learning means. Personality type has also been linked to social learning, with several studies finding that an individual's propensity to socially learn is related to how bold/shy they are (Carter et al., 2014; Kurvers et al., 2010; Marchetti & Drent, 2000; Nomakuchi et al., 2009; Rosa et al., 2012). Thus, social learning propensity may be a combined result of cognitive ability and personality type. While these individual attributes are of valid investigation, I was unable to explore them in relation to social learning performance in the experiments conducted within this thesis due to time constraints that prevented multiple testing required to assess cognition and personality. Future work should however continue exploring whether certain individuals hold a phenotype prone to using social information determined by inherent cognitive ability and personality.

Identifying how individuals differ in their social information use and how this may change across an individual's lifetime will help understand how behaviours spread across stable, long term natural groups and indicate which individuals are more likely to adopt and transmit novel behaviours. Knowledge which may be further applied to fields of conservation (reviewed by Greggor, Thornton, & Clayton, 2017), animal welfare and animal management (Nicol, 2004). For instance, it has been suggested that social learning can be applied to assist in species reintroduction programmes where pre-released individuals can socially learn from informed individuals about species-appropriate behaviours, such as responses to novel predators (Brown & Laland, 2001; Griffin, 2004), feeding and migratory behaviours (Brown & Laland, 2001) and human-avoidance behaviours (Walters et al., 2010). As with enhancing the spread of beneficial behaviours, social learning can be applied to limit the spread of detrimental behaviours across groups. For instance, certain species have become reliant upon human produce, raiding crops and waste, creating human-wildlife conflicts in wild populations (Chiyo, Moss, & Alberts, 2012; Donaldson, Finn, Bejder, Lusseau, & Calver, 2012; Mazur & Seher, 2008; Schakner, Lunsford, Straley, Eguchi, & Mesnick, 2014). Other problematic behaviours arise within captive zoo or farmed populations, such as cannibalistic ‘feather pecking’ behaviour seen in domestic chickens which can spread throughout flocks through social learning (Nicol, 2004; Zeltner, Klein, & Huber-Eicher, 2000). If certain individuals or classes of individuals (e.g. young, subordinate, female) are identified as more likely to facilitate the spread of behaviours this may be utilised in promoting or retarding behavioural spread through introducing or removing certain individuals from a group.

7.3.2 Social structure and a need for complex models of social transmission

The influence that the social structure of a population has on social learning and behavioural transmission was explored in both chapters 3 and 4. Chapter 3 looked at how group size during task interaction influenced social learning and spread of behaviour across the whole population. The chapter described experiments which tracked the spread of a novel behaviour across 4 populations of 48 pheasant chicks, in which 2 populations interacted with the task in large group sizes and 2 populations in small group sizes. These 4 populations were hatched from a well-mixed pool of eggs and so were likely of low relatedness, were all of the same age, consisted of an equal sex ratio and were reared under identical conditions. Thus, I limited and controlled for other influential factors that might affect results. Chapter 4 looked at how social structure, specifically how modular the network is, influenced social transmission of a novel foraging behaviour. The behaviour spread was monitored across 6 populations of domestic chicks (totalling 152), where 2 populations had an enforced network of high modularity, 2 populations of low modularity and 2 control populations in which only asocial learning was possible. All 6 populations were of a similar size (N=24-27), consisted of an equal sex ratio and were the same breed, age, and were reared under identical conditions. Again, by controlling these social and environmental factors, I was able to focus specifically on the population level and be confident in how the manipulated social structure affected social transmission.

The experiments conducted in Chapter 3 and 4 are unique in that they directly manipulated social structure and did so in a way that limited and controlled for other influential factors. Although many theoretical models have predicted the importance and effects of social structure on social transmission, very few studies have empirically tested these assumptions (Cantor & Whitehead, 2013). Some studies have indirectly manipulated social structure through the addition of physical barriers (Webster et al., 2013) and directly manipulated in a random manner (Firth & Sheldon, 2015; Firth et al., 2016; Morrell et al., 2008), but to my knowledge, experiments conducted in Chapter 3 and 4 were the first to manipulate a specific aspect of social structure to observe its effect on social transmission.

The number of connections between individuals is predicted to influence behavioural spread - an individual is more likely to learn a novel behaviour if they have multiple connections to others within the group (Firth, 2019; Hoppitt, 2017; Kurvers et al., 2014). Chapter 3 investigated the effect of associate number on social learning and behavioural spread. The results of this experiment found that interacting with a novel foraging task in larger groups did not result in an increase in behavioural spread as predicted. Instead I found the behaviour to spread throughout the wider population at a similar rate and this suggests that total number of connections to informed individuals may not best predict social learning. I tested between two differing hypotheses of social transmission; one where social learning is relative to the total number of connections an individual has to informed associates and the other to the proportional number of connections to informed individuals. I found equal support for both these hypotheses indicating that more complex factors, including the proportion of connections to informed individuals, can also play a role in social learning and behavioural transmission. While simple contagions are similar to and built upon disease infection models (where the likelihood of becoming informed/infected increases with the number of connections to informed/infected others), complex contagions add a level of complexity to these models by considering additional factors that affect the learning and spread of new behaviours (Firth, 2019). Although the notion of complex contagions is more developed within models of human behavioural cascades (Centola, 2018; Guilbeault et al., 2018; Montanaria & Saberi, 2010), evidence and models within animal literature is lacking and much needed (Firth, 2019). However, support for complex contagion does come from a study that shows pigeons to be increasingly more likely to socially learn with increasing numbers of informed individuals and decreasing numbers of uninformed bystanders (Lefebvre & Giraldeau, 1994), which suggests the proportion of informed individuals that an animal is in contact with plays an important role. More recently, the behavioural cascade of evasive manoeuvres displayed by the schooling fish *Notemigonus crysoleucas* was shown to spread via a ‘fractional contagion’, which is based on the proportion of neighbours displaying the behaviour and where individuals can be more strongly influenced by fewer strongly connected neighbours performing evasive behaviour (Rosenthal et al., 2015). Chapter 3 further highlights the need for new animal research and models to consider complex models of transmission, considering the proportion of informed associates in additional to total connections during learning.

Chapter 4 also provides evidence of the importance of additional factors within the transmission process, supporting a more complex transmission process. In this experiment, the modularity of populations was manipulated to create either populations of high or low modularity and I tracked the spread of a novel behaviour across these networks. I found again, contrary to prediction, that behaviour did not travel faster in the populations of low modularity. This result does not follow theoretical models predicting that less structured networks (those with multiple homogenous connections between individuals) allow for behaviours to transmit faster. The lack of difference in behaviour spread between my high and low modular networks indicates that additional factors such as behavioural reinforcement and forgetting rates may be playing an important role when socially learning a behaviour. The importance of behavioural reinforcement was indeed showcased by the results in Chapter 2 demonstrating that (on an almost identical task) most individuals required multiple exposures before they learnt the novel foraging behaviour. Social structure will influence both the number of interactions (and so behavioural reinforcement) and time-periods between behavioural demonstrations (affecting forgetting rates) which will interact to affect the likelihood of adopting and forgetting novel behaviours. Thus, predictions that arise from models based on simple contagion assumptions may not be accurate if they do not consider the amount of (and timings between) demonstrations of behaviour. The unexpected results from Chapter 4 therefore again highlight the need for complex contagion models in animal literature that include these additional factors (such as behavioural reinforcement and forgetting rates) that likely influence learning and behavioural spread.

Empirically investigating how social structure influences behavioural spread will allow us an understanding of how certain behaviours may arise rapidly within certain groups and give rise to group traditions. By developing an experimental system in this thesis that controlled the associations between individuals during a social learning task, I could uniquely test the effect of certain network properties. I found that group size during interaction and modularity of the whole network, did not necessarily affect behavioural spread as predicted by theoretical models, thus highlighting the importance of other complex factors that influence social transmission. Other network properties have also been highlighted as key influencers of behavioural spread and would therefore be worth further investigation. For instance decreasing average path length is predicted to increase spread (Cantor & Whitehead, 2013; Voelkl & Noë, 2010) and so would be a logical step for future work to manipulate this parameter in order to test model predictions.

7.3.3 Social dynamics and learning mechanisms deployed

The influence that social dynamics, specifically the adoption of differing foraging strategies, can have for social transmission was explored in Chapter 5. This chapter tracked the spread of a novel foraging behaviour across 4 populations, each of 24 domestic chicks, exploring how the opportunity to scrounge food interacts with social learning and social transmission. One population experienced low scrounging opportunities whilst interacting with the foraging task while the other three populations experienced greater scrounging opportunities (through the provision of multiple mini-mealworm rewards within each well of the task apparatus). While previous experiments have successfully manipulated scrounging opportunities, they have found differing results in how scrounging affects social learning, and none have linked these effects to the type of social learning mechanism demonstrated. Therefore, to investigate the social learning mechanisms involved, I recorded all the solving techniques performed by every individual and trained the initial seeded demonstrator bird of each population to solve the task in a particular way. This would allow me to investigate whether the learners accurately copied the actions of the model or were simply more likely to interact with the apparatus. In two populations the seeded demonstrator solved the task by pushing the red side of the door, while the other two populations had demonstrators that solved the door by pushing the blue side of the door. As with previous experiments, all 4 populations were of the same breed, same group size, equal sex ratio and reared under identical physical conditions experiencing identical timelines of experimenting. Thus, I can be confident that the effects observed were as a result of manipulated scrounging opportunity.

I found social foraging dynamics to be very influential for behavioural spread in domestic chicks. When scrounging food was permitted during task interaction, the novel foraging behaviour spread rapidly across the population with the majority of birds having solved the task by the end of the experiment. Conversely, when scrounging opportunity was restricted (through providing a single food item reward when birds performed the solving behaviour), the solving behaviour did not spread across the population with only a few individuals having learnt it by the end of the experiment. I also found that the specific solving technique (pushing at the red or blue side) was not conserved across the group, with no bias shown by the group to what method the initial seeded demonstrator was trained on. Even when looking at the individual level, a bird’s first solving technique was not dependent upon the proportion of red to blue solves they had observed. This indicates that birds were not imitating the exact actions demonstrated to them or emulating actions to achieve the same end result, but rather learning through mechanisms such as local or stimulus enhancement where an increase in overall attention to the task apparatus likely led them to solve the task. Overall, my result differs from those studies finding scrounging to prevent social learning (Beauchamp & Kacelnik, 1991; Fragaszy & Visalberghi, 1989, 1990, Giraldeau & Lefebvre, 1986, 1987; Lefebvre & Helder, 1997; Nicol & Pope, 1994; Stammbach, 1988) and instead agrees with those finding the ability to scrounge food facilitates social learning (Caldwell & Whiten, 2003; Midford et al., 2000; Thornton & Malapert, 2009a). I reason that scrounging might influence social learning differently dependent on the social learning mechanism deployed. This may therefore explain the conflicting results obtained by previous studies into social learning and scrounging. Future research should therefore take this into consideration when designing social transmission experiments that permit or restrict scrounging from others.

