Biased social learning and directed information transfer: a comparative approach.

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The candidate confirms that the work submitted is their own, except where work which has formed part of jointly authored publications has been included. The contribution of the candidate and the other authors to this work has been explicitly indicated below. The candidate confirms that appropriate credit has been given within the thesis where reference has been made to the work of others.

- The work in Chapter 2 of this thesis has appeared in publication as follows:

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Thesis structure and style

This is an 'alternative style' PhD thesis. Chapters 2-5 have been written in manuscript form intended for publication. I am lead author on all data chapters. Chapters 1 (General Introduction) and 6 (General Discussion) represent my sole work and so the terms 'I' and 'my' are used throughout. Reference lists are given at the end of each chapter. Supplementary Material, where applicable, is placed directly after the corresponding data chapter.

Chapters 2 and 3 have been approved for publication in peer-reviewed journals and so are included here as they would appear in their respective journals, using the terms 'we' and 'our' throughout to acknowledge the contributions of all authors. Chapter 2 is in the style of *Royal Society open science* and uses a numbered referencing style. Chapter 3 is in the style of *Ethology*. Chapters 1 and 3-6 use standard Harvard citations.

Chapters 4 and 5 have been written in manuscript form, but have not yet been submitted to journals and so have not been tailored to any specific journal style. As these chapters represent mostly my sole work, I use the terms 'I' and 'my', but acknowledge the contributions of my supervisors, W. Hoppitt and C. Hassall. Should these chapters be published, W. Hoppitt and C. Hassall will be included as co-authors on both manuscripts for their contributions to the work.

Chapters 2, 3 and 5 follow the standard 'introduction, methods, results, discussion' manuscript format. Chapter 4 is written as a methodological paper giving a detailed explanation of a novel research tool.

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Abstract

‘Social learning’ (learning from others) occurs across the animal kingdom and can affect not only individual fitness but also the patterns of information transmission through entire social groups. An individual’s ability to learn from others is determined not only by its own behaviour but by the behaviours of those in possession of the knowledge (the ‘demonstrator’) and by the structure of the underlying social network. In this thesis, I use theoretical and empirical approaches to investigate the physical, social and behavioural factors influencing social transmission within complex, spatially realistic environments. I find that individual variation in space use and tendency to transmit and receive information influence information transmission patterns in an agent-based model of social insect communication (Chapter 2). I also show that the characteristics of social bonds connecting individuals within the larger social network determine patterns of learning in zebra finches, which show biases towards learning from aggressors and mates (Chapter 3). Finally, a limitation of the human research is restrictive laboratory environments that offer little ecological validity and make generalisations across the human / non-human divide difficult. I tackle this limitation through the development (Chapter 4) and employment (Chapter 5) of novel, three-dimensional virtual research environments for studying human social learning, where I demonstrate that people are biased towards learning asocially (independently) and towards demonstrators greater in number and success rates. In Chapter 6, I discuss how individual variation in the aforementioned behaviours appears to play a particularly important role in determining the pathways of social transmission at the population level and, in some cases, can result in the existence of ‘keystone’ information transmitters, which have a disproportionate influence over the behaviours of others. I discuss ideas for future research and the potential application of these findings outside of behavioural ecology and evolution in fields including conservation, epidemiology and education.

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1.1. Learning from others

The way in which an individual interacts with its environment is crucially important for its survival, and so for the evolution of its species. These interactions can be as simple as temperature influencing the functioning of enzymes and as complex as socially connected networks of individuals harvesting resources using tools that have been developed over multiple generations of learning. For species capable of long-term memory – which include animals, plants, fungi and even unicellular organisms – learning can be a valuable way to increase fitness, allowing an individual to ascertain which behaviours bring about the best responses within their environment, build up a 'behavioural repertoire' and exploit these behaviours in the future (Witzany, 2018). However, learning comes with its own costs. The process of learning can involve experimenting with different behaviours and this experimentation comes with the risk of using maladaptive as well as adaptive behaviours – especially in fluctuating environments where optimal behaviours may vary – in addition to the additional time and energy costs associated with 'trying out' different behaviours (Warburton and Thomson, 2006; Dunlap and Stephens, 2016). Furthermore, trying to learn within potentially dangerous environments can increase the risk of predation (Kendal *et al.,* 2004; Webster and Laland, 2008) or ingesting toxins (Kikuchi and Sherratt, 2015). However, such risks can pay off if an individual manages to adopt adaptive behaviours which mean it can avoid these risks and additional expenses in the future. This behavioural refinement may be particularly beneficial in long-lived species, which have more time to benefit from early learning experiences – for example, long-lived migratory birds not only learn and remember migratory routes, but also gradually refine them over their lifetime (Fayet, 2020).

One way in which an individual can reduce or even avoid the costs of learning is to learn from others, thus reaping the benefits of a learned behaviour without paying the costs of having to trial multiple behaviours themselves. 'Social learning' is defined as learning which is facilitated by the interaction with or observation of another individual, or the products of its behaviour (Heyes, 1994; Hoppitt and Laland, 2013). Social learning includes direct copying, but also covers situations such as individuals being attracted to a particular object or location due to the presence of another individual (known as stimulus and local enhancement, respectively; Hoppitt and Laland, 2013) and individuals learning from products left over from another individual's behaviour (e.g. locating a novel food source that has been discovered, partially eaten or made accessible by another individual) (Heyes, 1994). All in all, this means that individuals learning socially are being influenced in their uptake of novel behaviours by other individuals in their social environment. Thus, social learning is in contrast to asocial (or independent) learning such as trial-and-error which is done without the influence of other individuals.

In addition to behavioural ecology and evolution, the study of social learning has important historical roots in the field of psychology. Albert Bandura's 'social learning theory', for example, was one of the first to acknowledge that humans – highly social animals by nature – learn about their environment not just through their individual experiences, but via 'observational learning' (Bandura, 1977). Observational learning involves first observing the behaviour of others and then making a cognitive decision concerning whether to adopt said behaviour – the latter being mediated, at least in humans, by internal cognitive processes such as positive/negative reinforcement and self-efficacy (Bandura, 1977; 1989). Thus, Bandura's principles align well with the slightly broader definition of 'social learning' in the evolutionary literature and, despite its focus on humans, many of Bandura's principles can be applied to other species as well.

From a cognitive perspective, social learning does not appear to require specialised adaptations relating to the learning process itself and instead utilises the same cognitive mechanisms as asocial learning (Heyes, 2012), e.g. both involve making associations between some stimulus and response. This idea is highlighted by the fact that social learning has even been demonstrated in entirely solitary animals (e.g. the red-footed tortoise, *Geochelone carbonaria*, Wilkinson *et al.,* 2010), which have no obvious reason to evolve specialised thought processes required to learn from others. Rather, what makes social learning 'social' are the input channels by which individuals obtain the information to be learned (Hill *et al.,* 2009; Heyes, 2012). More social animals may, therefore, evolve specialised 'input mechanisms' that favour the influx of social information (e.g. attentional biases towards the behaviour of conspecifics) over other aspects of the environment (Heyes, 2012).

Social learning is potentially a highly cost-effective way of gaining information, allowing novel behaviours to spread through a population (a process known as 'social transmission'), while reducing costs such as time, energy and predation risk that are associated with asocial learning (Hoppitt and Laland, 2013). Research suggests that social learning is adaptive in many biological contexts, from foraging to predator avoidance (Galef and Laland, 2005) and that organisms ranging from vertebrates to plants to slime moulds are capable of using information provided by others (Hoppitt and Laland, 2013; Gorzelak *et al.,* 2015; Briard *et al.,* 2020). At the population level, social transmission can benefit entire social groups by allowing them to respond effectively to changes in their environment and also allowing knowledge to be retained between generations. This is well illustrated by the lobtail feeding behaviour of humpback whales (*Megaptera novaeangliae*) in the Gulf of Maine, which appeared to originate in response to a sudden fluctuation in prey availability and has been retained in the population over three decades and multiple generations via social transmission (Allen *et al.,* 2013).

In their book "Animal Traditions: Behavioural Inheritance in Evolution", Avital and Jablonka (2000) argue that, beyond the benefits to the individual alone, social transmission offers an alternative form of inheritance (besides genetic inheritance), and that such 'behavioural inheritance' can have important impacts on the evolution of species. For humans in particular, social influences can impact not only what we do but how we think. Heyes (2018), for example, argues that various cognitive mechanisms (ways of thinking) in humans are not instinctive and are instead taken up by individuals via social learning – i.e. these mechanisms are 'cognitive gadgets' that are the product of cultural, as opposed to genetic, evolution. Exposure to social stimuli can also influence our social behaviour, as demonstrated by Albert Bandura's (1961) 'Bobo doll' experiments, where children observing adult models acting aggressively towards a toy showed more aggression towards the toy themselves. The uptake of aggressive behaviour was more likely when children viewed the models receiving a reward for their aggressive behaviour (i.e. learning was subject to 'vicarious enforcement'). Thus, social transmission has the potential to generate societies in which particular emotions, relationships or ways of interacting – especially those that are deemed more 'socially acceptable' – become more prominent than others. In cases where the social dynamics of a population both influence and are influenced by social learning, there is potential for interesting feedback loops to form – e.g. the learning of aggressive behaviours from others may either promote or inhibit an individual's likelihood of being copied in the future.

Through the sharing of information and behavioural norms, social transmission can result in the emergence of group-typical patterns of behaviour – thus, social learning underpins the evolution of local 'traditions' and 'culture' (Laland and Hoppitt, 2003). Culture and traditions have become an important part of human existence and understanding how we exchange information within our social communities is key to understanding how these cultures evolved. However, if culture is defined not by inherently human characteristics such as language, but by the underlying social processes that result in such group-typical behavioural patterns, its presence can be found across the animal kingdom (Laland and Hoppitt, 2003; Laland and Janik, 2006). According to Laland and Hoppitt (2003), culture can be broadly defined as "group-typical behaviour patterns shared by members of a community that rely on socially learned and transmitted information" (p.151). By this definition, any population-wide uptake of behavioural variants as the result of social – rather than solely genetic or environmental – influences can be considered a cultural tradition of that particular population. Aplin *et al*. (2015), for example, demonstrated how seeding sub-populations of wild great tits (*Parus major*) with alternate solutions to the same foraging task resulted in the development of stable local traditions. Other examples of similar 'foraging traditions' include differences in tool use between different populations of chimpanzees (*Pan troglodytes*) (Hobaiter *et al.,* 2014), as well as the lobtail feeding behaviour of Allen and colleagues' (2013) humpback whale population described above. 'Vocal cultures' (i.e. population-level differences in vocalisations that are mediated by social learning) have been identified in a number of species, including New Caledonian crows (*Corvus moneduloides*) (Bluff *et al.,* 2010), humpback whales (Noad *et al.,* 2000) and songbirds (Nelson *et al.,* 2004; Williams *et al.*, 2013; Whiten, 2019). Cultural traditions have the potential to set a population apart from its neighbours if the behavioural variations adopted by the population turn out to have adaptive benefits – in this sense, the cultures themselves may become subject to evolutionary selection (Whiten, 2019).

In some cases, cultural traditions may accumulate over time, with additions and modifications of the original behaviours building up into what is known as 'cumulative culture' (Dean *et al.,* 2014; Whiten, 2019; Miu *et al.,* 2018). Cumulative culture is often assumed to be a solely human process (e.g. human tools and technologies), although there is some evidence for this phenomenon in non-human animals, most notably tool manufacturing in New Caledonian crows (Hunt and Gray, 2003; Rutz *et al.,* 2018). Cultural traditions may even become paramount to the survival of a population if the adoption of local behaviours has a great enough impact on individual fitness. For example, the erosion of vocal culture in regent honeyeaters (*Anthochaera phrygia*) as a result of habitat fragmentation preventing young males from associating with song tutors has very recently been identified as a major contributor to the species' decline, as males singing atypical songs are less likely to attract females and so less likely to produce offspring (Crates *et al.,* 2021). An understanding of how information is transmitted through animal social groups, and the importance of cultural norms for the survival of the population, could therefore have crucial impacts on conservation efforts (Brakes *et al.,* 2019).

1.2. Social information transfer: from demonstrator to observer

In order to understand how information spreads through the population as a whole, we must first understand the individual-level factors influencing how social information transfers from a knowledged individual (the 'demonstrator') to a naïve individual (the 'observer'). The majority of current research focusses on information exchange from the observer’s perspective, examining how the observer gathers information from different potential demonstrators. However, this assumes that the observer has a choice between multiple sources of information in the first place, which may not always be the case, and does not take into account the underlying structure of the population social network. Here, I describe a framework in which social information transfer from demonstrator to observer is considered to occur across three stages (Figure 1.1), which aim to encompass some of the often overlooked complexities of social transmission.

First, demonstrator and observer must be appropriately connected within the social network, such that information transfer between them is possible. This will ultimately be determined by the underlying social network of the population. The definition of 'connected' here will depend on the social dynamics of the population in question and the type of information being transmitted. For example, in some cases, individuals may need to be in close proximity at the time a novel behaviour is being performed to learn this behaviour, while in others, information may be transmitted only within particular social groupings. These connections may also break and reform over time, resulting in a dynamic social network – particularly if information transfer is dependent on individuals being in close proximity, as individuals are likely to move away from and re-join each other over time. Second, the demonstrator must be in possession of information novel to the observer and must be willing and able to transmit this information (either actively or passively) to others. Third, the ability and inclination of an observer to learn from a particular source will dictate whether they ultimately take up the novel behaviour. Viewing social information transfer in this way accounts for the fact that the behaviours of both demonstrator and observer, plus the underlying social connections between them, can impact on who learns from whom at any given time.

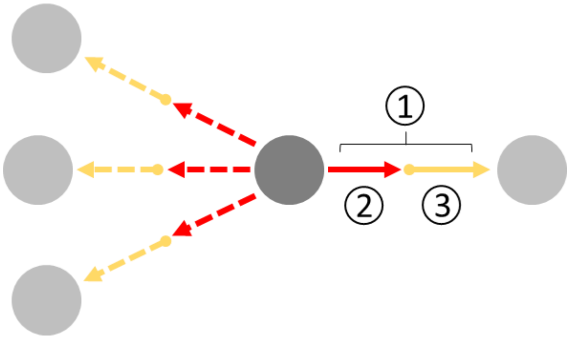

Figure 1.1. The three stages determining information transfer between an informed demonstrator (dark grey circle) and a naïve observer (light grey circle). **(1)** Demonstrator and observer must be appropriately connected within the social network, such that the novel information or behaviour in question can transmit between them. In this diagram, solid and dashed arrows represent two different types of connection, with information being transferred along the solid arrows only. This can be interpreted in different ways, depending on the social dynamics of the population and the type of information being transferred. For example, solid arrows could represent information transmission within family units, while dashed arrows represent inter-family information exchange. Alternatively, solid arrows could represent individuals being in close enough proximity to exchange information, while dashed arrows represent associations that are too distant to allow information transfer. **(2)** A demonstrator must be in possession of novel information, and must demonstrate this information to others. **(3)** A naïve observer must be receptive to the information being transmitted by the demonstrator in question and capable of learning this information.

The majority of research in this area is focussed around the third stage of information transfer – i.e. how an observer chooses which sources of information to learn from. Given the benefits of social learning discussed above, it may seem reasonable to assume that learning from others will always be more adaptive than independent learning. However, if all individuals copy each other indiscriminately, with nobody sampling directly from the environment, information is soon likely to become outdated, especially in fluctuating environments, thus reducing the fitness benefits of learning socially. Early theoretical analyses predicted that social learning would only be beneficial if it was rare, reaching an equilibrium with asocial learning at a point where there was enough reliable and up-to-date information coming in directly from the environment (Boyd and Richerson, 1985; Rogers, 1988). Furthermore, indiscriminate copying can lead to the uptake of maladaptive behaviours if, for example, the original demonstrator is unaware that a more beneficial option is available. Laland and Williams' (1998) study on guppies (*Poecilia reticulata*) illustrated this idea well. They demonstrated that individuals would copy the route-choice of trained demonstrators even when the demonstrated route was longer and more energetically costly than an available alternative. Evolutionary theory therefore predicts that, to optimise the social learning process, individuals should be selective about how they use social information through the use of 'social learning strategies' (Laland, 2004; Rendell *et al*., 2011; Boyd and Richerson, 1985).

1.3. Social learning strategies

Social learning strategies describe how individuals use social information, including when they favour social over asocial information and what types of individual they preferentially copy. First coined by Laland (2004), social learning strategies are traditionally split into two categories, "when" strategies and "who" strategies. "When" strategies describe the hypothesised situations in which individuals are expected to use social information over independent learning, such as when their own learning is unproductive or when asocial learning is costly. "Who" strategies (also referred to as "directed social learning"; Coussi-Korbel and Fragaszy, 1995) describe the types of demonstrator an individual preferentially learns from when learning socially, such as more successful individuals, older individuals or dominant individuals. We can also describe individuals as displaying "social learning biases" towards particular types of information ("content-based biases", e.g. a bias towards social information or more memorable behaviours), towards demonstrators with particular characteristics ("model-based biases") and towards behaviours based on their frequency ("frequency-dependent biases", e.g. copy the majority, copy rare behaviours) or associated payoffs ("payoff-based biases") (Boyd and Richerson, 1985; Rendell *et al*., 2011). Below I outline some of the specific social learning strategies identified through both theoretical and empirical research across a range of species.

Theoretical analyses have demonstrated a range of conditions which are expected to alter the use of social information. For example, an increased cost of asocial learning (Boyd and Richerson, 1985; Rendell, Fogarty, *et al*., 2010), uncertainty about the best behaviour to use (Boyd and Richerson, 1988) and the use of more successful variants by other individuals (Schlag, 1998) are all predicted to increase the adaptive value of social learning. In contrast, social learning is expected to be less adaptive when there is a large amount of spatial or temporal environmental variability (Enquist *et al.,* 2007; Rendell, Fogarty, *et al*., 2010; Feldman *et al.,* 1996). There is also a general consensus that the most adaptive behaviours should involve strategically switching between social and asocial learning. In particular, it is predicted that individuals will benefit from initially relying on social learning and switching to asocial learning if this proves unfavourable, even when asocial learning is not associated with a cost (Enquist *et* *al.,* 2007; Rendell, Boyd, *et al*., 2010; Rendell, Fogarty, *et al*., 2010) – although Rendell and colleagues 'social learning strategies tournament' additionally demonstrates that relying exclusively on social learning as a form of 'information parasitism' can prove the most successful individual strategy provided other members of the population are sampling the most optimal behaviours directly from the environment (Rendell, Boyd, *et al*., 2010). Theoretical analyses also suggest that a 'conformist bias' (a positive frequency-dependent strategy where individuals disproportionately copy the most common behaviour) should be adaptive under a wide range of conditions, including over spatially variable environments, as innately copying a common behaviour improves an individual's chance of acquiring a favoured variant for that particular area (Boyd and Richerson, 1985; Henrich and Boyd, 1998; Nakahashi, 2007). However, a conformist bias could also be maladaptive in some situations if it prevents or slows the spread of more adaptive innovations (Henrich and Boyd, 1998). This may be particularly apparent in rapidly changing or harsh environments (Nakahashi, 2007; Whitehead and Richerson, 2009; Perreault *et al.*, 2012).

Empirical research has revealed evidence for the use of several social learning strategies by humans and non-human animals, plus similarities in the use of social information between very different species, suggesting convergent evolution due to similar selection pressures promoting the selective use of social information (Rendell *et al.*, 2011). For example, human participants choosing the best arrowhead to use in a virtual hunting simulation tend to copy the most successful variant (Mesoudi, 2008; Mesoudi and O'Brien, 2008). Similarly, nine-spined sticklebacks (*Pungitius pungitius*) are more likely to copy the food patch choices of individuals which receive a higher payoff than themselves (Coolen *et al.,* 2005; Kendal *et al*., 2009; Pike *et al*., 2010). Both nine-spined sticklebacks subjected to foraging tasks (Pike and Laland, 2010) and humans subjected to abstract multiple-choice tasks (Morgan *et al*., 2012; Efferson *et al.*, 2008) conform to the majority when making decisions. There is additional evidence that humans copy variants which are increasing in frequency (Toelch *et al*., 2010) and that some individuals (known as 'mavericks') ignore social information completely (Efferson *et al.,* 2008). Both humans and non-human animals are also biased towards the types of demonstrators they learn from. For example, humans, guppies and zebra finches show learning biases towards familiar over non-familiar individuals (Corriveau and Harris, 2009; Swaney *et al*., 2001; Guillette *et al*., 2016); humans, common ravens and Siberian jays preferentially copy kin over non-kin (Henrich and Henrich, 2010; Schwab *et al.,* 2008; Griesser and Suzuki, 2016) and both humans and chimpanzees tend to copy high-ranking and/or older individuals (Henrich and Henrich, 2010; Kendal *et al.,* 2015). These model-based social learning biases can be a useful evolutionary strategy if focussing one's learning towards a certain type of individual tends to result in more profitable behaviours being acquired. For example, older individuals may offer a reliable source of adaptive behaviours because they have had more life experience to test different behaviours in different scenarios, and because these behaviours have enabled them to survive to an older age. Similarly, a dominant individual may represent a source of adaptive social information if their high dominance status is linked to their general success, while a prestigious individual who receives disproportionate attention from observers may do so because they are in possession of more desired skills. A naïve individual with an instinctive bias for copying demonstrators with characteristics that accurately predict their general success will theoretically learn adaptive behaviours without spending the time and effort either testing different behaviours themselves or assessing the actual success rates of behaviours used by others. Social learning biases have the potential to affect not just the information an individual gains, but also the pattern of information flow throughout the whole social group.

The methods used to investigate the use of social learning strategies, however, vary between animal and human studies, which make generalisations across the human / non-human divide difficult. The types of social learning experiments used in the animal versus human literature are discussed in more detail below.

1.4. Social learning experiments: animals

Traditionally, research into social learning strategies in non-human animals has involved laboratory experiments where a naïve individual is exposed to a small number of trained demonstrators, each demonstrating a different behaviour. One of the best examples of this is Galef's (2009) series of experiments on Norway rats (*Rattus norvegicus*). These experiments involved training a demonstrator to eat one of two different flavoured foods, pairing the trained demonstrator with a naïve observer, then giving the observer the choice between the two food types to establish whether the observer showed a significant preference for the demonstrated food type (or for the food type of one demonstrator over another). This same methodology was repeated across a number of different conditions and using pairs of demonstrators with different characteristics to determine when and from whom rats would selectively use social information. These 'demonstrator-observer' experiments give a lot of insight into the use of social learning strategies in animals but are also met with several limitations. Firstly, it could be argued that such highly controlled laboratory experiments limit natural behaviour by preventing free movement and natural interactions between individuals. Secondly, forcing a choice between two possible demonstrators does not tell us whether individuals would make such a choice in a natural context, where other alternatives, including learning entirely asocially, would also be available. Thirdly, because such experiments only consider a single learning event from demonstrator to observer, they do not tell us about the transmission of information through an entire population and whether social learning biases remain consistent during population-level information transfer.

In natural conditions, a variety of factors will influence how individuals learn from one another, from the general structure of the population's social network to where a naïve individual is looking at the time a novel behaviour is demonstrated. Spatial and temporal coordination of behaviours between multiple individuals in a population (i.e. whether an observer was in the right place at the right time to directly observe a behaviour being performed, rather than viewing the behaviour from a distance or observing only the products of a behaviour that has already been performed) can determine the amount of detail an observer can gain about a demonstrated behaviour and so the type of learning that can occur (Coussi-Korbel and Fragaszy, 1995). Even simple variation in individual personality traits, including movement patterns, can change an individual's position in a social network (Krause *et al.,* 2010; Aplin *et al*., 2013), thus influencing its access to social information (Aplin *et al*., 2012; Claidiere *et al.,* 2013) and ultimately determining the possible demonstrators that it is able to selectively learn from. Results from theoretical and empirical experiments that do not consider such factors may therefore be an unrealistic representation of social information use, representing an 'ideal' situation, where all individuals have access to all available social information and can selectively choose between different options.

More recently, studies on social learning strategies in non-human animals have used 'open diffusion' experiments to establish the natural patterns of information transfer in larger populations (Hoppitt and Laland, 2013). These experiments often involve introducing a novel task – for example, 'puzzle boxes' or 'artificial fruit' that can be solved using multiple techniques to access food rewards – to a free-roaming captive or wild population, sometimes after seeding the population with one or more trained demonstrators, and then analysing how information spreads naturally through the population (e.g. Whiten and Mesoudi, 2008; Claidiere *et al.,* 2013; Aplin *et al.,* 2015; Canteloup *et al.*, 2020). Open diffusion experiments are, in general, less restrictive on natural behaviour, allowing individuals to learn a task however they choose, be that socially (either indiscriminately or from particular demonstrators), independently, or not at all. Therefore, such experiments are likely to give a more accurate and ecologically relevant insight into the social learning strategies that are naturally used by a particular species. In addition, open diffusion experiments allow us to analyse the patterns of information transmission not just between pairs of individuals, but through whole populations. However, because these types of experiments are less controlled and often involve simply placing a novel task into a population and allowing social learning processes to occur naturally, deciphering when individuals are learning socially, and from whom, is more difficult. Statistical approaches have been adapted to tackle this issue, allowing researchers to fit models corresponding to different hypothesised social learning strategies to data on naturally occurring task solves as a way of inferring how individuals are learning (McElreath *et al.*, 2008; Franz and Nunn, 2009; Hoppitt *et al.,* 2010; Hoppitt, 2017). Such methods also allow investigations into the diffusion of non-introduced, naturally occurring innovations – for example, the social transmission of a foraging technique known as 'shelling' through dolphin (*Tursiops aduncus*) populations (Wild *et al.,* 2020). Such methods have allowed the study of social learning strategies in non-human animals to advance into more realistic and ecologically relevant scenarios.

1.5. Social learning experiments: humans

While animal studies have managed to move out of the lab and into field experiments where individuals can behave naturally to solve ecologically relevant tasks such as foraging or avoiding predators, studies on humans remain fixed in restrictive laboratory conditions. The vastly different methodologies used in human versus animal social learning experiments, particularly the lack of realism and natural relevance in human experiments (discussed below), make it difficult to compare human and non-human social learning strategies within a common evolutionary framework. Outside of social learning research, there is a general concern that laboratory studies on human behaviour may not accurately reflect how people would behave in real-life situations, that too much control over an experiment may inadvertently influence participants' decisions and that participants taken only from student pools may behave differently to members of the general public (Levitt and List, 2007a; Levitt and List, 2007b; Vicens *et al.,* 2018; Santos, 2009). In addition to this, there are several characteristics of human experiments that specifically make them difficult to consider in an ecological or evolutionary framework.

Firstly, human studies tend to use abstract tasks with no relevance to real-life situations that offer little insight into the adaptive benefit of social learning strategies for human survival. Examples of tasks used in human experiments on social learning strategies include choosing between coloured options with hidden values to receive the greatest payoff (Efferson *et al.,* 2008; Toelch *et al.,* 2010), deciding which of two lines are the longest (Morgan *et al*., 2012) and building towers as tall as possible using modelling clay and spaghetti (Caldwell and Eve, 2014). While these studies offer some insight into how and when humans use social information when given a simple, abstract task, they do not tell us how humans learn more complex skills or how our use of social information this might have contributed to our evolution. In addition, I argue that using abstract tasks where individuals are not able to use their own prior knowledge or skills might artificially increase participants' reliance on social information. For example, in the experiment by Toelch and colleagues (2010), participants had no way of independently learning which coloured card held the highest value other than to make a guess. In this case, it may have been preferable to use even potentially inaccurate social information. Very few laboratory-based experiments on human social learning strategies have used realistic or ecologically relevant tasks, with the major exception of a series of experiments by Mesoudi and colleagues, where participants were required to design arrowheads to use in a virtual hunting ground (Mesoudi, 2008; Mesoudi and O'Brien, 2008). In this case, the task is more realistic and so participants have a greater chance of using their own intuition or knowledge to attempt the task themselves.

Secondly, the methodologies used in lab-based human experiments tend to present social information in an unrealistic or overly simplistic way. Examples include using flashing tiles to represent demonstrator choices (Morgan *et al*., 2012) and giving a numeric value representing the frequency of demonstrators using a particular behaviour (Toelch *et al.*, 2010) or the success rates of different individuals (Mesoudi and O'Brien, 2008; Miu *et al.,* 2018). Essentially, this means that participants are being told what other individuals are doing and how useful certain behaviours are without having to infer this information themselves based on demonstrator behaviours. In addition, participants may be restricted as to when and how they are 'allowed' to use social information (e.g. Mesoudi and O'Brien, 2008). In reality, gaining social information requires actively observing and understanding the behaviours that are being displayed, which will be affected by simple factors such as the location of different individuals or where a naïve observer is looking at the time a particular behaviour is being demonstrated. Even something as simple as establishing the frequency of demonstrators using a particular behaviour would require observers to keep track of multiple demonstrators, potentially over large spatial and even temporal scales, which is relatively more complex than being given a single numerical value. Once in possession of social information, an individual must then decide whether, when and how to use that information. Furthermore, making use of social learning strategies requires an individual to gather and compare information from different sources – information that will not necessarily be displayed to them simultaneously – alongside their own experience. It could be argued, therefore, that the simplification of social information often used in human social learning experiments may make it ‘too easy’ for participants to gather, compare and use social information, and so may not reflect what would happen in reality.

The third characteristic of most human social learning experiments that makes it difficult to consider their findings in an evolutionary framework is spatial scale. Almost all human social learning experiments take place in the laboratory or some other relatively confined indoor space (e.g. Reader *et al.*, 2008; Wood *et al.,* 2013; Whiten *et al.,* 2016), and involve tasks such as puzzle boxes located in a single localised area. In reality, many tasks associated with human survival would take place over much larger spatial scales. In traditional hunter-gatherer communities, both today and in our evolutionary past, space use for activities such as foraging occurs over kilometre scales (Hamilton *et al*., 2007; Whallon, 2006). Allowing space use of this scale is not possible in the laboratory, but is likely to have a great influence on both an individual’s ability to make use of social information (e.g. are there demonstrators in the vicinity that can be learned from?) and the type of learning taking place (e.g. imitation, which requires close observation, versus local enhancement, which can likely be triggered over a longer distance) (Coussi-Korbel and Fragaszy, 1995). At the most extreme end of the scale, large-scale spatial movements may involve migrating from familiar to unfamiliar areas, which may influence how an individual responds to social information – e.g. migrating individuals may show an enhanced tendency to conform to local norms (Deffner *et al.,* 2020).

The study of human social learning very rarely manages to escape the lab into the field. A major exception to this is a set of experiments by Henrich and colleagues investigating the social influences on learning about toxic marine foods, crop growing and use of medicinal plants in Fijian hunter-gatherer populations (Henrich and Henrich, 2010; Henrich and Broesch, 2011). However, such an experiment cannot be easily generalised to contemporary human societies other than hunter-gatherers, where individuals are not routinely exposed to the same kinds of selection pressures. While animal research benefits from the ability to study populations in their natural habitats (using statistical analyses to decipher the pathways of learning) or alternatively to study captive individuals as an intermediate between laboratory experiments and studies on free-roaming individuals, human research does not benefit from such methodologies and so tends to be restricted to abstract lab-based tasks. Thus, human research tends to lack ecological validity compared to animal studies. Computer-based tasks are one way in which studies can incorporate evolutionary validity (e.g. Mesoudi, 2008; Mesoudi and O'Brien, 2008) and spatial factors (e.g. Deffner *et al*., 2020) into human social learning experiments. Later in this thesis

(Chapters 4-6), I advocate the use of complex, open-world virtual environments for studying human behaviour in more evolutionarily relevant scenarios than is often possible in laboratory settings.

1.6. Physical, social and behavioural factors influencing social information transmission

Social networks are dynamic and complex biological phenomena. A myriad of factors, including how novel information enters the population, who is in possession of this information at a particular time, and the spatial synchrony of different individuals at the time novel information is being communicated have the potential to influence exactly where and when information is available for an observer to learn, and how information is transmitted through social groups. In this thesis, I explore three key factors which I hypothesise to influence social transmission across the three stages of information transfer described above.

Firstly, spatial movement patterns determine which individuals are in close enough proximity to exchange information at any particular time (Figure 1.2A). Individuals are likely to interact more within submodules (local clusters of individuals) of the wider network than with individuals from other submodules, while spatial isolation is likely to block information transfer entirely. Thus, the spatial locations of individuals at the time a particular behaviour or piece of information is being demonstrated will be crucial in determining whether demonstrator and observer are appropriately connected (as illustrated in Figure 1.1) for information exchange to theoretically occur. While previous studies have used proximity and association networks to analyse whether individuals are more likely to learn from those who they spend more time with (e.g. Allen *et al.,* 2013; Aplin *et al.,* 2013), the influence of individual-level spatial movements and space-use behaviour on social transmission is often overlooked in the social learning research – particularly in the human literature, as discussed above. Social network analyses have revealed, however, that personality traits that correlate with movement patterns can impact on an individual's connectedness within its social network (Krause *et al.,* 2010; Aplin *et al.,* 2013). The influence of individual spatial movements on information transfer is explored using a spatially explicit movement model in Chapter 2.

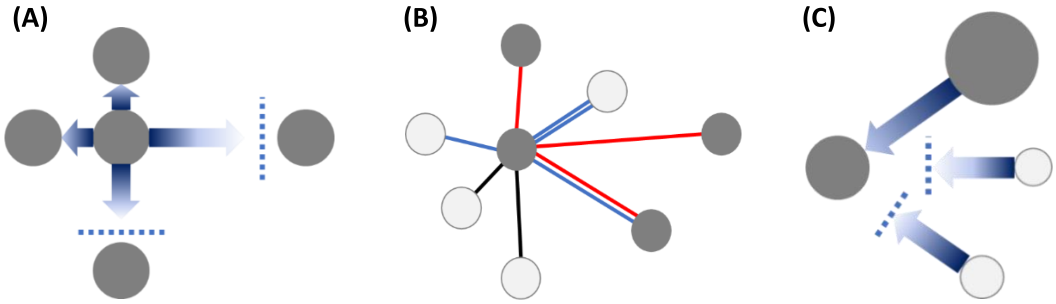

Figure 1.2. Three key factors predicted to influence social information flow by determining the structure of the underlying social network. **(A)** The spatial movements of individuals determine who is in close enough proximity to exchange information at any particular time. Spatial isolation is likely to block information flow between individuals who might normally learn from one another. **(B)** The types of connection between individuals. This example shows three hypothetical networks among seven individuals with knowledged individuals represented in dark grey. Here, the red network best predicts the presence of knowledge. **(C)** The characteristics of the demonstrators, regardless of the underlying social network structure. In this example, the focal individual learns preferentially from the larger demonstrator, despite similar proximity to smaller demonstrators.

Secondly, social networks can be structured by different types of connections, and some networks may predict the pathways of social learning better than others (Figure 1.2B). Some individuals may, for example, be more likely to exchange information with those they share specific social relationships with, e.g. learning from kin. The importance of social relationships on driving information transfer is thus far limited to just a handful of studies, with most research focussing instead on the individual characteristics of demonstrators and observers – or their associations – rather than the underlying social connections between them. The idea of relationship-based learning is explored using a multi-network analysis on zebra finches in Chapter 3.

Thirdly, regardless of the underlying social network, social learning might be determined by the characteristics of the demonstrators of information (Figure 1.2C). Certain types of demonstrators may, for example, be more prone to passing on information to others – thus influencing stage 2 of information transfer (Figure 1.1). Similarly, observers may be more prone to learning from specific types of demonstrator (e.g. large over small individuals, males over females, etc.) – thus influencing stage 3 of information transfer (Figure 1.1). I test several potential demonstrator preferences (size, dominance, gender, frequency) in a virtual reality experiment on humans in Chapter 5. In addition, in Chapter 2, I explore how variation in individuals’ tendency to pass on and receive information affects the patterning of information transfer through the social network.

1.7. Thesis aims and outlines

In this thesis, I investigate the impact of physical, social and behavioural factors on social transmission at the different stages of information transfer described above and consider how this impacts not only learning at the individual level, but also the transfer of information throughout entire populations. By conducting my investigations across different systems, I also make comparisons of social information use across different taxa. Throughout this thesis, I pay particular attention to the development of novel methodologies and expansion of past methodologies that aim to tackle some of the limitations of previous research and allow a more realistic portrayal of social transmission processes; especially by permitting more behavioural freedom than is typically possible in controlled, lab-based experiments and by incorporating the influence of spatial movements that may impact on who can learn from whom at a given time.

Throughout the following chapters, I will focus in on some specific aspects of social transmission within different model systems. Here, I will briefly outline the aims of these upcoming chapters:

- In Chapter 2, I devise an agent-based simulation model which aims to investigate how among-individual variation in simple behavioural axes (namely activity levels and movement patterns) influence the patterning of interactions and the resulting transfer of information at the population level. As described above, there is a serious gap in the literature concerning the role of individual spatial movements in the driving of information transfer through population networks. The agent-based simulation approach adopted here provides an empirical test of how the production of a particular network substructure – the “feed-forward loop” – is influenced by among-individual behavioural variations in space and time, and how the overproduction of this substructure affects the efficiency of information transfer through the simulated population. Thus, this chapter focusses on how the behaviours of the individuals can influence the structure of the social network at the group level.

- In Chapter 3, I investigate whether the pairwise social relationships that individuals share influence their tendency to learn from one another within a population of social birds, using network-based approaches. While similar analyses have been carried out before, they are usually restricted to the assessment of one or two types of association, e.g. proximity or affiliative interactions, rather than the influence of social relationships. In addition, the importance of mated pair bonds and aggressive interactions on social learning have received little attention in previous research. I further develop this network-based approach to evaluate a wide range of competing hypotheses concerning the importance of feeding associations, positive interactions, aggressive interactions and mated pair bonds in driving the transfer of information (solutions to a feeding task) through a freely-interacting population of zebra finches, thus building a comprehensive model of relationship-based social learning in this species. Thus, this chapter focusses on how the properties of the underlying social network can influence the transmission of novel information and behaviours through the population.

ξ In Chapter 4, I describe an innovative new tool for studying social learning in humans using realistic virtual environments: “Virtual Environments for Research into Social Evolution” (VERSE). As discussed above, human social learning research is often restricted to abstract, lab-based experiments which often involve unrealistic sources of social information and do not take into account the influence of spatial factors. In other words, these experiments generally do not provide a realistic representation of real life survival scenarios, where individuals would need to actively observe informed demonstrators across space and time in order to gather information. Participants may therefore act very differently during such experiments compared to how they might behave in complex environments that offer them a greater degree of behavioural freedom. VERSE tackles many of the issues of lab-based human social learning research by allowing human behaviour to be studied within ecologically relevant scenarios, in large-scale three-dimensional environments that they can navigate freely, using computer-controlled humanoid figures as realistic sources of social information that can be actively followed and observed. This chapter is structured as a methodological article, giving a detailed account of the features available in VERSE and how they can be used to conduct more realistic human behavioural experiments. Thus, this chapter focusses on improving the realism and ecological validity of human social learning experiments.

ξ In Chapter 5, I use VERSE to investigate human social learning strategies within complex environments in a series of experiments inspired by the animal literature. Specifically, I investigate whether humans are prone to using social over asocial information when faced with complex, ecologically relevant tasks and whether individuals are biased towards learning from demonstrators with particular characteristics, as demonstrated previously in the human and animal literature. I place a strong focus on allowing complete freedom of movement and behaviour that is often not possible in human experiments due to the restrictions of the laboratory environment. In doing so, I aim to gain a more accurate understanding of how humans use social information in complex, naturalistic environments, to test the findings of more restrictive, lab-based experiments against scenarios where participants are offered a greater degree of behavioural freedom and to allow generalisations to be made across the human / non-human divide. Thus, this chapter focusses on how demonstrator characteristics and observer biases can dictate the patterns of information exchange between individuals – and also on exploring the use of realistic, three-dimensional virtual environments for the study of human social behaviour.