Realising the effect scrounging has for social learning and thus social transmission will help further our understanding of how behaviours spread throughout groups. This knowledge can then be applied in experiments that wish to increase social transmission of behaviours and within fields that may utilise social learning for the transmission of certain beneficial behaviours. For instance, where individuals need to learn novel foraging behaviours or food preferences within species reintroduction/release programmes, then allowing scrounging to accompany social learning during preparatory training sessions may increase how quickly uninformed individuals adopt these behaviours. Given the substantial effects that social foraging dynamics can have for social learning and behavioural transmission, research should further investigate the effects of other social dynamics. For example, what influence do dominance hierarchies within animal groups have for social learning and behavioural spread? Chapter 2 highlighted that inherent dominant status may not affect social learning ability when opportunity for learning was experimentally controlled, but the role of dominance status in freely associating natural groupings in shaping opportunities for social learning and determining how novel behaviours spread through hierarchical structured groups remains largely unexplored.

7.3.4 Environment and social transmission

The environment an individual is living within can change the value of information and how it is acquired. It has been shown, both in theoretical models and empirical research, that individuals benefit from an increased reliance upon social information in an unpredictable or variable environment. For instance, bumblebees foraging on an array of artificial flowers that vary in reward quality will look more to where other bees are feeding compared to when the array is predictable in its rewards (Smolla et al., 2016). However, thus far studies have only tested social information reliance in relation to learning about the resource that have been varied. Chapter 6 explored how environmental predictability influences social information use and furthermore investigated whether an increased reliance on social information transfers over to other contexts. Two populations, each of 25 domestic chicks experienced differing predictability levels of the locations of rewarding feeders within their main living quarters. These populations were then presented with a novel foraging task in a location and context separate to that were their main food supplied was varied. Crucially, all aspects of the physical, social and testing environment were again equal across conditions except for the experimental manipulation varying the predictability of rewarded food locations.

Firstly, in accordance with theoretical models and previous empirical studies, I found some evidence for an increase in social information use in the population experiencing an unpredictable environment in locating the rewarding feeders. Although the median size of groups feeding together did not differ between conditions, those in the unpredictable environment would at times feed together in greater group sizes. It is possible that my manipulation of environment did not produce such obvious results as previous other studies, due to environmental predictability not varying enough or the costs not being large enough to produce observable differences in social information use. However, even with limited support it appears that increasing reliance upon social information when in an unpredictable environment is a commonly observed strategy exhibited by differing species. Second, I found no evidence that domestic chicks reared in the unpredictable environment relied more generally upon social information when learning about a different novel foraging behaviour in a separate location. While there is substantial evidence that animals will increase their reliance upon social information when in an unpredictable environment (Deygout et al., 2010; Jones et al., 2017; Rafacz & Templeton, 2003; Smolla et al., 2016; van Bergen et al., 2004; van der Post & Hogeweg, 2009) and evidence of bumblebees ‘learning to socially learn’ in that they increase their reliance on social information if it has previously proved beneficial (Dawson, Avarguès-Weber, Chittka, & Leadbeater, 2013), it appears this is still specific to a singular context. Animals may well vary their use of social and asocial information as appropriate to the specific conditions. For instance, when learning about resource location in a unpredictable environment, individuals may look more to the location where others are feeding, however this does not then mean they will deploy social learning as a general strategy to influence their predator responses or mate choice, unless these situations are themselves also unpredictable or variable.

Understanding how environmental conditions influence an individual's use of social information is key for predicting how socially learnt behaviours may spread across different environments and contexts. Studies thus far have explored how both the physical structuring of an environment and its level of variability or predictability can influence an individual's reliance on social information and the pathways of behavioural spread around a group. Understanding how features of the environment affect social transmission could refine how social learning is used as a tool for applied questions of conservation or animal management. For instance, the physical structuring of an environment may be adapted to reduce the social transmission of harmful behaviours in captive animals (such as feather pecking in domestic fowl) simply by the inclusion of barriers within enclosures. Likewise, manipulating the predictability of a novel resource can increase reliance upon social information when learning about that resource. If I had found a general increase in reliance upon social information following a manipulation of environmental predictability in a different context this could have been useful during programmes when individuals are socially learning species-appropriate behaviours. For example, increasing unpredictability in one context (e.g. food locations) could have then enhanced social learning of desirable behaviours from key demonstrator individuals in different contexts (such as learning predator identities). On a much broader, slower scale, social learning is considered important in enabling animals to adapt to human-induced environmental change such as habitat loss, climate change and exotic species (Tuomainen & Candolin, 2011). Some species appear to cope much better with environmental change, including changes in environmental predictability, than others and so it would be interesting to investigate where these species differ in their reliance upon social information, thus explaining some of this adaptability.

7.4 Generalisations and conclusions

Table 7.1 The effect different factors were found to have on social learning and transmission of behaviours tested within this thesis.

Factor	**Effect on social learning and transmission:**		
	Reducing	**No effect**	**Promoting**
Individual Individual attributes		Sex, Mass, Dominance Ranking, Social position (centrality) not related to likelihood or speed of social learning	
Social Group Size		Size of group interacting with the task did not affect behavioural spread	
Group Structure		Behavioural spread was not influenced by a population's modularity.	
Foraging dynamics			The opportunity to scrounge food during learning increased behavioural spread
Environment Environmental predictability		The learning of novel behaviours was not affected by the predictability of birds main living environment.	Evidence for an increase in social information use in the immediate context where the environment varied

Throughout this thesis I have explored factors that may influence the spread of socially learnt behaviours throughout a group. In order to understand the effects of different factors within this thesis, I devised controlled and replicated experiments that tested each of these factors in isolation (**Table 7.1**). This included investigating how certain attributes and characteristics of an individual might vary their likelihood of social learning, how social structure and social dynamics can influence social transmission of behaviours and finally how properties of the physical environment might affect reliance upon social information and thus behavioural spread. In natural settings these differing factors will all be acting in concert with one-another, with some likely exerting a greater influence than others. However, by studying factors in isolation via controlled experiments, I can be more confident about how each aspect affects social transmission and thus the results from these chapters allow for predictions to be made about how they may interact with one another and affect social transmission. For example, I found substantial inter-individual variation in speed of social learning (Chapter 2), and I also found scrounging to be essential for the spread of behaviour through the group (Chapter 5). It is therefore plausible that those individuals that can scrounge more in general, are more likely to acquire some socially learnt behaviours. Similarly, I found that the proportion of informed to uninformed individuals can contribute to the uptake of novel behaviours (Chapter 3). This proportion is a product of the social structure of the group, arising from associations and interactions between group members. For instance, I may expect to see differing phase-change points within clusters (in more modular networks) when the action of a few individuals provoke a switch in the majority of individuals from being uninformed to informed. Additionally, certain factors may be estimated to have been of importance when considering the spread of known socially learnt behaviours. For example, we may guess that scrounging, in the form of obtaining cream from previously opened milk bottle tops, might have played a vital role in allowing the piercing behaviour to spread across bird populations in the 20th century.

The experimental approach that I have taken in this thesis has permitted me to test some general predictions about factors shaping the use of social information and its spread around groups. However, the strength of my experimental and replicated approach is offset by the fact that it is a non-natural, model system and it is important to acknowledge that all the experiments were conducted on young pheasants and domestic chicks, providing them with a relatively simple food-extractive task. Therefore, it is important to recognise the limits to generalising my specific findings to all socially learnt behaviours across all species. Despite this caveat, my results illustrate and reveal some basic properties of the social and physical environment and allow for some pre-existing general assumptions about what shapes social learning to be challenged. Using a simple extractive-foraging task I found evidence that suggest that we should consider additional factors within transmission models, such as the proportion of informed to uninformed individuals, behavioural reinforcement and forgetting rates. While behavioural reinforcement appears to have been required in the task that I used, the amount of reinforcement will almost certainly vary dependent on the form and complexity of behaviour being transmitted and the cognitive capabilities of the species. I expect that some behaviours may follow standard simple contagion rules while other factors such as social reinforcement, forgetting rates and the number of informed individuals displaying a behaviour will play a larger role. Similarly, how a behaviour is acquired may dictate the influence these factors have. The definition of 'social learning' encompasses a large range of how behaviours are acquired and thus my results derived from one form of socially learnt behaviour do not necessarily apply to all. For instance, scrounging may well enhance the spread of some socially learnt behaviours, especially those involving food extraction from fixed locations, but it may also limit the spread of more complex behaviours, such as tool use and multi-stepped foraging behaviours, that are acquired through differing learning mechanisms. Indeed, it has been shown that animals will use social information differently depending on type of behaviour that is being practiced, with social learning assumed to be more heavily relied upon when learning about complex or risky behaviours (Boyd & Richerson, 1985, 1988; Day et al., 2003; Kendal et al., 2009; McElreath et al., 2005). Accumulating knowledge of how differing factors may act on a population will provide us with further understanding of how behaviours can spread throughout a group. This knowledge may then be applied to help aid or restrict the spread of certain behaviours and is crucial for understanding how group-level behaviours become traditions that underpin culture and create biodiversity among species.

References

Abbott, D. H., Keverne, E. B., Bercovitch, F. B., Shively, C. A., Mendoza, S. P., Saltzman, W., … Sapolsky, R. M. (2003). Are subordinates always stressed? A comparative analysis of rank differences in cortisol levels among primates. *Hormones and Behavior*, *43*(1), 67–82. https://doi.org/10.1016/S0018-506X(02)00037-5

Afshar, M., & Giraldeau, L.-A. (2014). A unified modelling approach for producer–scrounger games in complex ecological conditions. *Animal Behaviour*, *96*, 167–176. https://doi.org/10.1016/j.anbehav.2014.07.022

Allen, J., Weinrich, M., Hoppitt, W., & Rendell, L. (2013). Network-Based Diffusion Analysis Reveals Cultural Transmission of Lobtail Feeding in Humpback Whales, (April), 485–488.

Aplin, L. M., Farine, D. R., Morand-Ferron, J., Cockburn, A., Thornton, A., & Sheldon, B. C. (2015). Experimentally induced innovations lead to persistent culture via conformity in wild birds. *Nature*, *518*(7540), 538–41. https://doi.org/10.1038/nature13998

Aplin, L. M., Farine, D. R., Morand-Ferron, J., Cole, E. F., Cockburn, A., & Sheldon, B. C. (2013). Individual personalities predict social behaviour in wild networks of great tits (Parus major). *Ecology Letters*, *16*(11), 1365–1372. https://doi.org/10.1111/ele.12181

Aplin, L. M., Farine, D. R., Morand-Ferron, J., & Sheldon, B. C. (2012). Social networks predict patch discovery in a wild population of songbirds. *Proceedings. Biological Sciences / The Royal Society*, *279*(1745), 4199–205. https://doi.org/10.1098/rspb.2012.1591

Aplin, L. M., Firth, J. A., Farine, D. R., Voelkl, B., Crates, R. A., Culina, A., … Sheldon, B. C. (2015). Consistent individual differences in the social phenotypes of wild great tits, Parus major. *Animal Behaviour*, *108*, 117–127. https://doi.org/10.1016/J.ANBEHAV.2015.07.016

Aplin, L. M., & Morand-Ferron, J. (2017). Stable producer–scrounger dynamics in wild birds: sociability and learning speed covary with scrounging behaviour. *Proceedings of the Royal Society of London B: Biological Sciences*, *284*(1852).

Aplin, L. M., Sheldon, B. C., & McElreath, R. (2017). Conformity does not perpetuate suboptimal traditions in a wild population of songbirds. *Proceedings of the National Academy of Sciences of the United States of America*, *114*(30), 7830–7837. https://doi.org/10.1073/pnas.1621067114

Aplin, L. M., Sheldon, B. C., & Morand-Ferron, J. (2013). Milk bottles revisited: Social learning and individual variation in the blue tit, Cyanistes caeruleus. *Animal Behaviour*, *85*(6), 1225–1232. https://doi.org/10.1016/j.anbehav.2013.03.009

Appleby, M. C., Mench, J. A., & Hughes, B. O. (2004). *Poultry behvaiour and welfare*. Cambridge: CABI Publishing.

Ashton, B. J., Ridley, A. R., Edwards, E. K., & Thornton, A. (2018). Cognitive performance is linked to group size and affects fitness in Australian magpies. *Nature*, *554*(7692), 364–367. https://doi.org/10.1038/nature25503

Ashton, B. J., Thornton, A., & Ridley, A. R. (2019). Larger group sizes facilitate the emergence and spread of innovations in a group-living bird. *Animal Behaviour*, *158*, 1–7. https://doi.org/10.1016/j.anbehav.2019.10.004

Atton, N., Hoppitt, W., Webster, M. M., Galef, B. G., & Laland, K. N. (2012). Information flow through threespine stickleback networks without social transmission. *Proceedings. Biological Sciences / The Royal Society*, *279*(1745), 4272–8. https://doi.org/10.1098/rspb.2012.1462

Barnard, C. J., & Sibly, R. M. (1981). Producers and scroungers: A general model and its application to captive flocks of house sparrows. *Animal Behaviour*, *29*(2), 543–550. https://doi.org/10.1016/S0003-3472(81)80117-0

Barrett, B. J., McElreath, R. L., & Perry, S. E. (2017). Pay-off-biased social learning underlies the diffusion of novel extractive foraging traditions in a wild primate. *Proceedings. Biological Sciences*, *284*(1856). https://doi.org/10.1098/rspb.2017.0358

Bates, D., Maechler, M., Bolker, B., & Walker, S. (2015). Fitting Linear Mixed-Effects Models Using lme4. *Journal of Statistical Software*, *67*(1), 1–48. https://doi.org/10.18637/jss.v067.i01

Beauchamp, G. (2001). Should vigilance always decrease with group size? *Behavioral Ecology and Sociobiology*, *51*(1), 47–52. https://doi.org/10.1007/s002650100413

Beauchamp, G., & Kacelnik, A. (1991). Effects of the knowledge of partners on learning rates in zebra finches Taeniopygia guttata. *Animal Behaviour*, *41*(2), 247–253. https://doi.org/10.1016/S0003-3472(05)80476-2

Beck, M., & Galef, B. G. (1989). Social influences on the selection of a protein-sufficient diet by Norway rats (*Rattus norvegicus*). *Journal of Comparative Psychology*, *103*(2), 132–139. https://doi.org/10.1037/0735-7036.103.2.132

Biondi, L. M., García, G. O., Bó, M. S., & Vassallo, A. I. (2010). Social learning in the caracara chimango, milvago chimango (aves: Falconiformes): An age comparison. *Ethology*, *116*(8), 722–735. https://doi.org/10.1111/j.1439-0310.2010.01794.x

Boogert, N. J., Anderson, R. C., Peters, S., Searcy, W. A., & Nowicki, S. (2011). Song repertoire size in male song sparrows correlates with detour reaching, but not with other cognitive measures. *Animal Behaviour*, *81*(6), 1209–1216. https://doi.org/10.1016/j.anbehav.2011.03.004

Boogert, N. J., Giraldeau, L. A., & Lefebvre, L. (2008). Song complexity correlates with learning ability in zebra finch males. *Animal Behaviour*, *76*(5), 1735–1741. https://doi.org/10.1016/j.anbehav.2008.08.009

Boogert, N. J., Zimmer, C., & Spencer, K. A. (2013). Pre- and post-natal stress have opposing effects on social information use. *Biology Letters*, *9*(2), 20121088. https://doi.org/10.1098/rsbl.2012.1088

Bouchard, J., Goodyer, W., & Lefebvre, L. (2007). Social learning and innovation are positively correlated in pigeons (Columba livia). *Animal Cognition*, *10*(2), 259–66. https://doi.org/10.1007/s10071-006-0064-1

Boyd, R., & Richerson, P. J. (1985). *Culture and the Evolutionary Process* (Vol. 175). https://doi.org/10.1097/00005053-198702000-00018

Boyd, R., & Richerson, P. J. (1988). An evolutionary model of social learning: the effects of spatial and temporal variation. In T. R. Zentall & B. G. Galef (Eds.), *Social learning Psychological and Biological Perspectives* (pp. 29–48). Hillsdale, New Jersey: Lawrence Erlbaum Associates.

Boyd, R., & Richerson, P. J. (1995). Why does culture increase human adaptability? *Ethology and Sociobiology*, *16*(2), 125–143. https://doi.org/10.1016/0162-3095(94)00073-G

Bradshaw, R. H. (1991). Discrimination of group members by laying hens Gallus domesticus. *Behavioural Processes*, *24*(2), 143–151. https://doi.org/10.1016/0376-6357(91)90006-L

Bradshaw, R. H. (1992). Conspecific discrimination and social preference in the laying hen. *Applied Animal Behaviour Science*, *33*(1), 69–75. https://doi.org/10.1016/S0168-1591(05)80086-3

Brockman, J. H., & Barnard, C. J. (1979). Kleptoparasitism in birds. *Animal Behaviour*, *27*, 487–514.

Broom, M., & Ruxton, G. D. (1998). Evolutionarily stable stealing: game theory applied to kleptoparasitism. *Behavioral Ecology*, *9*(4), 397–403. https://doi.org/10.1093/beheco/9.4.397

Brown, C., & Laland, K. (2001). Social learning and life skills training for hatchery reared fish. *Journal of Fish Biology*, *59*(3), 471–493. https://doi.org/10.1111/j.1095-8649.2001.tb02354.x

Buchanan, K. L., Spencer, K. A., Goldsmith, A. R., & Catchpole, C. K. (2003). Song as an honest signal of past developmental stress in the European starling (Sturnus vulgaris). *Proceedings of the Royal Society B: Biological Sciences*, *270*(1520), 1149–1156. https://doi.org/10.1098/rspb.2003.2330

Burkart, J. M., Strasser, A., & Foglia, M. (2009). Trade-offs between social learning and individual innovativeness in common marmosets, Callithrix jacchus. *Animal Behaviour*, *77*(5), 1291–1301. https://doi.org/10.1016/j.anbehav.2009.02.006

Burnham, K. P., & Anderson, D. R. (2002). *Model Selection and Multimodel Inference: A Practical Information-Theoretic Approach* (2nd ed.). New York: Springer.

Burnham, K. P., & Anderson, D. R. (2004). Multimodel Inference. *Sociological Methods & Research*, *33*(2), 261–304. https://doi.org/10.1177/0049124104268644

Butcher, S. H. (1922). *The Poetics of Aristotle - Edited with Critical Notes and a Translation*. London: Macmillan and Co., Limited.

Byrne, R. W., & Russon, A. E. (1998). Learning by imitation: A hierarchical approach. *Behavioral and Brain Sciences*, *21*(05), 667–721. https://doi.org/10.1017/S0140525X98001745

Caldwell, C. A., & Whiten, A. (2003). Scrounging facilitates social learning in common marmosets, Callithrix jacchus. *Animal Behaviour*, *65*(6), 1085–1092. https://doi.org/10.1006/anbe.2003.2145

Campbell, E., & Salathé, M. (2013). Complex social contagion makes networks more vulnerable to disease outbreaks. *Scientific Reports*, *3*, 1–6. https://doi.org/10.1038/srep01905

Cantor, M., & Whitehead, H. (2013a). The interplay between social networks and culture : theoretically and among whales and dolphins The interplay between social networks and culture : theoretically and among whales and dolphins. *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences*, *368*(April), 1–10. https://doi.org/10.1098/rstb.2012.0340

Cantor, M., & Whitehead, H. (2013b). The interplay between social networks and culture: theoretically and among whales and dolphins. *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences*, *368*(1618), 20120340. https://doi.org/10.1098/rstb.2012.0340

Caraco, T., & Giraldea, L. A. (1991). Social foraging: Producing and scrounging in a stochastic environment. *Journal of Theoretical Biology*, *153*(4), 559–583. https://doi.org/10.1016/S0022-5193(05)80156-0

Carter, A. J., Marshall, H. H., Heinsohn, R., & Cowlishaw, G. (2014a). Personality predicts the propensity for social learning in a wild primate. *PeerJ*, *2*, e283. https://doi.org/10.7717/peerj.283

Carter, A. J., Marshall, H. H., Heinsohn, R., & Cowlishaw, G. (2014b). Personality predicts the propensity for social learning in a wild primate. *PeerJ*, *2*, e283. https://doi.org/10.7717/peerj.283

Catchpole, C. K., & Slater, P. J. B. (1995). *Bird Song: Biological Themes and Variations*. Cambridge: Cambridge University Press.

Centola, D. (2010). The spread of behavior in an online social network experiment. *Science (New York, N.Y.)*, *329*(5996), 1194–7. https://doi.org/10.1126/science.1185231

Centola, D. (2018). *How behavior spreads: The science of complex contagions*. Princeton University Press.