ξ In Chapter 6, I will bring the findings of these studies together into a general discussion about social learning, including the often overlooked social, behavioural and physical environmental factors influencing social transmission at both the individual and population level. I discuss the importance of individual behavioural variation in social learning in determining how information enters and transmits through the population and why an understanding of social influence and the patterns of information transmission is important both within and outside the field of behavioural ecology.

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Chapter 2 | Behavioural variation among workers promotes feed-forward loops in a simulated insect colony

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2.1. Abstract

Coordinated responses in eusocial insect colonies arise from worker interaction networks that enable collective processing of ecologically relevant information. Previous studies have detected a structural motif in these networks known as the feed-forward loop, which functions to process information in other biological regulatory networks (e.g., transcriptional networks). However, the processes that generate feed-forward loops among workers and the consequences for information flow within the colony remain largely unexplored. We constructed an agent-based model to investigate how individual variation in activity and movement shaped production of feed-forward loops in a simulated insect colony. We hypothesised that individual variation along these axes would generate feed-forward loops by driving variation in interaction frequency among workers. We found that among-individual variation in activity drove overrepresentation of feed-forward loops in the interaction networks by determining the directionality of interactions. However, despite previous work linking feed-forward loops with efficient information transfer, activity variation did not promote faster or more efficient information flow, thus providing no support for the hypothesis that feed-forward loops reflect selection for enhanced collective functioning. Conversely, individual variation in movement trajectory, despite playing no role in generating feed-forward loops, promoted fast and efficient information flow by linking together unconnected regions of the nest.

Keywords: network motif; social insects; feed-forward loop; agent-based model; personality; behavioural syndrome

2.2. Introduction

In many group-living species, social interaction patterns play an important role in shaping fitness outcomes, such as by impacting access to social information, the likelihood of cooperation, or exposure to pathogens [1]. Beyond an individual's direct connections, evolutionary fitness may further be influenced by the patterning of interactions at the group level. For instance, a minority of highly interactive individuals can accelerate the spread of information or disease throughout a population by linking together otherwise unconnected individuals [2] and modular social structures can contain the spread of information within tightly-knit communities [3]. These group-level properties are likely especially important in eusocial insect colonies in which only one or a few colony members reproduce, such that the fitness of individual workers is tightly linked to colony collective performance [4].

In the absence of any central control, interactions among workers regulate task allocation through a distributed process, ensuring that the effort devoted to various tasks matches a colony's internal needs and external conditions [5,6]. Meeting the demands of this regulatory role is likely to favour different interaction patterns to those that are observed in social systems where individual success is key. In other words, a social insect worker's position in the network is often less important for its fitness than higher-level network properties [5-7]. For instance, among-individual variation in interaction frequency in harvester ants (*Pogonomyrmex barbatus*) generates networks with a few highly interconnected individuals while the majority of workers remain only weakly connected [2]. Networks structured in this way permit rapid information transfer throughout a population and can thereby facilitate swift collective responses to changing conditions [2].

Social network analysis has emerged as a key approach for quantifying variation in social connectivity and investigating its ecological and evolutionary consequences [1,8,9]. A useful means to gain insight into a network's functionality is to deconstruct it into its constituent subcomponents [10]. A network can, for instance, be described in terms of the different 3-node subgraphs (or triads) from which it is composed. Because subgraphs differ in their functional properties [11-13], overrepresentation of a given subgraph within a network (relative to its typical representation within an ensemble of appropriately randomised networks) can suggest the processes or functions that have helped to shape that network. For example, food webs display an overrepresentation of simple chains derived from trophic interactions—e.g. species A consumes species B, which in turn consumes C [10]—whereas gene transcription networks contain an overabundance of a triadic configuration known as the "feed-forward loop" (Figure

2.1A; [12]), whereby a gene A transcriptionally regulates the activity of a second gene B, and both A and B jointly regulate a third gene C. As feed-forward loops are well-suited to carry out signal processing tasks (e.g. amplifying responses to external environmental cues), this structural feature may reflect the regulatory function of these networks [11].

The regulatory role of interaction networks within social insect colonies may likewise be reflected in their constituent subcomponents. In common with other biological regulatory systems, the antennation patterns of harvester ants (*Pogonomyrmex californicus*), which play a key role in transmitting task-relevant information between colony members, show an overrepresentation of feed-forward loops [7], at least relative to their appearance in size- and density-matched random graphs. Similarly, dominance relationships in the eusocial wasp *Ropalidia marginata* are made up predominately of feed-forward loops and are involved in regulating worker activity through agonistic interactions [14]. However, the way in which such network structures develop in social insect colonies is unclear.

In contrast to other biological regulatory networks, where the relationships between nodes are relatively stable (e.g. one gene produces a transcription factor that activates or inhibits another gene), the nodes in social insect interaction networks represent individual workers that engage in brief pairwise interactions with one another and often lack stable relationships. The patterning of interactions among workers instead arises from the behaviour of individuals that influence their likelihood of interacting. In some cases, the presence of feed-forward loops might simply reflect the tendency of a particular type of relationship to be transitive—e.g., in the dominance networks of *R. marginata* [14], if worker A is dominant over B and B is dominant over C, A is likely to also be dominant over C. Feed-forward loops consequently tend to form in the network. Yet even in this case, the formation of dominance relationships is dependent on other aspects of behaviour that influence individuals' likelihood of interacting, such as their spatial location on the nest. If A and C never interact, a feed-forward loop will never form between A, B, and C. Furthermore, the reason for the development of feed-forward loops in interaction networks that lack such hierarchical organization (e.g., the antennation patterns of *P. californicus*) is less clear, and suggests that more subtle behavioural mechanisms may be responsible for generating this structural feature in these populations.

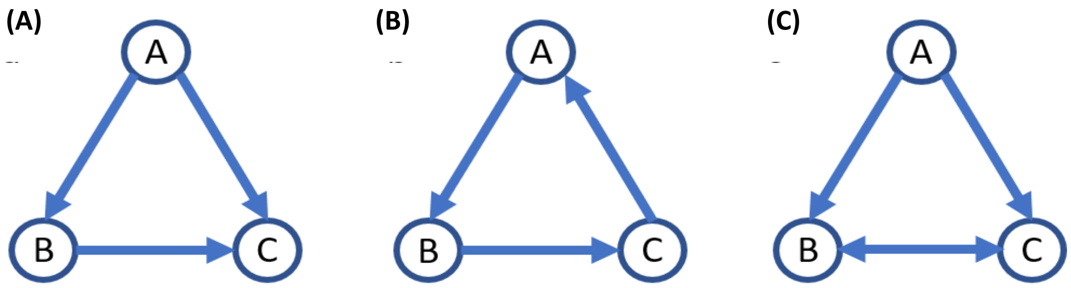

Figure 2.1. Examples of triangle configurations. **(A)** A transitive triangle, or feed-forward loop, in which one individual, A, has two outgoing edges and another, C, has two incoming edges. **(B)** A cyclic triangle, in which all individuals have one outgoing and incoming edge. **(C)** A triangle with a bidirectional edge connecting B and C.

The structure of a feed-forward loop inherently implies among-individual variation in contact patterns, as each node differs in the number of incoming and outgoing connections (or edges). Insect workers express substantial among-individual variation along a number of behavioural axes that may contribute to the generation of such network structures [15]. For instance, workers vary in the proportion of time that they are actively engaged in tasks: e.g. a minority of workers often carry out the majority of work [16-20], with some workers even appearing to specialise in inactivity [21]. Workers also vary in their spatial behaviour within the nest. This can partly be determined by activity levels—more active individuals will tend to cover more ground per unit time—but can also result from variation in movement patterns. Some *P. barbatus* workers, for example, walk very sinuous paths, causing them to occupy relatively restricted regions within the nest, while others walk straighter paths and so roam more extensively [2]. Such among-individual variation in activity and space-use may play central roles in shaping social contact patterns by influencing the likelihood that particular individuals will contact one another. For example, workers that move in straighter paths will likely contact a greater number of nestmates than workers that remain restricted to small regions within the nest. That different pairs of individuals vary in their likelihood of interacting further suggests that random graph models, which typically assume an equal probability of interaction between any pair of nodes, may not be the most appropriate null model with which to assess the presence of network motifs in empirical social insect interaction networks.

Here, we construct an agent-based model to investigate how among-individual variation in activity and movement patterns in a simulated insect colony contributes to the formation of interaction networks dominated by feed-forward loops. We further consider how this variation drives the speed and efficiency of information flow within the colony. Our model is not designed to reproduce the dynamics of any specific species. Rather, we seek to evaluate structural and functional consequences of patterns of behavioural variation that are commonly observed across eusocial insects [15,22], with a particular focus on how such variation shapes patterns of physical contact between workers (e.g., antennation), which are central in regulating collective behaviour [2,6,7]. We first predict that, by determining how frequently individuals contact others and how diverse those contacts are, among-individual variation in activity and movement will drive overrepresentation of feed-forward loops in the resulting interaction networks. We further predict that, when these sources of variation are treated as a 'behavioural syndrome' (i.e. individual activity and patterns of movement covary, such that that the most active agents walk the straightest paths, while the least active agents walk the most tortuous paths), they will have a synergistic effect on the production on feed-forward loops by emphasising among-individual variation in space-use (i.e. highly active, straight-walking individuals will traverse the entire nest, while inactive individuals with tortuous walking paths will remain in restricted areas). Second, due to the tendency of feed-forward loops to move information in a directional manner [11,12], we predict that patterns of behavioural variation that generate feed-forward loops will also lead to faster and more efficient information flow, in the sense that fewer interactions will be needed to drive the spread of information throughout a colony [7].

2.3. Methods

2.3.1. Agent-based model

Our model was created in the agent-based modelling platform NetLogo (V5.2.0; https://ccl.northwestern.edu/netlogo/) and is available at the Dryad Digital Repository, doi:10.5061/dryad.brv15dv8f [60]. We briefly describe the model's main processes below (also summarised in Figure 2.2). The full model description, which follows the ODD (Overview, Design concepts, Details) protocol [23], can be found in the Supplementary Material.

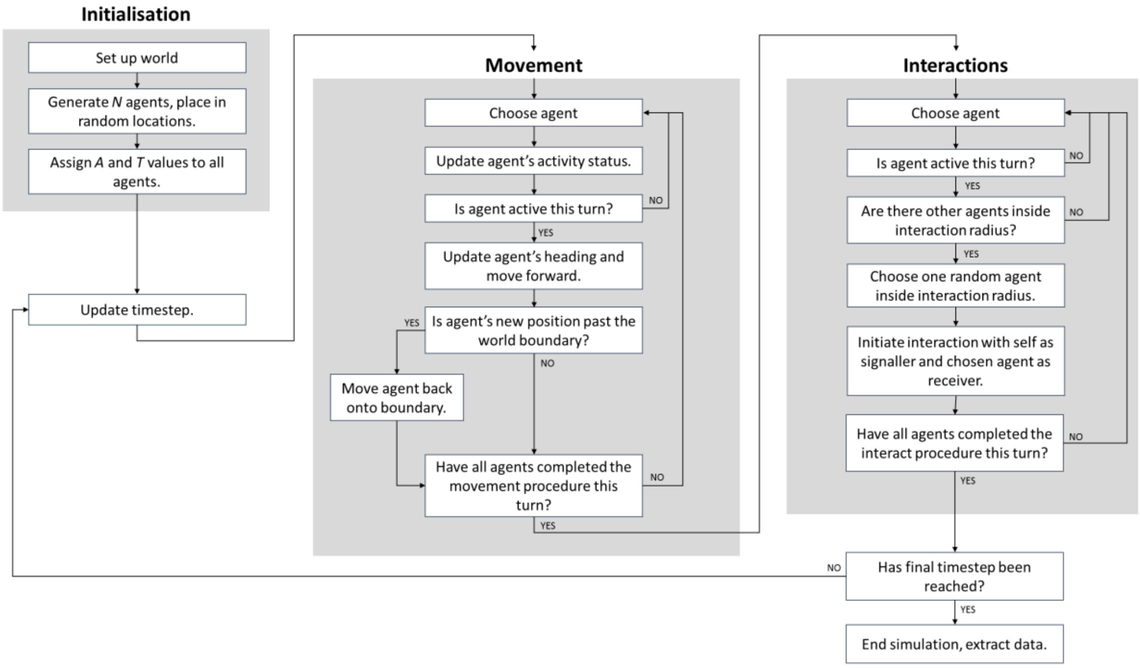

Figure 2.2. Flowchart describing the main model processes, including model initialisation, agent movement, agent interactions, timestep updates and data extraction.

Model initialisation. The model consists of a 50 x 50 grid of square 'patches' (the 'nest') containing the agent population ($N_{default}$ = 100), which represent workers within a social insect colony. At the beginning of each simulation, each agent (i) is placed in a random location and assigned its activity level (A_i) and turning index (T_i). The value of A_i determines how mobile an agent is within the nest and, under certain conditions, its likelihood of transmitting information to others upon physical contact. Conceptually, active agents represent individuals currently engaged in some task within the nest—e.g. nest construction, food distribution, recruitment—with the possibility of transmitting task-relevant information to individuals that they come into contact with. The value of T_i determines how sinuous an agent's walking path is—more sinuous paths result in greater spatial fidelity as individuals move away from their starting position more slowly. Agent movement occurs during discrete time steps ($t_{default}$ = 5000 steps) and the order in which agents act is selected randomly on each step. Once all agents have had the opportunity to move, agents can initiate interactions with nearby nestmates, with the order of action once more randomly determined. See 'Agent movement' and 'Agent interactions' below for an explanation of these processes.

Activity levels and turning indices can be either uniform or variable across the population and are centred around the population means, A_m and T_m respectively. When activity levels are uniform, all agents are assigned the same value, $A_i = A_m$. When activity levels are variable, values are randomly drawn from an exponential distribution with mean A_m, such that most agents are relatively inactive, while a few are highly active. Similar distributions of activity have been observed across multiple social insect species (e.g. ants [24]; stingless bees: [20]; bumblebees: [19]). When turning indices are uniform, all agents are assigned the same value, $T_i = T_m$. When turning indices are variable, values are first randomly drawn from an exponential distribution with mean T_m. These values are subsequently modified (see full ODD model in the Supplementary Material) such that most agents have relatively high turning indices, resulting in more tortuous movement paths, whereas a few agents have low turning indices, and so move in straighter paths (as observed in [2]). In addition, when both activity levels and turning indices are variable, values of A and T can either be uncorrelated or negatively correlated across agents. If uncorrelated, these values are assigned to agents independently of each other. If negatively correlated, these values are paired such that the agent with the highest value of A also has the lowest value of T, and so on, thus generating a population where more active agents also tend to move in straighter paths. This was done in order to explore whether such a behavioural syndrome [15] may especially contribute to the formation of feed-forward loops, given that active individuals with a greater potential to initiate contact (see ‘Agent interactions’ below) would also potentially contact a greater diversity of individuals, due to reduced spatial fidelity.

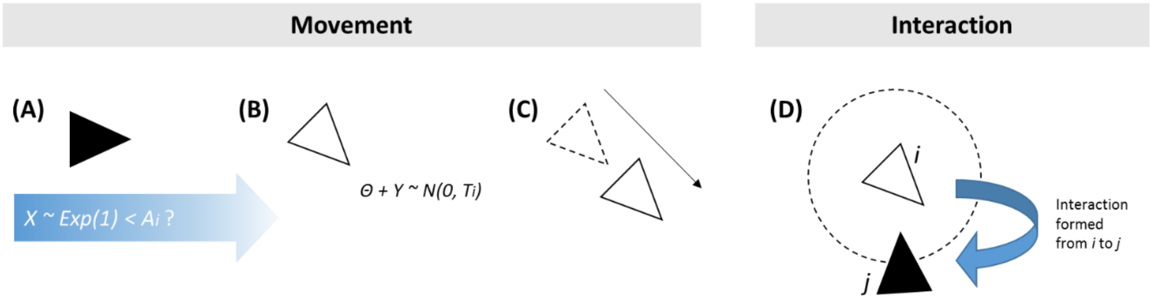

Figure 2.3. Movement and interaction processes performed by all agents each timestep. During the movement process, **(A)** an agent, *i*, begins the timestep as inactive (black shading). If a value, *X*, drawn from an exponential distribution with a mean of 1 is less than *i*’s activity level, A_i, **(B)** the agent becomes active (white shading) and updates its heading, then **(C)** moves forward. During the interaction process, **(D)** any agent that is currently active (white) forms a directed interaction to a randomly selected agent within its interaction radius (dashed circle). In this example, active agent *i* forms a directed interaction to inactive agent *j*.

Agent movement. Agents move in a correlated random walk [25] governed by their activity level and turning index (Figure 2.3A-C). Agent *i* will only move during time step *t* if it is 'currently active'. An agent is considered to be active on a given time step if $\propto < A_i$, where $\propto$ is randomly drawn from an exponential distribution with mean 1. Accordingly, if A_m is set to 1, half of the agents in the population will, on average, be active on any given time step, comparable to observed activity patterns in several social insect species [17,18,26]. If agent *i* is active during time step *t*, its current heading is updated as: $\theta_{i,t+1} = \theta_{i,t} + \delta\theta$, where $\delta\theta$ represents the change in direction drawn from normal distribution with mean 0 and standard deviation T_i (c.f. [27,28]). A higher value of T_i will therefore result in a more tortuous movement path and consequently greater spatial fidelity within the nest. After updating its heading, agent *i* then moves forward by one body length (equivalent to 0.5 patches). Agents are prevented from moving past the nest boundaries to capture the physical constraints present within a social insect nest. If forward movement would cause *i* to move past a boundary, its x and/or y coordinate is set to that of the boundary to ensure that it does not move past.

Agent interactions. Agents can form pairwise, directed interactions with one another upon coming into contact (Figure 2.3D). The formation and direction of interactions are both determined by agent activity by default (but see Experiment ii, where these constraints are relaxed). Each agent has an 'interaction radius' of 0.5 patches (equivalent to one body length) which determines when they are in physical contact with each other. An interaction radius equal to one body length was used because worker interactions often involve physical contact (e.g. antennation, food-sharing) and observations on multiple species suggest one body length is well within the range at which workers can detect nestmates [29,30]. If agent *i* is currently active and has at least one other agent within its interaction radius at timestep *t*, it forms an outgoing connection to one random agent, *j*, within its interaction radius. Agent *i* is therefore considered the information signaller and *j* the information receiver. Our assumption that information transfer is linked to activity in this way reflects a situation often seen in social insect species, where knowledgeable individuals actively transmit information to others, e.g. the honeybee waggle dance [31]. In other circumstances, greater activity can be positively related to the likelihood of acquiring information from nestmates—e.g., when an ant detects the cuticular hydrocarbons or food-associated odours borne by nestmates that it encounters [6]. We therefore investigated an alternative 'to-active' condition, where information tends to flow towards more active individuals, which produced qualitatively similar results (Figures 2.S1-2.S2).

2.3.2. Data collection

For every interaction that occurred throughout the simulations, we logged the following information: the ID of both agents involved, the interaction's direction, and the timestep during which the interaction occurred. This information was exported as a .csv file at the end of each simulation.

2.3.3. The experiments

Across several experiments, we investigated how the production of feed-forward loops within an interaction network is influenced by individual variation in activity and movement patterns, and the influence this has on within-colony information flow. Below, we describe the scenarios tested in each experiment and the statistical analyses of the data. In all cases, we used a population size of 100 agents and ran simulations for 5000 timesteps. All statistical analyses were carried out in R ver. 4.0.3 [32]. Generalized least squares (GLS) models were fit using maximum likelihood estimation in the *nlme* package [33]. A GLS framework allowed us to incorporate variance structures that modelled observed heterogeneity in residual spread where applicable [34]. Model selection was performed on the basis of Akaike's Information Criterion corrected for sample size (AICc) [35]. When a single model was strongly supported by the data (Akaike weight ≥ 0.95), inferences were based on that model. Otherwise, model-averaging was used across the minimal set of models whose summed Akaike weights were ≥ 0.95. Model selection was carried out using the *MuMIn* package [36].

2.3.3.1. Effects of behavioural variation on triangle transitivity

2.3.3.1.1. Model parameters and scenarios tested.

By determining how agents move, among-individual variation in activity and movement pattern is expected to influence how frequently (and with whom) individuals interact, thereby shaping the structure of the resulting interaction networks. We therefore compared simulations in which among-individual variation was present for activity level, turning index, or both to simulations in which these traits remained uniform across the population (Table 2.1). We ran 100 simulations for each of the following conditions: (i) Uniform, where A_i and T_i were set to A_m and

T_m respectively across all agents; (ii) Activity Variable, where A_i (but not T_i) varied across agents; (iii) TI Variable, where T_i (but not A_i) varied across agents; (iv) Uncorrelated, where both traits varied within a population, but activity variation was independent of variation in turning index; and (v) Correlated, where both traits varied within a population and A_i was negatively correlated with T_i. For each condition, interaction initiation was determined by agent activity and during interactions, active agents generated outgoing edges.

Table 2.1. The five behavioural conditions modelled in this experiment.

Condition	**Activity level, A_i**	**Turning index, T_i**	**Behavioural syndrome?**
Uniform	Uniform	Uniform	NA
Activity Variable	Varies	Uniform	NA
TI Variable	Uniform	Varies	NA
Uncorrelated	Varies	Varies	A_i and T_i are independent
Correlated	Varies	Varies	A_i and T_i are negatively correlated

For all conditions, $A_m = 1$ and $T_m = 60$. Setting A_m to 1 means that, on average, 50% of agents will be active on a given turn. Similar inactivity levels are commonly observed across social insect species [17,18,26]. A mean turning index of 60 is comparable to that observed in multiple ant species [2,37,38]. In addition, a sensitivity analysis showed that our results were robust to a range of values for A_m and T_m (Supplementary Material, Tables 2.S1-2.S5, Figure 2.S5).

2.3.3.2. Statistical analysis

To evaluate the role of among-individual variation in generating feed-forward loops, we compared mean triangle transitivity, t_{tri}, across the different conditions [13]. Triangle transitivity quantifies the tendency of triangles (i.e. triadic configurations in which all three dyads are connected) to be transitive (i.e. form a feed-forward loop) rather than cyclic (Figure 2.1A,B). This value is scaled relative to the expected proportion of transitive triangles, such that a value of 0 indicates that the proportion of transitive triangles does not differ from random expectations and a value of 1 indicates that all triangles are transitive (Figure 2.1A) and none are cyclic (Figure 2.1B).

We first extracted weighted time-aggregated networks from the interaction lists collected after each simulation (see ‘*Data collection’*) [39]. Time-aggregated networks were then converted into binary directed networks as follows: non-interacting dyads received a value of 0; dyads in which all interactions were in a single direction were linked by a binary edge with that same directionality; and for dyads in which interactions occurred in both directions, directionality of the binary edge corresponded to whichever direction >50% of interactions occurred in. If an equal number of interactions occurred in both directions, that dyad was linked by a bidirectional binary edge (Figure 2.1C). We acknowledge that assigning edge directionality using this method will have converted any edges that were close to being bidirectional (e.g. those with a 49/51 split) to edges with a single direction, which may have understated the abundance of bidirectional edges in our data, particularly when compared to naturally noisy ecological data. We therefore conducted a simple check to establish how often these ‘nearly bidirectional’ edges occurred in our data by calculating the proportion of dyads in which more than 0.45 but less than 0.5 of interactions occurred in one direction. As only 2-5% of dyads that were ultimately converted to single direction edges fell into this range, which we feel sufficiently low not to impact the overall interpretation of our results, we proceeded with the method of assigning the directionality of binary edges using a simple majority rule.

For each simulation run, time-aggregated networks were built over increasingly larger time windows (starting from $t = 0$) until the resulting binary network contained at least n edges, where n ranged from 150 to 1500 in increments of 150. For each combination of condition (Table 2.1) and network density ($n = 150, 300, \ldots, 1500$), ten binary networks were obtained; only one binary network was extracted from a given simulation run. Triangle transitivity was then calculated for each binary network as described in [13] (see the Supplementary Material for more details on triangle transitivity calculations). Triangle transitivity values were used as the response variable in a GLS model with behavioural condition (Table 2.1), network density, and their interaction as predictors. Prior to analysis, network density was standardised by subtracting the mean and dividing by the standard deviation.

To further compare the structure of the time-aggregated networks, triad significance profiles (TSP) for the 7 possible triangle configurations were also obtained for each non-Uniform behavioural condition. TSPs are vectors of normalized Z-scores that quantify the representation of each triangle configuration relative to that expected from a null model. Here, the Uniform condition represented the null model of interest, where all individuals expressed the same mean activity and turning index. Using time-aggregated networks containing 1000 binary edges, we first obtained Z-scores for each triangle configuration in each non-Uniform simulation as:

$$Z_i = \frac{N_{Obs.} - N_{Uniform}}{s.d._{Uniform}}$$

where N_{Obs} is the frequency of a given triangle configuration in the time-aggregated network and $N_{Uniform}$ and $s.d._{Uniform}$ are respectively the mean and standard deviation of the frequency of that triangle configuration across 100 networks from the Uniform condition. Z-scores were then normalized as follows:

$$Normalized\ Z - score = \frac{Z_i}{\sqrt{(\sum Z_i^2)}}$$

2.3.3.3. Effects of activity on triangle transitivity

2.3.3.3.1. Model parameters and scenarios tested

As well as determining an agent's probability of moving on timestep *t,* A_i also directly influences both the initiation and directionality of interactions. To disentangle the impact of these latter two elements on triangle transitivity, we modified the model to run the following four conditions: (i) Activity determines whether interactions are initiated, but not directionality. In this condition, interactions are initiated only by currently active agents as described above, but the interaction's direction is assigned randomly, such that both agents have a 0.5 probability of becoming the information signaller. (ii) Activity determines interaction directionality, but not initiation. In this condition, each agent, regardless of its activity status, has a 0.5 probability of initiating an interaction on each timestep, provided that there is at least one agent within its interaction radius. The direction of the interaction is then determined by the relative activity levels of the two agents, such that agents that tend to be more active are more likely to become signallers. Specifically, the probability of an interaction being directed from agent *i* to agent *j* is proportional to $\frac{A_i}{A_i+A_j}$. (iii) Neither interaction initiation nor directionality is determined by activity. In this condition, all agents have a 0.5 probability of initiating an interaction on each timestep, with the direction of any resulting interactions determined randomly. (iv) Both interaction initiation and directionality are determined by activity (this is the default condition, as described above). For each condition, we ran 100 simulations each for the Activity Variable and Uniform treatments (Table 2.1). For all conditions tested here, $A_m = 1$ and $T_m = 60$.

2.3.3.3.2. Statistical analysis

Network density had only a weak effect on triangle transitivity (see Results). As such, for each simulation we extracted a binary network that contained 1000 edges as previously described. Values of t_{tri} were then compared across conditions using GLS models.

2.3.3.4. Speed and efficiency of information flow

To evaluate how among-individual variation influenced information flow within the population, we simulated a simple diffusion process through 100 simulations for each condition specified in Table 2.1. The first agent to initiate an interaction in a simulation was treated as the initially informed individual. Naïve individuals that received an incoming interaction from an informed individual became informed themselves and capable of transmitting that information onwards. As in [40], we estimated transmission speed as the time step at which ≥ 50% of agents were informed in each simulation, T50. To evaluate how efficiently information spread, we also recorded the cumulative number of outgoing interactions from informed individuals (whether to naïve or informed agents) that occurred by T50. Our measure thus equates efficiency with maximizing the spread of information while minimizing the number of interactions.

Substantially more interactions occurred during simulations with uniform activity levels across agents than those in which activity levels varied. All else being equal, higher interaction rates should result in a more rapid spread of information [2]. To disentangle the effects of the patterning of interactions from the total number of interactions on the diffusion process, we randomly selected and removed 20% of interactions in each simulation run in which activity levels were uniform across agents, prior to simulating the diffusion process. This resulted in a similar interaction rate across all runs without systematically altering the patterning of interactions generated by different behavioural conditions. GLS models were used to compare T50 and the efficiency of information flow across behavioural conditions. Response variables were log-transformed to meet assumptions of normality.

2.4. Results

2.4.1. Effects of behavioural variation on triangle transitivity

There was strong evidence for an effect of behavioural condition on triangle transitivity, and the triadic configurations of the social network as a whole (Figure 2.4). Consistent across a range of network densities, networks were dominated by transitive (rather than cyclic) triangles (indicated by relatively greater t_{tri}) when activity levels varied among individuals, whereas when all individuals were equally active, the number of transitive triangles matched random expectations—i.e., $t_{\mathrm{tri}} \approx 0$ (Figure 2.4; Table 2.2). As binary networks became more dense (i.e. more connections), variation in t_{tri} decreased across simulations, though there was little change in mean t_{tri} (Figure 2.4A).

When individuals varied in only their turning indices, the abundance of fully-connected triads on the whole were reduced compared to the Uniform condition (Figure 2.4B). Among-individual variation in turning index also altered spatial structuring within the nest. Individuals with more sinuous walking paths (i.e., high T_i) tended to cluster into localised areas, while those with straighter walking paths navigated a greater proportion of the nest (Supplementary Material, Figure 2.S3).

Table 2.2. GLS model of triangle transitivity as a function of behavioural condition. Model-averaged estimates (MAE) and unconditional standard errors (USE) derived from the two best-supported models given in Table 2.S1 ($\sum w_i = 0.999$). Intercept taken as Condition = Uniform. A variance structure was incorporated that allowed for heterogeneous residual spread across network density, dependent on condition. *N* = 1000 simulations.

Parameter	MAE	USE	95% CI
Intercept	0.007	0.010	-0.012, 0.026
Condition = Activity Variable	0.538	0.016	0.506, 0.571
Condition = TI Variable	0.002	0.011	-0.020, 0.023
Condition = Uncorrelated	0.526	0.013	0.501, 0.552
Condition = Correlated	0.518	0.012	0.494, 0.542
Network density	-0.010	0.008	-0.027, 0.006
Activity Variable * Network density	0.024	0.016	-0.008, 0.056
TI Variable * Network density	0.003	0.009	-0.015, 0.020
Uncorrelated * Network density	0.013	0.012	-0.009, 0.036
Correlated * Network density	0.010	0.010	-0.011, 0.030

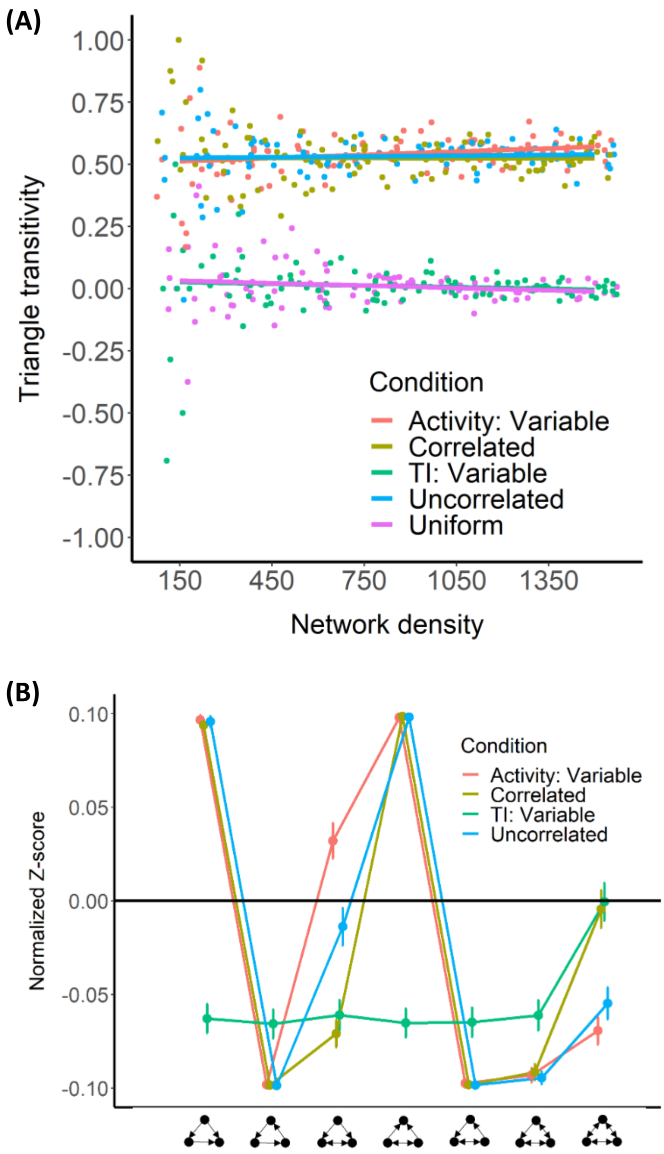

Figure 2.4. (A) Triangle transitivity as a function of behavioural condition and network density. Active agents generated outgoing edges. Lines depict predicted values. **(B)** Triad significance profiles comparing the relative significance of triangle configurations across the non-Uniform behavioural conditions, relative to the Uniform condition. Normalized Z-scores were averaged across 100 simulation runs for each condition; bars indicate the standard errors. For both graphs, points are horizontally jittered to improve clarity.

2.4.2. Effects of activity on triangle transitivity

Triangle transitivity varied according to a three-way interaction between condition (Uniform vs. Activity Variable) and activity-based influences on interaction initiation and directionality (Figure 2.5; Table 2.3). Triangle transitivity was significantly higher when activity levels varied among individuals and activity determined interaction direction (mean t_{tri} = 0.569) compared to instances in which these conditions were not met (mean t_{tri} = 0.001; Figure 2.5) (see Supplementary Material, Figure 2.S4, for triad significance profiles). Put simply, overrepresentation of feed-forward loops emerged when some individuals were more likely than others to generate directed network connections.

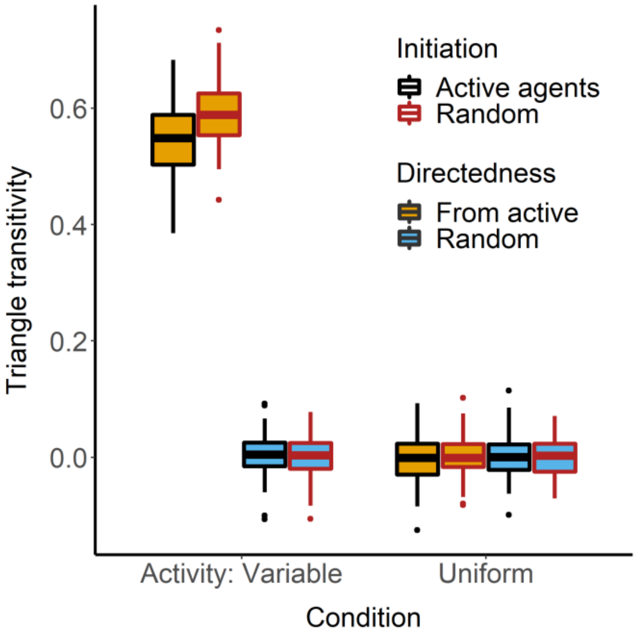

Figure 2.5. Boxplots depicting the effects of activity on triangle transitivity. Thick lines indicate medians, while the boxes indicate the interquartile range. Whiskers extend to 1.5x the interquartile range. Condition refers to whether activity levels varied or were uniform among agents. Interactions were either initiated randomly (red outlines) or by a currently active agent moving within the interaction radius of another agent (black outlines). The direction of an initiated interaction was either assigned randomly (blue fill) or according to an agent's current activity (yellow fill).

Table 2.3. Parameter estimates from GLS model of triangle transitivity as a function of behavioural condition, interaction initiation, and interaction directionality. Estimates derived from best-supported model ($\sum w_i = 0.999$). Intercept taken as Condition = Uniform with both initiation and direction of interactions determined by activity. A variance structure was incorporated that allowed for heterogeneous residual spread across both condition and directional variants. *N* = 800 simulations.

Parameter	Estimate	SE	95% CI
Intercept	-0.001	0.004	-0.008, 0.007
Condition = Activity Variable	0.547	0.006	0.534, 0.559
Random Initiation	-0.0004	0.006	-0.012, 0.011
Random Direction	0.003	0.005	-0.007, 0.013
Activity Variable * Random Initiation	0.046	0.009	0.028, 0.064
Activity Variable * Random Direction	-0.546	0.008	-0.562, -0.530
Random Initiation * Random Direction	-0.001	0.007	-0.015, 0.013
Activity Variable * Random Initiation * Random Direction	-0.045	0.012	-0.068, -0.023

2.4.3. Speed and efficiency of information flow

The speed of information flow—measured by T50, the time step at which 50% of agents were informed—varied across conditions (Figure 2.6A; Table 2.4). T50 was highest (i.e. information spread most slowly) when individuals varied only in activity level. When individuals independently expressed variation in both activity and turning index, the speed of information flow was similar to when no variation was present in either trait. T50 was lowest (i.e. information spread most rapidly) either when individuals varied in turning index alone or when this variation was negatively correlated with variation in activity levels.

Efficiency of information flow, measured by the number of outgoing interactions from informed agents that had occurred until T50 was reached, also varied across conditions (Figure 2.6B; Table 2.5). Information spread most efficiently (fewest outgoing connections) either when individuals varied only in turning index or when variation in activity level and turning index were negatively correlated with one another. When mean activity and turning index were uncorrelated, transmission efficiency was similar to the condition in which no individual variation was present. Information transmission was least efficient (most outgoing connections) when individuals varied in mean activity level alone.

Table 2.4. Parameter estimates from linear model of T50 (log-transformed) as a function of behavioural condition. Estimates derived from best-supported model ($\sum w_i > 0.999$). Intercept taken as Condition = Uniform. *N* = 500 simulations.

Parameter	Estimate	SE	95% CI
Intercept	6.611	0.025	6.562, 6.659
Condition = Activity Variable	0.148	0.035	0.080, 0.217
Condition = TI Variable	-0.136	0.035	-0.204, -0.068
Condition = Uncorrelated	-0.018	0.035	-0.086, 0.051
Condition = Correlated	-0.179	0.035	-0.248, -0.111

Table 2.5. Parameter estimates from linear model of transmission efficiency (log-transformed) as a function of behavioural condition. Estimates derived from best-supported model ($\sum w_i > 0.999$). Intercept taken as Condition = Uniform. *N* = 500 simulations.

Parameter	Estimate	SE	95% CI
Intercept	5.612	0.025	5.563, 5.660
Condition = Activity Variable	0.081	0.035	0.012, 0.149
Condition = TI Variable	-0.201	0.035	-0.270, -0.133
Condition = Uncorrelated	-0.080	0.035	-0.148, -0.011
Condition = Correlated	-0.216	0.035	-0.284, -0.148

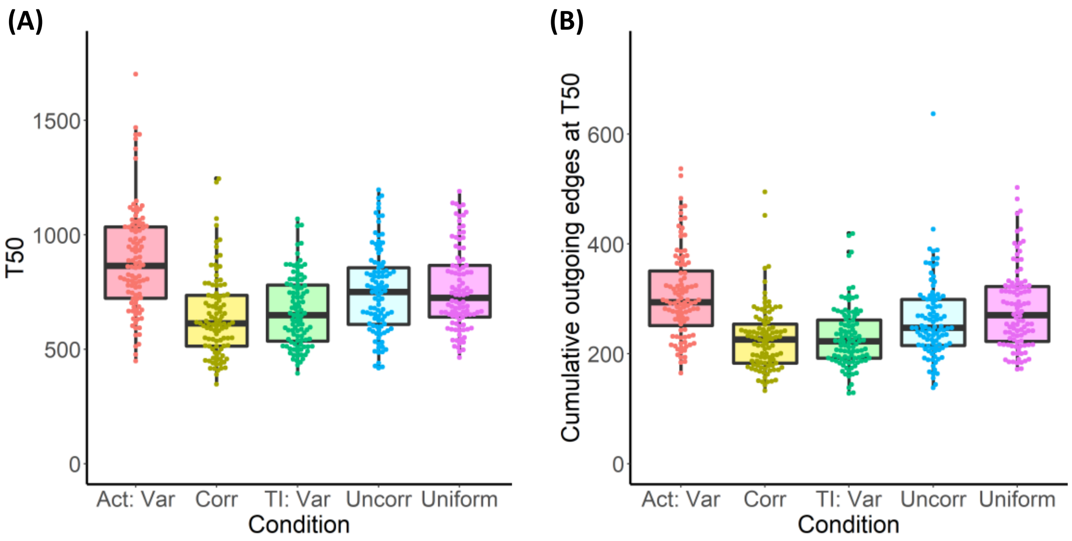

Figure 2.6. Speed and efficiency of information flow under different behavioural conditions. Boxplots show **(A)** T50, the timestep at which ≥ 50 individuals were informed, and **(B)** the cumulative number of outgoing interactions from informed individuals until T50. Lower values respectively correspond to faster and more efficient transmission. Thick lines indicate medians, while the boxes indicate the interquartile range. Whiskers extend to 1.5x the interquartile range.