Chase, I. D., & Seitz, K. (2011). Self-structuring properties of dominance hierarchies. A new perspective. In *Advances in Genetics* (Vol. 75, pp. 51–81). Academic Press Inc. https://doi.org/10.1016/B978-0-12-380858-5.00001-0

Chase, I. D., Tovey, C., Spangler-Martin, D., & Manfredonia, M. (2002). *Individual differences versus social dynamics in the formation of animal dominance hierarchies*. *PNAS April* (Vol. 16).

Chiyo, P. I., Moss, C. J., & Alberts, S. C. (2012). The Influence of Life History Milestones and Association Networks on Crop-Raiding Behavior in Male African Elephants. *PLoS ONE*, *7*(2), e31382. https://doi.org/10.1371/journal.pone.0031382

Chou, L.-S., & Richerson, P. J. (1992). Multiple models in social transmission of food selection by Norway rats, Rattus norvegicus. *Animal Behaviour*, *44*, 337–343. https://doi.org/10.1016/0003-3472(92)90039-C

Claidière, N., Messer, E. J. E., Hoppitt, W., & Whiten, A. (2013). Diffusion dynamics of socially learned foraging techniques in squirrel monkeys. *Current Biology*, *23*(13), 1251–1255. https://doi.org/10.1016/j.cub.2013.05.036

Clark, C. W., & Mangel, M. (1984). Foraging and flocking strategies: information in an uncertain environment. *American Naturalist*, *123*(5), 626–641. https://doi.org/10.1086/284228

Clark, C. W., & Mangel, M. (1986). The Evolutionary Advantages of Group Foraging, *30*, 45–75.

Coolen, I. (2002). Increasing foraging group size increases scrounger use and reduces searching efficiency in nutmeg mannikins (Lonchura punctulata). *Behavioral Ecology and Sociobiology*, *52*(3), 232–238. https://doi.org/10.1007/s00265-002-0500-4

Coussi-Korbel, S., & Fragaszy, D. M. (1995a). On the relation between social dynamics and social learning. *Animal Behaviour*, *50*(6), 1441–1453. https://doi.org/10.1016/0003-3472(95)80001-8

Coussi-Korbel, S., & Fragaszy, D. M. (1995b). On the relation between social dynamics and social learning. *Animal Behaviour*, *50*(6), 1441–1453. https://doi.org/10.1016/0003-3472(95)80001-8

Coussi-Korbel, S., & Fragaszy, D. M. (1995c). On the relation between social dynamics and social learning. *Animal Behaviour*, *50*(6), 1441–1453. https://doi.org/10.1016/0003-3472(95)80001-8

Croft, D. P., James, R., & Krause, J. (2008). *Exploring Animal Social Networks*. Princeton, New Jersey: Princeton University Press.

Croft, D. P., James, R., Ward, A. J. W., Botham, M. S., Mawdsley, D., & Krause, J. (2005). Assortative interactions and social networks in fish. *Oecologia*, *143*(2), 211–219. https://doi.org/10.1007/s00442-004-1796-8

Curio, E. (1988). Cultural transmission of enemy recognition by birds. In C. M. Heyes & B. G. Galef (Eds.), *Social Learning in Animals: The Roots of Culture* (pp. 75–97). San Diego: Academic Press.

D'Eath, R. B., & Stone, R. J. (1999). Chickens use visual cues in social discrimination: An experiment with coloured lighting. *Applied Animal Behaviour Science*, *62*(2–3), 233–242. https://doi.org/10.1016/S0168-1591(98)00216-0

Dall, S. R. X., Giraldeau, L.-A., Olsson, O., McNamara, J. M., & Stephens, D. W. (2005). Information and its use by animals in evolutionary ecology. *Trends in Ecology & Evolution*, *20*(4), 187–93. https://doi.org/10.1016/j.tree.2005.01.010

Dall, S. R. X., Houston, A. I., & McNamara, J. M. (2004). The behavioural ecology of personality: Consistent individual differences from an adaptive perspective. *Ecology Letters*.

https://doi.org/10.1111/j.1461-0248.2004.00618.x

Danchin, E., Giraldeau, L. A., Valone, T. J., & Wagner, R. H. (2004). Public Information: From Nosy Neighbours to Cultural Evolution. *American Association for the Advancement of Science*, *305*(5683), 487–491. https://doi.org/10.1126/science.1098254

Davies, N. B., & Welbergen, J. A. (2009). Social transmission of a host defense against cuckoo parasitism. *Science (New York, N.Y.)*, *324*(5932), 1318–20. https://doi.org/10.1126/science.1172227

Dawson, E. H., Avarguès-Weber, A., Chittka, L., & Leadbeater, E. (2013a). Learning by observation emerges from simple associations in an insect model. *Current Biology : CB*, *23*(8), 727–30. https://doi.org/10.1016/j.cub.2013.03.035

Dawson, E. H., Avarguès-Weber, A., Chittka, L., & Leadbeater, E. (2013b). Learning by observation emerges from simple associations in an insect model. *Current Biology*, *23*(8), 727–730. https://doi.org/10.1016/j.cub.2013.03.035

Day, R. L., Coe, R. L., Kendal, J. R., & Laland, K. N. (2003). Neophilia, innovation and social learning: a study of intergeneric differences in callitrichid monkeys. *Animal Behaviour*, *65*(3), 559–571. https://doi.org/10.1006/anbe.2003.2074

Day, R. L., MacDonald, T., Brown, C., Laland, K. N., & Reader, S. M. (2001a). Interactions between shoal size and conformity in guppy social foraging. *Animal Behaviour*, *62*(5), 917–925. https://doi.org/10.1006/anbe.2001.1820

Day, R. L., MacDonald, T., Brown, C., Laland, K. N., & Reader, S. M. (2001b). Interactions between shoal size and conformity in guppy social foraging. *Animal Behaviour*. https://doi.org/10.1006/anbe.2001.1820

Deygout, C., Gault, A., Duriez, O., Sarrazin, F., & Bessa-Gomes, C. (2010). Impact of food predictability on social facilitation by foraging scavengers. *Behavioral Ecology*, *21*(6), 1131–1139. https://doi.org/10.1093/beheco/arq120

Donaldson, R., Finn, H., Bejder, L., Lusseau, D., & Calver, M. (2012). The social side of human-wildlife interaction: wildlife can learn harmful behaviours from each other. *Animal Conservation*, *15*(5), 427–435. https://doi.org/10.1111/j.1469-1795.2012.00548.x

Duffy, G. A., Pike, T. W., & Laland, K. N. (2009). Size-dependent directed social learning in nine-spined sticklebacks. *Animal Behaviour*, *78*(2), 371–375. https://doi.org/10.1016/J.ANBEHAV.2009.05.015

Dugatkin, L. A., & Godin, J. G. J. (1993). Female mate copying in the guppy {poecilia reticulata): Age-dependent effects. *Behavioral Ecology*, *4*(4), 289–292. https://doi.org/10.1093/beheco/4.4.289

Dumke, M., Herberstein, M. E., & Schneider, J. M. (2016). Producers and scroungers: feeding-type composition changes with group size in a socially foraging spider. *Proceedings. Biological Sciences / The Royal Society*, *283*(1828), 20160114-. https://doi.org/10.1098/rspb.2016.0114

Dunlap, A. S., Nielsen, M. E., Dornhaus, A., & Papaj, D. R. (2016). Foraging Bumble Bees Weigh the Reliability of Personal and Social Information. *Current Biology*, *26*(9), 1195–1199. https://doi.org/10.1016/j.cub.2016.03.009

Evans, C. S., & Evans, L. (1999). Chicken food calls are functionally referential. *Animal Behaviour*, *58*(2), 307–319. https://doi.org/10.1006/anbe.1999.1143

Evans, C. S., Evans, L., & Marler, P. (1993). On the meaning of alarm calls: functional reference in an avian vocal system. *Animal Behaviour*, *46*(1), 23–38. https://doi.org/10.1006/anbe.1993.1158

Farine, D. R. (2013). Animal social network inference and permutations for ecologists in R using *asnipe*. *Methods in Ecology and Evolution*, *4*(12), 1187–1194. https://doi.org/10.1111/2041-210X.12121

Farine, D. R. (2014). Measuring phenotypic assortment in animal social networks: Weighted associations are more robust than binary edges. *Animal Behaviour*, *89*, 141–153. https://doi.org/10.1016/j.anbehav.2014.01.001

Farine, D. R., Aplin, L. M., Sheldon, B. C., & Hoppitt, W. (2015). Interspecific social networks promote information transmission in wild songbirds. *Proceedings. Biological Sciences / The Royal Society*, *282*(1803), 20142804. https://doi.org/10.1098/rspb.2014.2804

Feldman, M. W., Aoki, K., & Kumm, J. (1996). Individual versus social learning: Evolutionary analysis in a fluctuating environment. *Anthropological Science*, *104*(3), 209–323.

Firth, J. A. (2019). Considering complexity: animal social networks and behavioural contagions. *Trends in Ecology and Evolution*, *xx*(xx), 1–4. https://doi.org/10.1016/j.tree.2019.10.009

Firth, J. A. (2020). Considering Complexity: Animal Social Networks and Behavioural Contagions. *Trends in Ecology and Evolution*, *35*(2), 100–104. https://doi.org/10.1016/j.tree.2019.10.009

Firth, J. A., & Sheldon, B. C. (2015). Experimental manipulation of avian social structure reveals segregation is carried over across contexts. *Proceedings of the Royal Society B: Biological Sciences*, *282*(1802). https://doi.org/10.1098/rspb.2014.2350

Firth, J. A., Sheldon, B. C., & Farine, D. R. (2016). Pathways of information transmission among wild songbirds follow experimentally imposed changes in social foraging structure. *Biology Letters*, *12*(6), 20160144. https://doi.org/10.1098/rsbl.2016.0144

Flack, J. C., Girvan, M., De Waal, F. B. M., & Krakauer, D. C. (2006). Policing stabilizes construction of social niches in primates. *Nature*, *439*(7075), 426–429. https://doi.org/10.1038/nature04326

Food and Agriculture Organization of the United Nations. (2020). FAOSTAT.

Forsman, J. T., & Seppänen, J. T. (2011). Learning what (not) to do: Testing rejection and copying of simulated heterospecific behavioural traits. *Animal Behaviour*, *81*(4), 879–883. https://doi.org/10.1016/j.anbehav.2011.01.029

Foucaud, J., Philippe, A.-S., Moreno, C., & Mery, F. (2013). A genetic polymorphism affecting reliance on personal versus public information in a spatial learning task in Drosophila melanogaster. *Proceedings of the Royal Society of London B: Biological Sciences*, *280*(1760), 20130588.