2.5. Discussion

The superorganismal nature of eusocial insect colonies means that natural selection is increasingly expected to act on colony-level traits [4], such as the ability to generate robust, yet flexible, colony-level responses to ecological challenges. Collective coordination relies on interactions that transfer information between nestmates, raising the possibility that natural selection has acted on the behavioural algorithms that determine whether and how workers interact. Using a simple agent-based model, we demonstrate that among-individual variation in the likelihood of sending outgoing (or receiving incoming) links is sufficient to generate an over-abundance of a triadic network substructure known as the "feed-forward loop" (Figure 2.1A). This motif is commonly found in biological regulatory networks where it performs various signal processing tasks, e.g. discriminating persistent signals from short-lived pulses [10,11], and is also over-represented within social insect interaction networks, where similar regulatory roles have been demonstrated [7,14]. Nevertheless, our model found that feed-forward loops alone had little impact on information transmission processes. Rather, among-individual variation in movement patterns (either alone or as part of a behavioural syndrome) promoted faster and more efficient information transfer, despite contributing little to the production of feed-forward loops. Our model thus demonstrates how collective properties that support colony functioning can be tuned by modifying both the behavioural variation present among workers and correlations across traits.

Insect workers often vary considerably in their activity levels [16-19], with a minority of individuals generally carrying out most of the work [19,20,24]. These individuals can also play a key role in transmitting task-relevant information through interactions with nestmates [15]. Honeybee (*Apis mellifera*) foragers, for example, vary dramatically in their likelihood to produce recruitment dances, even when collecting from identical resources [41]. Similarly, highly active 'keystone individuals' catalyse worker activity in ant colonies [42]. We therefore linked activity in our model to the likelihood of directed information transfer between individuals and found that, when this criterion was satisfied, individual variation in activity drove production of feed-forward loops within the interaction networks. However, given that other effects of activity variation in our model (e.g. total distance moved) were unimportant for the generation of these motifs, it seems likely that any behavioural trait that (i) varies among individuals and (ii) directly influences the directionality of pairwise interactions (e.g. the direction of information transfer) could drive an over-abundance of feed-forward loops.

One such trait may be the propensity to interact with nestmates. For example, honeybees vary in their likelihood to engage in trophallactic food-sharing interactions [43], with some individuals potentially specialising in offering food [44]. Dominance interactions are also characterised by clear directional relationships—indeed, transitive relationships are a common feature in dominance hierarchies, in both insects [14] and other taxa [13]. In various ant species, for example, trophallaxis is generally directed from subordinate to dominant individuals [22]. Variation in knowledge or past experience is also likely to promote transitive network structures when it results in directed information transfer among workers. For example, more experienced *Temnothorax albipennis* ants are more likely to engage in tandem runs, where they directly lead naïve followers to a resource [45]. Similarly, it has been suggested that in the grass-cutting ant (*Acromyrmex heyeri*), workers initially sacrifice foraging efficiency in order to more rapidly provide nestmates with information about newly discovered foraging resources [46].

Nevertheless, while transitive network structures are a potentially common feature of social insect colonies, whether they offer any functional benefit remains unclear. Previous analyses of empirical social insect networks have shown that an overrepresentation of feed-forward loops could reflect selection for more efficient information transfer in insect colonies [7,14]. However, our model found that the speed and efficiency of information transfer was unrelated to the proportion of transitive triangles in the population social network. For example, among-individual variation in activity alone produced comparable triangle transitivity levels compared to when individuals varied in both activity and turning index, but the former was associated with relatively slow and inefficient transmission compared to the latter**.** This suggests that the effects of feed-forward loops on collective functioning are likely to be context-dependent.

It is also possible that feed-forward loops confer regulatory properties beyond those considered here. For instance, in transcriptional networks, feed-forward loops can dampen responses to external signals to ensure that transient signals are ignored [11]. A similar role may be present in insect colonies by limiting collective responses to weak signals about low-quality resources and thereby promote effective worker allocation. Workers often vary in their response thresholds to task-related stimuli, with some requiring relatively little stimulation to begin work, while others must experience substantially higher intensities of task-related stimuli before acting [22]. Feed-forward loops may regulate worker activation by limiting responses to weak task-relevant stimuli, while ensuring sufficient stimulation (e.g. multiple signals from active workers) is received by inactive workers when more help is truly needed. It is also possible that, in some cases, the production of feed-forward loops is simply an inadvertent by-product of the behavioural variation present within insect colonies and not itself a target of selection. Previous work has shown, for example, that the frequency and nature of lower-level dyadic interactions play a key role in determining the types of triadic configurations that can arise in a network [47].

It is worth noting that our model assumed that behavioural variation remained constant over time. In reality, an individual’s activity and/or propensity to interact with others may shift in response to factors such as worker loss, changes in colony food stores, or the discovery of a new resource, and these changes may in turn influence how information is transferred through the colony [19,29]. Nevertheless, while our model represents a simplified transmission scenario, it demonstrates clearly how variation in simple individual-level behaviours can significantly impact colony-level information transfer. It also highlights the challenge in inferring the functionality of dynamic systems from knowledge of the static network structure alone. Within insect colonies, interactions are often brief and stable relationships between particular individuals are generally absent. Under such conditions, very different patterns of interaction can give rise to similar network structures when aggregated over time [39]. Whereas previous analyses of the function of feed-forward loops have focused on systems with relatively fixed relationships (e.g. gene regulatory networks; [11]), within insect colonies, the timing and order of interactions is of critical importance. Indeed, when we simulated information flow on the static networks derived from our time-ordered interaction lists, rather than on the time-ordered interactions themselves, we found that in agreement with previous studies [11,14] information spread more efficiently on networks characterised by an overrepresentation of transitive triangles (Supplementary Material; Tables 2.S6–2.S7; Figure 2.S6).

In contrast to among-individual variation in activity, individual variation in movement paths often improved both the speed and efficiency of information transfer in our model, despite having limited impact on the generation of network transitivity. Spatial behavioural variation was included in our model in terms of walking path sinuosity, causing some individuals to remain in restricted areas of the nest, while others traversed the entire nest space [2,28] (Supplementary Material, Figure 2.S3). Under certain conditions, such variation in space-use allowed for faster and more efficient information transfer through the colony. In particular, these effects were observed either when individuals varied in path sinuosity alone or when activity levels were negatively correlated with turning indices across the population—that is, agents with sinuous walking paths tended to be inactive while those with straighter walking paths were often active. In many eusocial insect species, similar patterns of space-use variation have been observed. Bumblebees (*Bombus terrestris*), for example, perform irregular ‘excited’ runs throughout the nest after returning from successful foraging trips which serve to increase foraging activity in other workers by rapidly distributing pheromones and potentially through physical contacts [48,49]. Similarly, red harvester ants (*P. barbatus*) vary in the sinuosity of their walking trajectories, which influences their interaction frequency. Ants with straighter walking paths contact more nestmates than those with more tortuous paths [2]. Our model is consistent with the hypothesis that such variation in connectivity facilitates rapid information flow throughout the population due to workers with straighter walking paths linking isolated clusters of individuals [2].

It should be noted, however, that the adaptiveness of fast, efficient information transfer is highly context-dependent. In response to predation, for example, insect colonies are likely to benefit from rapid alarm propagation that can quickly marshal colony defences [50,51], whereas rapid information transfer may be less valuable in a foraging context. Instead, the *regulation* of information transmission in response to environmental feedback is key to ensuring worker effort is divided according to the quality of resources [52], and colonies that show restraint in foraging efforts can often be more successful [53,54]. In addition, behavioural variation that promotes fast and efficient information transfer may also promote faster transmission of pathogens. In this case, we would expect natural selection to favour collective responses to the infiltration of pathogens that limit unnecessary interactions. On exposure to pathogens, for example, some ant species switch from allogrooming to self-grooming – or even isolate themselves from other workers completely – thus reducing potential infection of healthy nestmates [55,56]. Similarly, nest architecture can influence disease spread throughout a colony, with physically or behaviourally segmented nests tending to dampen the spread of disease [56,57].

2.6. Concluding remarks and future directions

Further research is required to establish whether and how feed-forward loops impact the collective functioning of social insect colonies. Central to these efforts is quantifying the extent to which feed-forward loops and other network motifs are present within colony interaction networks. A common approach is to compare empirical networks with Erdős-Rényi random networks matched for size and density, yet these null models often lack biological and physical relevance [58, 59]. For example, random graphs typically assume that all individuals are equally likely to interact, thus ignoring spatial and temporal constraints on interactions (e.g., two individuals that generally occupy opposite sides of the nest are unlikely to interact). A potential application of our model lies in the generation of spatially explicit null models, tuned to a particular system, that will enable realistic comparison with empirical data. To illustrate this point, we reanalyzed previously published data on interaction networks of the ant *P. californicus* [7], using our agent-based simulations to generate spatially explicit null models that match the empirical data in network size and density (see Supplementary Material, section 2.7.5, for details on this analysis). Comparing the empirical networks with random graph models, the original study concluded that feed-forward loops were overrepresented, while three-cycles (Figure 2.1B) matched expected frequencies (see Fig. 3 in [7]). Conversely, our method suggests that both substructures are over-represented in the empirical data relative to the simulated data (Figure 2.7). We stress that our reanalysis does not invalidate the findings of [7]—indeed, our model is not parameterized appropriately for their data in terms of ant worker activity and movement. Rather, these results emphasize the important role that selecting a null model plays in the interpretation of network analyses. By offering a means to generate spatially explicit null models, we anticipate that our model will prove useful for future investigations into the mechanisms that drive the structure of animal social networks.

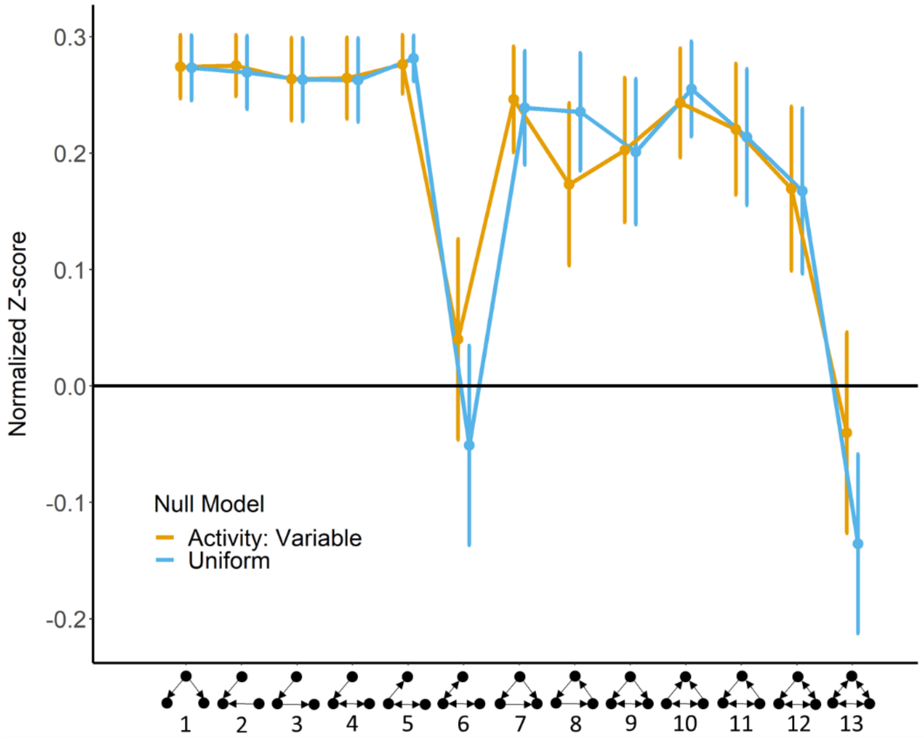

Figure 2.7. Triad significance profiles comparing the relative significance (measured by Z scores) of triangle configurations found in Waters and Fewell's [7] data compared to null models generated from our simulation using either Activity Variable or Uniform conditions. Normalized Z-scores were averaged across twelve networks with varied sizes, and across 100 simulation runs for each condition; bars indicate the standard errors.

Data accessibility. All supplementary analyses are available in the Supplementary Material of this manuscript. The simulation model, along with all data and code to reproduce our analyses are available from the Dryad Digital Repository, doi:10.5061/dryad.brv15dv8f [60].

Authors' contributions. CE and MH conceived the study, developed the model, and wrote the initial draft. All authors contributed towards interpreting the results and revising the manuscript.

Competing interests. We declare we have no competing interests.

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2.7. Supplementary Material

2.7.1. Full ODD model description

Our model was created in the agent-based modelling platform NetLogo (V5.2.0; https://ccl.northwestern.edu/netlogo/). The model description below follows the ODD (Overview, Design concepts, Details) protocol [23].

Purpose. The purpose of this model is to investigate how individual variation in worker movement in eusocial insect colonies, specifically in terms of activity levels and movement paths, contribute to the formation of networks characterised by a structural signature previously linked to information processing in regulatory networks, the feed-forward loop (Figure 2.1A), and what effect this has on the speed and efficiency of information flow within the colony.

Entities, state variables and scale. The model consists of a population of agents ($N_{default}$ = 100), which represent workers within a social insect colony. Each agent has a fixed activity level A_i and turning index T_i assigned at the beginning of the simulation (see *Initialisation* for details). The model is spatially explicit with agents contained within a 50 x 50 grid of square patches, representing an area within the nest in which workers move and interact with each other to share information.

Process overview and scheduling. Time is modelled in discrete time steps, until the specified end time ($t_{default}$ = 5000 steps) is reached. During each time step, two processes are executed in the following order: ‘movement’ and ‘interactions’. Each process is performed by all agents (selected in a random order) before moving to the next process. Both processes are described in more detail in the *Submodels* section below.

Design concepts. The structure of an insect colony’s interaction network emerges from the behaviour of the workers—specifically how they move through the nest and how they interact with one another [2,19,61]. By determining whether and how individuals move within the nest, among-individual variation in activity and space-use is expected to influence how frequently—and with whom—individuals interact. Agent movement is modelled as a correlated random walk [25] based on fixed parameters (i.e. A_i and T_i) and is therefore a partially stochastic process. A_i and T_i are random draws from exponential distributions with specified population means. The location of each agent at the beginning of the simulation is randomly assigned. When individuals come into contact (i.e. within 1 body length), worker activity then influences whether an interaction occurs and its directionality (i.e. incoming vs. outgoing). Data on pairwise interactions is collected continuously throughout the simulation. Specifically, each time an interaction occurs, the following information is logged by the model: the identities of the two agents involved, the direction of the interaction, and the time step on which it occurred.

Initialisation. During setup, a population of agents ($N_{default}$ = 100) is created and each agent is placed randomly within a 50 x 50 grid of square 'patches'. Each agent *i* is assigned an activity value (A_i) and turning index (T_i). Activity levels and turning indices can either be variable across the population (centred around population means, A_m and T_m, respectively) or set to the same value for all agents ('uniform').

When activity levels are uniform across the population, all agents are assigned the same value, $A_i = A_m$. When activity levels are variable, values are randomly drawn from an exponential distribution with mean A_m, meaning that while most agents are relatively inactive, a few are highly active. Similar distributions of worker activity have been observed across multiple social insect species (e.g. ants [24], stingless bees [20], bumblebees [19]).

When turning indices are uniform, all agents are assigned the same value, $T_i = T_m$. When turning indices are variable, the values t_i are first randomly drawn from an exponential distribution with mean T_m, and modified as follows:

$$r_i = t_{max} - t_i + 0.01$$

where t_{max} is the maximum value from all generated values of t_i. This results in the majority of individuals having a relatively high r_i, whereas a smaller number are assigned lower values of r_i. Adding a small constant ensures no individuals will be assigned a value of 0. Then, individuals are assigned a turning index, T_i, equal to:

$$T_i = \frac{r_i T_m}{r_m}$$

where r_m is equal to

$$r_m = \frac{\sum_{i=1}^{n} r_i}{n}$$

This procedure generates a distribution of turning indices such that most agents have relatively high turning indices, resulting in more tortuous movement paths, whereas a few agents have low turning indices (i.e. they tend to move in straighter paths).

N values of *A* and *T* are generated in the way described above and distributed across the *N* agents within the population. *A* and *T* can be either uncorrelated or negatively correlated across agents. If uncorrelated, the values of *A* and *T* are assigned randomly across agents. If negatively correlated, the highest value of *A* is paired with the lowest value of *T*, the second-highest value of *A* with the second-lowest value of *T*, and so forth. These paired values are then distributed randomly across the agents, generating a population where more active agents also move in straighter paths. This was done in order evaluate the potential for synergistic effects between activity level and turning index on the generation of feed-forward loops. In other words, if highly active agents not only interact more often, but also interact with a more diverse array of nestmates because they traverse the entire nest (while less active agents remain in more restricted areas), this might lead to greater overrepresentation of feed-forward loops than variation in activity acting alone.

Submodels. This model has two processes: ‘movement’ and ‘interactions’.

Movement. The ‘movement’ process is performed by all agents in a random order. An agent *i* moves through the nest in a correlated random walk [25] governed by its activity level, A_i, and turning index, T_i.

Agent *i* will only move during time step *t* if it is ‘currently active’. An agent is considered active on a given time step if: $\propto < A_i$, where $\propto$ is a random number drawn from an exponential distribution with mean 1. Therefore, the higher an agent’s activity level, the more likely they are to move in a given time step, and so will cover a greater distance across the entire simulation. According to these rules, if A_m is set to 1, half of the agents in the population will, on average, be active on any given time step. This is comparable to observed patterns of activity in several social insect species [17, 18, 26].

If agent *i* is active during time step *t*, its current heading is updated as: $\theta_{i,t+1} = \theta_{i,t} + \delta\theta$, where $\delta\theta$ represents the change in direction drawn from normal distribution with mean 0 and standard deviation T_i (c.f. 27, 28). A higher value of T_i means an agent tends to greatly modify its heading each time it moves, resulting in a more tortuous movement path. As this means an agent will be slower to move away from its starting location, higher values of T_i also correspond to greater spatial fidelity within the nest. After updating its heading, agent *i* then moves forward by one body length (equivalent to 0.5 patches). Agents are prevented from moving past the world boundaries to capture the physical constraints present within a social insect nest. If a forward movement causes *i* to move past a world boundary, its x and/or y coordinate is set to the position of the boundary to ensure it does not move past.

Interactions. The 'interactions' process is performed by all agents in a random order and involves two sub-processes, 'initiate interaction' and 'assign direction', which are executed differently depending on the inputs specified by the user.

The 'initiate interaction' sub-process determines whether the agent initiates an interaction with another agent and can be either 'based on activity' or 'random'. If based on activity, only a 'currently active' agent (see above) is permitted to initiate an interaction. If random, the agent will initiate an interaction at a 0.5 probability. When initiating an interaction, an agent (*i*) chooses another random agent (*j*) within its 'interaction radius' (0.5-patch radius, equal to one body length) to become its 'interaction partner'. If no agents are available within *i*'s interaction radius or if *i* does not meet the criteria required to initiate an interaction as outlined above, no interaction is initiated and the 'interaction' process for agent *i* for the current time step is ended. An interaction radius equal to 1 body length was used because interactions among social insect workers often involve physical contact (e.g. antennation, food-sharing) and observations on multiple species suggest one body length is well within the range at which workers can detect and respond to nestmates (e.g. ants [29, 30], honeybees [62]).

If an interaction is initiated, the 'assign direction' sub-process is executed, which determines which agent (*i* or *j*) becomes the signaller of the interaction and which becomes the receiver. In the model, directionality of an interaction can be assigned 'from active', 'to active', or 'at random'. When interaction direction is 'from active' or 'to active', the exact way in which directionality is assigned is dependent on how the interaction was initiated. If interaction initiation was determined by activity (see above) and interaction direction is 'from active', agent *i* (i.e. the agent initiating the interaction) automatically becomes the signaller and *j* the receiver. Likewise, if interaction direction is set to 'to active', agent *i* (the initiator) becomes the receiver and *j* the signaller. Note that, in both cases, the activity status of agent *j* has no impact on whether it is interacted with, thus an interaction could be formed between an active and a non-active agent, or between two active agents. If interaction initiation is random and interaction direction is set to either 'from active' or 'to active', the probability of agent *i* becoming the signaller or receiver respectively is instead proportional to $\frac{A_i}{A_i+A_j}$, meaning the direction of the interaction is determined by the relative activity levels of the two agents involved. If direction is chosen 'at random', agents *i* and *j* have an equal probability of becoming the signaller of the interaction. This allowed us to test hypotheses regarding the effect of activity-induced interactions on the formation of particular network structures.

In many social insect species, activity is often linked with information flow. The ‘from active’ condition described above may be viewed as representing a situation in which knowledgeable individuals actively transmit information to others—e.g. via evolved signalling behaviours such as the honeybee waggle dance [31]. However, increased activity may also be linked with information-seeking behaviours. For example, honeybee foragers actively solicit information from other foragers by “begging” for nectar samples [63]. This latter scenario was represented by the ‘to active’ condition. However, this modification produced qualitatively similar results to the ‘from active’ condition (Figures 2.S1-2.S2).

2.7.2. Calculation of triangle transitivity, t_{tri}

Triangle transitivity was calculated as described in Shizuka & McDonald [13]. For each binary network constructed from the simulated interaction lists (see main text), we first obtained the frequency of each of 7 possible triangle configurations using the *igraph* package in R ver. 4.0.3 [64]. We then calculated the proportion of transitive triangles among all triangles:

$$P_t = \frac{\sum_u w_u T_u}{N_{triangles}}$$

where T_u is the frequency of triangle type u, $N_{triangles}$ is the total number of triangles in the network, and w_u is a weighting factor. This weighting factor takes on values of 1 and 0 for transitive and cyclic triangles respectively. For triangle configurations containing one or more bidirectional edges, w_u corresponds to the probability that the configuration will become transitive if these ties are resolved. For example, $w_u = 1$ for the triangle depicted in Figure 2.1C since whichever direction the tie is ultimately resolved in will result in a transitive triangle. Triangle transitivity is then calculated as:

$$t_{tri} = 4(P_t - 0.75)$$

2.7.3. Additional results

Table 2.S1. Model set used to derive parameter estimates presented in Table 2.2. Cond. = Behavioural conditions; Dens. = Network density.

Model	Parameters	Df	log *L*	AICc	ΔAICc	w_i
1	Cond. + Dens. + Cond. * Dens.	16	594.19	-1239.4	0	0.753
2	Cond.	11	608.02	-1237.1	2.23	0.247

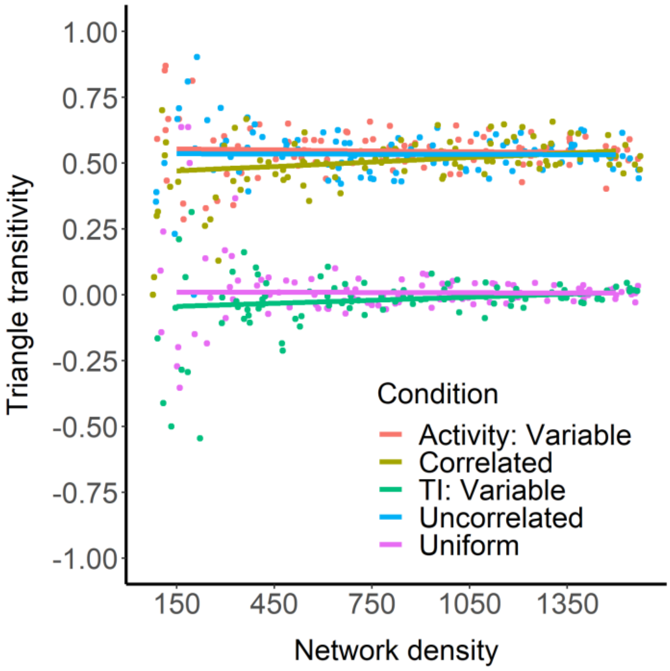

Figure 2.S1. Triangle transitivity as a function of behavioural condition and network density for the alternative 'to active' condition, where active agents generated incoming edges. Points are horizontally jittered to improve clarity. Lines depict predicted values.

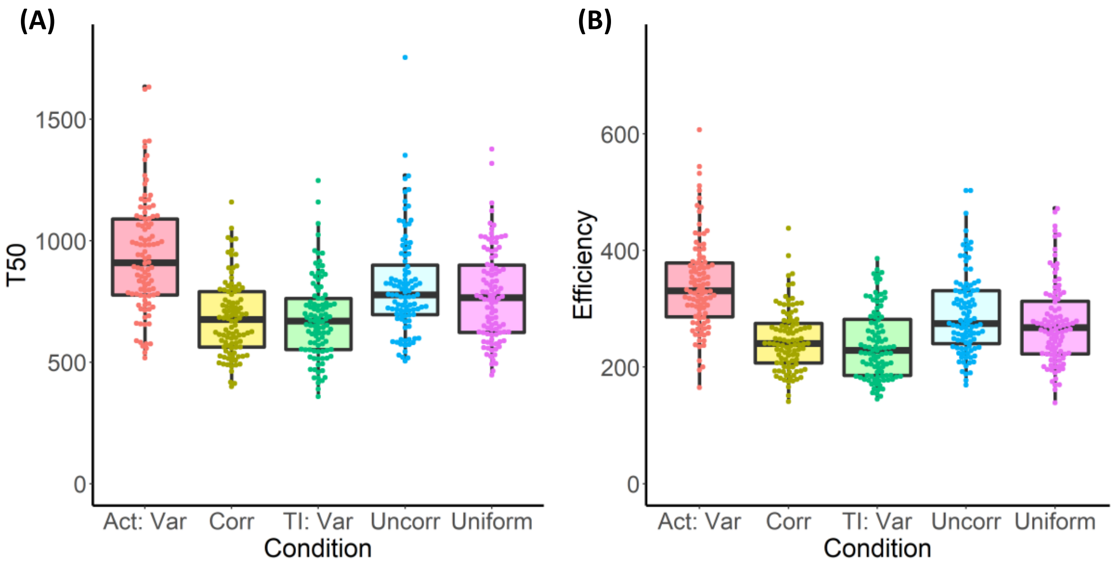

Figure 2.S2. Speed and efficiency of information flow under different behavioural conditions for the alternative 'to active' condition, where active agents generate incoming connections. Boxplots of **(A)** T50 (i.e., the time step at which ≥ 50% of agents are informed) and **(B)** efficiency, measured as the cumulative number of outgoing interactions from informed individuals until T50, for each behavioural condition. Thick lines indicate medians, while the boxes indicate the interquartile range. Whiskers extend to 1.5x the interquartile range.

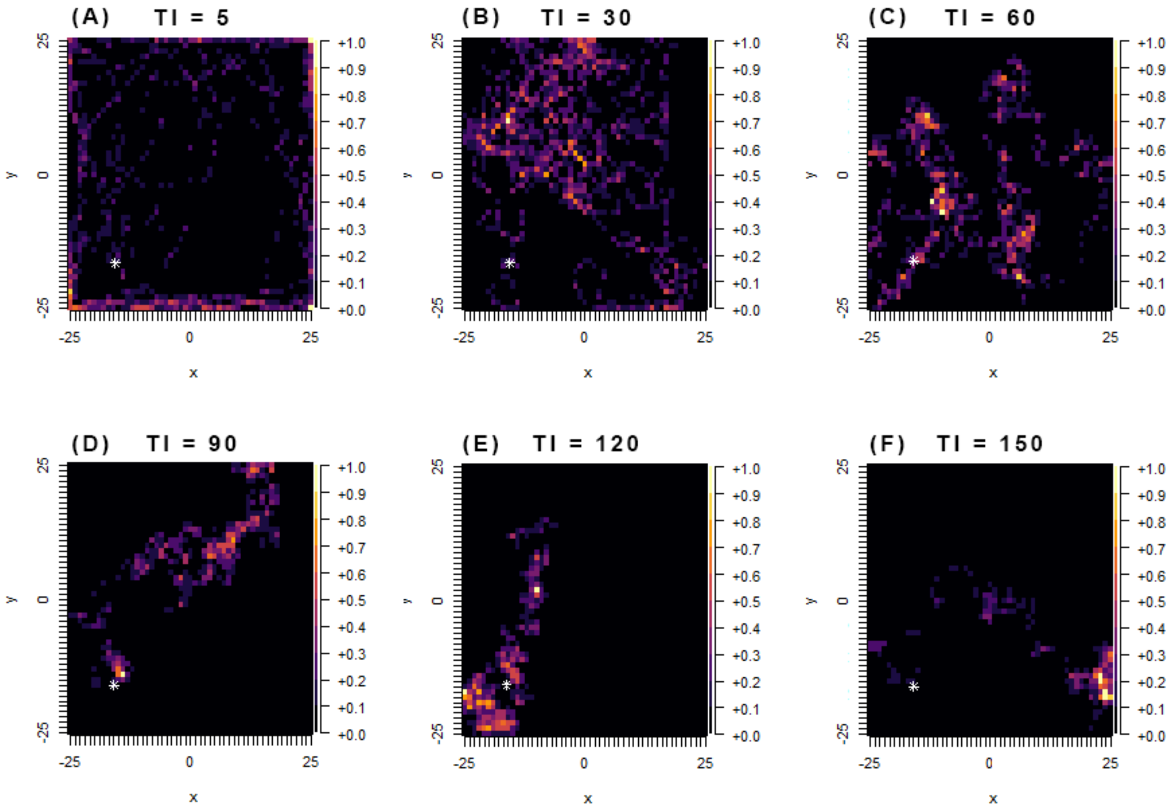

Figure 2.S3. Heatmaps showing examples of movement patterns of six agents with different turning indices (TI), within a 50x50 unit environment, over 5000 timesteps. **(A)** TI = 5; **(B)** TI = 30; **(C)** TI = 60; **(D)** TI = 90; **(E)** TI = 120; **(F)** TI = 150. Each individual started the simulation at position (-15,-15), which is marked by a white star. Each 1x1 unit within each map represents a patch within the environment, and is coloured according to the proportion of time the agent spent at this location, proportional to the maximum number of timesteps it spent at any one location.

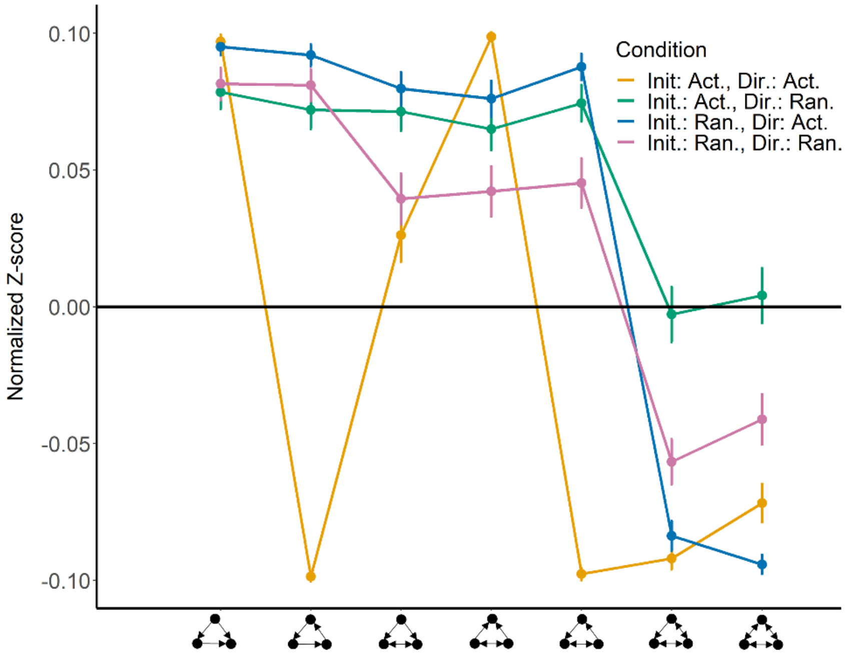

Figure 2.S4. Triad significance profiles comparing the relative significance of triangle configurations across the Activity Variable behavioural conditions, relative to the Uniform condition, when initiation and/or directionality of interactions were either determined at random or by the relative activity levels of the two interacting agents. Normalized Z-scores were averaged across 100 simulation runs for each condition; bars indicate the standard errors.

2.7.4. Additional analyses

2.7.4.1. Sensitivity analysis

Model parameters and scenarios tested. In the analyses described in the main text, the mean activity level of agents across the population, Am, was set to 1, such that on average, 50% of the population is active on any given time step and the mean turning index, Tm, was set to 60. To investigate the robustness of our results to these assumptions, we ran additional sets of simulations in which Am and Tm varied. For the former, we ran simulations with Am={0.5,0.75,1,…,2.5} for each behavioural condition (Table 2.1), keeping Tm = 60. Twenty simulations were run for each combination of behavioural condition and value for Am. We further ran an additional set of simulations with Tm = {15,30,45,…,150} for each behavioural condition (Table 2.1), keeping Am = 60. Twenty simulations were run for each combination of behavioural condition and value for Tm.

Statistical analysis. For each simulation run, t_{tri} was measured on a binary interaction network that contained 1000 edges. GLS models were fit with t_{tri} as the response variable and behavioural condition, mean activity level or mean turning index (depending on the analysis), and their interaction with condition as predictors.

Results: Mean activity. The relationship between triangle transitivity and the mean level of activity within a colony varied across conditions (Tables 2.S2-2.S3; Figure 2.S5A). As mean activity increased, triangle transitivity decreased only for conditions in which individuals varied in their activity level. Nevertheless, across the range of values for mean activity examined here, among-individual variation in activity always generated an overabundance of feed-forward loops, relative to conditions in which all individuals were similarly active (Figure 2.S5A).

Table 2.S2. Parameter estimates from GLS model of triangle transitivity as a function of behavioural condition, mean activity (*Am*), and their interaction. Estimates derived from best-supported model ($\sum w_i > 0.999$). Intercept taken as Condition = Uniform. A variance structure was incorporated that allowed for heterogeneous residual spread across condition. *N* = 900 simulations.

Parameter	Estimate	SE	95% CI
Intercept	0.012	0.006	0.001, 0.024
Condition = Activity Var	0.615	0.012	0.591, 0.638
Condition = TI Var	-0.01	0.008	-0.026, 0.006
Condition = Uncorrelated	0.601	0.012	0.577, 0.626
Condition = Correlated	0.616	0.012	0.593, 0.64
Am	-0.009	0.004	-0.016, -0.002
Activity Var * *Am*	-0.075	0.007	-0.089, -0.06
TI Var * *Am*	0.005	0.005	-0.005, 0.015
Uncorrelated * *Am*	-0.074	0.008	-0.088, -0.059
Correlated * *Am*	-0.087	0.007	-0.102, -0.073

Table 2.S3. Estimated slopes for effect of mean activity level on triangle transitivity for each behavioural condition. Model fitted with generalized least squares and restricted maximum likelihood. *N* = 900.

Behavioural condition	Trend	SE	95% CI
Uniform	-0.009	0.004	-0.016, -0.002
Activity Variable	-0.084	0.006	-0.097, -0.071
TI Variable	-0.004	0.004	-0.012, 0.003
Uncorrelated	-0.083	0.007	-0.096, -0.07
Correlated	-0.097	0.006	-0.109, -0.084

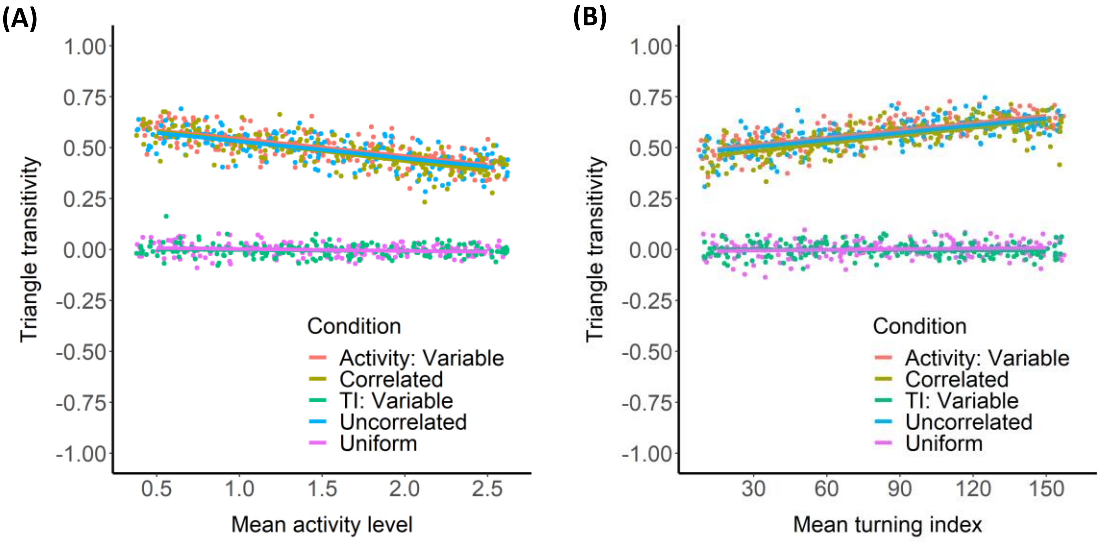

Figure 2.S5. Triangle transitivity as a function of behavioural condition for different values for **(A)** mean activity level and **(B)** mean turning index. Active agents generated outgoing edges. Points were horizontally jittered to improve clarity. Lines depict predicted values.

Results: Mean turning index. The relationship between triangle transitivity and the mean turning index also varied across conditions (Tables 2.S4-2.S5; Figure 2.S5B). As mean turning index increased, triangle transitivity correspondingly increased only for conditions in which individuals varied in their activity level. Nevertheless, across all tested values of Tm, triangle transitivity remained substantially higher for all conditions in which among-individual variation in activity was present, relative to those in which activity levels were uniform across agents (Figure 2.S5B).

Table 2.S4. Parameter estimates from GLS model of triangle transitivity as a function of behavioural condition, mean turning index (*Tm*), and their interaction.

Parameter	Estimate	SE	95% CI
Intercept	-0.007	0.006	-0.019, 0.005
Condition = Activity Var	0.483	0.01	0.464, 0.502
Condition = TI Var	0.009	0.008	-0.007, 0.02
Condition = Uncorrelated	0.475	0.01	0.455, 0.496
Condition = Correlated	0.452	0.01	0.432, 0.472
Tm	0.0001	0.00007	-0.00003, 0.0002
Activity Var * *Tm*	0.001	0.0001	0.0009, 0.0013
TI Var * *Tm*	-0.0001	0.0001	-0.0003, 0.00002
Uncorrelated * *Tm*	0.001	0.0001	0.0008, 0.0013
Correlated * *Tm*	0.001	0.0001	0.00096, 0.0014

Intercept taken as Condition = Uniform. A variance structure was incorporated that allowed for heterogeneous residual spread across condition. *N* = 1000 observations.

Table 2.S5. Estimated slopes for effect of mean turning index on triangle transitivity for each behavioural condition.

Behavioural condition	Trend	SE	95% CI
Uniform	0.0001	6.51×10^{-5}	-0.00003, 0.0002
Activity Variable	0.0012	8.08×10^{-5}	0.0011, 0.0014
TI Variable	-0.00005	5.7×10^{-5}	-0.0002, 0.00007
Uncorrelated	0.0012	9.07×10^{-5}	0.001, 0.0014
Correlated	0.0013	8.76×10^{-5}	0.0011, 0.0015

Model fitted with generalized least squares and restricted maximum likelihood. *N* = 1000.

2.7.4.2. Speed and efficiency of information flow on static networks

We further investigated how the network structures generated by the different behavioural conditions (Table 2.1) influenced the flow of information among agents within static networks, for comparison against our dynamic interacting populations. We first extracted 100 binary, directed networks with a density of 450 edges for each behavioural condition, following the procedure described in the main text (section 2.3.3.2). This density was selected as it required a similar number of time steps to reach as was needed to reach T50 when simulating information flow on the time-ordered interaction lists. The first agent to initiate an interaction in each simulation was treated as the initially informed individual. On each time step, each informed individual randomly selected one agent with which it shared an outgoing edge. If the latter was not yet informed, it became informed itself and would begin to transmit that information on the next time step. Informed agents with no outgoing edges did not interact. We recorded the number of time steps until ≥ 50% of agents were informed and the number of interactions that occurred up to that point (regardless of whether the recipient was already informed or not). As the number of informed individuals varied greatly when T50 was reached, efficiency was measured as the number of interactions per informed agent.

Statistical analysis. GLS models were used to compare the number of time steps needed to reach ≥ 50% informed and the efficiency of information flow across behavioural conditions. Response variables were log-transformed to meet assumptions of normality.

Results. The number of time steps needed to reach ≥ 50% informed agents varied across conditions, though differences were relatively modest (Table 2.S6; Figure 2.S6A). Information spread most rapidly when individuals varied in turning index. Efficiency of information flow at T50, measured by the number of outgoing interactions from informed agents per transmission event, also varied across conditions (Table 2.S7; Figure 2.S6B). Consistent with previous investigations [11,14], information tended to spread more efficiently (i.e. fewer interactions per transmission event) on networks characterised by an overrepresentation of feed-forward loops. Information spread least efficiently over networks in which individuals did not vary in activity level or turning index.

Table 2.S6. Parameter estimates from linear model of time steps needed to reach ≥ 50% informed agents (log-transformed) on static networks as a function of behavioural condition. Model-averaged estimates (MAE) and unconditional standard errors (USE) derived from the complete model set. Intercept taken as Condition = Uniform. A variance structure was incorporated that allowed for heterogeneous residual spread across behavioural condition. *N* = 500 simulations.

Parameter	MAE	USE	95% CI
Intercept	2.265	0.016	2.234, 2.295
Condition = Activity Var	0.016	0.025	-0.033, 0.064
Condition = TI Var	-0.052	0.024	-0.099, -0.004
Condition = Uncorrelated	-0.027	0.021	-0.069, 0.015
Condition = Correlated	-0.028	0.021	-0.068, 0.012

Table 2.S7. Parameter estimates from linear model of the efficiency of information flow (log-transformed) on static networks as a function of behavioural condition. Estimates derived from best-supported model ($\sum w_i > 0.999$). Intercept taken as Condition = Uniform. A variance structure was incorporated that allowed for heterogeneous residual spread across behavioural condition. *N* = 500 simulations.

Parameter	Estimate	SE	95% CI
Intercept	1.014	0.022	0.971, 1.056
Condition = Activity Var	-0.165	0.029	-0.223, -0.108
Condition = TI Var	-0.096	0.029	-0.153, -0.039
Condition = Uncorrelated	-0.211	0.028	-0.265, -0.156
Condition = Correlated	-0.239	0.027	-0.291, -0.186

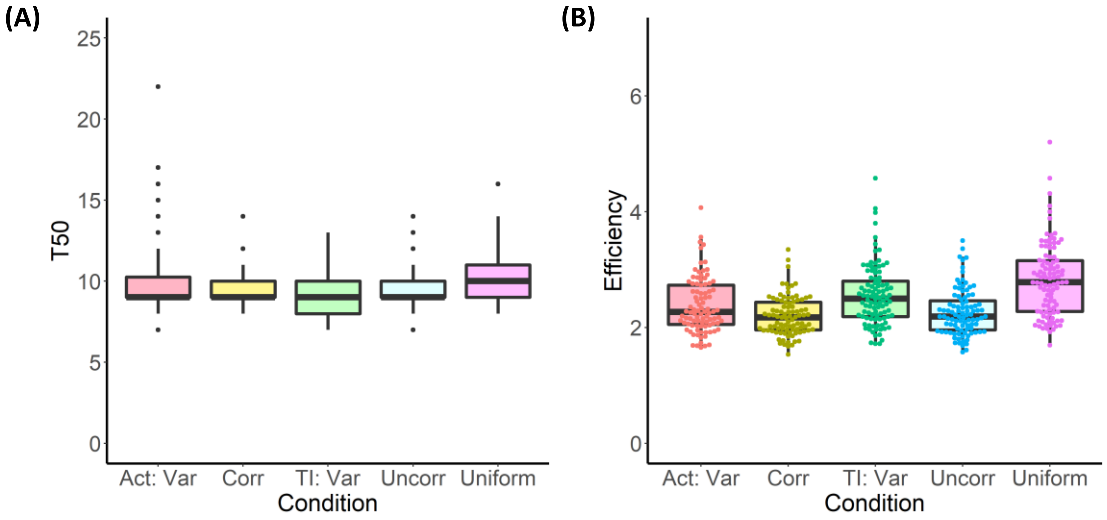

Figure 2.S6. Speed and efficiency of information flow on static networks under different behavioural conditions. Boxplots show **(A)** T50, the timestep at which at least 50 individuals were informed, and **(B)** the number of interactions per transmission event. Lower values respectively correspond to faster and more efficient transmission. Thick lines indicate medians, while the boxes indicate the interquartile range. Whiskers extend to 1.5x the interquartile range.

2.7.5. Potential model application: null models for empirical data

When calculating the relative significance of different network motifs in observed data, studies have traditionally used Erdős-Rényi random graphs – controlled for the number of nodes and edges – as their null model [10]. However, this method typically does not account for non-independence of data points commonly observed in real populations [58] and thus can lack biological relevance. For example, an Erdős-Rényi random graph assumes that any two individuals are equally likely to interact, which is often not the case (e.g., two insect workers that generally occupy different regions of the nest may be relatively unlikely to interact). Our model offers the potential to generate biologically relevant null models with spatial, temporal, and behavioural parameters matching the empirical data.

To illustrate this potential application of our model, we compared the representation of network motifs in a previously published dataset [7] to two null models generated using our simulation. We ran 100 simulations (5000 timesteps each) for our Uniform and Activity Variable conditions (Table 2.1), using population sizes matching the twelve networks from Water and Fewell's [7] experiment (*N* = {95, 200, 200, 200, 147, 81, 151, 113, 115, 118, 139, 147}; 2400 simulations in total). We then extracted networks from the simulated interaction lists with the number of edges matching the observed data (number of edges = {136, 158, 103, 164, 197, 131, 156, 238, 208, 247, 236, 324}). We generated triad significance profiles for each three-node subgraph for each empirical network, using our simulated networks to generate reference distributions. Normalized Z-scores for each subgraph were then averaged across trials.

2.8. References

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Chapter 3 | Aggression-based social learning in the zebra finch (*Taeniopygia guttata*)

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3.1. Abstract

Selectively learning from specific types of individuals may be adaptive if demonstrator characteristics can be used to identify more beneficial sources of social information. Such 'social learning biases' have been experimentally demonstrated in a number of species, but these experiments generally involve restricted laboratory conditions using a limited number of potential demonstrators and tend to consider only the characteristics of demonstrators rather than the importance of pairwise relationships on information transfer between individuals. In this study, we presented a novel foraging task to a large population of zebra finches (*Taeniopygia guttata*) housed in a free-flying aviary and used multi-network Network-Based Diffusion Analysis (NBDA) to establish whether birds learned from individuals they shared particular relationships with. Specifically, we investigated whether task solves followed social learning pathways representing the following relationships between individuals: feeding associations, aggressive interactions, positive associations (e.g. grooming) and mating pairs. We found strong evidence that zebra finches learn from their aggressors, irrespective of the outcome of that aggressive encounter. This has been previously suggested in laboratory-based studies on zebra finches, but never conclusively documented in a freely interacting population. We also found some weaker evidence to suggest that zebra finches learn from their mates – a social learning bias that has previously received little to no attention. However, we found that mates-based learning occurred infrequently and was secondary to aggression-based social learning biases. Our results therefore additionally highlight the importance of including combinations of multiple potential information pathways in social learning analyses to account for secondary learning pathways that may otherwise be missed.

Keywords: aggressive; directed social learning; Network-Based Diffusion Analysis; social learning strategies; personality; relationships

3.2. Introduction

Social learning (learning from others) is widespread across the animal kingdom and can be adaptive in a variety of biological contexts, from foraging to mate choice (Galef and Laland, 2005). This is because social learning permits the spread of adaptive behaviours without the higher risk and energetic costs associated with asocial (independent) learning. However, if individuals are indiscriminate as to when and from whom they learn, social learning can lead to the spread of maladaptive behaviours or outdated information (e.g. Laland and Williams, 1998). Evolutionary theory therefore predicts that natural selection will favour individuals that are selective in how they use social information over those that learn indiscriminately from others (Boyd and Richerson, 1985; Boyd and Richerson, 1988).

‘Social learning strategies’ describe how individuals choose to use social and asocial information (Laland, 2004); specifically, under what circumstances social learning is expected to be favoured (‘when’ strategies) and what types of individuals should be learned from (‘who’ strategies). ‘Who’ strategies, also referred to as ‘directed social learning’ (Coussi-Korbel and Fragaszy, 1995), consider that individuals may vary in their attractiveness as demonstrators for learning based on their individual characteristics and therefore that observers may display ‘social learning biases’ towards certain types of demonstrator. A variety of these biases have been demonstrated in animals. To give a few examples, nine-spined sticklebacks (*Pungitius pungitius*) and white-faced capuchins (*Cebus capucinus*) copy successful individuals when given novel foraging tasks (Coolen *et al*., 2005; Barrett *et al.*, 2017); common ravens (*Corvus corax*) and Siberian jays (*Perisoreus infaustus*) preferentially learn the behaviours of kin over non-kin (Schwab *et al*., 2008; Griesser and Suzuki, 2016); guppies and zebra finches (*Taeniopygia guttata*) copy individuals they are more familiar with (Swaney *et al*., 2001; Guillette *et al.*, 2016); and chimpanzees (*Pan troglodytes*) and domestic hens (*Gallus gallus domesticus*), according to some studies, preferentially copy high-ranking demonstrators (Nicol and Pope, 1994; Kendal *et al.,* 2015). In addition, individuals may be flexible in their use of social information, adaptively switching their preference of demonstrator depending on their situation. Juvenile zebra finches, for example, display a bias towards learning from their parents, but when exposed to early-life stress that indicates either a poor natal environment or low parental investment, they will instead learn from only unrelated adults (Farine, Spencer, *et al.*, 2015).

When considering who learns from whom within a population, studies almost always focus on how the individual characteristics of demonstrators affect their influence over the behaviour of others (e.g. do individuals preferentially copy those with higher dominance ranks?) and/or how different observers vary in their tendency to copy (e.g. are less dominant individuals more prone to copying?). Another approach is to consider how specific relationships or pairwise interactions between individuals influence their tendency to learn from one another (e.g. are individuals more likely to learn from demonstrators who actively showed them displays of aggression, irrespective of their overall dominance rank?). Social animals will likely share different types of relationships with different members of their group and this may influence who learns from whom; either because individuals who share specific relationships are more likely to associate with one another and so offer each other more opportunities for social learning, or because individuals favour information displayed by those they share certain relationships with over alternative demonstrators. This will in turn affect how information transmits through the entire social group.

For example, any relationship that results in two individuals tending to be in close proximity over prolonged periods will likely provide those individuals with plenty of opportunities to learn from each other. Individuals who tend to forage together may be more likely to learn novel foraging behaviours from one another, as demonstrated in wild songbirds (Aplin *et al.,* 2012). Similarly, individuals who share positive associations, such as grooming or huddling, are likely to tolerate each other in close proximity, thus offering each other more opportunities for social learning. For example, patterns of information transfer have been shown to follow proximity and affiliative networks in zebra finches (Williams, 1990), ravens (Kulahci *et al.*, 2016) and red-fronted lemurs (*Eulemur rufifrons*) (Schnoell and Fichtel, 2012). Some species have been shown to selectively copy kin and/or familiar individuals (e.g. Schwab *et al*., 2008; Griesser and Suzuki, 2016; Swaney *et al*., 2001; Guillette *et al.*, 2016), which may again be due to close associations, but may also be explained by a selective bias towards learning from individuals who are likely to share similar genetics (and so similar behavioural capacities) and/or the same territory (and so similar environmental pressures). Depending on the mating system of a species, individuals that form part of a mated pair may also be more likely to learn from each other if they spend prolonged periods of time together. In addition, for species that choose their mates based on indicators of fitness (which suggests a tendency to use successful behaviours), selectively learning from these individuals is also likely to be adaptive. Despite this, studies of information transfer in groups of individuals tend not to include learning pathways between mates.

Aggressive interactions have also been noted as potentially important for social learning in several bird species (Payne, 1981; Baptista and Petrinovich, 1984; Kulahci *et al.*, personal communication). Thus, it is possible that individuals may learn from those they share aggressive interactions with, either selectively learning from or passing information to their aggressors. The influence of negative pairwise relationships on social learning remains understudied, with most studies instead focussing on how an individual's dominance rank affects their social influence. There are, however, some discrepancies in the reported influence of dominance on social learning. Several studies have suggested, for example, that individuals will preferentially copy higher-ranking demonstrators (e.g. Nicol and Pope, 1999; Kendal *et al.,* 2015; Horner *et al*., 2010; Coelho *et al*., 2015), possibly because dominance is linked to general success; while others have suggested that dominant individuals restrict subordinate access to a novel task and, in the absence of this limitation, subordinates can actually have a greater influence over the behaviours of others (e.g. Watson *et al.,* 2017).

Research into dominance-related social learning biases almost always involves using calculated dominance ranks to infer the direction of learning events, regardless of whether the individuals involved actively engage in aggressive interactions with one another. As dominance is inherently linked to aggression, it is possible that the aggressive interactions between dominants and subordinates play a larger part in information transfer than the calculated dominance ranks of demonstrators. For example, individuals who display aggression towards one another may do so because they compete over resources, which may make them more likely to be in close proximity at a novel foraging task and so more likely to learn from one another. The outcome of said aggressive interactions (i.e. who tends to win against whom) may or may not be important in determining the direction of information transfer (e.g. individuals who win aggressive interactions may be viewed as stronger, and so more likely to be in possession of adaptive behaviours, causing them to be more attractive as demonstrators), which could explain some of the discrepancies between previous studies on the influence of dominance on social learning.

Over the past decade, Network-Based Diffusion Analysis (NBDA) has become a popular way of detecting social learning within freely-interacting populations, allowing social learning studies to escape the laboratory and move into more natural conditions. NBDA infers social transmission (the spread of novel behaviours via social learning) if the order in which individuals learn a novel behaviour follows the association network of the population (Franz and Nunn, 2009), under the assumption that, if social learning is occurring, individuals who associate more are more likely to learn from one another. Networks representing different types of connections between individuals can be tested to determine whether social transmission follows a particular pathway (Hoppitt and Laland, 2011; Hoppitt, 2017) or combination of pathways (Farine, Spencer, *et al.*, 2015; Farine, Aplin, *et al.,* 2015). Altogether, this makes NBDA perfect for investigating whether freely-interacting individuals learn from those they share specific connections with, without the need for highly-controlled laboratory conditions that may mask natural behaviours or degrade stable relationships. However, despite statistical advancements in the field, very few studies compare among networks (and even fewer among combinations of networks) to establish which aspect of social interaction is the primary route for social information transfer (notable exceptions include Farine, Spencer, *et al.*, 2015; Farine, Aplin, *et al.,* 2015; Barrett *et al.*, 2017).

Here, we investigate the influence of pairwise relationships on social transmission in a model species, the zebra finch. Zebra finches are highly gregarious, form strong mating pairs, display aggressive, dominance-related behaviours (Zann, 1996; Bonoan *et al.*, 2013) and are capable of strategic social information use (e.g. Benskin *et al.*, 2002; Katz and Lachlan, 2003; Farine, Spencer, *et al.*, 2015; Guillette *et al.*, 2016), making them an ideal study species for such research. Specifically, we investigate whether zebra finches preferentially learn from (i) individuals they associate with while feeding, (ii) individuals they share aggressive interactions with, (iii) individuals they share positive interactions with and/or (iv) individuals they form part of a mating pair with, as determined by observations of pairwise interactions. Using multi-network NBDA, we build a comprehensive model of relationship-based learning pathways across our zebra finch population.

3.3. Methods

3.3.1. Study system

Our study was carried out on a population of captive zebra finches housed at Harewood House Bird Garden in Leeds, UK. In total, 53 individual birds were present in the population over the study period, although the population size at a given time fluctuated slightly due to three natural deaths and one birth during the study period. Finches were housed in a semi-natural, free-flying aviary measuring approximately 3m x 3m x 3m (with an additional hut attached to provide shelter) and containing various plants, trees and rocks as well as a shallow water pool. The population was well-established and the finches had been housed together for their entire lives (since 2015), thus allowing any stable relationships to form. Housed in the same aviary was a small population of eight diamond doves (*Geopelia cuneate*), which did not form part of our study. The diamond doves very rarely interacted with the zebra finches, tended to isolate themselves at the top of the aviary and were never observed interacting with any the equipment we introduced, making it highly improbable that they contributed to zebra finch learning. Birds had free access to food from their usual feeders at all times. Individual finches were identified by a combination of colour morphs and leg rings. We collected data on several types of social interaction and conducted a diffusion experiment to investigate patterns of social learning of a novel foraging task, as detailed below. In general, data collection was carried out during 1-2 hour sessions over 57 non-consecutive days between 12th November 2018 and 21st March 2019 – allowing us to capture evidence of any stable, long-lasting relationships in the population and giving the majority of finches time to learn the novel task.

3.3.2. Data collection of social interactions

We collected data on four types of interactions between individuals as follows (for a more detailed account of this data collection, see Supplementary Material, section 3.7.1).

3.3.2.1. Feeding associations.

Feeding activity was recorded over 21 days between 12th November 2018 and 19th February 2019 using two GoPro cameras placed at either side of each of the birds' two regular feeders. In total, we recorded 30.3 hours of cumulative video footage over 21 days for feeder 1 (average: 1.4h per day; range: 0.3-2.2h per day) and 28.3 hours of footage over 20 days for feeder 2 (average: 1.3h per day; range: 0.6-2h per day. We analysed the entire footage, recording every visit to the feeders. For each visit, we recorded the bird's ID, the time it landed and the time it left the feeder. Times were recorded as cumulative times across the entire set of videos. If a bird could not be confidently identified by either of the researchers, the visit was removed from the dataset prior to analysis. A measure of the propensity each dyad of birds had for feeding together (henceforth, 'feeding association') was calculated by analysing the overlap in times for each dyad, as the actual versus expected proportion of time (F_{ij}) individuals *i* and *j* spent feeding together, as follows:

$$F_{ij} = \frac{A_{ij}}{E_{ij}}$$

where A_{ij} is the actual proportion of time individuals *i* and *j* were observed on the same feeder together and E_{ij} is the expected proportion of time they would have spent together if they had been feeding independently, calculated as:

$$A_{ij} = P_{1,ij} + P_{2,ij}$$

where $P_{1,ij}$and $P_{2,ij}$are the proportions of time individuals *i* and *j* were observed together on feeders 1 and 2, respectively, and

$$E_{ij} = (P_{1,i}P_{1,j}) + (P_{2,i}P_{2,j})$$

where $P_{1,i}$ and $P_{2,i}$ are the proportions of time individual *i* was observed on feeders 1 and 2, respectively. In all cases, proportions were calculated relative to the total cumulative video time for the feeder in question. Thus we obtain a measure that is $F_{ij} > 1$ for birds that preferentially feed at the same time and $0 \leq F_{ij} < 1$ for birds that preferentially feed apart.

3.3.2.2. Aggressive interactions.

To record aggressive interactions, we presented the birds with a small, 6.9cm x 6.7cm platform (Figure 3.1A) on which a sprig of millet was placed. The platform was small enough so that only a few birds could fit on it at one time and so would encourage expression of natural aggressive behaviours over food in an area that could be monitored closely (zebra finches generally engage in aggressive interactions with those who are 5-15cm from themselves; Evans, 1970). The platform was present in the aviary during 19 days between 23th November 2018 and 19th March 2019 and was re-constructed halfway through the experiment due to poor weather conditions causing it to break. The sprig of millet was secured to the platform initially using two crossed nails and, after reconstruction, using an elastic band. When the millet became depleted or fell off the platform, the researcher entered the aviary to replace it once all birds had dispersed from the platform. A single GoPro camera was used to record activity on the platform – in total, we recorded approximately 27.7 hours of video footage over 20 days (average: 1.3h per day; range: 0.8-2.6h per day). We analysed the entire footage, recording the ID of each visiting bird, the times at which they landed on and left the platform and all aggressive interactions they engaged in. This included biting but was mostly in the form of 'beak fencing' (two birds clashing their beaks together). (Note that we did not include displacements as displays of aggression, because they occurred infrequently and because it was difficult to determine whether they were intentional, or simply a case of individuals losing balance when there were too many birds on the platform). As previous studies have demonstrated an influence of an individual's dominance rank on who learns from whom, we were also interested to know whether the outcome of aggressive interactions influenced the direction of information transfer between aggressors. Thus, when an aggressive behaviour occurred, we recorded the ID of both birds involved and the winner of the fight. A bird was said to have 'won' the fight if the other bird fell or jumped off the platform. If two birds stopped fighting without one falling off, the fight was considered to have no winner. We then calculated the overall tendency of bird *i* to win a fight against bird *j* – bird *i* was considered the 'winning aggressor' of the pair and bird *j* the 'losing aggressor' if the two engaged in at least one fight and *i* won more fights than it lost against *j*.

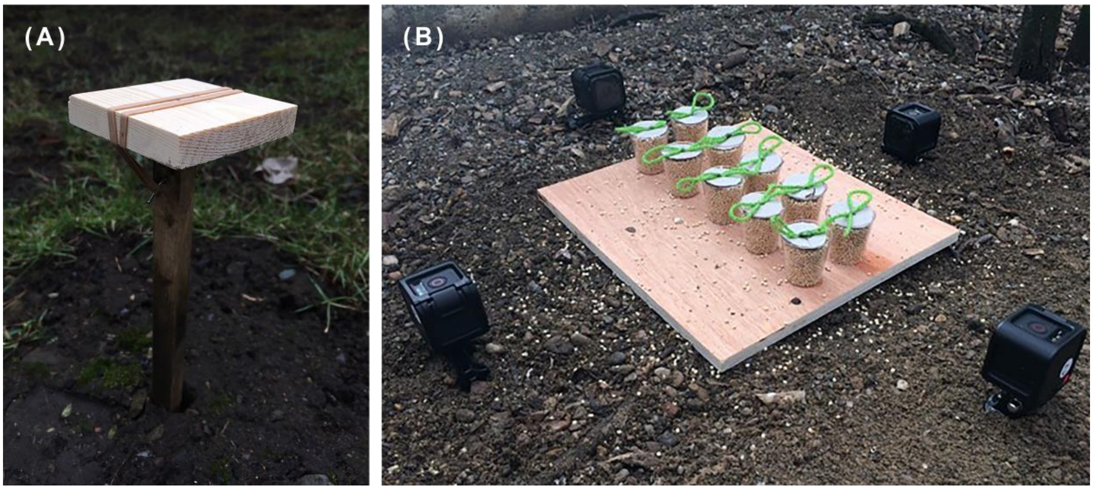

Figure 3.1. (A) The platform used to monitor pairwise aggressive interactions in finches. Millet spray was held onto the platform using an elastic band. **(B)** The foraging task presented to the finches, along with the placement of four GoPro cameras. The task consisted of 10 transparent plastic cups stuck to a wooden board. Each glass contained millet seed and was covered with a cardboard lid which birds needed to remove to solve the task and access the seed

3.3.2.3. Positive interactions and mating pairs.

Live observations were made during 1-2 hour sessions on 17 days between 14th November 2018 and 21st March 2019 to determine which birds engaged in positive interactions and which belonged to mating pairs. Positive interactions were defined as two birds either preening each other or perching together with their bodies touching. Mates were defined as pairs that were observed either copulating or nesting together. The principle investigator (who had the most experience identifying the birds based on their morph and leg rings) was positioned at the front of the aviary with a pair of binoculars. When a positive interaction or mating behaviour was observed occurring anywhere inside the aviary, the type of behaviour and the identity of the two birds involved were recorded. If both birds could not be confidently identified, the observation was discounted. Live observations were used rather than filming with cameras because, unlike feeding associations and aggressive interactions, it wasn't possible for us to focus positive interactions and mating/nesting into a single, easy-to-film area, and so live observations allowed us to record these interactions from across the entire aviary. In addition, these two types of interaction were easier to record live than feeding associations, which involved many individuals in a single area that were difficult to track live, or aggressive interactions, which were comparatively brief and easy to overlook. A total of 215 observations of positive interactions and 25 observations of mating / nesting behaviour were made. It is likely that birds who tended to interact closer to the front of the aviary were more likely to be accurately recorded as they were easier to see. To combat the effect of this, we used only the presence / absence of connections between each dyad of birds, rather than the frequency of interactions, in our generation of social networks below.

3.3.3. Generation of social networks

We constructed nine social networks based on the pairwise social interactions described above (Table 3.1; Figure 3.2). Each network represents a different social learning pathway and so a different hypothesis concerning how individuals learn from each other based on their social relationships. In the ‘feeding associations’ network, connections between dyads were equal to F_{ij}, reflecting the hypothesis that birds learned from all other birds in proportion to their propensity to feed together. For the remaining types of social interaction (aggressive, positive, mates), we constructed two versions of the social network that made different assumptions about the influence of feeding associations on learning opportunities – a binary version, where a connection of a particular type either existed or didn’t exist between two individuals, and a feeding association-weighted version (henceforth, shortened to ‘feeder version’), where any non-zero connection between individuals was equal to F_{ij}. The binary version reflects the hypothesis that the finches learned from those they share particular relationships with, e.g. individuals learning from their mates. The feeder version reflects the hypothesis that birds learned from those they share particular relationships with at a rate proportional to their propensity to feed together. In the case of aggressive interactions, we additionally considered that information flow may be directional (i.e. transfer from the winning aggressor to the losing aggressor of the dyad, or vice versa) and so divided both versions of this network into two – a ‘winning to losing aggressor’ network and a ‘losing to winning aggressor’ network.

Table 3.1. Descriptions of the social networks used in the analysis, constructed from five types of social interaction between zebra finch individuals.

Network name	**Description**
FeedingAssociations	Undirected network where the strength of connections between each pair of individuals is proportional to the amount of time they were observed feeding together.
WinningToLosingAggressor (Binary and feeder versions)	Directed network where individuals who were aggressive towards each other are connected and information is assumed to flow from the winning to losing aggressor. Birds that are not connected were either never observed engaging in aggressive interactions with each other or there was no overall fight winner (i.e. they both won an equal number of fights against each other or the fights ended in a 'draw').
LosingToWinningAggressor (Binary and feeder versions)	Directed network where individuals who were aggressive towards each other are connected and information is assumed to flow from the losing to winning aggressor. Birds that are not connected were either never observed engaging in aggressive interactions with each other or there was no overall fight winner (i.e. they both won an equal number of fights against each other or the fights ended in a 'draw').
Positive (Binary and feeder versions)	Undirected network where individuals are equally connected to birds with which they were observed engaging in positive interactions. Birds that are not connected were never observed engaging in positive interactions with one another.
Mates (Binary and feeder versions)	Undirected network where individuals are equally connected to birds they were observed mating or nesting with. Birds that are not connected were never observed engaging in mate-related interactions with one another.

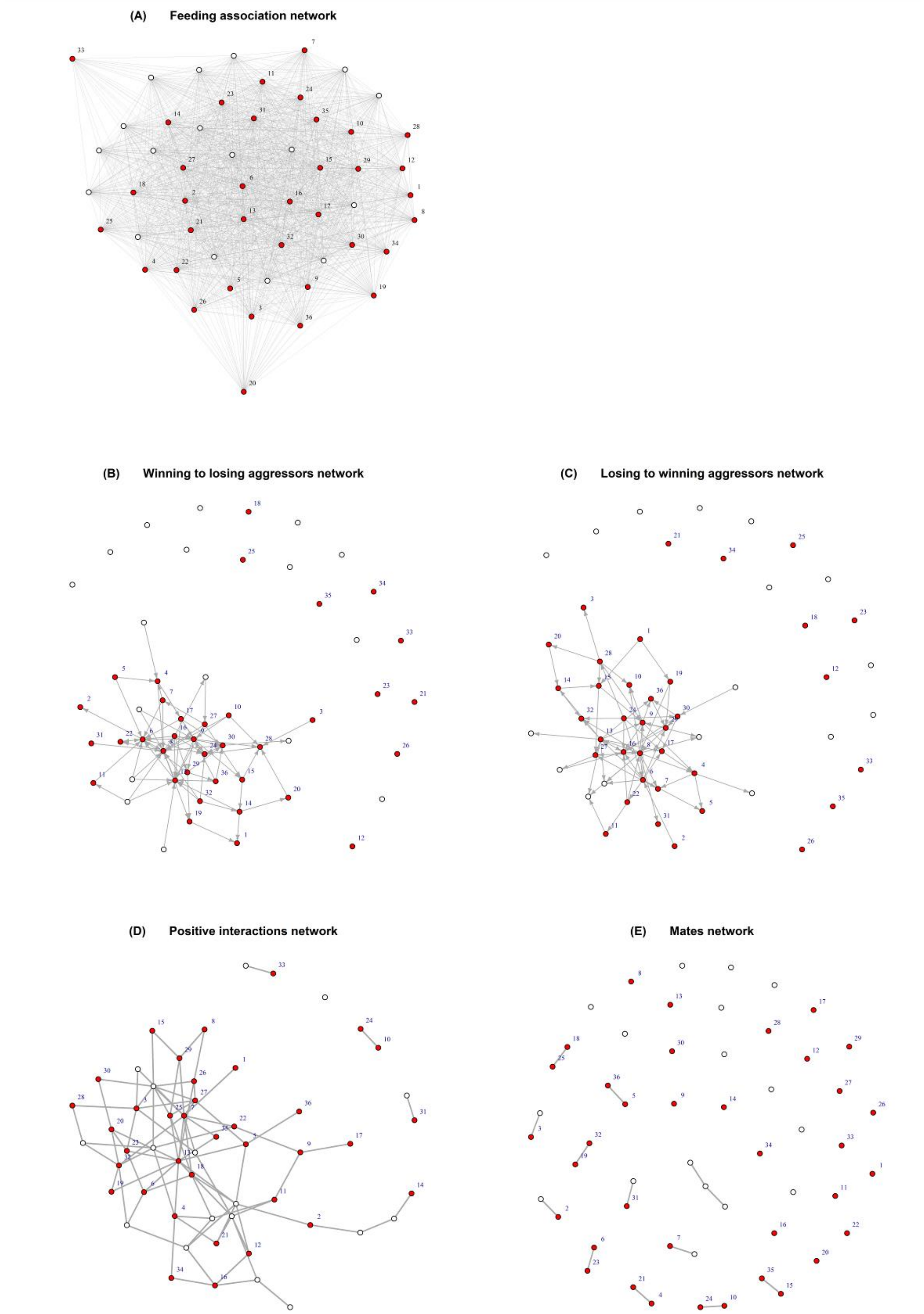

Figure 3.2. The five types of network used in our analysis. **(A)** Feeding association-based network. **(B)** Winning to losing aggressor network. **(C)** Losing to winning aggressor network. **(D)** Positive network. **(E)** Mates network. Networks B-E are shown in their binary forms. All networks are spring-embedded. White nodes represent individuals that did not solve the task. Shaded (red) nodes represent individuals that did solve the task, and are numbered according to the order at which they first solved the task. Lines represent

undirected connections between individuals (networks A, D and E). Arrows represent directed connections between individuals (networks B and C). Unconnected dyads were not observed interacting in the manner represented by that network.

3.3.4. Individual-level variables (ILVs)

In our analysis, we considered five ILVs which may have influenced individual rates of asocial and/or social learning. (i) The total time (seconds) each individual was recorded at the regular feeders was used as a measure of motivation to feed. (ii) A measure of the individual's overall tendency to win aggressive encounters was calculated based on the total number of fights won minus the total number of fights lost while on the introduced platform. (iii) The total number of fights engaged in while on the platform was used as a measure of aggression. (iv) Solving of a former task was used as a measure of learning proficiency and past experience. This was a binary ILV describing whether or not each individual solved a puzzle box task (by either lifting a lid or pulling a door) introduced to the same population during a previous, unpublished study that took place between 31st October 2017 and 20th January 2018 (see Supplementary Material, section 3.7.1 for details). (v) Suspected sex. In absence of genetic information, this was based on morphological differences and singing behaviour and was used as a general indicator of differences in sex.

3.3.5. Diffusion experiment

The finches were given a novel foraging task during 23 days between 5th February 2019 and 21st March 2019. The task (Figure 3.1B) consisted of 10 transparent plastic cups (volume 50ml) glued to a wooden base. Each glass was filled with millet seed and covered with a round cardboard lid. Each lid had a loop of green string attached to make it easier for the birds to remove. We were interested in the diffusion of lid-removing behaviours through the population. We therefore defined a solve as an individual removing or partially removing the lid from one of the cups, regardless of whether the bird fed from the cup afterwards. Presentation of our task and platform was alternated so that the two were never in the aviary at the same time. This is because the platform attracted a lot of attention from the finches and so may have distracted the birds from the task. During the task presentation, birds were allowed to solve and feed from the task freely. In order to avoid interrupting possible learning events, the researcher would only go into the aviary and replace any removed lids either when the birds had completely dispersed from the task or if all lids had been removed. Four GoPro cameras were used to record the task from all sides (positions of the cameras are shown in Figure 3.1B). We collected a total of 47.1 hours video footage for the task across the 23 days (average: 2.0h per day; range: 1.2-2.4h per day). We studied the entire footage and documented each solve (i.e. when a bird removed or partially removed a lid from one of the cups), noting the time of solve and the identity of the bird. Solve times were recorded as cumulative times across the entire set of videos (i.e. the time, in seconds, from the start of the experiment, discounting periods of time when the task was not present).

3.3.6. Statistical analysis

We used NBDA to determine whether the acquisition of the novel foraging behaviour during our diffusion experiment followed any of our interaction-based social networks. NBDA was carried out in the R statistical software (v.3.5.3), using the NBDA package (Hoppitt *et al.*, 2019) available at https://github.com/whoppitt/NBDA. We applied a specific type of NBDA known as Order of Acquisition Diffusion Analysis (OADA), which determines whether the order at which individuals learn the novel behaviour follows a specific social network. We used a multi-network approach (c.f. Farine, Spencer, *et al.*, 2015; Farine, Aplin, *et al.,* 2015), where multiple social networks can be considered in one model, which allows for the possibility that social learning may transmit via more than one possible pathway at the same time. We constructed separate models for all combinations of binary social networks and for all combinations of feeding association-based networks. Each network combination was considered to be a separate hypothesis as to the pathways of social transmission. For models which included more than one social network, we modelled two situations, one where the influence of each network on learning was constrained to be the same and one where the influence of each network was presumed to be different (as measured by the *s* parameter, described below).

For each network combination, we ran models for all combinations of ILVs, except in the case of the two fights-based ILVs (number of fights engaged in and tendency to win fights). Because these variables were derived from the same data, we considered them as an ‘either/or’ variable and so did not include models with both of these ILVs at the same time. For each ILV combination, we generated two types of model which assume different effects of ILVs on learning: additive models, which assume ILVs affect the rate of asocial learning only, and multiplicative models, which assume ILVs have a combined effect on the rate of both asocial and social learning. For comparison, we also generated asocial models, which included no social networks and therefore assumed individuals learned entirely asocially, for each ILV combination. Asocial models required only an additive version, since ILVs cannot affect social learning if learning is assumed to be entirely asocial. Finally, we ran a model which included no social networks and no ILVs. All models were generated using the 'AICtable' function of the NBDA package.

Models were compared using the corrected Akaike information criterion (AICc), where lower values indicate better-fitting models. Akaike weights were calculated giving a measure of support for each model. Due to the large number of individual models considered, we obtained a measure of support for each network combination and for each ILV by summing the Akaike weights across any models which included that network or variable. To allow fair comparison, we accounted for differences in model number as follows: Firstly, when comparing network combinations, Akaike weights were summed separately across the additive and multiplicative model sets and then the best-performing version (additive/multiplicative; henceforth referred to as the 'best model set') for each network combination was selected for model comparison (see Supplementary Material, Table 3.S1). For the final analysis, Akaike weights were recalculated as percentages based on only the best model sets. This ensured that model sets for each social network combination contained the same number of models as the asocial set, which only required an additive version since social learning was absent in these models. Secondly, when comparing the influence of ILVs, social models with no ILVs were included twice in the model set to allow fair comparison (i.e. an equal model number) to with-ILV model sets, which included both additive and multiplicative variations. Thirdly, when assessing the performance of the binary versus feeder versions of the *WinningToLosingAggressor, LosingToWinningAggressor*, *Positive* and *Mates* networks, we removed the asocial models and any models that included the full *FeedingAssociations* network to ensure equal model numbers and then recalculated the Akaike weights.

For our best social network combinations (those with the highest Akaike weights), we obtained model-averaged estimates for the social learning parameter (*s*) for each of the social networks included. The social learning parameter represents the increase in the rate at which a naïve individual will learn the novel behaviour per unit of association with informed individuals, relative to the baseline asocial rate of learning. The *s* parameter can, however, be difficult to interpret for proportional networks (as is the case for our feeding association-based networks) because it is scaled relative to the scale of the network itself (Hasenjager *et al,* 2021). This also means that *s* parameters estimated from networks of different scales cannot be directly compared (e.g. our binary and feeding-association based networks cannot be compared directly from the estimated *s* parameters). Therefore, to facilitate comparison between binary and feeding association-based networks, which were modelled separately, we also calculated the estimated proportion of learning events to have occurred via social transmission (propST) via each network in our best network combinations (Hasenjager *et al,* 2021). This was calculated as a model-weighted average across all models for each network combination. We also calculated lower limit estimates for both *s* and propST parameters. For further information on the lower limit estimates and additional calculations involving propST estimates, see Supplementary Material, section 3.7.2.

Note that we also ran a number of additional analyses (available in the Supplementary Material, section 3.7.6) to test the robustness of our findings and to explore some alternative explanations for the observed patterns of information transmission. The results of these analyses are referred to only briefly in the main text and so we refer the reader to the Supplementary Material (section 3.7.6) for the full discussion.

3.3.7. Ethical note

This study was approved by the Animal Welfare and Ethical Review Board at the University of Leeds and the Harewood House Trust. The study was in line with the Harewood House Trust Research Policy and research guidelines. We did not physically handle the birds in any way or restrict their access to regular feeders. No physical injury was observed as a result of the presence of any of our equipment. The task provided to the study population was in no way invasive and may have also acted as environmental enrichment. The presence of the wooden platform did not appear to incite aggressive interactions, but rather focus naturally-occurring behaviours into an area where we could monitor them. In addition, aggressive behaviours were mainly limited to beak fencing and were not observed causing physical injury.