Fragaszy, D. M., & Visalberghi, E. (1989). Social Influences on the Acquisition of Tool-Using Behaviors in Tufted Capuchin Monkeys (Cebus apella). *Journal of Comparative Psychology*, *103*(2), 159–170. https://doi.org/10.1037/0735-7036.103.2.159

Fragaszy, D. M., & Visalberghi, E. (1990). Social processes affecting the appearance of innovative behaviors in capuchin monkeys. *Folia Primatologica*, *54*(3–4), 155–165. https://doi.org/10.1159/000156439

Franks, V. R., & Thorogood, R. (2018). Older and wiser? Age differences in foraging and learning by an endangered passerine. *Behavioural Processes*, *148*(August 2017), 1–9. https://doi.org/10.1016/j.beproc.2017.12.009

Franz, M., & Nunn, C. L. (2009). Network-based diffusion analysis: a new method for detecting social learning. *Proceedings. Biological Sciences / The Royal Society*, *276*(1663), 1829–36. https://doi.org/10.1098/rspb.2008.1824

Fritz, J., & Kotrschal, K. (1999). Social learning in common ravens, *Corvus corax*. *Animal Behaviour*, *57*(4), 785–793. https://doi.org/10.1006/anbe.1998.1035

Gajdon, G. K., Mundwiler, B., & Stauffacher, M. (2015). Development of early foraging behaviour of domestic chicks in varying social contexts. *Applied Animal Behaviour Science*, *164*, 29–40. https://doi.org/10.1016/j.applanim.2014.08.012

Galef, B. G. (2009). Chapter 4 Strategies for Social Learning (pp. 117–151).

https://doi.org/10.1016/S0065-3454(09)39004-X

Galef, B. G., Dudley, K. E., & Whiskin, E. E. (2008). Social learning of food preferences in ‘dissatisfied’ and ‘uncertain’ Norway rats. *Animal Behaviour*, *75*(2), 631–637. https://doi.org/10.1016/j.anbehav.2007.06.024

Galef, B. G., & Giraldeau, L.-A. (2001). Social influences on foraging in vertebrates: causal mechanisms and adaptive functions. *Animal Behaviour*, *61*(1), 3–15. https://doi.org/10.1006/anbe.2000.1557

Galef, B. G., & Laland, K. N. (2005). Social Learning in Animals: Empirical Studies and Theoretical Models. *BioScience*, *55*(6), 489. https://doi.org/10.1641/0006-3568(2005)055[0489:SLIAES]2.0.CO;2

Galef Jr., B. G. (1988). Imitation in animals: history, definition, and interpretation of data from the psychological laboratory. In *Social Learning: Psychological and Biological Perspectives* (pp. 3–28).

Gastwirth, J. L., Gel, Y. R., Wallace Hui, W. L., Lyubchick, V., Miao, W., & Noguchi, K. (2019). lawstat: Tools for Biostatistics, Public Policy, and Law.

Gelman, A. (2008). Scaling regression inputs by dividing by two standard deviations. *Statistics in Medicine*, *27*(15), 2865–2873. https://doi.org/10.1002/sim.3107

Gelman, A., Su, Y.-S., Yajama, M., Hill, J., Pittau, M. G., Kerman, J., … Dorie, V. (2018). arm: Data Analysis Using Regression and Multilevel/Hierarchical Models.

Gilman, R. T., Johnson, F., & Smolla, M. (2020). Competition for resources can promote the divergence of social learning phenotypes. *Proc. R. Soc. B*, *287*.

Giraldeau, L. A. (1984). Group Foraging : The Skill Pool Effect and Frequency-Dependent Learning. *The American Naturalist*, *124*(1), 72–79.

Giraldeau, L. A., & Beauchamp, G. (1999). Optimal Joining Policy, *14*(3), 102–106.

Giraldeau, L. A., & Caraco, T. (2000). *Social Foraging Theory*. Princeton, New Jersey: Princeton University Press.

Giraldeau, L. A., & Dubois, F. (2008). Chapter 2 Social Foraging and the Study of Exploitative Behavior. *Advances in the Study of Behavior*, *38*(08), 59–104. https://doi.org/10.1016/S0065-3454(08)00002-8

Giraldeau, L. A., & Lefebvre, L. (1986). Exchangeable producer and scrounger roles in a captive flock of feral pigeons: a case for the skill pool effect. *Animal Behaviour*, *34*(3), 797–803. https://doi.org/10.1016/S0003-3472(86)80064-1

Giraldeau, L. A., & Lefebvre, L. (1987a). Scrounging prevents cultural transmission of food-finding behaviour in pigeons. *Animal Behaviour*, *35*(2), 387–394. https://doi.org/10.1016/S0003-3472(87)80262-2

Giraldeau, L. A., & Lefebvre, L. (1987b). Scrounging prevents cultural transmission of food-finding behaviour in pigeons. *Animal Behaviour*, *35*(2), 387–394. https://doi.org/10.1016/S0003-3472(87)80262-2

Giraldeau, L. A., & Templeton, J. (1991). Food Scrounging and Diffusion of Foraging Skills in Pigeons, Columba livia: The Importance of Tutor and Observer Rewards. *Ethology*, *89*(1), 63–72. https://doi.org/10.1111/j.1439-0310.1991.tb00293.x

Giraldeau, L. A., Valone, T. J., & Templeton, J. J. (2002). Potential disadvantages of using socially acquired information. *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences*, *357*(1427), 1559–66. https://doi.org/10.1098/rstb.2002.1065

Greenberg, R. (2012). The Role of Neophobia and Neophilia in the Development of Innovative Behaviour of Birds. In *Animal Innovation*. https://doi.org/10.1093/acprof:oso/9780198526223.003.0008

Greggor, A. L., Thornton, A., & Clayton, N. S. (2017). Harnessing learning biases is essential for applying social learning in conservation. *Behavioral Ecology and Sociobiology*. https://doi.org/10.1007/s00265-016-2238-4

Griffin, A. S. (2004). Social learning about predators: a review and prospectus. *Animal Learning & Behavior*, *32*(1), 131–140. https://doi.org/10.3758/BF03196014

Grüter, C., Czaczkes, T. J., & Ratnieks, F. L. W. (2011). Decision making in ant foragers (Lasius niger) facing conflicting private and social information. *Behavioral Ecology and Sociobiology*, *65*(2), 141–148. https://doi.org/10.1007/s00265-010-1020-2

Guhl, A. M. (1958). The development of social organisation in the domestic chick. *Animal Behaviour*, *6*(1–2), 92–111. https://doi.org/10.1016/0003-3472(58)90016-2

Guilbeault, D., Becker, J., & Centola, D. (2018). Complex contagions: a decade in review. In S. Lehmann & Y. Y. Ahn (Eds.), *Complex SPreading Phenomena in Social Systems* (pp. 3–25). Springer.

Heyes, C. M. (1994). Social learning in animals: categories and mechanisms. *Biological Reviews of the Cambridge Philosophical Society*, *69*(2), 207–31.

Heyes, C. M., & Galef Jr., B. G. (1996). *Social Learning in Animals: The Roots of Culture*. *Developmental Biology* (Vol. 43). https://doi.org/10.1017/CBO9781107415324.004

Hinde, R. A., & Fisher, J. (1951). Further observations on the opening of milk bottles by birds. *British Birds*, *44*(12), 393–396. https://doi.org/10.1038/1691006a0

Hobaiter, C., Poisot, T., Zuberbühler, K., Hoppitt, W., & Gruber, T. (2014). Social network analysis shows direct evidence for social transmission of tool use in wild chimpanzees. *PLoS Biology*, *12*(9), e1001960. https://doi.org/10.1371/journal.pbio.1001960

Hogue, M. E., Beaugrand, J. P., & Laguë, P. C. (1996). Coherent use of information by hens observing their former dominant defeating or being defeated by a stranger. *Behavioural Processes*, *38*(3), 241–252. https://doi.org/10.1016/S0376-6357(96)00035-6

Hoppitt, W. (2017). The conceptual foundations of network-based diffusion analysis: choosing networks and interpreting results. *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences*, *372*(1735), 20160418. https://doi.org/10.1098/rstb.2016.0418

Hoppitt, W., Boogert, N. J., & Laland, K. N. (2010). Detecting social transmission in networks. *Journal of Theoretical Biology*, *263*(4), 544–55. https://doi.org/10.1016/j.jtbi.2010.01.004

Hoppitt, W., & Laland, K. N. (2013). *Social learning: An introduction to mechanisms, methods, and models*. Princeton University Press.

Hoppitt, W., Photopoulou, T., Hasenjaer, M., & Leadbeater, E. (2020). NBDA: A Package For Implementing Network-Based Diffusion Analysis.

Horner, V., Proctor, D., Bonnie, K. E., Whiten, A., & de Waal, F. B. M. (2010). Prestige affects cultural learning in chimpanzees. *PLoS ONE*, *5*(5), 1–5. https://doi.org/10.1371/journal.pone.0010625

Huffman, M. A. (1996). Acquisition of Innovative Cultural Behaviors in Nonhuman Primates: A Case Study of Stone Handling, a Socially Transmitted Behavior in Japanese Macaques. In H. C. M & Galef Jr B. G (Eds.), *Social Learning in Animals* (pp. 267–289). London: Elsevier. https://doi.org/10.1016/b978-012273965-1/50014-5

Ikeda, Y., Hasegawa, T., & Nemoto, K. (2010). Cascade dynamics on clustered network. *Journal of Physics: Conference Series*, *221*(1), 012005. https://doi.org/10.1088/1742-6596/221/1/012005

Jacoby, D. M. P., Fear, L. N., Sims, D. W., & Croft, D. P. (2014). Shark personalities? Repeatability of social network traits in a widely distributed predatory fish. *Behavioral Ecology and Sociobiology*, *68*(12), 1995–2003. https://doi.org/10.1007/s00265-014-1805-9

Johnston, A. N. ., Burne, T. H. ., & Rose, S. P. . (1998). Observation learning in day-old chicks using a one-trial passive avoidance learning paradigm. *Animal Behaviour*, *56*(6), 1347–1353. https://doi.org/10.1006/anbe.1998.0901

Jones, C. M., Braithwaite, V. A., & Healy, S. D. (2003). The evolution of sex differences in spatial ability. *Behavioral Neuroscience*, *117*(3), 403–411. https://doi.org/10.1037/0735-7044.117.3.403

Jones, T. B., Aplin, L. M., Devost, I., & Morand-Ferron, J. (2017). Individual and ecological determinants of social information transmission in the wild. *Animal Behaviour*, *129*, 93–101. https://doi.org/10.1016/j.anbehav.2017.05.011

Kappeler, P. M. (1987). The acquisition process of a novel behavior pattern in a group of ring-tailed lemurs (Lemur catta). *Primates*, *28*(2), 225–228. https://doi.org/10.1007/BF02382571