3.4. Results

3.4.1. General observations

The task was solved a total of 207 times (at an average rate of 4.4 times per hour) by 36 of the 53 zebra finches. Each solver solved the task an average of 5.75 times, but this was highly skewed, with only four birds solving more than 10 times. The task was solved the most times by individual “CrL”, who solved the task 39 times over the course of the study period. Behaviours used to remove or partially remove the lid included pulling the cardboard or string with the beak, removing lid with feet while standing on top of the task, and wedging beak into a small gap at the side of the lid. Solvers fed from the cup (within 10 seconds after solving) during only 55 of the 207 solve events.

3.4.2. Presence of social learning

There was strong evidence that social learning occurred in our study group. Our best social model (AICc = 236.48) fit the data substantially better than our best asocial model (AICc = 243.72) (ΔAICc = 7.24, corresponding to 37.3x more support for the best social learning model). In addition, the total Akaike weight (summed across all ILV combinations) of the best-performing social network combination (Akaike weight = 0.107) was over 80x that of the asocial model set (Akaike weight = 0.001). Across the top fifteen best-performing network combinations, the average summed propST estimate across all included networks was 0.498 (± 0.16 SD) and the average summed propST lower limit estimate was 0.179 (± 0.07 SD). This suggests that, on average, approximately half of the learning events in the study occurred due to social learning via the included learning pathway(s). This provides further evidence for the presence of social learning in the study population, but also suggests that a large proportion of learning occurred either asocially or socially via a pathway not included in our analysis.

3.4.3. ILVs

There was little evidence that any of the ILVs included in this analysis had an effect on individual learning (Table 3.2). Models performed better without the inclusion of *FeederTimes, LastYearSolves* and *SuspectedSex* and the fights-based ILVs had little effect on the total Akaike weight. The estimated proportion of social learning events via each network were also largely unaffected by the inclusion of different ILV combinations (Supplementary Material, Table 3.S3). Additional analysis also showed that social networks based on these five ILVs did not convincingly explain the observed patterns of social transmission between individuals (Supplementary Material, Table 3.S15).

Table 3.2 Summed Akaike weights across all models with and without the inclusion of each ILV. *NumberOfFights* and *NetFightWin* were treated as a three-way either/or variable and so models without either of these variables are grouped together.

	Summed Akaike Weight	
ILV	*With ILV*	*Without ILV*
FeederTimes	0.270	0.730
NumberOfFights	0.384	0.334
NetFightWin	0.283	
LastYearSolves	0.238	0.762
SuspectedSex	0.257	0.743

3.4.4. Social learning pathways

Table 3.3 shows the support, measured by summed Akaike weights, for the fifteen best-performing social network combinations (see also Supplementary Material, Table 3.S1). The top fifteen network combinations accounted for >75% of the summed Akaike weights across all 84 network combinations used in our analysis, beyond which the summed Akaike weights dropped below 0.012 (~1/10 the support of the best model set) (Supplementary Material, Figure 3.S1). The full set of network combinations is available in Supplementary Material (Table 3.S6).

Of all the network combinations we tested, that which included the *WinningToLosingAggressor* and *LosingToWinningAggressor* networks (feeder versions), with the *s* parameters of each network constrained to be the same, received the most support (total Akaike weight = 0.107; 15.9% of best model set weights; Table 3.3). This corresponds to the hypothesis that individuals were most likely to learn from those with whom they shared aggressive interactions (at a rate proportional to their propensity to feed together) and that the rate of learning was unaffected by the direction of the aggressive interaction within a dyad. The model-averaged *s* parameter estimate was 0.28 (95% C.I. lower limit estimate = 0.08) for both networks, meaning that a naïve individual learned the task an estimated 0.28x faster (relative to the baseline asocial rate of learning) per unit of connection to an informed aggressor, proportional to their feeding associations. Since the *s* parameter can be difficult to interpret for proportional networks (Hasenjager *et al.,* 2021), the propST estimate offers a more intuitive measure of social transmission via each included network. The model-averaged propST estimate is 0.277 (± 0.017

SD) for the *WinningToLosingAggressor* network and 0.183 (± 0.01 SD) for the *LosingToWinningAggressor* network (Supplementary Material, Table 3.S2). In other words, an estimated 28% of learning events involved individuals learning from those who generally won against them during aggressive encounters and an estimated 18% involved individuals learning from those who generally lost to them during aggressive encounters – with the remainder of learning events being either asocial or via a social learning pathway not considered here. The propST lower limit estimate is 0.133 (± 0.031 SD) for the *WinningToLosingAggressor* network and 0.090 (± 0.02 SD) for the *LosingToWinningAggressor* network, providing further evidence that social transmission occurred via both networks.

Table 3.3 Total Akaike weight (summed across all ILV combinations) for our top fifteen network combinations, as a percentage of the summed Akaike weights across all network combinations in the analysis. Binary and feeding association-weighted networks were always modelled separately and so are grouped together. For each network included in each network combination, the estimated *s* parameter values are given. This is an estimate of the rate of social information transfer along the network in question, per connection to an informed individual. Where *s* parameters were estimated to be different across networks, higher values are additionally indicated by darker shading. The summed weights for all remaining social network combinations and for the asocial model (ranked 43; no social networks) are also included for comparison.

	Social networks present									
	Feeder networks					**Binary networks**				
Network combination	*FeedingAssociations*	*WinningToLosingAggressor*	*LosingToWinningAggressor*	*Positive*	*Mates*	*WinningToLosingAggressor*	*LosingToWinningAggressor*	*Positive*	*Mates*	**Summed Akaike weight (%)**
1		0.28	0.28							15.86
2						1.46	1.46		1.46	14.87
3						1.11	1.11			10.61
4		0.26	0.38							5.97
5	48.9	721.2	1600.67							4.70
6						0.89	1.66			4.38
7		0.39								3.61
8		0.17	0.17		0.17					2.59
9							1.75			2.55
10						1.63			1.63	2.01
11						1.53				1.96
12		0.31	0.43		0.04					1.96
13	0.04	1.21								1.88
14						1.29	2.02		0.85	1.84
15			0.44							1.78
NA	*Remaining 68 social model sets*									23.21
43										0.20

The second best network combination included the *WinningToLosingAggressor, LosingToWinningAggressor* and *Mates* networks (binary versions) with the *s* parameters constrained to be the same (total Akaike weight = 0.100; 14.9% of best model set weights; Table 3.3). This corresponds to the hypothesis that individuals learned both from their mates and their aggressors at a rate that was unaffected by either the type of interaction, direction of information transfer or the birds' propensity to feed together. The model-averaged *s* estimate was 1.46 (95% C.I. lower limit estimate = 0.38) for each network. The model-averaged propST estimate is 0.297 (± 0.02 SD) for the *WinningToLosingAggressor* network, 0.189 (± 0.01 SD) for the *LosingToWinningAggressor* network and 0.083 (± 0.01 SD) for the *Mates* network (Supplementary Material, Table 3.S2). This suggests that an estimated 30% of learning events involved individuals learning from those who generally won against them in fights, 20% involved individuals learning from those who generally lost against them in fights and 8% involved individuals learning from their mates. The propST lower limit estimate is 0.146 (± 0.04 SD) for the *WinningToLosingAggressor* network, 0.090 (± 0.02 SD) for the *LosingToWinningAggressor* network and 0.035 (± 0.01 SD) for the *Mates* network.

Overall, out of all the networks we tested, we found the strongest evidence for social transmission between individuals that shared aggressive interactions, in that every one of the top fifteen network combinations included either the *WinningToLosingAggressor* or *LosingToWinningAggressor* network and nine of the fifteen included both (Table 3.3). This includes the top two network combinations described above, which account for 31% of the model support over the 84 tested network combinations and, after which, model support rapidly drops (Supplementary Material, Figure 3.S1). Additional analyses clarified that simple associations on the aggression platform did not explain this pattern of social transmission (Supplementary Material, Tables 3.S12-3.S13), suggesting that the pairwise connections between aggressors were important in predicting the pattern of task solves. In addition, the removal of pre-task recordings of aggression had little impact on the explanatory power of these networks, suggesting that aggressive relationships were relatively stable in this population (Supplementary Material, Table 3.S14).

Learning events occurring through the aggression-based pathways did, however, appear to occur more often in the winner to loser direction. The average propST estimate for the *WinningToLosingAggressor* network (averaged over the top fifteen network combinations in which either the binary or feeder version of this network is present) is 0.297 (± 0.06 SD), with an estimated lower limit of 0.121 (± 0.08 SD) (Supplementary Material, Table 3.S2). The average propST estimate for the *LosingToWinningAggressor* network is 0.220 (± 0.05 SD), with an estimated lower limit of 0.089 (± 0.04 SD). This provides strong support that social transmission occurred via both of these pathways, and suggests that the *WinningToLosingAggressor* pathway was responsible for an estimated 1.35x as many learning events, on average, as the *LosingToWinningAggressor* pathway. The reason for this, despite the equal *s* parameters which indicate equal rates of learning along both pathways, appears to be due to three individuals with a disproportionate number of connections to losing aggressors acting as 'hubs' of information. All three successfully learned the task – and also learned the task quickly – giving them the potential to provide their many connected losing aggressors with early learning opportunities and promote information transfer along the *WinningToLosingAggressor* pathway. In addition, one of these highly-connected individuals, "CrL", solved the task considerably more times than any other individual, allowing it to act as a particularly strong source of social information. (Supplementary Material, Tables S8-S11).

In addition to aggression-based social learning, we found some support for social transmission between mates – five of the top fifteen network combinations contained the *Mates* network, including the second-best model. However, propST estimates for the *Mates* network tended to be < 0.1, suggesting that very little social information was actually transmitted via this pathway, and social transmission between mates was only apparent when the *Mates* network was included with at least one of the aggression-based networks. In addition, when interactions recorded prior to task introduction were removed from the analysis, the *Mates* networks received less support, suggesting either that finches learned novel behaviours from both past and present mates, or simply that removal of a subset of interactions made the *Mates* networks, which already contained only a few pairwise connections, too sparse to add any explanatory power to our models (Supplementary Material, Table 3.S14).

We found little to no support for social transmission via pathways based on positive associations (none of the top fifteen network combinations included the *Positive* network) or via a purely feeding-association-based network (only two of the top fifteen network combinations included the *FeedingAssociation*s network and *s* parameter and propST estimates were extremely varied). In addition, the binary and feeder versions of the *WinningToLosingAggressor, LosingToWinningAggressor*, *Positive* and *Mates* networks received a similar level of support (summed Akaike weights, binary: 0.529 ± 0.001 SD, feeder: 0.471 ± 0.001 SD, when asocial models and models including the full feeder network are disregarded), suggesting that a dyad's propensity to feed together did not greatly influence their likelihood of learning from one another.

3.5. Discussion

Within complex social groups, individuals are connected via different relationships, which may in turn determine the potential social learning pathways within the population. In this study, we examined the influence of pairwise relationships on social transmission of novel behaviours in zebra finches. Our results suggest that social learning in zebra finches is not homogenous, i.e. it does not occur indiscriminately among individuals. We also found no evidence to suggest that it was based primarily on simple feeding associations, as has been demonstrated in wild songbirds (Aplin *et al.,* 2012). Rather, we found evidence that specific social interactions between pairs of individuals determine who they learn from. In particular, in our study population, zebra finches appeared to learn from individuals with whom they share aggressive interactions, regardless of the overall outcome of aggression. It is possible that this pattern occurred because aggressive individuals were simply more likely to interact with the task (e.g. due to correlated personality traits such as boldness and exploratory tendency; David *et al.*, 2011) and so more likely to learn from each other; however our analysis indicated that this wasn't the case, as we found no evidence to suggest that aggression affected an individual's learning rate. In addition, since we were unable to control the number of learning opportunities provided by different types of individuals, it was difficult to say whether individuals selectively copied their aggressors over non-aggressors when given the opportunity to learn from either, or whether aggressors simply associated more often, making them more likely to witness each other performing novel behaviours. However, our analysis did suggest that patterns of association on the feeders and aggression platform did not explain the pattern of task solves, suggesting that the former is more likely. Either way, we have demonstrated that information about the novel task appeared to transmit between individuals who share aggressive interactions. We also found evidence to suggest that a subset of highly-connected aggressive individuals within our study population acted as 'hubs' of information that offered increased social learning opportunities for individuals whom they tended to win fights against.

Aggression-based directed social learning has been previously suggested in zebra finches. Clayton (1987) placed broods of juvenile zebra finches with two adult males and monitored their behaviour to determine whether juveniles preferentially learn songs from individuals with certain characteristics. The results showed that the majority of juveniles copied the song of the demonstrator that was the most aggressive towards them. This was irrespective of the dominance rank of the demonstrator, measured by the level of aggression between the two potential demonstrators. Clayton was unable to confirm whether juveniles were actively choosing more aggressive individuals to learn from or whether the aggressive behaviour of chosen demonstrators was simply a response to being followed in close proximity by their observers. However, Jones and Slater (1996) later replicated and confirmed the results of Clayton's experiment, additionally demonstrating that aggression was not simply a response to being followed by observers. Thus, rather than displaying directed social learning based on the dominance rank of demonstrators, it appears to be the actual aggressive interaction between two individuals that is important for social learning in zebra finches, as suggested by our own findings.

Our study expands on the findings of Clayton (1987) and Jones and Slater (1996) in several ways. Firstly, we have demonstrated that aggression-based directed social learning appears to be generalised across different types of behaviours – in our study, a foraging task, and in Clayton's (1987) and Jones and Slater's (1996) studies, song learning. Secondly, we demonstrated that that social learning between zebra finch aggressors, in a feeding context, was not influenced by the outcome of aggressive interactions. Clayton (1987) and Jones and Slater (1996) both studied song learning in juvenile zebra finches, in scenarios where both aggression and information transfer occurred in only one direction, from adult to juvenile, and so the importance of the directionality of aggressive interactions on learning was not a focus of their investigations. Furthermore, as our study population was almost entirely made up of adult finches, our results demonstrate that this social learning bias is not specific to juvenile learning, but is also present in adulthood. Our results also clarify that aggression-based demonstrator choice is not simply an artefact of confined laboratory conditions, a suggestion put forward by Clayton (1987). The birds used in our study inhabited a large, spacious aviary with natural features, enabling more natural movement and interaction than is likely to occur in the lab. They had lived together for their entire lives and so any relationships should be well-established. Birds were not given specific pre-selected demonstrators to choose from and had complete freedom to learn from any demonstrator they chose, much like a natural population. In addition, access to the introduced platform was completely voluntary, meaning that birds could easily have avoided aggressive interactions. Overall, this strongly suggests that aggressive interactions are not necessarily an artefact of being forced into close proximity together, and that aggression-based directed social learning occurs naturally in freely interacting populations.

The reasons for social learning between aggressors in our study population are unclear. It is possible that aggression leads to hormonal changes that promote learning. For example, steroid hormones are believed to be associated with both aggression (Soma *et al.*, 2008) and song learning (Brainard and Doupe, 2002) in male birds. It seems unlikely, however, that sex-specific hormones were responsible for the patterns of social learning found in our study, since we found no influence of suspected sex on learning and since the task we introduced to the population was not sex-specific like song-learning. Rather, our results suggest that individuals were actively choosing to learn from, or paying more attention to, demonstrators that were aggressive towards them. Several studies have demonstrated that more aggressive individuals tend to solve cognitive tasks more quickly, potentially because they tend also to be bolder, more exploratory and less neophobic (David *et al.*, 2011; Sih and Del Giudice, 2012; Guenther *et al*., 2014), thus making them more likely to approach and attempt novel tasks. While this could make more aggressive individuals more attractive as demonstrators of novel behaviours, we found no evidence to suggest this was the case in our study group, as an individual's level of aggression did not influence its rate of either social or asocial learning. Alternatively, aggression may be used as a simple and reliable way of assessing an individual's fitness. Aggression is often linked to reproductive fitness in male individuals (Darwin, 1896) and an individual who voluntarily takes part in an aggressive encounter, regardless of the outcome of the fight, may theoretically be stronger and healthier than those who avoid unnecessary confrontation. In our study, access to the platform where fights were recorded was entirely voluntary and an alternative food supply was constantly available. Thus, birds that chose to land on the platform may represent healthier or stronger individuals and therefore more attractive demonstrators for social learning.

An alternative explanation for social transmission along aggression-based pathways in our zebra finch population, rather than aggression having a direct impact on or acting as an indicator of learning ability, is that aggressive individuals were more likely to observe each other perform the novel behaviour. This may be because aggressive acts were a direct result of close association, and it was these close associations specifically that resulted in increased learning opportunities. This, however, does not seem likely, since none of our other measures of association (including associations on the aggression platform itself, as analysed in the Supplementary Material, section 3.7.6) offered a convincing explanation for the observed pattern of social transmission. A more likely explanation is that birds were displaying cognitive biases towards aggressors as sources of social information (as described by Heyes, 2012; Coussi-Korbel and Fragaszy, 1995). Perhaps these individuals were more salient demonstrators due to their aggressive behaviour towards observers, or perhaps observers actively paid them more attention to avoid unnecessary conflict and learned from them as a byproduct of this surveillance. Alternatively, the aggressive interactions that we documented may have been an indicator of which birds were in competition over resources – and so the aggression-based networks used in our analysis may also represent context-specific association networks. For example, since our task was a foraging task, aggressors who compete over food may have been more likely to be present at the task at the same time and so able to observe each other performing novel behaviours. Since our focus was purely on the importance of relationship-based pathways of social transmission, we did not document the identities of task observers – only task solvers – and so we are unable to comment on whether aggressors actively associated or competed with each other at the task location.

While aggressive interactions had the largest influence on social transmission between zebra finches in our study, we also found evidence of social transmission between mates. Beauchamp and Kacelnik (1991) demonstrated evidence that female zebra finches with more knowledgeable mates are less likely to learn a novel foraging task than those with naïve mates, because a female foraging closely alongside an informed male is provided with more opportunities for scrounging, thus overshadowing opportunities for her own learning. In contrast, we found evidence that zebra finches, to a degree, actively learn a novel task from their mates. This may be because mates are more likely to follow each other around the aviary (as suggested by our personal observations), thus increasing the likelihood that they will learn from one another. In line with this, previous studies have suggested that female zebra finches tend to prefer the foraging choices of male over female demonstrators, which was attributed to females paying more attention to male conspecifics (Katz and Lachlan, 2003; Benskin *et al.,* 2002). Avital and Jablonka (2000) argue that information exchange between monogamous mates can be a crucial component in reducing male-female conflict and permitting parental cooperation, and that the formation of stable, long-term pair bonds can result in the development of pair-specific preferences and behaviours. Thus, mate-mate information exchange may have significant evolutionary importance, despite receiving relatively little attention in the social learning literature to date.

Our results suggested, however, that learning from mates was not the main pathway of social learning, offering additional explanatory power only when combined with the aggression-based social networks. This may be because the *Mates* networks were comparatively small, containing only a few isolated pairwise connections (see Figure 3.2E), thus restricting the number of possible opportunities for social learning via this pathway. This would explain why the proportion of social learning events attributed to mates learning from one another tended to be low. This result additionally reflects the importance of considering multiple pathways of learning at the same time when studying animal social learning, as the effect of the *Mates* networks may not have been noticeable if they were not combined with the aggression-based networks.

Furthermore, research into directed social learning between mates is currently lacking and we encourage further research into such behaviour in zebra finches and other species, keeping in mind that social transmission between mates may be difficult to detect if only a few pairwise connections exist.

Positive relationships (specifically preening and perching in close proximity) did not have a strong influence on social learning in zebra finches in our study. This is in contrast to a former study by Williams (1990), which demonstrated that juveniles tended to learn song elements from adult males with whom they shared positive interactions such as preening, clumping and parental care. Similarly, experiments on various other species (e.g. *Sturnus vulgaris*; Boogert *et al.*, 2014; *Gasterosteus aculeatus*, Atton *et al.*, 2012; *E. rufifrons*, Schnoell and Fichtel, 2012; *C. corax,* Kulahci *et al.*, 2016) have demonstrated evidence that social information spreads through populations via proximity and/or affiliative networks. This did not appear to be the case in our study, which could suggest that the particular task provided to the study population did not require birds to be in such close proximity that they could only learn from their affiliates. For example, individuals may have been learning merely to interact with the task apparatus via stimulus or local enhancement (Heyes, 1994) rather than learning specific motor skills required to solve the task, which only required behaviours to be observed from afar, rather than imitating specific behaviours. This would account for the fact that the birds completed the task using a variety of behaviours (e.g. using either their beak or feet). More complex behaviours such as song learning might require demonstrators to be more familiar and have a higher tolerance of close observers. Alternatively, discrepancies between studies could indicate that different populations of the same species differ in how they learn from each other – essentially a ‘culture of learning’.

3.6. Conclusion

In this study, we investigated the influence of pairwise relationships on social learning in a freely interacting population of zebra finches in a semi-natural aviary environment. We found strong evidence that individuals learned a novel foraging task from demonstrators with which they had shared aggressive interactions, irrespective of the outcome of aggression. This has been previously suggested in laboratory experiments on zebra finches – and our study demonstrates that these previous findings are not simply an artefact of confined laboratory conditions. Instead, it appears to be a specific social learning strategy that also occurs in free-flying zebra finches. We also found evidence for a weak, secondary social learning pathway between mates, which was only apparent when combined with aggression-based pathways.

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Conflicts of interest/Competing interests. The authors have no conflicts of interest to declare that are relevant to the content of this article.

Ethical approval. This study was approved by the Animal Welfare and Ethical Review Board at the University of Leeds. We additionally carried out the research in line with the Harewood House Trust Research Policy and their research guidelines

Availability of data and material. The datasets generated during and/or analysed during the current study are available in the FigShare repository, https://doi.org/10.6084/m9.figshare.13570559. Additional information is included in Supplementary Material.

Authors' contributions. All authors contributed to the study conception and design. Data collection was carried out by CE and AR. Video footage of feeders were coded by CE. Video footage of tasks were coded by AR and CE. Data analysis was conducted by CE, with additional contributions from all authors. The first draft of the manuscript was written by CE. All authors contributed to, read and approved the final manuscript.

3.7. Supplementary Material

3.7.1. Details of a 2017-18 puzzle box study on the same zebra finch population.

During a previous, unpublished experiment, which took place between October 2017 and January 2018, the same population of zebra finches as used in our experiment were presented with a foraging task with two possible solve options. At the time of this experiment, the zebra finch population consisted of 120 individuals. The task was a wooden 'puzzle box' with two holes on top, each covered by a circular cardboard lid, and two holes at the side, each covered by a cardboard door (Figure 3.S1). Both lids and doors had a loop of string attached to make them easier for the birds to pull. This puzzle box was not novel to the population at the time and had in fact been presented to the same population three and a half months before, thus allowing naïve birds to learn how to solve the task for the first time and informed birds to reinforce any previously acquired knowledge. Birds were presented with two of these puzzle boxes during twelve 1.5-2 hour sessions, during which time each box was filmed from two angles using Go Pro cameras. The boxes were filled with seed and the lids and doors were closed. Birds could therefore 'solve' the task and gain access to the seed by either lifting one of the lids or pulling open one of the doors. The task was reset and refilled by the experimenter as and when the doors and lids were opened, provided the birds had dispersed from the task and so would not be disturbed. A record of which birds solved the task and which solve option they used was then made from the video footage of the puzzle boxes.

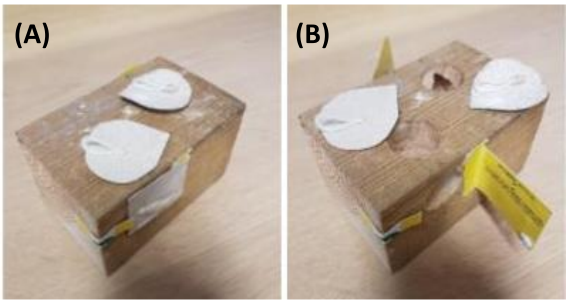

Figure 3.S1. Puzzle box task presented to the same zebra finch population during a previous, unpublished study which took place between October 2017 and January 2018. The task consisted of a wooden block into which seed was placed, with two holes on top covered by cardboard lids and a hole at either side covered with cardboard doors. **(A)** Task in its 'unsolved' state. **(B)** Task in its 'solved' state, with lids and doors removed.

The task used in our experiment was novel in its appearance, but the cardboard lids covering the plastic glasses in our task were similar to those on top of the puzzle box in the 2017-18 experiment. It was therefore possible that birds could be using previously learned behaviours to solve our task. To test this, we used a binary ILV representing whether each bird in our study population had previously solved the 2017-18 task (using the lid-lifting and/or door-pulling behaviour) in our analysis to establish whether birds who had solved the previous task were faster to learn the new task, either asocially or socially. As explained in the main text, we found no evidence to suggest that knowledge of how to solve the 2017-18 task influenced a bird's tendency to learn our task.

3.7.2. Additional information on statistical analyses

3.7.2.1. Best model sets.

Table 3.S1. The best-performing model type (additive/multiplicative) used for each of the top 15 network combinations shown in Table 3.2.

Network combination rank	**Best ILV model type**
1	multiplicative
2	multiplicative
3	multiplicative
4	multiplicative
5	additive
6	multiplicative
7	multiplicative
8	multiplicative
9	multiplicative
10	multiplicative
11	multiplicative
12	multiplicative
13	multiplicative
14	multiplicative
15	multiplicative

3.7.2.2. PropST calculations.

We calculated the estimated proportion of learning events to have occurred via social transmission (propST) via each network in the top fifteen network combinations (Table 3.S2). This was calculated as a model-weighted average across all twenty-four models in the best model set (i.e. using either multiplicative or additive models) for each network combination. To provide robustness to model-selection uncertainty, we also calculated an estimate for the lower limit of the propST parameter, based on the 95% confidence interval for the *s* parameter (Hasenjager *et al.*, In Press) for each network in each of the top fifteen network combinations. The model-weighted average of each lower limit estimate was calculated for each network combination.

For each network in each of the top fifteen network combinations, we used the variation in the propST estimate and propST lower limit estimate among models which incorporated different ILV combinations to assess whether the proportion of social transmission events attributed to a particular network was affected by the inclusion of different ILVs. We found that the standard deviations of the propST estimate across the twenty-four models used for each network combination were very low, always less than 0.1 (Table 3.S3).

Table 3.S2. propST estimates (upper cells, in bold) and propST lower limit estimates (lower cells) for each network in each of the top fifteen network combinations, and as a total across all networks in the combination. Grey cells indicate that a network was not included in a particular network combination. Also shown are the averages and standard deviations for each network, taken across the fifteen network combinations where a network of this type is present, and the combined average and standard deviation across binary and feeder-based networks (where applicable).

Network combination	Network									Total propST across networks
	FeedingAssociations	*WinningToLosingAggressor* (Binary version)	*LosingToWinningAggressor* (Feeder version)	*WinningToLosingAggressor* (Binary version)	*LosingToWinningAggressor* (Feeder version)	*Positive* (Binary version)	*Positive* (Feeder version)	*Mates* (Binary version)	*Mates* (Feeder version)	
1			**0.28**		**0.18**					**0.46**
			0.13		0.09					0.22

2		**0.30**		**0.20**				**0.08**		**0.57**
		0.15		0.09				0.04		0.27
3		**0.28**		**0.18**						**0.47**
		0.13		0.09						0.21
4			**0.25**		**0.21**					**0.46**
			0.04		0.05					0.09
5	**0.40**		**0.24**		**0.25**					**0.88**
	0.0003		0.12		0.15					0.26
6		**0.24**		**0.23**						**0.47**
		0.01		0.06						0.07
7			**0.38**							**0.38**
			0.21							0.21
8			**0.22**		**0.15**				**0.10**	**0.47**
			0.08		0.05				0.03	0.16
9				**0.30**						**0.30**
				0.15						0.15
10		**0.38**						**0.09**		**0.48**
		0.19						0.04		0.23
11		**0.38**								**0.38**
		0.20								0.20
12			**0.26**		**0.21**				**0.04**	**0.52**
			0.06		0.05				0	0.11
13	**0.41**		**0.37**							**0.78**
	0		0.24							0.24
14		**0.27**		**0.23**				**0.06**		**0.55**
		0.03		0.06				0		0.10
15					**0.29**					**0.29**
					0.14					0.14
Combined network average	**0.40**	**0.30**		**0.22**		**0**		**0.08**		
	0.0001	0.12		0.09		0		0.02		
Combined network SD	**0.02**	**0.06**		**0.05**		**0**		**0.03**		
	0.0002	0.08		0.04		0		0.02		

Table 3.S3. Standard deviation of the propST estimate for each network in each network combination. Standard deviations are calculated across the twenty-four models containing the specific network combination, where each model represents a different ILV combination. Grey cells indicate that a particular network was not used in this network combination and so a standard deviation was not calculated.

Network combination	Network								
	FeedingAssociations	*WinningToLosingAggressor* (Binary version)	*LosingToWinningAggressor* (Feeder version)	*WinningToLosingAggressor* (Binary version)	*LosingToWinningAggressor* (Feeder version)	*Positive* (Binary version)	*Positive* (Feeder version)	*Mates* (Binary version)	*Mates* (Feeder version)
1			0.017		0.010				
2		0.018		0.009				0.007	
3		0.019		0.010					
4			0.053		0.043				
5	0.098		0.007		0.007				
6		0.060		0.043					
7			0.050						
8			0.021		0.012				0.009
9				0.024					
10		0.048						0.015	
11		0.056							
12			0.055		0.045				0.008
13	0.084		0.041						
14		0.063		0.046				0.008	
15					0.025				

In addition, for each network, we used variation in the model-averaged propST estimate (Table 3.S4) and propST lower limit estimate (Table 3.S5) between all network combinations that included this network to assess whether the proportion of social transmission events attributed to a particular network varied depending on the other networks included in the combination. Again, SDs are always low, less than 0.1, suggesting that there is little variation in the estimates for each network, regardless of the other networks included in the combination.

Table 3.S4. The average propST estimate and SD for each network, averaged across the top fifteen network combinations where the network is present (shown in 'number of appearances' column). Also shown is the propST estimate average and SD combined across networks of the same type (e.g. the two Mates networks).

Network	**Number of appearances**	**Average propST estimate**	**SD**	**Combined average propST**	**Combined SD**
FeedingAssociations	2	0.400	0.015	0.400	0.015
WinningToLosingAggressor (Binary)	6	0.308	0.061	0.297	0.062
WinningToLosingAggressor (Feeder)	7	0.287	0.061		
LosingToWinningAggressor (Binary)	5	0.226	0.047	0.220	0.047
LosingToWinningAggressor (Feeder)	6	0.215	0.051		
Positive (Binary)	0	0	0	0	0
Positive (Feeder)	0	0	0		
Mates (Binary)	3	0.080	0.017	0.077	0.025
Mates (Feeder)	2	0.073	0.044		

Table 3.S5. The average propST lower limit estimate and SD for each network, averaged across the top fifteen network combinations where the network is present. Also shown is the propST lower limit estimate average and SD combined across networks of the same type.

Network	**Average propST lower limit estimate**	**SD**	**Combined average lower limit estimate**	**Combined SD**
FeedingAssociations	0.000	0.000	0.000	0.000
WinningToLosingAggressor (Binary)	0.119	0.081	0.121	0.078
WinningToLosingAggressor (Feeder)	0.126	0.076		
LosingToWinningAggressor (Binary)	0.091	0.036	0.089	0.040
LosingToWinningAggressor (Feeder)	0.088	0.047		
Positive (Binary)	0	0	0	0
Positive (Feeder)	0	0		
Mates (Binary)	0.025	0.022	0.021	0.020
Mates (Feeder)	0.016	0.023		

3.7.3. Akaike weights for all network combinations.

Figure 3.S2 shows the total Akaike weight, summed across models using the best-performing ILV type, for all 84 network combinations, ranked in order of their performance. Model support dropped off rapidly after the best two network combinations. Therefore, rather than display the Akaike weights for all of our 84 network combinations, we used this drop in model support to determine the number of individual network combinations to display, in an analogous way to using a scree plot to determine how many components to retain in a Principle Components Analysis. The top fifteen network combinations were chosen to display individually in Table 3.3, beyond which, the summed Akaike weights dropped below 0.012 (>8.9x less support than the best combination). When considering only the best model set for each network combination, these top fifteen combinations accounted for over 75% of the summed Akaike weights across combinations.

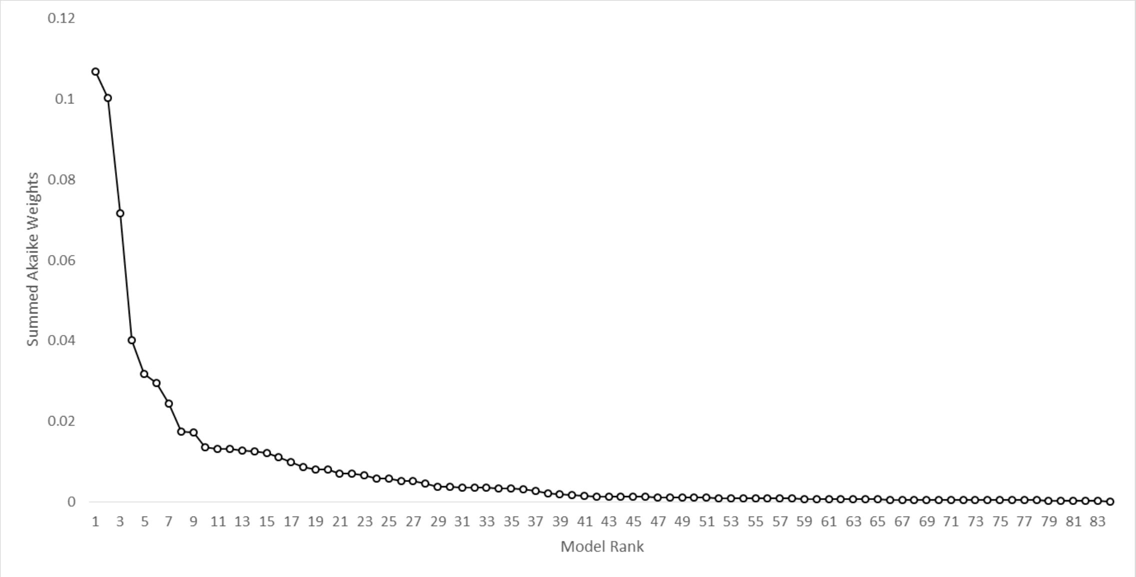

Figure 3.S2. Summed Akaike weight of each network combination in the analysis, summed across the 24 models in the combination's best model set.

3.7.4. Additional information and ‘raw’ Akaike weights for all network combinations considered.

Table 3.S6. The summed Akaike weight for each network combination. Akaike weights were summed across the best-performing ILV type (additive versus multiplicative) for each network combination. The Akaike weight is also given as a percentage compared to only the best model sets. The asocial model is highlighted in grey.

Rank	Network combination†	Best ILV model type	Summed Akaike weight	Percentage compared to model sets using only best ILV type
1	0:0:1:0:1:0:0:0:0	multiplicative	0.106923587	15.85605404
2	0:1:0:1:0:0:0:1:0	multiplicative	0.100302664	14.87421536
3	0:1:0:1:0:0:0:0:0	multiplicative	0.071569111	10.6132213
4	0:0:1:0:2:0:0:0:0	multiplicative	0.040230301	5.965885026
5	1:0:2:0:3:0:0:0:0	additive	0.031705297	4.701683853
6	0:1:0:2:0:0:0:0:0	multiplicative	0.029569621	4.384977362
7	0:0:1:0:0:0:0:0:0	multiplicative	0.024361714	3.612679526
8	0:0:1:0:1:0:0:0:1	multiplicative	0.017498639	2.594931328
9	0:0:0:1:0:0:0:0:0	multiplicative	0.017188013	2.548867566
10	0:1:0:0:0:0:0:1:0	multiplicative	0.013570336	2.012390222
11	0:1:0:0:0:0:0:0:0	multiplicative	0.013213354	1.959452174
12	0:0:1:0:2:0:0:0:3	multiplicative	0.013201174	1.957645962
13	1:0:2:0:0:0:0:0:0	multiplicative	0.012701101	1.883488475
14	0:1:0:2:0:0:0:3:0	multiplicative	0.012428752	1.843100937
15	0:0:0:0:1:0:0:0:0	multiplicative	0.012008063	1.780715567
16	0:0:1:0:2:0:3:0:0	multiplicative	0.011068787	1.641427207
17	0:0:1:0:0:0:0:0:2	multiplicative	0.009754974	1.446597512
18	0:1:0:2:0:3:0:0:0	multiplicative	0.008634465	1.280433508
19	1:0:2:0:3:0:4:0:0	additive	0.007992919	1.18529652
20	1:0:2:0:3:0:0:0:4	additive	0.007988052	1.184574776
21	0:0:1:0:0:0:2:0:0	multiplicative	0.006990143	1.036591535
22	0:0:0:1:0:0:0:1:0	multiplicative	0.006968518	1.033384692
23	0:1:0:0:0:0:0:2:0	multiplicative	0.006495746	0.963275761
24	0:1:0:1:0:1:0:0:0	multiplicative	0.005752445	0.853049185
25	0:0:0:1:0:0:0:2:0	multiplicative	0.00570693	0.846299615

26	0:0:0:1:0:2:0:0:0	multiplicative	0.005124901	0.7599886
27	0:1:0:1:0:1:0:1:0	multiplicative	0.005033042	0.746366524
28	1:0:0:0:2:0:0:0:0	multiplicative	0.004609367	0.68353835
29	0:1:0:0:0:2:0:0:0	multiplicative	0.003783189	0.561021669
30	0:0:0:0:1:0:0:0:2	multiplicative	0.003719138	0.551523333
31	1:0:2:0:0:0:0:0:3	multiplicative	0.003562747	0.528331592
32	0:0:0:0:1:0:2:0:0	multiplicative	0.003506584	0.520002994
33	0:0:1:0:0:0:0:0:1	multiplicative	0.003442222	0.510458539
34	1:0:2:0:0:0:3:0:0	multiplicative	0.003359213	0.498148859
35	0:0:1:0:2:0:3:0:4	multiplicative	0.003326556	0.493306044
36	0:1:0:2:0:3:0:4:0	multiplicative	0.00313007	0.464168482
37	0:0:1:0:0:0:2:0:3	multiplicative	0.002583404	0.383101564
38	0:0:1:0:1:0:1:0:0	multiplicative	0.002058444	0.305253501
39	1:0:2:0:3:0:4:0:5	additive	0.001840613	0.272950618
40	0:1:0:0:0:2:0:3:0	multiplicative	0.001713348	0.254078069
41	0:0:0:1:0:2:0:3:0	multiplicative	0.001544711	0.229070327
42	1:0:1:0:1:0:0:0:0	multiplicative	0.00133941	0.19862556
43	0:0:0:0:0:0:0:0:0	NA	0.001334995	0.197970845
44	0:0:1:0:1:0:1:0:1	multiplicative	0.001303429	0.193289818
45	1:0:0:0:2:0:0:0:3	multiplicative	0.001248273	0.185110551
46	1:0:0:0:2:0:3:0:0	multiplicative	0.001247873	0.185051234
47	1:0:1:0:1:0:0:0:1	multiplicative	0.001078417	0.159922041
48	0:1:0:0:0:1:0:0:0	multiplicative	0.001033647	0.153282949
49	0:0:0:0:1:0:0:0:1	multiplicative	0.001028284	0.152487651
50	0:1:0:0:0:1:0:1:0	multiplicative	0.001015882	0.150648518
51	0:0:0:0:1:0:2:0:3	multiplicative	0.001004082	0.148898656
52	0:0:0:1:0:1:0:0:0	multiplicative	0.000916878	0.135966886
53	1:0:1:0:0:0:0:0:0	multiplicative	0.000879927	0.130487299
54	0:0:0:1:0:1:0:1:0	multiplicative	0.00087949	0.130422495
55	1:0:2:0:0:0:3:0:4	multiplicative	0.000865374	0.128329186
56	1:0:1:0:1:0:1:0:0	multiplicative	0.000799231	0.118520621
57	0:0:1:0:0:0:1:0:0	multiplicative	0.000785949	0.116550989
58	1:0:1:0:0:0:0:0:1	multiplicative	0.000739659	0.109686491
59	1:0:1:0:1:0:1:0:1	multiplicative	0.000698707	0.103613583
60	0:0:1:0:0:0:1:0:1	multiplicative	0.000666408	0.098823857
61	1:0:0:0:1:0:0:0:0	multiplicative	0.000590336	0.087542887
62	1:0:1:0:0:0:1:0:0	multiplicative	0.000583163	0.086479179
63	1:0:1:0:0:0:1:0:1	multiplicative	0.000543437	0.080588079

64	1:0:0:0:1:0:0:0:1	multiplicative	0.000540479	0.080149427
65	0:0:0:0:1:0:1:0:0	multiplicative	0.000524915	0.07784139
66	0:0:0:0:1:0:1:0:1	multiplicative	0.000493321	0.07315621
67	1:0:0:0:1:0:1:0:0	multiplicative	0.000478404	0.070944119
68	1:0:0:0:1:0:1:0:1	multiplicative	0.000468322	0.069449026
69	1:0:0:0:0:0:0:0:0	multiplicative	0.000451621	0.066972379
70	1:0:0:0:0:0:0:0:1	multiplicative	0.0004442	0.065871894
71	0:0:0:0:0:0:0:1:0	additive	0.000424975	0.063020955
72	0:0:0:0:0:0:0:0:1	multiplicative	0.000423762	0.062841075
73	1:0:0:0:0:0:1:0:1	multiplicative	0.000423511	0.062803854
74	1:0:0:0:0:0:1:0:0	multiplicative	0.000422823	0.062701828
75	0:0:0:0:0:1:0:1:0	multiplicative	0.000413013	0.06124707
76	0:0:0:0:0:0:1:0:1	multiplicative	0.000412089	0.061110047
77	0:0:0:0:0:1:0:0:0	additive	0.000412083	0.061109157
78	0:0:0:0:0:0:1:0:0	additive	0.000412047	0.061103819
79	1:0:0:0:2:0:3:0:4	multiplicative	0.000311315	0.046165936
80	1:0:0:0:0:0:0:0:2	multiplicative	0.000129568	0.019214069
81	1:0:0:0:0:0:2:0:0	multiplicative	0.000129568	0.019214069
82	0:0:0:0:0:1:0:2:0	additive	0.000122102	0.018106911
83	0:0:0:0:0:0:1:0:2	multiplicative	0.00012167	0.018042849
84	1:0:0:0:0:0:2:0:3	multiplicative	3.43E-05	0.005086461

[†] Network combinations are displayed in the following format *FeedingAssociations* : *WinningToLosingAggressor*(binary) : *WinningToLosingAggressor*(feeder) : *LosingToWinningAggressor*(binary) : *LosingToWinningAggressor*(feeder) : *Positive*(binary) : *Positive*(feeder) : *Mates*(binary) : *Mates*(feeder). If a network is included in the combination, it is indicated by a number > 0. If a network is absent, it is indicated by a 0. Where all *s* parameters were constrained to be equal, all included networks are indicated by a 1 (e.g. 0:1:0:1:0:0:0:0:1). Where *s* parameters were different, all included networks are indicated by different numbers (e.g. 0:1:0:2:0:0:0:0:3).

3.7.5. Investigation into the distribution of social learning events along aggression-based pathways.

In our analysis (see main text), we found evidence that a higher proportion of social learning events occurred along the *WinningToLosingAggressor* pathway compared to the *LosingToWinningAggressor* pathway when both of these pathways were included in the NBDA model. This occurred even when *s* parameters were constrained to be the same (i.e. suggesting an equal influence of both social learning pathways). Here, we investigate the possible reasons for this result.

Firstly, we investigated whether there was evidence that fight winners tended to learn the task first, thus providing earlier opportunities for information transfer from winning to losing aggressors. For each dyad that shared an aggressive interaction, we calculated which bird(s) successfully learned the task and, if both, which one learned the task first. We found evidence that winning aggressors in a dyad were more likely to learn the task and also tended to learn the task before their losing aggressor (Table 3.S7). This is somewhat surprising, given that the NBDA results found no effect of fight wins on the rate at which individuals learned the task. Overall, this suggests that any influence of aggression or fight wins on individual learning ability was not strong enough for NBDA to detect.

Table 3.S7. Which individual(s) successfully learned the task and which individual learned the task first in each aggression-based dyad.

Scenario	Number of occurrences
Both learn, winning aggressor learns first.	37
Both learn, losing aggressor learns first.	28
Only winning aggressor learns.	11
Only losing aggressor learns.	2
Neither learn task.	0

We then considered that there may be a difference in the distribution of connections from winning to losing aggressors versus those from losing to winning aggressors that might explain the difference in propST estimates along the different pathways. For each connected bird in the aggression-based networks, we counted how many of its connections were to losing aggressors and how many to winning aggressors. Within the aggression-related networks, there are a total of 78 links connecting birds who engaged in aggressive interactions. We found that connections to losing aggressors are distributed differently across the individuals in the network compared to connections to winning aggressors. Table 3.S8 shows the number of outgoing connections to losing aggressors and to winning aggressors for each individual in the network (which is equivalent to the number of birds that each individual tended to win fights against or tended to lose fights against, respectively).

In the network, there are 30 individuals with outgoing connections to winning aggressors and most of these have only a few connections (>90% of connected individuals in the network have between one and four birds who tended to beat them in fights). In contrast, fewer individuals

(24 in total) had any outgoing connections to losing aggressors and these connections were more skewed in their distribution, with some birds winning fights against considerably more individuals than others. The majority of individuals (64%) had only one or two birds who tended to lose against them, but there were a few very highly connected individuals who tended to win fights against many birds. Specifically, there were three birds (ID numbers 20, 27 and 51) that had a large number of losing aggressors (>10, shown in bold in Table 3.S8). These three individuals accounted for >40% of all connections within the *WinningToLosingAggressors* network.

Table 3.S8. The number of outgoing links to losing aggressors (i.e. the number of birds who tended to lose to the individual) and to winning aggressors (i.e. the number of birds who tended to win against the individual) for each individual in the aggression-based networks. Highly-connected individuals with >10 links are shown in bold.

Bird ID	Number of losing aggressors	Number of winning aggressors
1	1	3
2	2	1
3	1	4
4	0	0
5	0	0
6	0	0
7	0	0
8	0	0
9	0	0
10	0	0
11	0	0
12	1	1
13	2	0
14	1	0
15	0	0
16	5	6
17	0	3
18	2	1
19	0	0
20	**10**	3
21	0	0
22	0	0
23	0	1
24	0	4
25	5	1
26	1	1

27	**12**	4
28	1	4
29	2	3
30	1	1
31	3	3
32	2	2
33	0	3
34	0	0
35	1	3
36	0	0
37	0	1
38	0	0
39	0	2
40	0	3
41	0	0
42	1	8
43	0	1
44	0	1
45	1	0
46	0	0
47	2	4
48	0	2
49	5	2
50	0	0
51	**10**	2
52	6	0
53	0	0

Overall, this means there were a greater number of fight losers linked to a smaller number of fight winners, thus the learning of the task by a bird who tended to win fights against a lot of individuals would offer a greater opportunity for their losing aggressors to learn than vice versa. The three highly-connected individuals in particular could have acted as hubs of social information transfer, particularly if they learned the task early on in the experiment. Indeed, all three of these individuals succeeded in learning the task, and each learned the early in the experiment (Table 3.S9). Individuals 20, 27 and 51 first learned the task at 2162, 6171 and 8374 seconds, respectively (taken as cumulative time across all task videos). As the entire experiment was approximately 170000 seconds in cumulative time, this means that these three individuals learned the task in the first 5% of the experiment duration, with individuals 20 and 27 learning particularly early on, thus giving their connected losing aggressors an early source of social information. This may also go some way to explaining the discrepancy between our results in Table 3.S7, which suggest that fight winners learned faster than their losing aggressors, and the results of the NBDA, which suggest no effect of aggression or fight wins on learning. If there are only a few winning aggressors that tended to learn faster than a large number of losing aggressors, NBDA may not find an overall effect on the rate of learning.

Table 3.S9. The order at which the birds first learned the task. Small numbers in the grey rows represent the order, large numbers in the white rows are the birds' ID numbers, which correspond to the first column of Table 3.S7. Highly-connected winning aggressors (ID numbers 20, 27 and 51) are shown in bold.

Solve order	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18
Bird ID	13	14	37	31	39	**20**	35	**27**	16	17	12	19	**51**	32	29	42	3	11
Solve order	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36
Bird ID	18	30	5	2	8	52	38	10	28	25	47	49	44	24	22	6	53	1

Table 3.S10 shows the cumulative number of outgoing links to winning aggressors and to losing aggressors as each new individual learns to solve the task. This can be used as a representation of the potential learning opportunities along each pathway – i.e. as a new individual becomes informed, this individual will become a source of information for its connected winning and losing aggressors. Table 3.S10 shows that the cumulative number of connections from winning to losing aggressors is consistently higher than those from losing to winning aggressors (except in one early instance, where they are equal). In addition, the first individuals to solve the task had some outgoing connections to losing aggressors, but no connections to winning aggressors, thus providing early opportunities for social transmission from winning to losing aggressors. Taken together, this may explain why an average of 1.36x more social learning events followed the *WinningToLosingAggressor* pathway compared to the *LosingToWinningAggressor* pathway, despite the estimated *s* parameters being equal.

Table 3.S10. The cumulative number of connections from winning to losing aggressors and from losing to winning aggressors as the number of birds learning the task increases.

Number of birds to solve the task	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18
Win->Lose	2	3	3	6	6	16	17	29	34	34	35	35	45	47	49	50	51	51
Lose->Win	0	0	1	4	6	9	12	16	22	25	26	26	28	30	33	41	45	45

	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36
Win->Lose	53	54	54	56	56	62	62	62	63	68	70	75	75	75	75	75	75	76
Lose->Win	46	47	47	48	48	48	48	48	52	53	57	59	60	64	64	64	64	67

In addition, individual 51 (”CrL”) solved the task the most times during the course of the experiment (Table 3.S11). This individual solved the task a total of 39 times (which is 17 more times than the next most frequent solver) and these solves occurred over a large timespan (159913 seconds from when it first learned the task to almost the end of the experiment). Again, this likely allowed individual 51 to act as an information hub. Individuals 20 and 27 also ranked within the top ten in terms of how often they solved the task.

Table 3.S11. The number of times each bird solved the task, ordered from most to least solves. The three highly-connected winning aggressors are shown in bold.

Bird ID	Number of solves
51	39
39	22
30	16
52	16
13	15
20	12
35	9
19	8
27	8
29	7
37	7
8	6
17	5
1	3
16	3
28	3
42	3
3	2

6	2
11	2
14	2
31	2
49	2
2	1
5	1
10	1
12	1
18	1
22	1
24	1
25	1
32	1
38	1
44	1
47	1
53	1
4	0
7	0
9	0
15	0
21	0
23	0
26	0
33	0
34	0
36	0
40	0
41	0
43	0
45	0
46	0
48	0
50	0

3.7.6. Additional analyses.

3.7.6.1. The influence of associations on the aggression platform

It is possible that the pattern of learning between aggressors was because of associations on the aggression platform, rather than the aggressive interactions themselves. For example, the aggression platform and the introduced task both share the characteristic of being novel; thus birds who choose to visit the platform may also be more likely to visit and subsequently solve the task. To investigate this, we generated association networks for the aggression platform in the same way that feeding associations on the normal feeders were generated – by using landing and leaving times to calculate how long each dyad of birds spent together, and then calculating F_{ij} (the actual versus expected proportion of time birds were together) as detailed in the main text. We then constructed models to test two hypotheses: (i) the *FeedingAssociations* network will receive a greater level of support if associations on the aggression platform are included in addition to associations on the normal feeders; and (ii) the network of associations on the aggression platform will receive approximately the same level of support as the combined *WinningToLosingAggressor* and *LosingToWinningAggressor* networks (i.e. aggressive interactions predict the order of learning due to associations between birds visiting novel objects, rather than directed learning towards aggressors).

To test hypothesis (i), we generated a combined network of associations (*FeederAndPlatformAssociations*) where F_{ij} represented the actual versus expected proportion of time each dyad of birds were together across the aggression platform and two regular feeders. We then substituted the *FeedingAssociation* network for the new *FeederAndPlatformAssociations* network and reran all NBDA models that included this network. Models were constructed the same way as in the main text – with all network combinations using both equal and differing *s* parameters, and all ILV combinations using both additive and multiplicative model versions. We then recalculated the Akaike weights for each network combination using their best versions (additive or multiplicative) in the same way as the main analysis (sections 3.3.6 and 3.3.7.2). The top model in this analysis was the same as in our original analysis – multiplicative model, using the feeder versions of the *WinningToLosingAggressor* and *LosingToWinningAggressor* networks, with total fight number as an ILV, which had an AICc of 236.48 – and the overall pattern of the results (i.e. that aggression-based networks offered the best explanation for the pattern of social transmission) remained the same (Table 3.S12). Incorporating associations at the platform did, however, slightly improve the explanatory power of the feeding associations network. The most supported model that included the *FeederAndPlatformAssociations* network had an AICc of 237.30 (additive model, using *FeederAndPlatformAssociations* network and the feeder version of the *WinningToLosingAggressor* and *LosingToWinningAggressor* networks, with fight wins and suspected sex as ILVs); whereas the most supported model that included the original *FeedingAssociations* network (model using the *FeedingAssociations* network and the feeder versions of the *WinningToLosingAggressor* and *LosingToWinningAggressor* networks, no ILVs included) had an AICc of 238.87 (ΔAICc = 1.57). Overall, this suggests that, while support for feeding-association-based social learning was improved by including associations at the platform, social learning pathways based on the actual aggressive interactions still offered a better explanation for the pattern of information transmission that we observed.

Table 3.S12. The top fifteen network combinations when the original *FeedingAssociations* network was substituted with the *FeederAndPlatformAssociations* network, which represented the proportion of time each dyad of birds associated either on one of the feeders or on the aggression platform. Feeder and binary versions of the networks were modelled separately and so are grouped to reflect this. The networks included in each network combination are indicated by either S_D or S_E, depending on whether the *s* parameters of the model in question were different or constrained to be equal. Akaike weights for each network combination are given as a percentage of Akaike weights across all network combinations. Only the best-performing ILV model type (additive or multiplicative) for each network combination were used in these calculations.

	Social networks present									
	Feeder networks					**Binary networks**				
Network combination	*FeederAndPlatformAssociations*	*WinningToLosingAggressor*	*LosingToWinningAggressor*	*Positive*	*Mates*	*WinningToLosingAggressor*	*LosingToWinningAggressor*	*Positive*	*Mates*	**Summed Akaike weight (%)**
1		S_E	S_E							15.11
2						S_E	S_E		S_E	14.17
3						S_E	S_E			10.11
4	S_D	S_D	S_D							8.73
5		S_D	S_D							5.68
6						S_D	S_D			4.18
7		S_E								3.44
8		S_E	S_E		S_E					2.47
9							S_E			2.43
10	S_D	S_D	S_D		S_D					2.14
11	S_D	S_D	S_D	S_D						2.13
12						S_E			S_E	1.92
13						S_E				1.87
14		S_D	S_D		S_D					1.87
15						S_D	S_D		S_D	1.76

To test hypothesis (ii), we generated a network of associations on the aggression platform (*PlatformAssociations*) and reran our analysis, replacing the feeder versions of the *WinningToLosingAggressor* and *LosingToWinningAggressor* networks with this new network. In other words, we tested whether the associations on the aggression platform, without taking into account the actual aggressive encounters between birds, offered a better (or equally convincing) explanation for the pattern of learning events, or whether the more important factor was the connection between the aggressors themselves. The most supported model that included the *PlatformAssociations* network (additive model, using only the *PlatformAssociations* network, with total fight number included as an ILV) had an AICc of 245.96. This is substantially larger than the most supported model in our original model set (AICc = 236.48; ΔAICc = 9.48). As shown in Table 3.S13, replacing the original aggressor networks with this network resulted in the binary versions of the *WinningToLosingAggressor* and *LosingToWinningAggressor* networks receiving more support, while the new *PlatformAssociations* network received little to no support. Replacing the original aggressor networks with a network representing associations on the aggression platform therefore does not offer a better fit for our data, suggesting that the tendency of individuals to learn from their aggressors was not simply due to birds who visited the novel aggression platform together being more likely to also visit the novel task together.

Overall, these additional analyses show that individuals learning from their aggressors remains the most supported explanation for the observed pattern of solves, and that this does not appear to be due to simple associations on the aggression platform itself.

Table 3.S13. The top fifteen network combinations, but with the feeder versions of the *WinningToLosingAggressor* and *LosingToWinningAggressor* networks replaced with a new *PlatformAssociations* network, which represents the proportion of time dyads of birds were together on the aggression platform, without taking into account any aggressive interactions taking place between them. Feeder and binary versions of the networks were modelled separately and so are grouped to reflect this. The networks included in each network combination are indicated by either S_D or S_E, depending on whether the *s* parameters of the model in question were different or constrained to be equal. Akaike weights for each network combination are given as a percentage of Akaike weights across all network combinations. Only the best-performing ILV model type (additive or multiplicative) for each network combination were used in these calculations.

	Social networks present								
	Feeder networks				**Binary networks**				
Network combination	*FeedingAssociations*	*PlatformAssociations*	*Positive*	*Mates*	*WinningToLosingAggressor*	*LosingToWinningAggressor*	*Positive*	*Mates*	**Summed Akaike weight (%)**
1					S_E	S_E		S_E	30.82
2					S_E	S_E			22.00
3					S_D	S_D			9.09
4						S_E			5.28
5					S_E			S_E	4.17
6					S_E				4.06
7					S_D	S_D		S_D	3.82
8					S_D	S_D	S_D		2.65
9						S_E		S_E	2.14
10					S_D			S_D	2.00
11					S_E	S_E	S_E		1.77
12						S_D		S_D	1.75
13						S_D	S_D		1.57
14					S_E	S_E	S_E	S_E	1.55
15					S_D		S_D		1.16

3.7.6.2. Removal of associations and interactions recorded prior to task introductions

If the relationships between individuals in a population are not stable over time, with connections between different individuals breaking and forming, the possible pathways of social transmission may also change over time. In our main analysis, we began recording data on associations and interactions almost three months prior to the introduction of the task itself. It is therefore possible that, by the time the task was introduced, some of the connections present in our tested social networks no longer existed in the population network. We investigated this by regenerating all of our social networks, but with the removal of interactions that were observed prior to task introduction on the 5th February 2019, and then rerunning our analysis as described in the main text.

As shown in Table 3.S14, the most favoured network combinations were altered somewhat by the removal of pre-task recordings from the social networks, although aggression-based social learning pathways still remain the most supported. In this analysis, there is more support for social transmission along the *WinningToLosingAggressor* networks than the *LosingToWinningAggressor* networks. The *Mates* network received less support than in the original analysis, including no longer appearing in the second best model. For example, the best model that included the *Mates* network in this analysis (multiplicative model including feeder versions of the *WinningToLosingAggressor* and *Mates* network, with total fight number as an ILV) had an AICc of 241.46; substantially higher than the best model which included the *Mates* network in our original analysis (multiplicative model including binary versions of the *WinningToLosingAggressor, LosingToWinningAggressor* and *Mates* networks, with total fight number as an ILV), which had an AICc of 236.61 (ΔAICc = 4.85).

The *Positive* network, on the other hand, received slightly more support, now appearing in three of the top fifteen network combinations, although was still substantially less supported than the aggression-based networks alone. However, the best model including the *Positive* network in this analysis (multiplicative model which included the feeder versions of the *WinningToLosingAggressor* and *Positive* networks, with pre-task interactions removed, and with total fight number as an ILV; AICc = 241.46) and the original analysis (multiplicative model including the binary versions of the *WinningToLosingAggressor, LosingToWinningAggressor* and *Positive* networks, with total fight number as an ILV; AICc = 241.05) received similar levels of support; suggesting that the removal of the pre-task interactions did not improve the explanatory power of the *Positive* networks, but more likely reduced the explanatory power of the aggression-based networks, thus making the *Positive* networks more supported by comparison.

Overall, however, the networks used in this analysis fit the data less well than those used in the original analysis. The most supported model in this analysis, for example, (multiplicative model which included the feeder version of the *WinningToLosingAggressor* network, with pre-task interactions removed, and total fight number as an ILV) had an AICc of 239.07 (ΔAICc = 2.59 compared to the best model in our original analysis). The higher support for the networks in our original analysis could suggest that both past and present relationships are important for transmission of information about a novel task. For example, the higher level of support for the *Mates* network in the original analysis could suggest that birds learned from both past and present mates. Alternatively, the removal of pre-task connections may have simply made the networks too sparse to account for as much of the information transfer – especially in the case of the *Mates* network, which already contained very few pairwise connections.

Table 3.S14. The top fifteen network combinations, using social networks in which any pre-task connections were removed. Feeder and binary versions of the networks were modelled separately and so are grouped to reflect this. The networks included in each network combination are indicated by either S_D or S_E, depending on whether the *s* parameters of the model in question were different or constrained to be equal. Model 15 is the asocial model, where no social learning pathways were included. Akaike weights for each network combination are given as a percentage of Akaike weights across all network combinations. Only the best-performing ILV model type (additive or multiplicative) for each network combination were used in these calculations.

	Social networks present									
	Feeder networks					**Binary networks**				
Network combination	*FeedingAssociations*	*WinningToLosingAggressor*	*LosingToWinningAggressor*	*Positive*	*Mates*	*WinningToLosingAggressor*	*LosingToWinningAggressor*	*Positive*	*Mates*	**Summed Akaike weight (%)**
1		S_E								11.87
2						S_E				11.47
3						S_E	S_E			8.47
4		S_E	S_E							6.57
5						S_D	S_D			3.97
6		S_D	S_D							3.63
7						S_D		S_D		3.54
8	S_D	S_D								3.41
9		S_D		S_D						3.41
10		S_D			S_D					3.41
11						S_D			S_D	3.30
12						S_E			S_E	3.14
13						S_E	S_E			2.67
14						S_E		S_E		1.33
15										1.21

3.7.6.3. The influence of ILVs on information transmission

In our main analysis, ILVs were only included to account for any differences in learning rates between certain types of individuals. However, it is also possible that the ILVs we recorded may have influenced information transmission between individuals – e.g. information may have passed between individuals with the characteristics described by the ILVs. To investigate this, we first generated the following sets of binary networks from our five recorded ILVs:

(i) Two directional networks based on each individual's time spent on the regular feeders (i.e. their motivation to feed):
  a. *HighToLowFeeder* network. Each individual has an incoming binary connection from those who spent more time on the feeder than themselves.
  b. *LowToHighFeeder* network. Each individual has an incoming binary connection from those who spent less time on the feeder than themselves.

(ii) Two directional networks based on each individual's tendency to win fights:
  a. *HighToLowNetFightWin* network. Each individual has an incoming binary connection from those with a higher net fight score (fight wins – fight losses) than themselves.
  b. *LowToHighNetFightWin* network. Each individual has an incoming binary connection from those with a lower net fight score (fight wins – fight losses) than themselves.

(iii) Two directional networks based on each individual's total number of fights on the aggression platform (i.e. general aggression levels):
  a. *HighToLowFightNumber* network. Each individual has an incoming binary connection from those who fought more often than themselves.
  b. *LowToHighFightNumber* network. Each individual has an incoming binary connection from those who fought less often than themselves.

(iv) Two bidirectional networks connecting individuals based on whether they solved a previous task (see section 3.7.1 for details).
  a. *Solves* network. Binary connections between those who solved the previous task.
  b. *NoSolves* network. Binary connections between those who did not solve the previous task.

(v) Four directional networks based on suspected sex.
  a. *MaleToMale* network. Males have incoming binary connections only from other males.

b. *FemaleToFemale* network. Females have incoming binary connections only from other females.
c. *FemaleToMale* network. Males have incoming binary connections only from females.
d. *MaleToFemale* network. Females have incoming binary connections only from males.

We then took the top-performing binary model from our original analysis (multiplicative model including the binary versions of the *WinningToLosingAggressor, LosingToWinningAggressor* and *Mates* networks, with *s* parameters constrained to be the same, and with total fight number as an ILV) and re-ran this model with the inclusion of each of the five sets of networks described above, to establish whether the inclusion of any of these networks improved the model's fit to the data. Each of the five sets of networks described above were modelled separately, but with every possible combination of their included networks alongside the original *WinningToLosingAggressor, LosingToWinningAggressor* and *Mates* networks. The *s* parameters for the *WinningToLosingAggressor, LosingToWinningAggressor* and *Mates* networks were constrained to be the same, as in the original best model; however the *s* parameters of any additional networks were permitted to be different to account for variation in social transmission between the networks.

As shown in Table 3.S15, the addition of these ILV-based networks into the top-performing binary model from our original analysis did not improve the fit of the original model. We therefore have no reason to suspect that any of our recorded ILVs influenced the pathways of transmission between individuals in the population.

Table 3.S15. AICc values for our top-performing binary model when networks constructed from our five recorded individual-level variables (ILVs) were added to the original model. For each ILV, a set of additional networks were constructed, representing different social learning pathways between individuals with the characteristics described by the ILV, which were added to the original model in different combinations to establish if the fit of the original model was improved. ΔAICc is given relative to the original model.

	ILV	Networks added	AICc	ΔAICc
Original model			**236.61**	**0**
	Feeder times	*HighToLowFeeder* only	238.38	1.77
		LowToHighFeeder only	239.00	2.39
		HighToLowFeeder + *LowToHighFeeder*	240.33	3.72
	Net fight win	*HighToLowNetFightWin* only	237.41	0.8
		LowToHighNetFightWin only	239.00	2.39
		HighToLowNetFightWin + *LowToHighNetFightWin*	239.80	3.19
	Total fight number	*HighToLowFightNumber*	239.00	2.39
		LowToHighFightNumber	237.67	1.06
		HighToLowFightNumber + *HighToLowFightNumber*	240.21	3.60
	Past task solves	*Solves*	238.15	1.54
		NoSolves	239.00	2.39
		Solves + *NoSolves*	239.93	3.32
	Sex	*MaleToMale* only	238.15	1.54
		FemaleToFemale only	239.00	2.39
		MaleToFemale only	237.99	1.38
		FemaleToMale only	239.00	2.39
		MaleToMale + *FemaleToFemale* (same-sex learning)	240.55	3.94
		MaleToMale + *MaleToFemale* (male-biased learning)	240.52	3.91
		MaleToMale + *FemaleToMale*	239.76	3.15
		FemaleToFemale + *MaleToFemale*	240.24	3.63
		FemaleToFemale + *FemaleToMale* (female-biased learning)	241.54	4.93

	MaleToFemale + *FemaleToMale* (opposite-sex learning)	239.64	3.03
	MaleToMale + *FemaleToFemale* + *MaleToFemale*	242.95	6.34
	MaleToMale + *FemaleToFemale* + *FemaleToMale*	242.47	5.86
	FemaleToFemale + *MaleToFemale* + *FemaleToMale*	242.35	5.74
	MaleToMale + *FemaleToFemale* + *MaleToFemale* + *FemaleToMale*	245.20	8.59

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Chapter 4 | Virtual Environments for Research into Social Evolution (VERSE): A novel experimental environment for the study of human social learning

4.1. Abstract

Social learning (learning from others) can be a cost-effective way of gaining information compared to asocial (independent) learning. However, learning from others indiscriminately can lead to the acquisition of maladaptive behaviours or outdated information. Evolutionary theory therefore predicts that individuals will use social information adaptively through the use of 'social learning strategies'. Restrictive laboratory conditions, however, make studying human learning strategies problematic. Abstract tasks, unrealistic sources of social information and methodologies that do not take into account the influence of physical location over large spaces make it difficult to ascertain if previous findings are representative of the way we would use social information in reality. Here I describe a novel platform for studying human social behaviour within immersive virtual environments: "Virtual Environments for Research into Social Evolution" (VERSE). Through the use of gaming technology, VERSE allows researchers to build realistic, three-dimensional, open world environments where participants can complete ecologically relevant tasks while actively observing computer-controlled artificial intelligence agents (AIs) that act as realistic yet controllable sources of social information. This methodological chapter begins by exploring what social learning strategies are and the problems with studying social learning behaviour in humans (compared to animal populations, for example). I then discuss how gaming technology can be used in behavioural research and follow on with a detailed account of the specific functionalities available in VERSE. I conclude with a worked example of how VERSE can be used to construct a novel behavioural experiment. Altogether, VERSE has great potential to give us insight into how human individuals learn within novel environments in a way that has never before been possible.

4.2. Background

Social learning (learning from others) occurs in many species and can be a highly cost-effective way of gaining information (Hoppitt and Laland, 2013), making it adaptive in many biological contexts (Galef and Laland, 2005) over independent, or ‘asocial’, learning. There are many ways in which individuals can gain information from one another – from direct observation of an individual to interactions with the products of its behaviour – and many specific mechanisms of social learning – from ‘local enhancement’, where a demonstrator’s behaviour attracts an observer’s attention to a particular stimulus, to direct imitation of a specific behaviour or set of behaviours (Heyes, 1994). Research suggests that both animals and humans are also selective in the way they use social information, deploying ‘social learning strategies’ that dictate when, what and from whom they learn socially (Laland, 2004; Rendell *et al.*, 2011). The use of such selective social information use is expected to be adaptive compared to copying individuals indiscriminately (Boyd and Richerson, 1988; Schlag, 1998; Rendell *et al.*, 2010), as a constant lack of direct sampling from the environment can lead to the spread of maladaptive or outdated behaviours through the population (Laland and Williams, 1998; Rogers, 1988). Evidence suggests that both humans and non-human animals are capable of using social information adaptively and that there are similarities in the use of social learning strategies between different taxa.

However, making direct comparisons between the way humans and animals use social information is difficult, not least because of the hugely different methodologies used to study humans versus non-human animals. In Chapter 1, I made the case for a lack of ecological validity in human social learning experiments. In summary, while animal experiments generally involve individuals learning ecologically relevant survival skills (e.g. foraging, predator avoidance) through the observations of informed demonstrators during either traditional ‘demonstrator-observer’ experiments or larger scale, more naturalistic ‘open diffusion’ experiments, most human experiments are limited by highly abstract tasks that offer little in the way of behavioural flexibility, unrealistic sources of social information and extremely localised spatial scales. This makes it difficult to establish how we would use social information in real-world scenarios, as well as the importance of social learning for human survival in our evolutionary past.

One largely unexploited methodology that may allow humans to be studied in more ‘natural’, spatially realistic conditions, and in a framework more comparable to field experiments on animals, is virtual reality (VR). Computer-based experiments, in general, offer a greater possibility of extending their reach to the general public, and hence a more diverse pool of participants, than lab-based experiments (Vicens *et al.*, 2018). Relatively simple computer-based tasks have already proved useful in the field for the creation of novel tasks (e.g. Mesoudi 2008; Mesoudi and O’Brien, 2008; Morgan *et al.*, 2012). Mesoudi and colleagues’ research in particular demonstrates how virtual tasks can be created that would represent real-life challenges in traditional human communities – in this case, designing virtual arrowheads to use in a virtual hunting ground (Mesoudi 2008; Mesoudi and O'Brien, 2008). Such computer-based methodologies have even extended to the study of human cumulative culture – as in Miu and colleagues' (2018) study of collaborative computer programming. Perhaps most importantly for the study of human behavioural ecology and social evolution, VR also gives us a unique opportunity to study human behaviour in survival situations that cannot be replicated under experimental conditions, e.g. the outbreak of a fire (Arias *et al.,* 2018) or evacuation scenarios (Moussaïd *et al.,* 2016).

Large, open world, three-dimensional environments that participants can navigate freely have the potential to allow realistic social interactions between networks of individuals across realistic spatial scales, without the need to leave the lab. Massively multiplayer online role-playing games (MMORPGs) such as *World of Warcraft* offer a particularly exciting opportunity to study real world social dynamics within VR. This potential was highlighted by a virtual 'disease outbreak' that plagued *World of Warcraft* in 2005 (Lofgren and Fefferman, 2007; Balicer, 2007). Due to the realistic movement patterns and social interactions of players, the disease was able to spread through the virtual population in a way analogous to real world disease dynamics. The virtual outbreak also gave insights into human behavioural responses to unexpected events – something that is notoriously difficult to model due to the complexity and unpredictability of human nature. MMORPGs could also act as experimental environments for studying the development of cultural norms across different 'societies' (Strimling and Frey, 2020). However, despite the immense potential of commercial multiplayer games for the study of human social evolution, these games are not purpose built for behavioural experiments. Ideally, social learning researchers could benefit from a VR platform built specifically to study human social behaviour within realistic, ecologically relevant environments. Developing complex, realistic virtual worlds for behavioural research is not a simple task and requires game coding expertise not readily available to most researchers – hence the full potential of VR for studying human social learning within realistic three-dimensional spaces has not been fully exploited.

Here, I describe a novel tool specifically developed for the purpose of studying human social learning using virtual reality: "Virtual Environments for Research into Social Evolution" (VERSE). Developed using Unity3D game development technology, VERSE gives researchers the ability to create complex, immersive 3D environments containing ecologically relevant tasks and challenges, without the need for game coding knowledge. Within VERSE environments, participants take control of a virtual player to explore and learn within realistic 3D spaces. Computer-controlled artificial intelligence agents (AIs), programmed by the researcher to behave in a certain way, offer optional sources of social information. VERSE is designed with the limitations of laboratory-based human social learning experiments in mind and offers a novel way for human behaviour to be studied in 'wild' environments. In particular, VERSE is designed to give participants the freedom to navigate 3D environments; allow tasks to span large spatial scales; provide more realistic sources of social information, in the sense that participants must actively observe an individual's behaviour and decide how to use this information; allow humans to be studied in naturalistic environments and survival scenarios; expose participants to realistic, ecologically-relevant tasks that can optionally require cumulative behaviours to complete; and provide researchers with a flexible toolkit that can be used to create potentially infinite new environments, tasks and types of social information due to its modular design. VERSE, therefore, has great potential for human social learning research, allowing humans to be studied in a comparable framework to animal research, allowing the replication of animal studies using human subjects and giving us a glimpse into how our social behaviour may have aided us in our evolutionary past.

What follows is a detailed account of VERSE, including the features already available in Unity3D that make it a suitable program for this type of research and features created specifically for VERSE to provide researchers with the ability to generate their own complex social learning environments. A detailed empirical experiment within VERSE can be found in Chapter 5.

4.3. Unity3D in Behavioural Research

Unity3D[1] is one of a series of virtual reality packages that have been used to create realistic environments for use as educational tools (e.g. Houghton *et al.*, 2015) and systems for studying human behaviour (e.g. Arias *et al.,* 2018). Unity3D boasts a range of features that make it suitable for use within research projects on social evolution. Here, I outline some of these key features. Table 4.1 describes some of the main Unity3D terminology intended to aid the reading of this document.

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[1] https://unity.com/

Table 4.1. Descriptions of some of the Unity terminology referred to in this document.

Feature	**Description**
GameObject[2]	Any object within the game, either a 'physical' object or an 'empty' placeholder. Can be set to 'active' or 'inactive'. 'Deactivating' a GameObject makes it invisible and disables all functionality. 'Activating' an inactive GameObject makes it visible and enables all functionality. 'Destroying' a GameObject removes it from the environment entirely.
Script[3]	A set of code (written in *C#* language), which is added to a GameObject to make it behave in a certain way. Multiple scripts can be added to a single GameObject. When attached to a GameObject, the script becomes a 'component' of that object.
Scene[4]	Essentially a game 'level', containing the environment and all the objects that will be present when the game is played. A single game can have multiple scenes.
Camera[5]	An object that dictates the view of the scene during gameplay.
Collider[6]	An invisible shape that defines the physical presence of a GameObject, allowing it to 'collide' with other GameObjects that also have colliders. GameObjects without colliders will not detect collisions and so will pass through other objects.
Trigger[6]	A type of collider that does not behave as a solid object, but rather detects when another object (with a collider attached) passes through it.
Rigidbody[7]	A component that allows a GameObject to be affected by physics forces, including gravity.
AI	'Artificial Intelligence'. A broad term used to describe an agent whose behaviour is controlled entirely by code.
Canvas[8]	A 2D user interface (UI) component that is displayed over the top of the game screen. Can be used, for example, to display text or clickable 2D objects (such as buttons) to the user.
Build[9]	The process of generating a game by compiling the scenes and scripts from the Unity interface into a playable application. The scenes to be included in the game should be specified in Unity's 'build settings'.

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[2] https://docs.unity3d.com/Manual/GameObjects.html
[3] https://docs.unity3d.com/Manual/CreatingAndUsingScripts.html
[4] https://docs.unity3d.com/Manual/CreatingScenes.html
[5] https://docs.unity3d.com/ScriptReference/Camera.html
[6] https://docs.unity3d.com/ScriptReference/Collider.html
[7] https://docs.unity3d.com/Manual/class-Rigidbody.html
[8] https://docs.unity3d.com/2020.1/Documentation/Manual/UICanvas.html
[9] https://docs.unity3d.com/Manual/PublishingBuilds.html

4.3.1. Flexible coding, ScriptableObjects and inheritance

Unity3D uses *C#* game coding which offers a high level of flexibility for the creation of tasks and character behaviours. Each section of code is contained within a script and so can be attached to different GameObjects in different combinations, thus allowing scripts to act as 'building blocks' for more complex character behaviour and task functionalities. Data containers called 'ScriptableObjects' can also be used to store particular properties within the Unity interface, allowing them to be shared between different scripts or objects during gameplay[10]. ScriptableObjects are notably used within VERSE for applying modifications to 'interactable objects' (section 4.4.3) and creating 'weather conditions' within the environment (section 4.4.7.1). In addition, Unity's 'inheritance' system[11] is particularly useful for creating 'parent' scripts which contain a number of functions and properties that are shared with (or 'inherited' by) any number of 'child' scripts. Thus, one can easily create multiple scripts of a particular type with shared functionality without having to repeat blocks of code. For example, inheritance is used within VERSE to create 'interactable objects' of various different types (section 4.4.3).

4.3.2. The Asset Store

Unity3D's Asset Store[12] allows game developers to obtain additional features for their games, such as 3D models or specialised scripts. VERSE uses one feature from the Asset Store, a third-person character controller (see below), that was modified for purpose and is included within the VERSE system. VERSE is an inclusive package, containing all the features and coding required for researchers to generate their own social learning environments, and so the Asset Store is not essential for its use. However, researchers can benefit from the Asset Store, for example, if they wish to obtain 3D models to use in tasks or as other features within the environment.