Katsnelson, E., Motro, U., Feldman, M. W., & Lotem, A. (2008). Early experience affects producer-scrounger foraging tendencies in the house sparrow. *Animal Behaviour*, *75*(4), 1465–1472. https://doi.org/10.1016/j.anbehav.2007.09.020

Katsnelson, E., Motro, U., Feldman, M. W., & Lotem, A. (2011). Individual-learning ability predicts social-foraging strategy in house sparrows. *Proceedings of the Royal Society B: Biological Sciences*, *278*(1705), 582–589. https://doi.org/10.1098/rspb.2010.1151

Kendal, R. L., Coolen, I., & Laland, K. N. (2004). The role of conformity in foraging when personal and social information conflict. *Behavioral Ecology*, *15*(2), 269–277. https://doi.org/10.1093/beheco/arh008

Kendal, R. L., Coolen, I., van Bergen, Y., & Laland, K. N. (2005). Trade-Offs in the Adaptive Use of Social and Asocial Learning. *Advances in the Study of Behavior*, *35*, 333–379. https://doi.org/10.1016/S0065-3454(05)35008-X

Kendal, R. L., Hopper, L. M., Whiten, A., Brosnan, S. F., Lambeth, S. P., Schapiro, S. J., & Hoppitt, W. (2015). Chimpanzees copy dominant and knowledgeable individuals: implications for cultural diversity. *Evolution and Human Behavior : Official Journal of the Human Behavior and Evolution Society*, *36*(1), 65–72. https://doi.org/10.1016/j.evolhumbehav.2014.09.002

Kendal, R. L., Kendal, J. R., Hoppitt, W., Laland, K. N., & Horner, V. (2009). Identifying Social Learning in Animal Populations: A New ‘Option-Bias’ Method. *PLoS ONE*, *4*(8), e6541. https://doi.org/10.1371/journal.pone.0006541

Krause, J., Croft, D. P., & James, R. (2007). Social network theory in the behavioural sciences: potential applications. *Behavioral Ecology and Sociobiology*, *62*(1), 15–27. https://doi.org/10.1007/s00265-007-0445-8

Krause, J., James, R., Franks, D. W., & Croft, D. P. (2015). *Animal Social Networks*. Oxford: Oxford University Press.

Krause, J., & Ruxton, G. D. (2002). *Living in Groups*. Oxford: Oxford University Press. https://doi.org/10.1093/sysbio/sys022

Krause, S., Wilson, A. D. M., Ramnarine, I. W., Herbert-Read, J. E., Clément, R. J. G., & Krause, J. (2016). Guppies occupy consistent positions in social networks: mechanisms and consequences. *Behavioral Ecology*, *28*(2), arw177. https://doi.org/10.1093/beheco/arw177

Kulahci, I. G., Ghazanfar, A. A., & Rubenstein, D. I. (2018a). Consistent individual variation across interaction networks indicates social personalities in lemurs. *Animal Behaviour*, *136*, 217–226. https://doi.org/10.1016/j.anbehav.2017.11.012

Kulahci, I. G., Ghazanfar, A. A., & Rubenstein, D. I. (2018b). Knowledgeable Lemurs Become More Central in Social Networks. *Current Biology*, 1–5. https://doi.org/10.1016/j.cub.2018.02.079

Kulahci, I. G., & Quinn, J. L. (2019). Dynamic Relationships between Information Transmission and Social Connections. *Trends in Ecology and Evolution*, *34*(6), 545–554.

https://doi.org/10.1016/j.tree.2019.02.007

Kulahci, I. G., Rubenstein, D. I., Bugnyar, T., Hoppitt, W., Mikus, N., & Schwab, C. (2016). Social networks predict selective observation and information spread in ravens. *Royal Society Open Science*, *3*(7), 160256. https://doi.org/10.1098/rsos.160256

Kurvers, R. H. J. M., Krause, J., Croft, D. P., Wilson, A. D. M., & Wolf, M. (2014). The evolutionary and ecological consequences of animal social networks: Emerging issues. *Trends in Ecology and Evolution*, *29*(6), 326–335. https://doi.org/10.1016/j.tree.2014.04.002

Kurvers, R. H. J. M., Van Oers, K., Nolet, B. A., Jonker, R. M., Van Wieren, S. E., Prins, H. H. T., & Ydenberg, R. C. (2010a). Personality predicts the use of social information. *Ecology Letters*, *13*(7), 829–837. https://doi.org/10.1111/j.1461-0248.2010.01473.x

Kurvers, R. H. J. M., Van Oers, K., Nolet, B. A., Jonker, R. M., Van Wieren, S. E., Prins, H. H. T., & Ydenberg, R. C. (2010b). Personality predicts the use of social information. *Ecology Letters*, *13*(7), 829–837. https://doi.org/10.1111/j.1461-0248.2010.01473.x

Lachlan, R. F., Crooks, L., & Laland, K. N. (1998). Who follows whom? Shoaling preferences and social learning of foraging information in guppies. *Animal Behaviour*, *56*(1), 181–190. https://doi.org/10.1006/anbe.1998.0760

Laland, K. N. (2004). Social learning strategies. *Animal Learning & Behavior*, *32*(1), 4–14. https://doi.org/10.3758/BF03196002

Laland, K. N., & Hoppitt, W. (2003). Do Animals Have Culture? *Evolutionary Anthropology*, *12*(3), 150–159. https://doi.org/10.1002/evan.10111

Laland, K. N., & Janik, V. M. (2006). The animal cultures debate. *Trends in Ecology & Evolution*, *21*(10), 542–7. https://doi.org/10.1016/j.tree.2006.06.005

Laland, K. N., & Kendal, J. R. (2003). What the models say about social learning. In Fragaszy D M & S. Perry (Eds.), *The Biology of Traditions* (pp. 33–55). Cambridge University Press. https://doi.org/10.1017/cbo9780511584022.003

Laland, K. N., & Kendal, J. R. (2009). What the models say about social learning. *The Biology of Traditions*, 33–55. https://doi.org/10.1017/cbo9780511584022.003

Laland, K. N., & Williams, K. (1997). Shoaling generates social learning of foraging information in guppies. *Animal Behaviour*, *53*(6), 1161–1169. https://doi.org/10.1006/anbe.1996.0318

Langley, E. J. G., van Horik, J. O., Whiteside, M. A., & Madden, J. R. (2018). Individuals in larger groups are more successful on spatial discrimination tasks. *Animal Behaviour*, *142*, 87–93. https://doi.org/10.1016/J.ANBEHAV.2018.05.020

Lefebvre, L., & Bolhuis, J. J. (2012). Positive and Negative Correlates of Feeding Innovations in Birds: Evidence for Limited Modularity. In *Animal Innovation*. https://doi.org/10.1093/acprof:oso/9780198526223.003.0002

Lefebvre, L., & Giraldeau, L.-A. (1994). Cultural transmission in pigeons is affected by the number of tutors and bystanders present. *Animal Behaviour*. https://doi.org/10.1006/anbe.1994.1046

Lefebvre, L., & Helder, R. (1997). Scrounger numbers and the inhibition of social learning in pigeons. *Behavioural Processes*, *40*(3), 201–7.

Lévy, F., Melo, A. I., Galef, B. G., Madden, M., & Fleming, A. S. (2003). Complete maternal deprivation affects social, but not spatial, learning in adult rats. *Developmental Psychobiology*, *43*(3), 177–191. https://doi.org/10.1002/dev.10131

Liker, A., & Bókony, V. (2009). Larger groups are more successful in innovative problem solving in house sparrows. *Proceedings of the National Academy of Sciences*, *106*(19), 7893–7898. https://doi.org/10.1073/PNAS.0900042106

Lindeyer, C. M., Meaney, M. J., & Reader, S. M. (2013). Early maternal care predicts reliance on social learning about food in adult rats. *Developmental Psychobiology*, *55*(2), 168–175. https://doi.org/10.1002/dev.21009

Lonsdorf, E. V, Eberly, L. E., & Pusey, A. E. (2004). Sex differences in learning in chimpanzees. *Nature*, *428*(6984), 715–716. https://doi.org/10.1038/nature02527

Lupfer, G., Frieman, J., & Coonfield, D. (2003). Social Transmission of Flavor Preferences in Two Species of Hamsters (Mesocricetus auratus and Phodopus campbelli). *Journal of Comparative Psychology*, *117*(4), 449–455. https://doi.org/10.1037/0735-7036.117.4.449

Lusseau, D., & Newman, M. E. J. (2004). Identifying the role that animals play in their social networks. *Proceedings. Biological Sciences*, *271 Suppl 6*(Suppl 6), S477-81. https://doi.org/10.1098/rsbl.2004.0225

Marchetti, C., & Drent, P. J. (2000). Individual differences in the use of social information in foraging by captive great tits. *Animal Behaviour*, *60*(1), 131–140. https://doi.org/10.1006/anbe.2000.1443

Marcoux, M., Whitehead, H., & Rendell, L. (2006). Coda vocalizations recorded in breeding areas are almost entirely produced by mature female sperm whales (Physeter macrocephalus). *Canadian Journal of Zoology*, *84*(4), 609–614. https://doi.org/10.1139/Z06-035

Marino, L. (2017). Thinking chickens: a review of cognition, emotion, and behavior in the domestic chicken. *Animal Cognition*. https://doi.org/10.1007/s10071-016-1064-4

Mazur, R., & Seher, V. (2008). Socially learned foraging behaviour in wild black bears, Ursus americanus. *Animal Behaviour*, *75*(4), 1503–1508. https://doi.org/10.1016/j.anbehav.2007.10.027

McElreath, R., Lubell, M., Richerson, P. J., Waring, T. M., Baum, W., Edsten, E., … Paciotti, B. (2005). Applying evolutionary models to the laboratory study of social learning. *Evolution and Human Behavior*, *26*(6), 483–508. https://doi.org/10.1016/j.evolhumbehav.2005.04.003

Melo, A. I., Lovic, V., Gonzalez, A., Madden, M., Sinopoli, K., & Fleming, A. S. (2006). Maternal and littermate deprivation disrupts maternal behavior and social-learning of food preference in adulthood: Tactile stimulation, nest odor, and social rearing prevent these effects. *Developmental Psychobiology*, *48*(3), 209–219. https://doi.org/10.1002/dev.20130

Mench, J., & Keeling, L. J. (2001). The social behaviour of domestic birds. In L. J. Keeling & H. W. Gonyou (Eds.), *Social behaviour in farm animals* (pp. 177–209). Wallingford, UK: CABI Publishing.