4.3.3. Environment creation

Creating VERSE in Unity means that researchers can take advantage of Unity3D's built-in terrain tool[13], which is particularly helpful if a researcher is wishing to conduct (or replicate) a study

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[10] https://docs.unity3d.com/Manual/class-ScriptableObject.html

[11] https://learn.unity.com/tutorial/inheritance

[12] https://assetstore.unity.com

[13] https://docs.unity3d.com/2017.4/Documentation/Manual/script-Terrain.html

within a naturalistic environment. The terrain tool allows the easy creation of realistic environments with varied topology and allows the rapid addition of trees, vegetation and surface textures (Figure 4.1). This tool can also be used to convert real Ordnance Survey 2D map data to 3D virtual terrains (Robinson *et al.,* 2015). Terrains can potentially be any size – the creation of large terrains being of particular use if a researcher wishes to allow their participants to have free movement over large scales. Hunter-gatherer processes, for example, occur over kilometre scales (90km^2 to 730,000km^2 according to Hamilton *et al.*, 2007). Such scales are not possible in conventional lab experiments, but become relatively easy to achieve, subject to computational demands, in virtual reality. Terrains can also be generated that vary in their complexity, allowing hypotheses concerning the effect of environmental complexity on social information use to be investigated. Such hypotheses have been tested in animals – for example, Webster *et al*. (2013) demonstrated that threespine sticklebacks (*Gasterosteus aculeatus*) were more likely to use social information in structured environments – but current methodologies make comparative studies on humans difficult.

Figure 4.1. Example of a realistic, large-scale environment created using the terrain tool within Unity3D.

4.3.4. Physics

Unity's physics system[14] allows entities within the game to respond realistically to forces such as gravity and collisions with other objects. This is achieved by the simple addition of a Rigidbody

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[14] https://docs.unity3d.com/Manual/PhysicsSection.html

component[15] which can be used to alter aspects such as the object's mass or the drag applied during movement. This is one way in which Unity can aid researchers to move away from abstract tasks and towards more immersive environments which better represent reality.

4.3.5. Navigation and pathfinding

Unity's navigation system[16] allows the user to create agents that can intelligently find their way around an environment using 'navigation meshes' that are automatically generated from the environment's geometry. When moving to a particular destination, agents will move over the geometry of the environment, using the shortest or most efficient path and avoiding obstacles, including each other. VERSE makes extensive use of Unity's navigation system in programming artificial intelligence agents (AIs) which act as sources of social information. Unity's navigation system makes AI movement much easier for researchers to achieve than, for example, hard-wiring agents with a highly specific path. This also adds more realism, randomness and inter-individual variability to AI movement by allowing them to, within the constraints of the specified parameters, find their own path to their target location. VERSE can also extract the 3D location information of individuals at runtime, including the exact paths taken by AIs (see 'Tracking values and logging data', section 4.4.6, below).

4.3.6. Visual effects

Unity comes with a variety of visual effects that can add an extra dimension to the environment by increasing the level of realism. Examples that VERSE explicitly makes use of are lights[17] and particle systems[18]. Lights are glowing effects that illuminate the surrounding objects, while particle systems are used to emit a number of small meshes to produce a visual effect (e.g. fire, smoke, water splashes) according to the properties inputted by the user.

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[15] https://docs.unity3d.com/Manual/class-Rigidbody.html
[16] https://docs.unity3d.com/Manual/Navigation.html
[17] https://docs.unity3d.com/Manual/Lighting.html
[18] https://docs.unity3d.com/Manual/ParticleSystems.html

4.3.7. Building an application with multiple scenes

Unity allows the user to build a game or application with multiple levels or scenes. For the purpose of human behavioural research, this can be a useful way of organising several replicates into a single application, so a participant can take part in all replicates one after the other without the researcher having to generate many different builds.

4.4. “Virtual Environments for Research into Social Evolution” (VERSE)

The remainder of this chapter describes how I brought together these elements of Unity3D functionality to produce a custom tool for research. VERSE is a research tool, created using Unity3D (version 2017.4.23f1), designed to allow researchers to create their own realistic virtual environments for studying human social learning. VERSE is designed to be flexible, providing researchers with many different ‘building blocks’ that can be used to create tasks of different types, generate AIs with particular behaviours and allow environmental fluctuations. VERSE is also designed to give participants free movement over potentially large-scale environments, allowing experiments comparable to those involving wild animal populations or human hunter-gatherer communities to be produced. VERSE has been developed in a way that makes it widely available to all researchers, avoiding the use of costly equipment such as VR headsets and providing all the code necessary to build social learning environments without the need for game coding knowledge. While VERSE was specifically created with the study of human social learning in mind, it could feasibly be expanded to study other subjects, such as epidemiology or other aspects of human behaviour. VERSE can be accessed at the following figshare repository: https://figshare.com/s/c97c305736c9a3d1c8b9 (Easter, 2022) and requires Unity to open.

VERSE uses a combination of the standard Unity3D features, as described above, and a catalogue of specialised scripts coded specifically for the tool. Using VERSE will therefore require some basic knowledge of the Unity interface, but largely involves altering the properties of pre-created objects and so does not require any coding knowledge unless the researcher wishes to make substantial changes. What follows is an account of the novel features and their associated scripts coded specifically for VERSE (summarised in Figure 4.2). Script names are given in *italics*, VERSE-specific GameObjects are given in `courier font` and computer keys are highlighted in **bold**. A basic account of the function of each script is given in the main text. For researchers wishing to use VERSE, a detailed instruction manual / tutorial can also be found in the figshare repository.

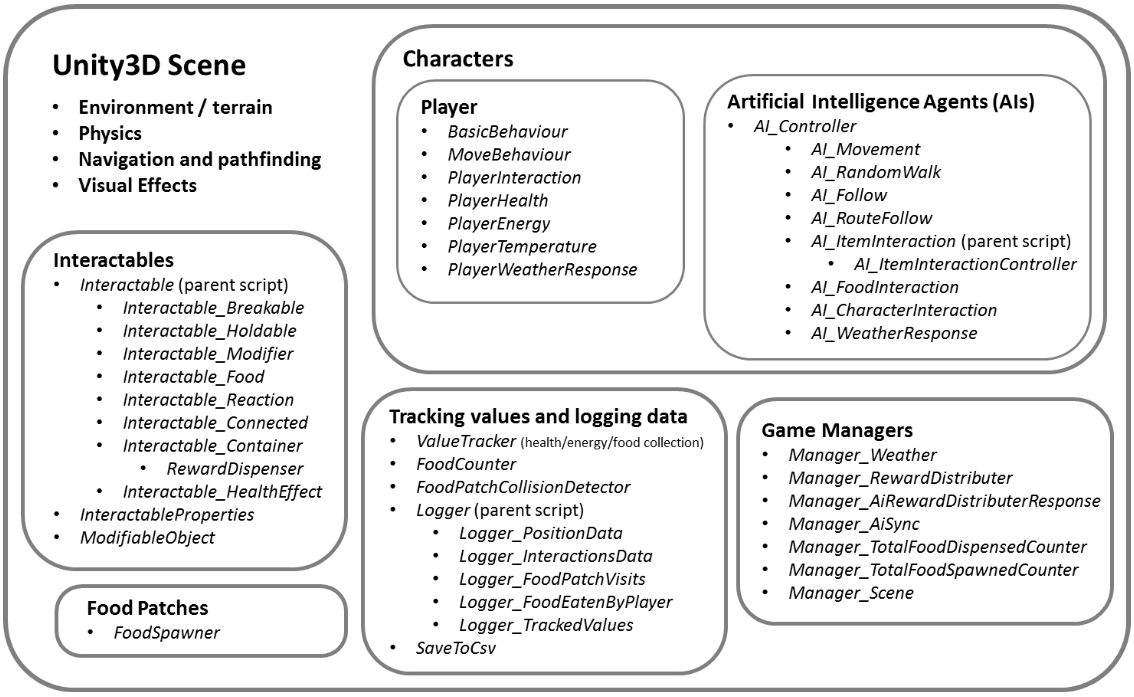

Figure 4.2. Schematic showing the main features of VERSE and the various scripts that control them. Script names are shown in italics and their descriptions and functioning can be found in the main body of the manuscript.

4.4.1. Characters

VERSE uses a third person character controller asset from the Unity Asset Store[19], which is modified to produce two different types of character – the `player` (which is controlled by the participant) and Artificial Intelligence agents (`AIs`; controlled by the game code and programmable by the researcher). The `player` and `AIs` share the same general appearance and animations. Some of the animations were in-built features of the third person character controller asset[19], including walking, running, jumping and idle animations. Other animations were created specifically for use in VERSE, including interacting and crouching animations. Both character types have a 'collider', which gives them a physical presence and stops them being able to walk through solid objects, and a 'trigger', which allows them to register when other objects are nearby (Table 4.1). The `player`, `AIs` and the scripts that can be applied to each of them are described in more detail below.

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[19] https://assetstore.unity.com/packages/templates/systems/3rd-person-controller-fly-mode-28647

4.4.2. The Player

The `player` is the virtual human that a participant takes control of using the computer keys and is followed by a camera. The `player` is capable of various behaviours and can be affected by various elements of the game, according to the needs of the researcher. The scripts relating to `player` movement and behaviour are detailed below. Note that all computer keys described below are default options and can be changed via the Unity settings (e.g. to improve accessibility).

4.4.2.1. *BasicBehaviour* and *MoveBehaviour*

Two scripts that work in conjunction to allow a participant to control the `player` using the computer keys. These scripts are slightly modified versions of those available in the third-person character controller[19]. Default `player` controls are given in Table 4.2. Movement, sprinting and jumping behaviours were all taken from the original code. Crouching behaviour is a VERSE addition – its only function is to serve as an additional behaviour that can be required to complete certain tasks (see 'Interactables', section 4.4.3, below). The options within the Unity interface allow the researcher to alter aspects of `player` movement, such as walk, run and sprint speed. An additional option allows the researcher to disable jumping, as this may be unnecessary or undesirable in certain studies.

Table 4.2. Default `player` controls according to the *BasicBehaviour and MoveBehaviour* scripts and Unity settings.

Player control	Description	Computer key (default)
Movement	Player moves along Unity's (x,z) plane, which changes from walking to running depending on how long the key is held down.	Arrow keys (**←,↑,→,↓**)
Sprint	Speeds up movement.	**Left Shift**
Crouch	Player crouches down.	**Left Ctrl**
Jump	Player jumps. Distance is further if walking or running at the time.	**Spacebar**

4.4.2.2. *CameraControl*

Script that is placed on a camera to allow camera rotation. The camera itself must be positioned correctly and connected to the `player` via Unity's hierarchy system to allow player movement to be tracked by the camera (see instruction manual in the figshare repository for more information). The camera can be rotated left and right using the **A** and **D** keys, and rotated up and down using the **W** and **S** keys. The researcher can alter the vertical and horizontal rotation speeds within the Unity interface. In addition, depending on the task in question, the vertical rotation may be unnecessary or distracting in some studies and so can be switched off completely.

4.4.2.3. *PlayerInteraction*

Script that allows the `player` to interact with specific 'interactable' objects (see 'Interactables' below). By default, this involves the `player` approaching the object and pressing the 'Interact' button (default: **?** key, modifiable in the Unity settings), however alternative requirements can be programmed for each individual interactable object, as discussed below.

4.4.2.4. *PlayerHealth*

Stores a numeric value representing the `player`'s current health and displays this as a health bar onscreen, which updates during gameplay. This script contains functions to add or remove health from the `player` which can be called on by interactable objects. This script also logs when the `player`'s health reaches zero, which can be used to end the level or game prematurely (see *Manager_Scene*, section 4.4.7.7, below). Adding a health component to the `player` can be useful for assessing how humans learn behaviours based on their consequences. One way in which a `player`'s health can be affected is by collecting `Food interactables` (see *Interactable_Food* in the 'Interactables' section below, section 4.4.3.3.4) – poisonous `Food` that depletes health and/or nutritious `Food` that increases health by different amounts can be created and used to study human learning about food preferences. Thus, VERSE allows the possibility of creating tasks with clear evolutionary significance, comparable to foraging tasks used in animal studies.

4.4.2.5. *PlayerEnergy*

Stores a numeric value representing the `player`'s current energy level and displays this as a bar onscreen, which updates during gameplay. Whenever the `player` moves (i.e. whenever the participant presses down any of the movement keys), the `player`'s energy depletes at a specified rate. When running (i.e. if the participant holds down the **Shift** key while moving), the energy depletion rate is multiplied by a specified 'sprint multiplier'. The researcher can also specify how much energy should be used while jumping. Energy recovery can also be enabled – meaning that the `player`'s energy value will increase by a specified rate up to a specified maximum whenever the `player` is not moving, thus giving participants the option of 'resting' when their energy is low. The researcher can also specify whether energy depletion should be linked to player health. If player energy is linked to player health, once the `player`'s energy reaches zero, the `player`'s health starts to deplete at a specified rate. Adding an energy component is useful in tasks that require a participant to make energetically efficient choices, such as the route choice tasks, mazes or foraging tasks used in some animal studies (e.g. Laland and William, 1998). Allowing energy depletion to have an effect on health can further reinforce the choices that participants make.

4.4.2.6. *PlayerTemperature*

Stores a numeric value representing the `player`'s current temperature, which is displayed as a temperature gage onscreen. The researcher can specify the values for the `player`'s ideal body temperature and for minimum and maximum possible temperatures, as well as the visual properties of the temperature bar. By default, the `player`'s body temperature is set to 37 and the minimum and maximum temperatures are set to 35 and 39, representing the temperatures that lead to hypothermia and hyperthermia in humans, but this can be changed according to the researcher's requirements. As discussed below, the temperature of the `player` can be programmed to fluctuate in different ways according to different `weather conditions`, which can optionally be detrimental to health.

4.4.2.7. *PlayerWeatherResponse*

Determines how the `player` reacts to changes in the 'weather' (see *Manager_Weather*, section 4.4.7.1, below). Weather can affect the `player` in the following ways: (i) raise/lower temperature at a specified rate; (ii) raise/lower health at a specified rate; or (iii) raise/lower temperature to a specified maximum/minimum (according to the *PlayerTemperature* script, see above), beyond which health begins to deplete at a specified rate. These effects only occur when the specified `weather condition` is currently active. Once the `weather condition` has deactivated, or if the `player` moves into a `weather shelter` (see *Manager_Weather* below), the `player`'s temperature gradually returns to the ideal body temperature. However, any health effects incurred by the `weather condition` remain even after the `weather condition` has been deactivated.

4.4.3. Interactables

This section refers to objects that can be interacted with in various ways by either the `player` or `AIs` with interaction capabilities enabled. To interact with an `interactable`, a character (the `player` or an `AI`) must approach it and meet a specified set of requirements for a successful interaction to occur. Each `interactable` is surrounded by a trigger[6] which senses when an object moves through it (Table 4.1). The size of this trigger determines how close a character needs to be to the `interactable` in order to attempt an interaction (this will henceforth be referred to as the `interactable`'s 'trigger area'). `Interactables` can also be 'modified' to affect their appearance and functionality (through the use of the *ModifiableObject* script; section 4.4.3.2), which provides VERSE with further flexibility for constructing novel tasks. Unless otherwise specified by the researcher, all `interactables` are coded to behave in the same way towards any character, whether it is a `player` or `AI`. This ensures that social information is realistic – i.e. a participant can observe an `AI` performing a particular set of behaviours and imitate these behaviours to achieve the same result. What follows are descriptions of all `interactable`-related scripts within VERSE.

4.4.3.1. *InteractableProperties*

This script is automatically added to a GameObject when any one of the *Interactable* scripts (below) is attached, and holds information about the `interactable` in question, including its 'item type'. This script also determines the fate of an `interactable` object once it has been destroyed (i.e. removed from the environment); which can occur in a number of circumstances, including if it is a `Breakable interactable` that has been broken or a `Holdable interactable` that has been deposited into a `Container` (see below). After an `interactable` object is destroyed, it can either be removed from the environment entirely or regenerated, either in its current position or in its original position, after a specified number of seconds. Having an `interactable` regenerate once it has been destroyed may be useful if, for example, the researcher wishes the participant to complete the same task multiple times in succession without creating multiple versions or replicates. This can be likened to situations in animal social learning research where the researcher routinely adds an object to the subject's environment during the study period (e.g. Horner *et al*., 2010). Regeneration can also be synced with that other `interactables` (i.e. this object will only regenerate when a set of specified `interactables` are also regenerated), which is useful if a researcher wishes to add a set of `interactables` back into the environment only when they have all been removed.

4.4.3.2. *ModifiableObject*

This script allows an `interactable` to be modified by the addition of a '`modification`' (`interactables` with the ability to be modified in this way will henceforth be referred to as `Modifiable Objects`). `Modifications` can alter the `interactable`'s appearance and influence how it interacts with other `interactables` (via their 'required items', as discussed in the description of *Interactable,* below). For each `Modifiable Object`, the researcher specifies a list of 'possible modifications' that can be applied and how each of these should affect the `interactable`. Each `modification` can alter the appearance by the addition of extra object(s) or by switching the material (colour/texture) of the object. A researcher can create any number of novel `modifications` using a VERSE-specific menu in the Unity interface and have these `modifications` affect different `Modifiable Objects` in different ways. `Modifications` are stored as ScriptableObjects[10], allowing them to be easily added to the *ModifiableObject* component of an object within the Unity interface. `Modifications` can also be added to a `Modifiable Object` during gameplay via interaction with an appropriate `Modifier interactable` (see *Interactable_Modifier*, section 4.4.3.3.3, below) making it possible to allow learning of cumulative behaviours within VERSE. An example of a `Modifiable Object` may include a 'stick' that can be modified using a 'burning' `modification` by the addition of a 'flame' at the end and a change in functionality.

4.4.3.3. *Interactable* (parent script)

This script acts as a base (or ‘parent’) script for all `interactables` and dictates several properties and functions that are inherited by all the ‘child’ scripts listed below (and summarised in Table 4.3). For each `interactable` object, a particular set of conditions can be specified that must be fulfilled during an attempted interaction for that interaction to be successful. Firstly, the researcher can specify a set of ‘required keys’ that must be pressed when the `player` is within the `interactable`’s trigger area to attempt an interaction (by default, this is the ‘Interact’ key: **?**) and, secondly, a set of ‘required items’ that must be held by the `player` or `AI` during an attempted interaction for that interaction to be successful (e.g. a stick may be required to reach a high-up object). Each required item can either be a specific `interactable` object within the scene or can be a general item type, as identified by the ‘item type’ in an `interactable`’s *InteractableProperties* script (see above). For example, there are a group of ‘keys’ (all with the item type ‘key’) located in the environment which the `player` can pick up and use to attempt to open a ‘chest’. If the chest has a specific key object set as a required item, the `player` must pick up and use that specific key for the interaction to be successful. On the other hand, if the required item has a general item type of ‘key’, which matches the item type of all the keys in the environment, any one of those keys could be used to successfully open the chest. In addition, for each required item, the researcher can also specify a particular `modification` (see *ModifiableObject,* above) that must be applied for the condition to be met (e.g. a ‘stick’ must have the ‘burning’ `modification` to allow an interaction with a ‘flammable’ `interactable`). For `interactables` that are intended for `AI` use only, `player` interaction can be completely disabled.

The *Interactable* parent script contains functions that check whether all interaction conditions have been met and, if so, initiates a successful interaction. The response to a successful interaction depends on the type of `interactable` concerned, as explained below. What follows are the various types of `interactables` available in VERSE (summarised in Table 4.3). Each `interactable` type is a ‘child’ of the *Interactable* ‘parent’ script. When one of the following *Interactable* child scripts is added to an object, that object becomes an `interactable` of a specified type, ‘inheriting’ the properties and functions detailed above, while also containing their own individual functionality. Each type of `interactable` responds to a successful interaction in a different way and this response is dictated by its own properties, as specified by the researcher.

Table 4.3: Summary of the different types of `interactable` available in VERSE, how they respond to a successful interaction, and an example of use.

Interactable type	**Response to successful interaction**	**Optional responses**	**Example of use**
`Breakable`	Object breaks and disappears.	Any number of 'held items' can be released from the object after it has been broken.	Breakable 'fruit' that releases 'seeds'.
`Holdable`	Object is picked up and held by the player or an AI.	n/a	A 'stick' that can be picked up by the player.
`Modifier`	Applies a specified 'modification' to a compatible Modifiable Object currently in the character's hand.	Modification can be either added to or removed from the Modifiable Object.	A 'fire' modifier that can change a held 'stick' into a flaming 'torch' by the addition of a 'burning' modification.
`Food`	Object is 'eaten' by the player, affecting their health. Disappears after interaction.	Different food objects can increase or decrease player health by different amounts. This can occur instantaneously or after a delay.	A 'poisonous seed' released by a breakable 'fruit' that lowers player health on interaction.
`Reactable`	A visual reaction is switched on.	Reaction can be a light or a release of 'particles'. Can switch on and off upon successive interactions, or alternatively switch on only once.	A 'fire' that releases sparks when interacted with.
`Connected`	A connected object is affected. Possible effect on connected object: GameObject is 'activated'; physics is enabled on object; interactable object is interacted with.	Connected object can be affected just once or multiple times.	Interaction with a 'tree' applies gravity to a separate 'fruit' object, causing it to fall to the ground.
`Container`	Holdable interactable currently in the character's hand is deposited into the Container, provided it is one of the Container's 'accepted objects'.	Can double up as a 'reward dispenser' that gives out reward(s) on deposition of a correct object. AI rewards can be disabled.	A 'vending machine' that gives out a 'food' reward on deposition of a 'coin'.
`Health Effect`	Adds or removes health when the player interacts.	Can be instantaneous or after a specified delay.	A poisonous 'flower' that lowers health that the player should learn to avoid.

4.4.3.3.1. *Interactable_Breakable* (child script, inherits from *Interactable*)

An `interactable` that breaks open after a successful interaction. The `interactable` is destroyed and replaced with a 'broken parts' GameObject that acts as a visual representation of the broken object. These broken parts can either remain indefinitely or disappear after a specified number of seconds. One element of social learning is the influence of the products of a demonstrator's behaviour on observer behaviour (Heyes, 1994). Having the broken parts of a `Breakable` object remain may therefore be useful if the researcher wishes to explore this type of social learning (e.g. does finding the broken remains of a 'fruit' encourage participants to try breaking the same type of fruit open themselves?). However, if a large number of `Breakable` objects are to be present in the scene and the influence of their broken remains are not a focus of the research in question, their removal is recommended to keep computational costs down. A `Breakable interactable` can optionally contain a number of 'held objects' which are released once the `interactable` has been broken. Examples may include a 'fruit' that breaks open when interacted with to release a number of 'seeds', or a 'barrel' that breaks open to release a number of collectable 'coins'.

4.4.3.3.2. *Interactable_Holdable* (child script, inherits from *Interactable*)

An `interactable` that can be picked up and carried by a character (`player` or `AI`). Each character can hold a maximum of two items (one in each hand) at any given time and can therefore only successfully interact with a `Holdable interactable` if at least one of its hands is free. Objects held by the `player` can be released from the left or right hand by pressing the **[** or **]** key, respectively. `AIs` can be programmed to release `Holdable interactables` according to certain conditions (see *AI_ItemInteractionController*, section 4.4.5.6.1, below). `Holdable interactables` are especially useful because they can be specified as 'required items' for interacting with other `interactables` (see above). An example may be a 'stick' that can be picked up by the `player` or `AI` and used to interact with other objects.

4.4.3.3.3. *Interactable_Modifier* (child script, inherits from *Interactable*)

An `interactable` that applies a specified `modification` to a `Modifiable Object` (see above). The researcher specifies the `modification` to apply and whether it should be added to or removed from the `Modifiable Object`. The `Modifier` can only modify compatible objects (i.e. a `Modifiable Object` with the same `modification` listed in its set of 'possible modifications'). An example may be a 'fire' that, when interacted with by a character holding a compatible 'stick' object, modifies that stick by adding a 'burning' `modification`, which turns the stick into a flaming 'torch'.

4.4.3.3.4. *Interactable_Food* (child script, inherits from *Interactable*)

An `interactable` that can be 'eaten' (or collected) by the `player` or `AI`. Each `Food` item has a 'nutrition value', a 'nutrition delay' and a 'food type' specified by the researcher. Upon successful interaction, the `Food` object disappears and is considered eaten or collected by the character interacting with it. When a `player` with a *PlayerHealth* script attached eats a `Food` item, it can optionally affect the `player`'s health, adding the nutrition value to the `player`'s current health value after a delay equivalent to the nutrition delay. This effect on health can be either positive or adverse, allowing researchers to create foraging tasks comparable to studies on animals and hunter-gatherer communities, e.g. learning to avoid poisonous foods (Galef, 2009; Henrich and Henrich, 2010). By including a nutrition delay, one can assess how social information use is impacted by the time taken to process information about payoffs (e.g. in reality, the effects of eating a toxic or inedible food item would not necessarily be instantaneous) or by the unpredictability of rewards gained by using a particular behaviour (c.f. Caldwell and Eve, 2014). The nutrition value and food type variables are also used by `AIs` when making decisions on what `Food` items to eat (see *AI_FoodInteraction,* section 4.4.5.7, below), thus allowing specific social information to be conveyed to participants. An example of a `Food interactable` may be an edible 'seed' released from a `Breakable` 'fruit' `interactable`, which increases the `player`'s health when eaten. Food rewards are often given to animals completing tasks in social learning studies and the addition of `Food interactables` in VERSE offer a comparable way of rewarding human participants – although note that the *Interactable_Food* script could also be used to create collectable, non-food items (e.g. collectable coins). Additional functionality relating to `Food interactables`, such as logs that keep track of the number of `Food interactables` collected (see *FoodCounter,* section 4.4.6.2, below), are also available in VERSE to aid data collection and allow participants to see how well they are doing in a task.

4.4.3.3.5. *Interactable_Reaction* (child script, inherits from *Interactable*)

An `interactable` that reacts to successful interactions with a visual display. This display can involve a light[17] and/or particle system[18]. Successful interactions can either switch the display on and off (which may be more appropriate for a light or a looping particle system), or only switch it on (which may be more appropriate for a non-looping particle system that switches off itself after a certain amount of time). This type of `interactable` is entirely visual. It could be used to draw a participant's attention to a particular area or simply to visually enrich the environment. The use of a light display could also be used to illuminate a dark area as part of a task. An example of this type of `interactable` may be a 'campfire' that is lit (by switching on a particle system designed to look like fire) after a character interacts with it while holding a burning stick.

4.4.3.3.6. *Interactable_Connected* (child script, inherits from *Interactable*)

An `interactable` that affects a connected object upon successful interaction. The connected object can be affected in one of three ways: (i) the connected GameObject is 'activated', meaning it becomes visible if it isn't already and all its components and behaviours are enabled[20]; (ii) the connected object's Rigidbody component[7] is enabled, allowing it to respond to physics forces including gravity; or (iii) the connected object, provided it is a VERSE `interactable`, is interacted with as though the `player` is interacting with it directly, but bypassing its usual conditions for interaction such as required keys or close proximity to the object. The researcher can additionally specify whether the effect on the connected object can occur multiple times or whether it should happen only once. Examples of where `Connected interactables` could be used include a 'tree' that, when interacted with, causes a connected 'fruit' object hidden in the canopy to drop by enabling gravity; or a 'button' that breaks open a connected `Breakable interactable` that would normally require a required item to be held upon interaction, thus offering an alternative, perhaps faster, way of completing the task.

4.4.3.3.7. *Interactable_Container* (child script, inherits from *Interactable*)

An `interactable` into which `Holdable interactables` can be deposited. A list of 'accepted objects' can be specified. Only if a character is holding an accepted object while interacting with the `Container` will a successful interaction occur. A successful interaction causes the `Holdable interactable` currently in the character's hand to be deposited into the `Container` and subsequently destroyed from the game scene entirely (the fate of the `Holdable interactable` after this is then determined by its *InteractableProperties,* as

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[20] https://docs.unity3d.com/ScriptReference/GameObject.SetActive.html

discussed in section 4.4.3.1, above). The researcher can optionally program a `Container` to give out a reward upon deposition of an accepted object. This requires the addition of an extra script, *RewardDispenser*, which contains a 'DispenseRewards' function that *Interactable_Container* can call on during a successful interaction:

4.4.3.3.7.1. *RewardDispenser*

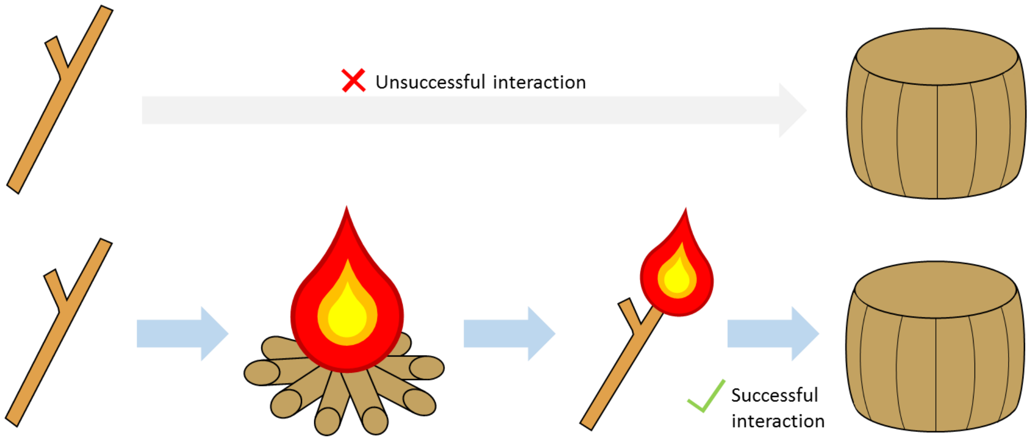
This script allows the researcher to specify a list of 'possible rewards' – where each possible reward consists of a GameObject and quantity – and a 'reward location'. It contains the function 'DispenseRewards', which chooses one of the possible rewards at random and generates the chosen reward object in the specified quantity at the specified reward location. The 'DispenseRewards' function is called on by the *Interactable_Container* script during a successful interaction, provided the `Container` has been set to give out rewards. A reward may, for example, consist of a number of `Food interactables` that can then be collected by the `player`. In some cases, it may be useful to have 'dynamic' `reward dispensers`, where the possible rewards swap and change between 'rounds'. For example, a researcher may give a participant the task of choosing between multiple `reward dispensers` over a number of rounds and may wish to investigate how social information is being used during this task. If the location of the best reward was always fixed to a particular `reward dispenser`, it would be difficult to determine whether the participant was using social information or simply learning which `reward dispenser` was more profitable. To disentangle these effects, the *Manager_RewardDistributer* can be used to randomly swap the possible rewards between a set of specified `reward dispensers` (see *Manager_RewardDistributer*, section 4.4.7.2, below).

4.4.3.3.8. *Interactable_HealthEffect* (child script, inherits from *Interactable*)

An `interactable` that increases or reduces the `player`'s health by a specified amount after a specified delay upon successful interaction by the `player`. A `Health Effect interactable` could be used, for example, to investigate avoidance behaviour – e.g. an environment could feature 'toxic' plants or animals that reduce the `player`'s health when interacted with and that the participant must learn to avoid. Alternatively, `Health Effect interactables` that increase player health could be used to explore hypotheses concerning how humans use social information about medicinal plants, as in Henrich and Broesch's (2011) field study on Fijian village populations.

Interactables example

To illustrate how interactable scripts work together to allow complex tasks to be created, consider the following example: A participant is located in an environment and given a task to open a small wooden barrel using only the tools available. Those tools include a stick and a campfire. The participant is required to learn the following behaviours in order: pick up the stick, use the campfire to light the stick, and use the burning stick to destroy the barrel (as illustrated in Figure 4.3). In VERSE, this is possible using the extensive 'interactables' system. The stick, campfire and box are all different types of `interactable`, each containing scripts derived from the *Interactable* parent script and each requiring particular conditions for a successful interaction to occur. The stick is a `Holdable interactable`, containing the *Interactable_Holdable* script, with 'Interact' and 'Crouch' as required keys and no required items. This means that, if the `player` approaches the stick and presses the 'Crouch' and 'Interact' keys, they will pick the stick up. The stick is also a `Modifiable Object` with one possible `modification`: 'burning', which alters the stick's appearance by the addition of a 'flame' at the top. The campfire is a Modifier, containing the *Interactable_Modifier* script. It has 'Interact' as a required key and has no required items. It is capable of adding the 'burning' `modification` to any compatible `Modifiable Object`. In this case, this means that, if the `player` approaches the campfire and presses the 'Interact' key while holding the stick in hand, because the stick is a compatible `Modifiable Object`, the 'burning' `modification` will be added to it. The barrel is a `Breakable interactable`, containing the *Interactable_Breakable* script. It has 'Interact' as a required key and has the stick with the 'burning' `modification` as a required item. This means that the `player` must be holding the modified stick `interactable` for a successful interaction to take place and so must have completed the aforementioned behaviours in the correct order to break open the barrel. This example illustrates how different types of `interactable`, derived from the same parent script, can be used to assess cumulative learning through the use of the interaction conditions and object modifications available in VERSE.



Stick	Campfire	Stick (burning)	Barrel
Holdable interactable	*Modifiable interactable* (Adds 'burning' modification)	*Holdable interactable*	*Breakable interactable*
Required keys: 'Interact', 'Crouch' **Required items:** none	**Required keys:** 'Interact' **Required items:** none	**Required keys:** 'Interact', 'Crouch' **Required items:** none	**Required keys:** 'Interact' **Required items:** Stick (burning)
Possible modification: 'burning'	**Possible modification:** none	**Possible modification:** 'burning'	**Possible modification:** none
Current modification: none	**Current modification:** none	**Current modification:** 'burning'	**Current modification:** none

Figure 4.3. An example of how `interactables` work within VERSE. In this example, the participant is required to pick up the 'stick' (a `Holdable interactable`) and modify it with the 'burning' `modification` using the 'campfire' (a `Modifier interactable`) in order to break open the 'barrel' (a `Breakable interactable`) to receive a reward. Attempting to interact with the barrel while holding the unmodified stick results in an unsuccessful interaction. The participant therefore needs to use the correct behaviours in the correct order to complete the task.

4.4.4. Creating food patches

In VERSE, it is possible to create any number of `food patches` within the environment, which the `player` is required to find and exploit – thus allowing researchers to assess human foraging behaviour over large, complex envrionments. `Food patch` creation can be done simply by creating a number of `Food` objects and distributing manually around the environment. Alternatively, a researcher may wish to have `Food` items that are generated during gameplay and/or that regenerate after being 'eaten' (examples may include seasonal or temporal food supplies). This can be done using the *FoodSpawner* script.

4.4.4.1. *FoodSpawner*

Spawns a specified number of a specified `Food` item at a specified 'spawn location'. This occurs on a timer, with each spawn occurring after a specified time. Each individual `Food` item is spawned in a random position within a specified radius from the spawn location. The *FoodSpawner* can be programmed to spawn the `Food` items instantly at the beginning gameplay or wait until after the spawn time is reached before the first spawn occurs. It can also be programmed to reset its timer the instant it has spawned its last lot of `Food` items or, alternatively, wait until all the `Food` it previously spawned has become depleted before the timer is reset. The researcher can also limit the total number of `Food` items that can be spawned to a specified maximum. A number of *FoodSpawners*, each with their own specified `Food` items, can be added to the environment, or even to the exact same area to produce a patch of mixed `Food` items. It is worth noting that *FoodSpawners* can be programmed to spawn any object in this manner, not just `Food` items, and so can be repurposed for any task which requires objects to be generated on a timer during gameplay.

4.4.5. Artificial Intelligence agents (AIs)

In VERSE, social information about a task is conveyed in the form of Artificial Intelligence agents (`AIs`) with programmable behaviours. These `AIs` are designed to offer realistic sources of social information often not possible in lab-based or simple computer-based experiments by allowing participants to observe human figures moving around the environment and actively performing tasks, while also offering the researcher control over demonstrator behaviour and the social information being conveyed. A number of scripts are available in VERSE which control different aspects of `AI` behaviour, which can be added to each `AI` in different combinations depending on the behaviours that are appropriate for the given environment or task (e.g. for some environments, the researcher may only require movement-based behaviours, while others may require more complex behaviours).

4.4.5.1. *AI_Controller*

This script is automatically added to a GameObject with any other `AI`-related script attached. Its purpose is to store a number of functions that offer overarching control over the `AI` and its behaviour and that can be called on by other `AI` scripts where appropriate. Functions include enabling and disabling `AI` scripts, pausing and unpausing `AI` behaviours and altering the parameters or properties of `AI` behaviours. The *AI_Controller* is especially important for ensuring that different `AI` behaviours do not interfere with one another.

4.4.5.2. *AI_Movement*

A script containing functions used to instruct an `AI` to move to a specified destination at a particular walking speed, while updating character animation accordingly. The researcher can optionally specify whether an `AI` should move at an increased speed if they are moving further than a specified distance, which is a useful way of maintaining realistic movement speeds when `AI` behaviours span various distances. The functions in *AI_Movement* are called on by any `AI` scripts that require the `AI` to walk to a particular location.

4.4.5.3. *AI_RandomWalk*

Programs an `AI` to move around according to a random walk that is controlled by several parameters inputted by the researcher. The researcher can also specify a set of ‘attractive areas’ – locations that are favoured in the random walk procedure over choosing a completely random point to walk to. For each attractive area specified by the researcher, the `AI` is given a ‘level of attraction’ which determines the probability that the `AI` will choose to visit that area. The researcher can also instruct the `AI` to favour less-visited attractive areas.

The random walk procedure is as follows. For each random walk cycle, the `AI` first waits for a random delay between a specified minimum and maximum. The `AI` then decides whether to visit an attractive area or walk to a random location. The probability of visiting an attractive area over choosing a random location is: $\frac{\sum_i^n A_i}{n}$ where A_i is the level of attraction towards a particular attractive area, *i*, and *n* is the total number of attractive areas in the list. If the `AI` chooses to visit an attractive area, it then decides which area in its list it should visit. It iterates through all the attractive areas in its list and the probability of choosing attractive area *i* is: $\frac{A_i}{\sum_i^n A_i}$. This formula ensures that an area is chosen and that areas further up in the list are not favoured over those at the bottom. If the researcher has instructed the `AI` to favour less-visited attractive areas, attractive area *i* will then be temporarily removed from the attractive areas list (thus ensuring it isn’t visited again) until all other attractive areas in the list have been visited. If the

`AI` chooses not to visit an attractive area, or if no attractive areas are specified, the `AI` will instead walk a random distance between a specified minimum and maximum in a random direction from their its position. Movement to the chosen destination is executed via the *AI_Movement* script. Once the `AI` has reached its chosen destination, the random walk procedure is executed again, and this repeats continuously while ever the random walk script is enabled (i.e. unless it is disabled by the *AI_Controller* while another behaviour is being executed).

This random walk behaviour is designed to provide `AIs` with stochastic movement, while also allowing researchers to program `AIs` that provide social information about particular locations (e.g. foraging patches or other areas of interest). The 'attractive areas' feature could also be used for investigations into 'local enhancement', a social learning mechanism where a demonstrator's behaviour attracts an observer to stimuli in a particular location (Heyes, 1994). In addition, the researcher can specify whether to allow `Food` detection during a random walk. When enabled, if an `AI` detects a compatible `Food` object while walking to its chosen location, it will abandon its current path and instead execute its `Food` interaction procedures (see *AI_FoodInteraction,* section 4.4.5.7, below). When disabled, an `AI` will ignore any `Food` items while on route to its chosen location. A researcher may use the first option if, for example, they are programming an `AI` that is designed to do a random search of the environment and stop off at any food sources that they pass by. Whereas the second option may be preferable if the researcher is programming an `AI` that is designed only to visit specific `food patches`, without becoming distracted by any other food sources it may pass.

4.4.5.4. *AI_Follow*

Script that instructs an `AI` to walk to the location of a specified target object after a specified delay. Movement to this location is executed via the *AI_Movement* script. Once it has reached the location of the target object, the `AI` will repeat the behaviour. This behaviour can be used in conjunction with the random walk behaviour – the `AI` will switch between walking to the location of the target object and walking to a random location according to the respective time delays programmed into the two behaviours. One example of where this behaviour might be useful is if the researcher wishes to create a number of `AIs` that move as a group – one `AI` can be programmed with behaviours that determine the group's chosen destination (e.g. via the *AI_RandomWalk* script) while the remaining `AIs` are instructed to follow the 'leader' using the *AI_Follow* script.