Menzel, E. W. (1974). A group of young chimpanzees in a 1-acre field: Leadership and communication. In *Behaviour of Non-Human Primates* (pp. 83–153).

Mesoudi, A., Chang, L., Dall, S. R. X., & Thornton, A. (2016). The Evolution of Individual and Cultural Variation in Social Learning. *Trends in Ecology & Evolution*, *31*(3), 215–25. https://doi.org/10.1016/j.tree.2015.12.012

Midford, P. E., Hailman, J. P., & Woolfenden, G. E. (2000). Social learning of a novel foraging patch in families of free-living Florida scrub-jays. *Animal Behaviour*, *59*(6), 1199–1207. https://doi.org/10.1006/anbe.1999.1419

Mineka, S., & Cook, M. (1988). Social learning and the acquisition of snake fear in monkeys. *Social Learning: Psychological and Biological Perspectives*, 51–97.

Montanaria, A., & Saberi, A. (2010). The spread of innovations in social networks. *Proceedings of the National Academy of Sciences of the United States of America*, *107*(47), 20196–20201. https://doi.org/10.1073/pnas.1004098107

Morand-Ferron, J., & Quinn, J. L. (2011). Larger groups of passerines are more efficient problem solvers in the wild. *Proceedings of the National Academy of Sciences of the United States of America*, *108*(38), 15898–903. https://doi.org/10.1073/pnas.1111560108

Morand-Ferron, J., Sol, D., & Lefebvre, L. (2007). Food stealing in birds: brain or brawn? *Animal Behaviour*, *74*(6), 1725–1734. https://doi.org/10.1016/j.anbehav.2007.04.031

Morgan, M. J. (1988). The influence of hunger, shoal size and predator presence on foraging in bluntnose minnows. *Animal Behaviour*, *36*(5), 1317–1322. https://doi.org/10.1016/S0003-3472(88)80200-8

Morinay, J., Forsman, J. T., Germain, M., & Doligez, B. (2020). Behavioural traits modulate the use of heterospecific social information for nest site selection: experimental evidence from a wild bird population. *Proceedings of the Royal Society B: Biological Sciences*, *287*(1925), 20200265. https://doi.org/10.1098/rspb.2020.0265

Morrell, L. J., Croft, D. P., Dyer, J. R. G., Chapman, B. B., Kelley, J. L., Laland, K. N., & Krause, J. (2008). Association patterns and foraging behaviour in natural and artificial guppy shoals. *Animal Behaviour*, *76*(3), 855–864. https://doi.org/10.1016/j.anbehav.2008.02.015

Nematzadeh, A., Ferrara, E., Flammini, A., & Ahn, Y. Y. (2014). Optimal network modularity for information diffusion. *Physical Review Letters*, *113*(8), 1–5. https://doi.org/10.1103/PhysRevLett.113.088701

Newman, M. E. J. (2004). Analysis of weighted networks. *Physical Review E - Statistical Physics, Plasmas, Fluids, and Related Interdisciplinary Topics*, *70*(5), 9. https://doi.org/10.1103/PhysRevE.70.056131

Nicol, C. J. (2004). Development, direction, and damage limitation: Social learning in domestic fowl. *Animal Learning & Behavior*, *32*(1), 72–81. https://doi.org/10.3758/BF03196008

Nicol, C. J. (2015). *The Behavioural Biology of Chickens*. Wallingford, UK: CABI Publishing.

Nicol, C. J., & Pope, S. J. (1992). Effects of social learning on the acquisition of discriminatory keypecking in hens. *Bulletin of the Psychonomic Society*, *30*(4), 293–296. https://doi.org/10.3758/BF03330468

Nicol, C. J., & Pope, S. J. (1994). Social learning in small flocks of laying hens. *Animal Behaviour*, *47*(6), 1289–1296. https://doi.org/10.1006/anbe.1994.1177

Nicol, C. J., & Pope, S. J. (1996). The maternal feeding display of domestic hens is sensitive to perceived chick error. *Animal Behaviour*, *52*(4), 767–774. https://doi.org/10.1006/anbe.1996.0221

Nicol, C. J., & Pope, S. J. (1999). The effects of demonstrator social status and prior foraging success on social learning in laying hens. *Animal Behaviour*, *57*(Caro 1980), 163–171. https://doi.org/10.1006/anbe.1998.0920

Nomakuchi, S., Park, P. J., & Bell, M. A. (2009). Correlation between exploration activity and use of social information in three-spined sticklebacks. *Behavioral Ecology*, *20*(2), 340–345. https://doi.org/10.1093/beheco/arp001

Nunn, C. L., Thrall, P. H., Bartz, K., Dasgupta, T., & Boesch, C. (2009). Do transmission mechanisms or social systems drive cultural dynamics in socially structured populations? *Animal Behaviour*, *77*(6), 1515–1524. https://doi.org/10.1016/J.ANBEHAV.2009.02.023

Perlman, R. F., Borries, C., & Koenig, A. (2016). Dominance relationships in male Nepal gray langurs (*S emnopithecus schistaceus*). *American Journal of Physical Anthropology*, *160*(2), 208–219. https://doi.org/10.1002/ajpa.22958

Perry, S. E., Barrett, B. J., & Godoy, I. (2017). Older, sociable capuchins (Cebus capucinus) invent more social behaviors, but younger monkeys innovate more in other contexts. *Proceedings of the National Academy of Sciences of the United States of America*, *114*(30), 7806–7813. https://doi.org/10.1073/pnas.1620739114

Pike, T. W., & Laland, K. N. (2010). Conformist learning in nine-spined sticklebacks' foraging decisions. *Biology Letters*, *6*(4), 466–468. https://doi.org/10.1098/rsbl.2009.1014

Pitcher, T. J., Magurran, A. E., & Winfield, I. J. (1982). Fish in larger shoals find food faster.

Behavioral Ecology and Sociobiology, *10*(2), 149–151. https://doi.org/10.1007/BF00300175

R Core Team. (2016).

Rafacz, M., & Templeton, J. . (2003). Environmental Unpredictability and the Value of Social Information for Foraging Starlings. *Ethology*, *109*, 951–960.

Raouf, S. A., Smith, L. C., Brown, M. B., Wingfield, J. C., & Brown, C. R. (2006). Glucocorticoid hormone levels increase with group size and parasite load in cliff swallows. *Animal Behaviour*, *71*(1), 39–48. https://doi.org/10.1016/J.ANBEHAV.2005.03.027

Reader, S. (2003). Innovation and social learning: individual variation and brain evolution. *Animal Biology*, *53*(2), 147–158. https://doi.org/10.1163/157075603769700340

Reader, S. M., & Laland, K. N. (2000). Diffusion of foraging innovations in the guppy. *Animal Behaviour*, *60*(2), 175–180. https://doi.org/10.1006/anbe.2000.1450

Reader, S. M., & Laland, K. N. (2003). *Animal Innovation*. Oxford: Oxford University Press.

Rendell, L., Fogarty, L., Hoppitt, W. J. E., Morgan, T. J. H., Webster, M. M., & Laland, K. N. (2011). Cognitive culture: theoretical and empirical insights into social learning strategies. *Trends in Cognitive Sciences*, *15*(2), 68–76. https://doi.org/10.1016/j.tics.2010.12.002

Robertson, P. (1997). *A natural history of the pheasant*. Swan Hill Press.

Rogers, A. R. (1988). Does Biology Constrain Culture. *American Anthropologist*, *90*(4), 819–831. https://doi.org/10.1525/aa.1988.90.4.02a00030

Romanes, G. J. (1884). *Mental evolution in animals*. New York: AMS Press.

Rosa, P., Nguyen, V., & Dubois, F. (2012). Individual differences in sampling behaviour predict social information use in zebra finches. *Behavioral Ecology and Sociobiology*, *66*(9), 1259–1265. https://doi.org/10.1007/s00265-012-1379-3

Rosenthal, S. B., Twomey, C. R., Hartnett, A. T., Wu, H. S., & Couzin, I. D. (2015). Revealing the hidden networks of interaction in mobile animal groups allows prediction of complex behavioral contagion. *Proceedings of the National Academy of Sciences*, *112*(15), 4690–4695. https://doi.org/10.1073/pnas.1420068112

Rowe, C., & Healy, S. D. (2014). Measuring variation in cognition. *Behavioral Ecology*, *25*(6), 1287–1292. https://doi.org/10.1093/beheco/aru090

RStudio Team. (2016). RStudio: Integrated Development for R. Boston, MA: RStudio, Inc.

Rushen, J. (1982). The peck orders of chickens: How do they develop and why are they linear? *Animal Behaviour*, *30*(4), 1129–1137. https://doi.org/10.1016/S0003-3472(82)80203-0

Ryer, C. H., & Olla, B. L. (1991). Information transfer and the facilitation and inhibition of feeding in a schooling fish. *Environmental Biology of Fishes*, *30*(3), 317–323. https://doi.org/10.1007/BF02028847

Ryer, C. H., & Olla, B. L. (1992). Social mechanisms facilitating exploitation of spatially variable ephemeral food patches in a pelagic marine fish. *Animal Behaviour*, *44*(1), 69–74. https://doi.org/10.1016/S0003-3472(05)80756-0

Salathé, M., & Bonhoeffer, S. (2008). The effect of opinion clustering on disease outbreaks. *Journal of the Royal Society, Interface*, *5*(29), 1505–8. https://doi.org/10.1098/rsif.2008.0271

Salathé, M., & Jones, J. H. (2010). Dynamics and control of diseases in networks with community structure. *PLoS Computational Biology*, *6*(4), e1000736. https://doi.org/10.1371/journal.pcbi.1000736

Salva, O. R. (2011). Social cognition and learning mechanisms: Experimental evidence in domestic chicks. *Interaction Studies*, *12*(2), 208–232. https://doi.org/10.1075/is.12.2.02dai

Sapolsky, R. M. (2005). The influence of social hierarchy on primate health. *Science*. https://doi.org/10.1126/science.1106477

Sarin, S., & Dukas, R. (2009). Social learning about egg-laying substrates in fruitflies. *Proceedings of the Royal Society B: Biological Sciences*, *276*(1677), 4323–4328. https://doi.org/10.1098/rspb.2009.1294

Schakner, Z. A., Lunsford, C., Straley, J., Eguchi, T., & Mesnick, S. L. (2014). Using Models of Social Transmission to Examine the Spread of Longline Depredation Behavior among Sperm Whales in the Gulf of Alaska. https://doi.org/10.1371/journal.pone.0109079

Schakner, Z. A., Petelle, M. B., Tennis, M. J., Van Der Leeuw, B. K., Stansell, R. T., & Blumstein, D. T. (2017). Social associations between California sea lions influence the use of a novel foraging ground. *Royal Society Open Science*, *4*(5). https://doi.org/10.1098/rsos.160820

Schnoell, A. V., & Fichtel, C. (2012). Wild redfronted lemurs (Eulemur rufifrons) use social information to learn new foraging techniques. *Animal Cognition*, *15*(4), 505–16. https://doi.org/10.1007/s10071-012-0477-y

Schwab, C., Bugnyar, T., Schloegl, C., & Kotrschal, K. (2008). Enhanced social learning between siblings in common ravens, Corvus corax. *Animal Behaviour*, *75*(2), 501–508. https://doi.org/10.1016/j.anbehav.2007.06.006

Seppanen, J.-T., Forsman, J. T., Monkkonen, M., Krams, I., & Salmi, T. (2011). New behavioural trait adopted or rejected by observing heterospecific tutor fitness. *Proceedings of the Royal Society B: Biological Sciences*, *278*(1712), 1736–1741. https://doi.org/10.1098/rspb.2010.1610

Shaw, R. C. (2017a). Testing cognition in the wild : factors affecting performance and individual consistency in two measures of avian cognition. *Behavioural Processes*, *134*, 31–36. https://doi.org/10.1016/j.beproc.2016.06.004

Shaw, R. C. (2017b, January 1). Testing cognition in the wild: factors affecting performance and individual consistency in two measures of avian cognition. *Behavioural Processes*. Elsevier B.V. https://doi.org/10.1016/j.beproc.2016.06.004

Shaw, R. C., Boogert, N. J., Clayton, N. S., & Burns, K. C. (2015). Wild psychometrics: evidence for ‘general’ cognitive performance in wild New Zealand robins, Petroica longipes. *Animal Behaviour*, *109*, 101–111. https://doi.org/10.1016/j.anbehav.2015.08.001

Sih, A., Bell, A., & Johnson, J. C. (2004, July 1). Behavioral syndromes: An ecological and evolutionary overview. *Trends in Ecology and Evolution*. Elsevier. https://doi.org/10.1016/j.tree.2004.04.009

Sih, A., & Watters, J. V. (2005). *The mix matters: behavioural types and group dynamics in water striders*. *Behaviour* (Vol. 142).

Smolla, M., Alem, S., Chittka, L., & Shultz, S. (2016). Copy-when-uncertain: bumblebees rely on social information when rewards are highly variable. *Biology Letters*, *12*(6), 20160188-. https://doi.org/10.1098/rsbl.2016.0188

Smulders, T. V. (2018). Smarter through group living ?, 100–101. https://doi.org/10.3758/s13420-018-0335-0

Stammbach, E. (1988). Group Responses to Specially Skilled Individuals in a Macaca fascicularis Group, *107*(3), 241–266.

Stroeymeyt, N., Giurfa, M., & Franks, N. R. (2017). Information Certainty Determines Social and Private Information Use in Ants. *Scientific Reports*, (January), 1–13. https://doi.org/10.1038/srep43607

Sugita, Y. (1980). IMITATIVE CHOICE BEHAVIOR IN GUPPIES. *Japanese Psychological Research*, *22*(1), 7–12. https://doi.org/10.4992/psycholres1954.22.7

Swaney, W., Kendal, J., Capon, H., Brown, C., & Laland, K. N. (2001). Familiarity facilitates social learning of foraging behaviour in the guppy. *Animal Behaviour*, *62*(3), 591–598. https://doi.org/10.1006/anbe.2001.1788

Therneau, T. (2015). A Package for Survival Analysis in S. version 2.38.

Therneau, T. (2018). coxme: Mixed Effects Cox Models.

Therneau, T., & Grambsch, P. M. (2000). *Modelling Survival Data: Extending the Cox Model*. New York: Springer.

Thornton, A., & Malapert, A. (2009a). Experimental evidence for social transmission of food acquisition techniques in wild meerkats. *Animal Behaviour*, *78*(2), 255–264. https://doi.org/10.1016/j.anbehav.2009.04.021

Thornton, A., & Malapert, A. (2009b). The rise and fall of an arbitrary tradition: an experiment with wild meerkats. *Proceedings. Biological Sciences / The Royal Society*, *276*(1660), 1269–1276. https://doi.org/10.1098/rspb.2008.1794

Tuomainen, U., & Candolin, U. (2011). Behavioural responses to human-induced environmental change. *Biological Reviews*. https://doi.org/10.1111/j.1469-185X.2010.00164.x

van Bergen, Y., Coolen, I., & Laland, K. N. (2004). Nine-spined sticklebacks exploit the most reliable source when public and private information conflict. *Proceedings of the Royal Society B: Biological Sciences*, *271*(1542), 957–962. https://doi.org/10.1098/rspb.2004.2684

van de Waal, E., Renevey, N., Favre, C. M., & Bshary, R. (2010). Selective attention to philopatric models causes directed social learning in wild vervet monkeys. *Proceedings of the Royal Society B: Biological Sciences*, *277*(1691), 2105–2111. https://doi.org/10.1098/rspb.2009.2260

van der Post, D. J., & Hogeweg, P. (2009). Cultural inheritance and diversification of diet in variable environments. *Animal Behaviour*, *78*(1), 155–166. https://doi.org/10.1016/j.anbehav.2009.04.009

van Horik, J. O., Beardsworth, C. E., Laker, P. R., Whiteside, M. A., & Madden, J. R. (2019). Response learning confounds assays of inhibitory control on detour tasks. *Animal Behaviour*, (0123456789). https://doi.org/10.1017/CBO9781107415324.004

van Horik, J. O., Langley, E. J. G., Whiteside, M. A., Laker, P. R., & Madden, J. R. (2018). Intra-individual variation in performance on novel variants of similar tasks influences single factor explanations of general cognitive processes. *Royal Society Open Science*, *5*(7), 171919. https://doi.org/10.1098/rsos.171919

van Horik, J. O., Langley, E. J. G., Whiteside, M. A., & Madden, J. R. (2016). Differential participation in cognitive tests is driven by personality, sex, body condition and experience. *Behavioural Processes*, *134*, 22–30. https://doi.org/10.1016/j.beproc.2016.07.001

van Horik, J. O., & Madden, J. R. (2016). A problem with problem solving: motivational traits, but not cognition, predict success on novel operant foraging tasks. *Animal Behaviour*, *114*, 189–198. https://doi.org/10.1016/j.anbehav.2016.02.006

Vickery, W. L., Giraldeau, L.-A., Templeton, J. J., Kramer, D. L., & Chapman, C. A. (1991). Producers, Scroungers, and Group Foraging, *137*(6), 847–863.

Vital, C., & Martins, E. P. (2009). Using graph theory metrics to infer information flow through animal social groups: A computer simulation analysis. *Ethology*, *115*(4), 347–355. https://doi.org/10.1111/j.1439-0310.2009.01613.x

Voelkl, B., & Noë, R. (2008). The influence of social structure on the propagation of social information in artificial primate groups: A graph-based simulation approach. *Journal of Theoretical Biology*, *252*(1), 77–86. https://doi.org/10.1016/j.jtbi.2008.02.002

Voelkl, B., & Noë, R. (2010). Simulation of information propagation in real-life primate networks: longevity, fecundity, fidelity. *Behavioral Ecology and Sociobiology*, *64*(9), 1449–1459.

https://doi.org/10.1007/s00265-010-0960-x

Walters, J. R., Derrickson, S. R., Michael Fry, D., Haig, S. M., Marzluff, J. M., & Wunderle, J. M. (2010). Status of the California Condor Gymnogyps californianus and Efforts to Achieve Its Recovery. *The Auk*, *127*(4), 969–1001. https://doi.org/10.1525/auk.2010.127.4.969

Watson, S. K., Vale, G. L., Hopper, L. M., Dean, L. G., Kendal, R. L., Price, E. E., … Whiten, A. (2018). Chimpanzees demonstrate individual differences in social information use. *Animal Cognition*, *21*(5), 639–650. https://doi.org/10.1007/s10071-018-1198-7

Webster, M. M., Atton, N., Hoppitt, W. J. E., & Laland, K. N. (2013). Environmental complexity influences association network structure and network-based diffusion of foraging information in fish shoals. *The American Naturalist*, *181*(2), 235–44. https://doi.org/10.1086/668825

Webster, M. M., & Laland, K. N. (2008). Social learning strategies and predation risk: minnows copy only when using private information would be costly. *Proceedings. Biological Sciences*, *275*(1653), 2869–76. https://doi.org/10.1098/rspb.2008.0817

Webster, M. M., & Laland, K. N. (2011). Reproductive state affects reliance on public information in sticklebacks. *Proceedings of the Royal Society B: Biological Sciences*, *278*(1705), 619–627. https://doi.org/10.1098/rspb.2010.1562

Wey, T., Blumstein, D. T., Shen, W., & Jordán, F. (2008). Social network analysis of animal behaviour: a promising tool for the study of sociality. *Animal Behaviour*, *75*(2), 333–344. https://doi.org/10.1016/j.anbehav.2007.06.020

Whitehead, H., & Lusseau, D. (2012). Animal social networks as substrate for cultural behavioural diversity. *Journal of Theoretical Biology*, *294*, 19–28. https://doi.org/10.1016/j.jtbi.2011.10.025

Whitehead, H., & Rendell, L. (2014). *The Cultural Lives of Whales and Dolphins*. Chicago: The University of Chicago Press.

Whiten, A., Caldwell, C. A., & Mesoudi, A. (2016). Cultural diffusion in humans and other animals. *Current Opinion in Psychology*, *8*, 15–21. https://doi.org/10.1016/j.copsyc.2015.09.002

Whiten, A., & Mesoudi, A. (2008). Review. Establishing an experimental science of culture: animal social diffusion experiments. *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences*, *363*(1509), 3477–88. https://doi.org/10.1098/rstb.2008.0134

Whiteside, M. A., van Horik, J. O., Langley, E. J. G., Beardworth, C. E., Laker, P. R., & Madden, J. R. (2017). Differences in social preference between the sexes during ontogeny drive segregation in a precocial species. *Behavioral Ecology and Sociobiology*, *71*(7), 103. https://doi.org/10.1007/s00265-017-2332-2

Wilkinson, G. S. (1992). Information transfer at evening bat colonies. *Animal Behaviour*, *44*(PART 3), 501–518. https://doi.org/10.1016/0003-3472(92)90059-I

Zeltner, E., Klein, T., & Huber-Eicher, B. (2000). Is there social transmission of feather pecking in groups of laying hen chicks? *Animal Behaviour*, *60*(1999), 211–216. https://doi.org/10.1006/anbe.2000.1453

Zentall, T. R., & Galef, B. G. (1988). *Social learning: Psychological and biological perspectives*. Psychology Press.