4.4.5.5. *AI_RouteFollow*

Script that instructs an `AI` to follow a route through any number of specified waypoints, after an initial start delay randomly selected between a specified minimum and maximum number of seconds. This behaviour can be used in conjunction with the random walk behaviour – the random walk behaviour will be temporarily disabled via the *AI_Controller* script until the `AI` has followed the route to its end point. This behaviour is especially useful if a researcher wishes to investigate social information use during route-choice tasks, as has been investigated in both animals (Laland and Williams, 1998) and humans (Reader *et al.*, 2008).

4.4.5.6. *AI_ItemInteraction* (parent script)

Script containing functions to instruct an `AI` to interact with an `interactable`. If instructed to interact with a specified `interactable`, the `AI` will first check if the specified `interactable` is 'available'. An `interactable` may become unavailable if (a) it is not present in the environment, e.g. if it has been destroyed, or (b) it is a `Holdable interactable` that is currently being held by the `player`, another `AI` or this `AI` itself. An `AI` will not attempt to walk to the location of or interact with an unavailable `interactable`. If the `interactable` is available, the `AI` will walk to the `interactable`'s location via the *AI_Movement* script, first disabling any random walk procedures via the *AI_Controller* script. The `AI` will then perform a second check to ensure the `interactable` has not become unavailable during the time the `AI` has taken to walk to it. If it is still available, the `AI` will attempt to interact with the `interactable`. As with the `player`, a successful interaction will only occur if the `AI` meets the required items condition for interacting. However, since the `AI` is computer-controlled, the required keys condition does not apply. The `AI` is assumed to be 'pressing' the correct keys and will play the appropriate animations associated with the required keys (e.g. playing the interaction animation if the 'Interact' key would be required by the `player`, or the crouching animation if the 'Crouch' key would be required). This provides a realistic source of social information, enabling participants to watch and imitate demonstrated behaviours to successfully complete a task.

4.4.5.6.1. *AI_ItemInteractionController* (child script, inherits from *AI_ItemInteraction*)

This script gives the researcher control over what `interactables` an `AI` is able to interact with and how they interact with them, thus determining how social information about `interactables` is conveyed to participants. The researcher specifies a list of ‘potential interactables’ that the `AI` is able to interact with. For each `interactable` in the list, the researcher specifies whether the `AI` should interact with it only once or if multiple interactions are allowed. The basic procedure is as follows: An `AI` will interact with the `interactables` in its potential interactables list on a timer. After a random delay between a specified minimum and maximum number of seconds, the `AI` will choose an `interactable` (*i*) from its potential interactables list, then walk to its location and interact with it using functions inherited from the *AI_ItemInteraction* script. Once it has interacted with its chosen `interactable`, the timer will reset and the behaviour is repeated. If the researcher has specified that the `AI` should only interact with `interactable` *i* once, *i* is removed from the `AI`’s potential interactables list after the interaction occurs, regardless of whether said interaction was successful or not.

The researcher has a number of options concerning how an `AI` will choose between the `interactables` in its potential interactables list:

1. **Interact in order.** The `AI` will loop through the `interactables` in its potential interactables list in the order they have been inputted by the researcher within the Unity interface. This can be particularly useful if a researcher wishes to convey social information to a participant about cumulative behaviours or tasks that require multiple steps in a specific order to complete. The researcher can also specify whether the `AI` should continuously loop through its potential interactables list, returning to the first `interactable` once it has interacted with the last, or whether it should only iterate through the list once. In addition, the researcher can specify whether the `AI` should skip past any unavailable `interactables`, or whether it should wait for the next `interactable` in the list to become available again.
2. **Favour closest interactable.** The `AI` will calculate the distance between itself and all currently available `interactables` in its potential interactables list, choosing the one that is currently closest.
3. **Favour most recent interactable.** In this case, the `AI` will always choose the `interactable` with which it last interacted – provided that `interactable` is currently available, else it will choose its next `interactable` from its potential interactables list at random instead. This option may be useful, for example, if a

researcher wishes to program an `AI` with a repertoire of possible behaviours, but have it preferentially repeat the same behaviour / option once it has been selected.

4. **Choose random interactable.** An `interactable` is selected at random from the currently available `interactables` in the `AI`'s potential interactables list.

An `AI` can also be programmed to add new `interactables` to its potential interactables list during gameplay if it comes in contact with them. An `AI` is considered as coming into contact with an `interactable` if it has entered the `interactable`'s trigger area. Having an `AI` add new `interactables` to its potential interactables list may be useful if a researcher wishes to add an element of randomness to an `AI`'s behaviour. Alternatively, a researcher may not wish the `AI` to interact with objects straight away at the start of the game and instead have the `AI` 'learn' about the `interactable` only after coming into contact with it, the likelihood of which can be controlled by the `AI` movement (e.g. by setting the location of the `interactable` as an attractive area, as described in *AI_RandomWalk*, above).

This script also instructs the `AI` how to treat any `Holdable interactables` it has picked up. An `AI` can carry a maximum of two `Holdable interactables` at a time (one in each hand). An `AI` will carry a `Holdable interactable` around indefinitely unless the researcher programs the `AI` to either deposit it into a `Container`, or drop it given a specified condition. An `AI` can be programmed to drop a `Holdable interactable` according to any of the following conditions: (a) after a random number of seconds between a specified minimum and maximum; (b) after a specified number of interactions with other `interactables` in their potential interactables list; or (c) after the `interactable` has been successfully 'used' a specified number of times – with a 'use' defined as a successful interaction with another `interactable`, for which this `Holdable interactable` and its modification(s) were a 'required item'. Allowing an `AI` to pick up, use and drop `Holdable interactables` can be useful if a researcher wishes to create an environment where the `player` is required to observe how an `AI` uses a `Holdable interactable` and then attempt to replicate the demonstrated behaviour.

4.4.5.7. *AI_FoodInteraction*

This script allows `AIs` to collect specific `Food` items in order to transmit social information about `Food` types to the `player` or allow `AIs` to collect rewards after completing tasks. Despite being a type of `interactable`, `Food` items are dealt with in a separate `AI` script than other `interactables` since different parameters and `AI` behaviours are required – and to allow the collection of `Food` items (which are likely to act as rewards for the successful completion of tasks) to be completely independent of interactions with other types of `interactable`.

An `AI` has a specified `Food` detection radius and can only react to `Food` items within this radius. After a specified delay, the `AI` will first pause the timer in the *AI_ItemInteractionController* script to avoid interactions being missed during `Food` consumption, then the `AI` will choose a `Food interactable` within its detection radius and interact with it. If the interaction is successful, the `Food` will be collected (or 'eaten') by the `AI`, as discussed in *Interactable_Food* (section 4.4.3.3.4) above. The actual interactions with `Food` items are dealt with via the *AI_ItemInteraction* script.

The researcher has a number of additional options concerning how an `AI` responds to `Food` items:

1. **High value preference.** The `AI` interacts with the `Food` items in its detection radius in order of their nutritional values – interacting with the highest value `Food` first, then the second highest, and so on.
2. **Avoid poisonous food.** The `AI` will ignore any `Food` item that has a negative nutritional value (i.e. a 'poisonous' `Food` that would deduct health from the `player` if the `player` was to eat it).
3. **Specific food preferences.** The `AI` will only respond to specified types of `Food` items within a 'food preferences' list specified by the researcher, and will ignore all other `Food` types. This can be a useful way of researching whether human food preferences are spread via social transmission (i.e. do people favour food types that they have witnessed another individual eating?), as has been investigated in various animal species.
4. **Leave food behind.** Instructs an `AI` not to eat all the `Food` items in the area. An `AI` will only respond to `Food` if there are more than a specified number of `Food` items in its detection radius. This option is useful in situations where an informed `AI` is likely to visit a `food patch` before the uninformed `player`, to ensure there is still `Food` available when the `player` arrives.

4.4.5.8. *AI_CharacterInteraction*

Script that instructs the `AI` to respond in certain ways towards other `AIs` and the `player`. `AIs` can respond to other characters in three ways: an aggressive display (stand up straight and punch outwards); a submissive display (hunch over, shield face and turn away); and a positive display (waving). When the `AI` comes within a certain distance of a character (i.e. within its trigger area), they turn to the character and, after a specified delay, perform one of the displays above. The type of display towards the `player` is explicitly chosen by the researcher, meaning a particular `AI` will always respond in the same way to the `player`. The `AI` also has a specified 'aggression level', which determines how it acts towards other `AIs`. If two interacting `AIs` both have an aggression level of zero, each with interact with a positive display. If both have aggression levels above zero and there is a difference in their aggression levels, the `AI` with the highest aggression level will use an aggressive display and the one with the lowest aggression level will use a submissive display. If both have an aggression level of above zero, but their aggression levels are equal, they will both use an aggressive display. If one of the `AIs` does not possess the *AI_CharacterInteraction* script, no interaction will occur. Alternatively, the researcher can specify a 'specific response' towards a particular `AI`, which will override any response based on aggression levels.

Previous research has that both human and non-human individuals are more likely to copy demonstrators with particular characteristics, such as dominant or familiar individuals (e.g. Henrich and Henrich, 2010; Horner *et al*., 2010; Kendal *et al*., 2015; Corriveau and Harris, 2009; Swaney *et al*., 2001; Guillette *et al*., 2016). Creating `AIs` within VERSE that interact with other characters using particular displays can enable participants to distinguish between `AIs` of different characteristics or personalities and investigate what influence this has on social information use. In addition, `AI` aggression levels and the resulting behaviours towards one another can also be used to generate a dominance hierarchy, which have been experimentally demonstrated as having an influence on social learning in animals (e.g. Kendal *et al.,* 2015).

4.4.5.9. *AI_WeatherResponse*

Determines how an `AI` responds to different `weather conditions` (see *Manager_Weather*, section 4.4.7.1, below). The researcher specifies which `weather condition(s)` the `AI` will respond to and a list of 'known weather shelters'. When one of these `weather conditions` is activated, the `AI` will, after a specified delay, run to one of the `weather shelters` in its list and stay in that shelter until the `weather condition` is deactivated. All other behaviours are disabled via the *AI_Controller* while an `AI` is shielding itself from the weather. The researcher can also specify whether the `AI` should favour the closest of its known shelters. This behaviour allows researchers to supply participants with social information about appropriate responses to unfavourable environmental conditions within environments where these `weather conditions` have been programmed.

4.4.6. Tracking values and logging data

Several scripts are available in VERSE for collecting and exporting various types of data that correspond to different types of task used in social learning research.

4.4.6.1. *ValueTracker*

Tracks a specified numeric value during gameplay, updating continuously and additionally recording the value as a percentage of a 'maximum value', which is calculated differently depending on the type of *ValueTracker. ValueTrackers* are useful for continuously monitoring important information that the researcher may, for example, wish to display to the participant during gameplay. There are currently three types of *ValueTracker*:

1. **Player energy tracker.** Requires the *PlayerEnergy* script to be attached to the `player`. Tracks the `player`'s current energy as a percentage of the starting energy value. This can be used to monitor how energy-efficient a participant's choices are – for example, in a route choice task where a number of routes of different length are available.
2. **Player health tracker.** Requires the *PlayerHealth* script to be attached to the `player`. Tracks the `player`'s current health as a percentage of the maximum health. This can be used to monitor how adaptive a participant's behavioural choices are – for example, in a foraging task where a number of possible `Food` types, including potentially poisonous items, are available.
3. **Food collection tracker.** Tracks the number of `Food` items obtained by the `player` as a percentage of the total number of available `Food` items in the environment. This type of *ValueTracker* requires an additional *FoodCounter* script (see below) and updates its tracked value according to the current `player` food count. In environments where `Food` is generated during gameplay, calculating the total number of available `Food` items will require the *Manager_TotalFoodDispensedCounter* and/or *Manager_TotalFoodSpawnedCounter* scripts, depending on the way in which `Food` items are added to the environment (see sections 4.4.7.5 and 4.4.7.6, below). The food

collection tracker is a useful way of assessing how 'well' a participant is doing in terms of food / rewards collected.

4.4.6.2. *FoodCounter*

Counts the number of `Food` items collected by the `player` within the current environment. The researcher can specify whether this count should include the nutritional information of `Food` items or whether it should be based solely on the number of items collected.

4.4.6.3. *FoodPatchCollisionDetector*

Detects when a character visits a `food patch` (or any other specified area). This script must be added to a GameObject that has a trigger[6] around it (Table 4.1).

4.4.6.4. *Logger* (parent script)

Creates a log of a specific dataset in preparation for export from the application.

4.4.6.4.1. *Logger_PositionData* (child script, inherits from *Logger*)

Records the position (x, y, z coordinates) of a specified set of monitored objects. The position of each object and the current time in seconds is logged throughout gameplay at a specified time interval. A separate dataset is created for each monitored object in preparation for export. This can be used to assess how a participant uses social information about particular locations or routes. (Note: In Unity, y coordinates corresponds to the up/down direction, while x and z are the left/right and forward/backward directions, which may differ from statistical programs).

4.4.6.4.2. *Logger_InteractionsData* (child script, inherits from *Logger*)

Records any interactions that a specified set of monitored characters (i.e. `player` or `AIs`) make with a specified set of monitored `interactables`. Each time a character successfully interacts with an `interactable`, the current time, the character name and the `interactable` name are recorded. One dataset is produced containing all the interactions made by all the monitored characters towards any monitored `interactable`, in the order at which they occurred. This can be used to assess how a participant uses social information about particular `interactables`.

4.4.6.4.3. *Logger_FoodPatchVisits* (child script, inherits from *Logger*)

Records each time a character from a set of specified monitored characters visits one of a set of specified `food patches`. Requires a *FoodPatchCollisionDetector* script (section 4.4.6.3) to be added to each monitored `food patch` to register visits. A single dataset is produced showing all the visits made by any of the monitored characters to any of the monitored `food patches` and the times at which the visits occurred. This can be used to assess how a participant uses social information about the locations of `food patches`. (Note: This *Logger* can be repurposed to log visits to any area according to the researcher's needs).

4.4.6.4.4. *Logger_FoodEatenByPlayer* (child script, inherits from *Logger*)

Records all the `Food` items 'eaten' by the `player` during the course of the game. The name of the `Food` object, its nutritional value and the time at which it was eaten are all recorded. In addition, a cumulative nutritional value across all consumed `Food` items is recorded. If `AIs` are programmed to prefer certain food types, this *Logger* can be a useful way of assessing whether participant choices have been influenced by `AI` preferences.

4.4.6.4.5. *Logger_TrackedValues* (child script, inherits from *Logger*)

Records the final tracked value, maximum possible value and percentage value of any *ValueTrackers* (see *ValueTracker* above) at the end of the current scene.

4.4.6.5. *SaveToCsv*

Takes the dataset from all *Loggers* in the current scene and exports each as a .csv file at the end of gameplay. All datasets are exported to the game's directory with descriptive file names to make data easy to recognise and sort. The researcher can also give participants a 'reference number' and have this number automatically added to all file names to allow data from the same participant to be linked together. VERSE comes with a dedicated scene where participants can input their reference number, which can be added to the start of the build – the *SaveToCsv* script will then save a record of this inputted number and add it to the filename of every outputted dataset.

4.4.7. Game managers

Several game managers are available in VERSE which add additional features to the environment as a whole and/or allow a greater level of control over some of the functions already discussed.

4.4.7.1. *Manager_Weather*

Controls `weather conditions` within a VERSE environment. Each `weather condition` is saved as a ScriptableObject[10] containing the following properties: *visual effect, duration, time interval* and *initial delay*. The *Manager_Weather* takes any number of `weather conditions` and enables and disables them on a loop according to their respective properties. Each `weather condition` has its own timer within the *Manager_Weather*. The `weather condition` is enabled after *time interval*, except at the beginning of the scene, when it is enabled after a delay equivalent to: *initial delay* + *time interval.* Once enabled, the `weather condition` is disabled again after *duration*, after which the timer restarts. Enabling a `weather condition` involves 'switching on' the *visual effect* associated with it. Visual effects for `weather conditions` are created using particle systems[18] that are placed directly in front of the camera so they are continuously visible to the participant while ever the `weather condition` is enabled, without the high computational demands of creating a visual effect over the entire environment. The effects of the weather on the `player` and `AIs` can be altered through the *PlayerWeatherResponse* (section 4.4.2.7) and *AI_WeatherResponse* (section 4.4.5.9) scripts as previously discussed.

Any number of `weather shelters` can be added to an environment. These are areas or objects which protect the `player` from all `weather conditions` and which `AIs` can be programmed to run for when a particular `weather condition` is enabled. Each `weather shelters` is surrounded by a trigger[6] (Table 4.1) which senses when a character enters it. Adding `weather conditions` to a social learning environment can be used both as a task in itself to establish how participants use social information to learn about adverse environments or to increase the difficulty of another, unrelated task through environmental complexity and uncertainty. This function aids VERSE in generating realistic environmental features only currently possible in field studies, while providing researchers with experimental control only possible in lab studies.

4.4.7.2. *Manager_RewardDistributer*

Gives additional control over a set of specified `reward dispensers` (see *RewardDispenser*, section 4.4.3.3.7.1, above), allowing their rewards to be swapped and changed over a number of ‘rounds’. The researcher specifies a set of `reward dispensers` and, for each one, a set of ‘possible rewards’. The researcher also specifies the total number of rounds and can optionally have this displayed as text onscreen for the participant to see during gameplay. At the beginning of each round, the *Manager_RewardDistributer* randomly selects a reward for each `reward dispenser` from its set of possible rewards. This reward will override any possible rewards already set in the *RewardDispenser* script of the specified `reward dispenser`. The researcher can optionally specify that equal rewards should be distributed to all `reward dispensers`, in which case the *Manager_RewardDistributer* will randomly select a single reward from all sets of possible rewards and distribute this reward to all `reward dispensers`.

The *Manager_RewardDistributer* can also be programmed to swap the set of possible rewards between `reward dispensers` at a specified probability (where a probability of 1 means a definite swap) at the beginning of each round. The specific reward for each `reward dispenser` is then chosen as described above from the newly distributed sets of possible rewards. When swapping rewards between more than two `reward dispensers`, the set of possible rewards from each `reward dispenser` is distributed to one of the alternative `reward dispensers` at random. Programming a situation where rewards are swapped between rounds can allow a researcher to create a task where a participant is required to locate the `reward dispenser` with the highest reward and where the location of the highest reward is randomised, thus preventing the participant from simply learning a single location.

The researcher is also required to specify how the *Manager_RewardDistributer* should define the beginning of a new round. A new round can begin on a timer after a specified number of seconds or can be synced with the regeneration of a specified `interactable` (see *InteractableProperties*, section 4.4.3.1, above). An example of a situation where the second option would be favourable is a task where a `Holdable` ‘token’ must be deposited into one of two `Containers` to receive a reward, and where the token has been set to regenerate in its original position after being placed into a container. In this case, it may be favourable to sync the redistribution of rewards between the two containers with the regeneration of this token, therefore ensuring that the beginning of a new round, and so any change in the rewards dispensed by the containers, only occur after the participant has made their choice. This method is used for the ‘Container task’ in the experiment described in Chapter 5.

Once the total number of rounds have been completed, all rewards are removed from the set of `reward dispensers` and no new rounds will be initiated. In addition, the *Manager_RewardDistributer* can optionally be instructed to remove a number of objects from the scene once all rounds are completed. This can be useful in a situation where the beginning of each round is defined by the regeneration of an `interactable` object. When all rounds are completed, said `interactable` may become redundant and having it disappear from the environment can make it clear to the participant that the task is complete.

4.4.7.3. *Manager_AiRewardDistributerResponse*

Controls how `AIs` respond to the reward distributions in the *Manager_RewardDistributor* script. A set of specified `AIs` are instructed to choose between a set of specified reward dispensers after a specified number of rounds. The researcher has several options influencing how `AI` choice is distributed between the specified reward dispensers:

1. **Frequency-distributed.** The researcher specifies the frequency of `AIs` that should visit each `reward dispenser`, and `AIs` are distributed randomly according to this frequency at the beginning of each round. The specified frequencies can either be fixed to a particular `reward dispenser` across all rounds (e.g. dispenser A is always visited by two `AIs` and dispenser B by three `AIs`) or can be set to swap randomly between rounds. Note that a 1:1 frequency can be used if a researcher wishes to investigate biases towards particular demonstrators while controlling for the frequency of demonstrators using choosing each option.
2. **Payoff-based.** Each `AI` is given a ‘tracking ability’ that determines how well it is able to detect the `reward dispenser` with the highest payoff. At the beginning of the round, each `AI`’s probability of choosing a `reward dispenser` with a higher payoff over one with a lower payoff is equal to its tracking ability.

3. **Frequency-distributed and payoff-based.** The researcher specifies the frequency of `AIs` that should visit each `reward dispenser` and `AIs` are distributed according to this frequency at the beginning of each round. The tracking ability of each `AI` acts as a weight that determines the likelihood that it will be chosen over other `AIs` to visit a higher-payoff `reward dispenser` within the specified frequency distribution. The frequencies assigned to each `reward dispenser` can be either fixed across rounds, set to swap randomly, or distributed according to payoff (so that the highest-payoff `interactable` is always visited by the most `AIs`).
4. **Assigned at random.** Each `AI` randomly chooses one of the specified reward dispensers at the beginning of each round.

For each `AI`, the chosen `reward dispenser` is added to the list of potential interactables within its *AI_ItemInteractionController* script (see section 4.4.5.6.1, above), allowing the `AI` to interact with the `reward dispenser` according to the rules and functions of this script. Increasing the number of rounds that elapse before choices are redistributed among `AIs` can be used to represent a delay in demonstrators responding to changes in their environment, thus adding a level of uncertainty about the social information being provided.

Overall, this manager allows the researcher to control how social information about reward dispensers is conveyed to the participant in a way that is specifically designed for investigating human social learning strategies. Frequency-, success- and model-based social learning biases have been demonstrated in many species (e.g. Pike and Laland, 2010; Kendal *et al.*, 2009; Pike *et al.*, 2010; Seppänen *et al.*, 2011; Horner *et al.*, 2010; Kendal *et al.*, 2015), including humans (e.g. Morgan *et al.*, 2012; Efferson *et al.*, 2008; Mesoudi, 2008; Mesoudi and O'Brien, 2008; Henrich and Henrich, 2010; Miu *et al.,* 2018), but are generally difficult to assess in humans in a realistic environment, using ecologically relevant tasks. VERSE makes it possible to test such hypotheses within complex and naturalistic, yet highly controlled, environments.

4.4.7.4. *Manager_AiSync*

Synchronises the item interaction behaviours within the *AI_ItemInteractionController* scripts of a specified set of `AIs`. For each `AI`, the researcher specifies a particular ‘sync interactable’ from the potential interactables list in its *AI_ItemInteractionController* script. When an `AI` interacts with this specified `interactable`, any further item interactions normally dictated by the *AI_ItemInteractionController* script are paused (via the *AI_*Controller) until all `AIs` have interacted with their own sync `interactables`. When all `AIs` have reached their sync `interactable`, item interaction is enabled again. Syncing `AI` item interaction behaviour is particularly helpful in cases where multiple `AIs` are required to display multiple options to the participant at the same time and/or where differences in the timing of `AI` choices may cause confusion or influence the choice of the participant.

4.4.7.5. *Manager_TotalFoodDispensedCounter*

Calculates the maximum possible reward value that a `player` could collect from `reward dispensers` in the environment, which is used to update the maximum value in any food collection *ValueTrackers* (see *ValueTracker,* section 4.4.6.1, above) and to assess how 'well' a participant has completed a task involving `reward dispensers`. The researcher can specify which `reward dispensers` to monitor or, alternatively, specify that all `reward dispensers` in the environment should be included. The researcher can also specify whether `AI` rewards should be included in the total. A researcher may wish to include `AI` rewards in the total if they consider rewards dispensed to `AIs` as 'extra opportunities' for gaining rewards (e.g. if investigating 'scrounging' behaviour, which has been most notably demonstrated in pigeons; Giraldeau and Lefebvre, 1987). However, if a researcher wishes to base this total only on successful completion of tasks by the `player`, they may wish to avoid including `AI` rewards in the count.

The maximum number of rewards from `reward dispensers` is calculated as follows: `reward dispensers` are defined as 'managed' or 'unmanaged' depending on whether their rewards are managed by a *Manager_RewardDistributer* script (section 4.4.7.2). For unmanaged `reward dispensers`, the total number of possible `Food` rewards equate to the actual number of rewards dispensed during gameplay. Therefore, each time an unmanaged `reward dispenser` dispenses a reward into the environment, the reward value is added to the running total. For managed `reward dispensers`, rewards are distributed between a number of `reward dispensers` across a number of rounds (see *Manager_RewardDistributer*, section 4.4.7.2) and the participant is expected to choose only one `reward dispenser` per round. Therefore, for each round, only the maximum reward distributed amongst the managed `reward dispensers` (i.e. the maximum possible reward a `player` would gain if they chose the 'best' `reward dispenser` in the set) is added to the running total. If a researcher specifies that `AI` rewards should be included, any additional rewards dispensed to `AIs` from managed dispensers are viewed as opportunities to scrounge and so are added to the total as well. When calculating the total possible value from dispensed rewards, *Manager_TotalFoodDispensedCounter* can either count `Food` rewards by their quantity alone or can include each `Food` item's nutritional value. This is determined by the options inputted into the *FoodCounter* script (see section 4.4.6.2, above).

4.4.7.6. *Manager_TotalFoodSpawnedCounter*

Calculates the number of `Food` rewards spawned from any *FoodSpawners* in the environment (see *FoodSpawner,* section 4.4.4.1, above) during gameplay, which is used to update the maximum value in any food collection *ValueTrackers* (see *ValueTracker,* section 4.4.6.1, above) and to assess how 'well' a participant has completed a foraging task. `Food` rewards can either be counted based on their quantity alone or based on each `Food` item's nutritional value. This is determined by the options inputted into the *FoodCounter* script (see section 4.4.6.2, above).

4.4.7.7. *Manager_Scene*

Automates the process of moving to the next scene and/or ending gameplay so that the researcher does not need to do this manually. The application is instructed to end the current scene according to one or more of the following conditions: (i) after a specified amount of time has elapsed since the beginning of the scene; (ii) a specified delay after a *Manager_RewardDistributer* (see section 4.4.7.2, above) has completed all its rounds; (iii) if the `player`'s health reaches zero. Once a scene has ended, all functionality is paused pending the beginning of the next scene. If the current scene is the last in the build, the *Manager_Scene* displays an 'end game canvas', a 2D canvas[8] (Table 4.1) that lets the participant know they have completed all tasks in the application. If the current scene is not the last in the build, the *Manager_Scene* can either move automatically on to the next scene, or optionally display an 'end scene canvas' which contains a button that allows the participant to decide when to move to the next scene. An end scene canvas may be preferred if the researcher wishes to allow participants a short break between scenes. In addition, one or more tracked values (see *ValueTracker*, section 4.4.6.1, above) can be optionally displayed on the end scene canvas and/or end game canvas, either as an absolute value or as a percentage of its maximum, to give the participant an idea of their performance during tasks.

4.5. Worked example

What follows is an example of a social learning environment created in VERSE (shown in Figure 4.4), which demonstrates some of the features described above. In this example, a single participant is placed into a small forest environment and given the task to find and break open fruits to collect seeds. The fruits are located in three trees within the environment and require a stick to reach and dislodge them. Hidden in the environment is a pile of sticks the participant can use. Two `AIs` provide a source of social information – both know the location of the stick pile and how to access fruit and break them open to get to the seeds, but each `AI` chooses to gather their fruit from a different tree. Data on the location of the `player` and `AIs` and all the `interactables` each character interacted with throughout gameplay are collected using the *Logger_PositionData* and *Logger_InteractionsData* scripts. This example environment could be used to investigate how social information is used when learning to use tools in a novel, realistic environment – and offers some direct comparisons to research on tool-use and foraging in animal communities (e.g. tool-use in chimpanzees; Biro *et al.,* 2003; Musgrave *et al.,* 2016).

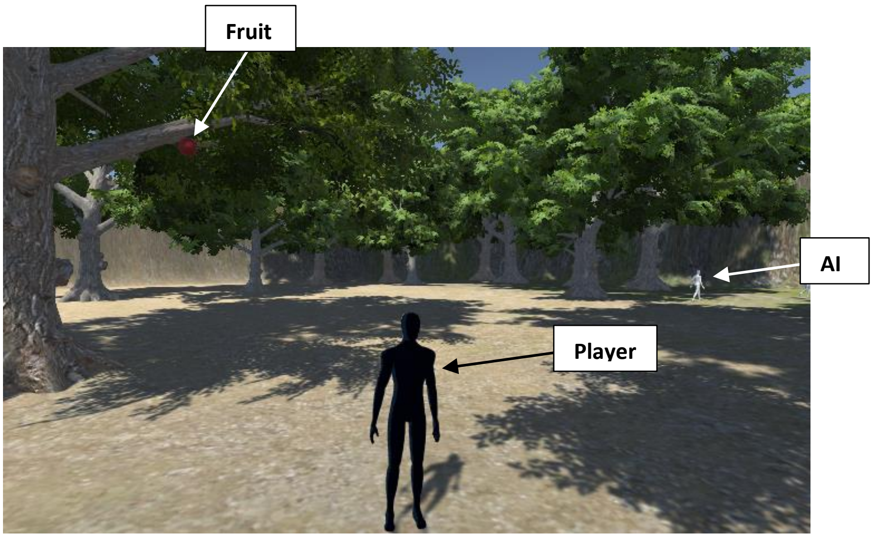


Figure 4.4. Example of a VERSE environment where the `player` (black figure, controlled by the participant) is required to obtain seeds by accessing and breaking open fruit hidden in trees. Computer-controlled `AIs` (white figures) provide social information about how to complete the task.

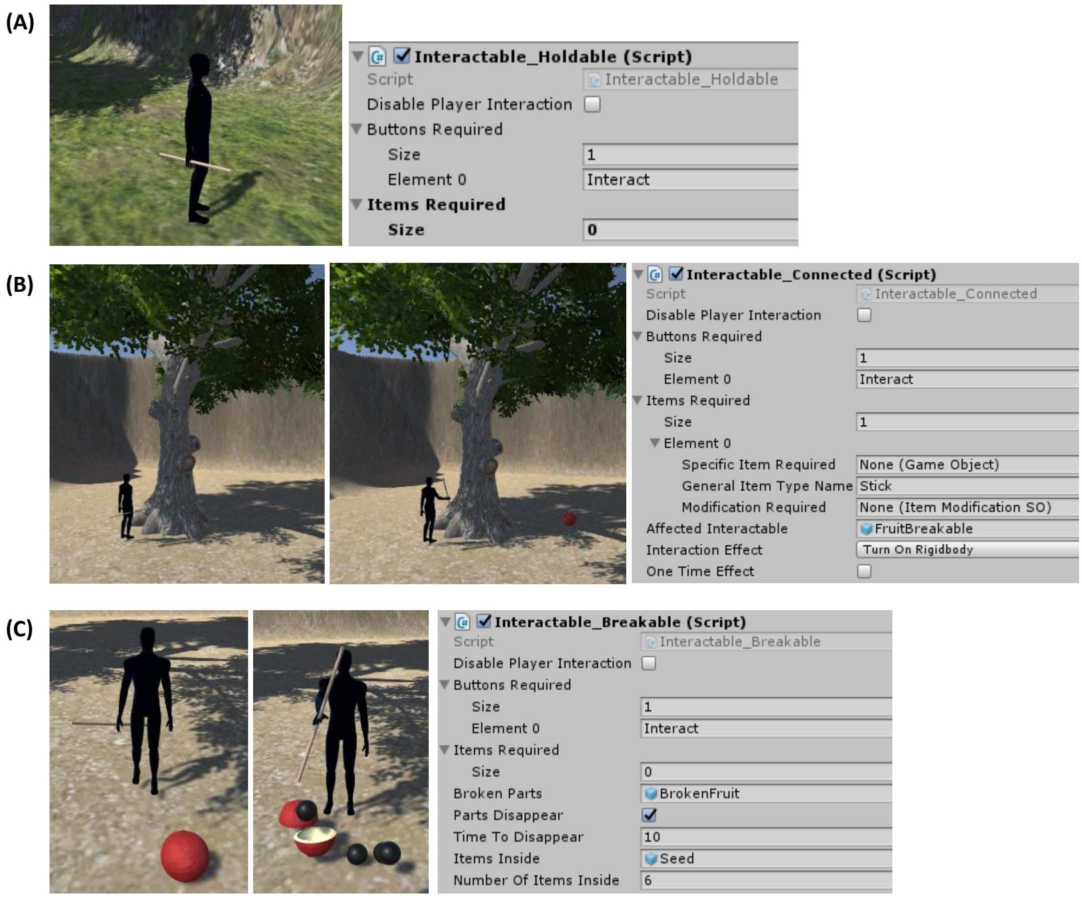
To achieve this, the environment is first created in VERSE using Unity's terrain tool. A `player` is added to the environment that has the following three scripts attached: *BasicBehaviour, MoveBehaviour* and *PlayerInteraction*, which allow the participant to move the `player` and interact with `interactable` objects within the environment. A camera is added to the `player`, which follows the `player` around during gameplay. The *CameraControl* script is attached to the camera to allow camera rotation.

Three types of `interactable` are added to the environment: sticks, trees and fruit (Figure 4.5). Each `interactable` contains the *Interactable_Properties* script and one of the *Interactable* child scripts, as described below. A number of sticks are hidden in the environment. Three trees are placed in the environment, each with a fruit hidden in their branches. The fruit `interactables` have their 'Rigidbody' component disabled so they do not respond to gravity and so remain in the branches of the tree and out of reach of the `player` or `AIs`.

Each stick is a `Holdable interactable`, containing the *Interactable_Holdable* script (Figure 4.5A). One required key ('Interact') and no required items are specified, meaning the `player` simply needs to approach the stick and press the 'Interact' key (default: **?**) to interact with it. A successful interaction results in the `player` picking up and carrying the stick. The stick also has an 'item type' of 'Stick' specified in its *Interactable_Properties* component.

Each tree is a `Connected interactable`, containing the *Interactable_Connected* script (Figure 4.5B). It has one required key ('Interact') and one required item (any `interactable` with the general item type 'Stick'). This means that, in order to interact with the tree, the `player` must approach the tree with a stick in hand (any stick with the correct item type, since a general item type has been specified rather than a specific object) and press the 'Interact' key for a successful interaction to take place. If the `player` attempts to interact with the tree without the required item in hand, the interaction will be unsuccessful. The *Interactable_Connected* script is programmed so that a successful interaction will enable the Rigidbody component of a connected fruit object, allowing the fruit to respond to forces such as gravity. This means that, when the `player` successfully interacts with the tree using the stick, the fruit will drop out of the tree, thus allowing the `player` to access it and break it open.

Each fruit is a `Breakable interactable`, containing the *Interactable_Breakable* script (Figure 4.5C). It has one required key ('Interact') and no required items. It is also set to release six 'seeds' when broken. This means that the `player` needs to approach the fruit and press the 'Interact' key to break open the fruit and gain access to the seeds. The seeds themselves are examples of `Food interactables`, containing the *Interactable_Food* script. Seeds have no required keys or required items, meaning the `player` simply needs to walk into them to collect them. To gain access to the seeds, the `player` must therefore learn to perform the correct series of behaviours, first picking up the stick and then using the stick to interact with the tree so that the fruit drops to the floor, then breaking open the fruit to access the seeds. The fruit also has an additional property specified in its *Interactable_Properties* script – it is set to regenerate in its original position after it is destroyed (i.e. when it is broken open, it will reappear back in the tree again). This gives the impression that the fruit 'regrows' after being hit out of the tree with the stick and gives both the `player` and `AIs` multiple opportunities to access fruit from the same tree.



(A)

Interactable_Holdable (Script)
Script: Interactable_Holdable
Disable Player Interaction: ☐
Buttons Required
Size: 1
Element 0: Interact
Items Required
Size: 0

(B)

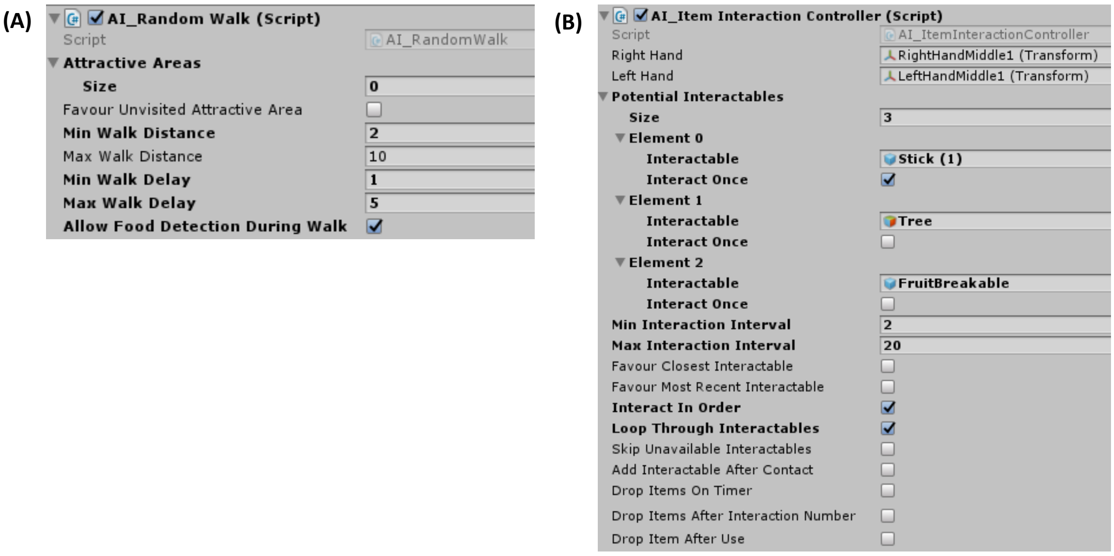
Interactable_Connected (Script)
Script: Interactable_Connected
Disable Player Interaction: ☐
Buttons Required
Size: 1
Element 0: Interact
Items Required
Size: 1
Element 0
Specific Item Required: None (Game Object)
General Item Type Name: Stick
Modification Required: None (Item Modification SO)
Affected Interactable: FruitBreakable
Interaction Effect: Turn On Rigidbody
One Time Effect: ☐

(C)

Interactable_Breakable (Script)
Script: Interactable_Breakable
Disable Player Interaction: ☐
Buttons Required
Size: 1
Element 0: Interact
Items Required
Size: 0
Broken Parts: BrokenFruit
Parts Disappear: ☑
Time To Disappear: 10
Items Inside: Seed
Number Of Items Inside: 6

Figure 4.5. The three main types of `interactable` within the example VERSE environment. Left-hand images show their in-game representations and right-hand images show the particular *Interactable* script attached to the object, along with its properties. **(A)** A `Holdable` 'stick' `interactable` which can be picked up by the `player` by pressing the 'Interact' key. **(B)** A `Connected` 'tree' `interactable` that turns on the Rigidbody component of a connected 'fruit' (red ball), thus allowing it to be influenced by gravity and causing it to fall from the top of the tree onto the ground. The tree has one required item for a successful interaction to occur – the `player` must have a 'stick' in hand while interacting using the 'Interact' key. **(C)** A `Breakable` 'fruit' `interactable` which breaks open upon pressing the 'Interact' key is when the player is in close vicinity. The fruit becomes a 'broken fruit' object (two broken halves) and releases six 'seeds' – a `Food` `interactable` that can be collected by the `player`.

Social information is provided to the participant in the form of two `AIs` that already 'know' how to complete the task. Participants are able to observe these `AIs` performing the correct series of behaviours and imitate these behaviours to gain access to the fruit seeds. Both `AIs` contain the following scripts: *AI_Controller, AI_Movement, AI_RandomWalk, AI_ItemInteractionController,* and *AI_FoodInteraction.* For each `AI`, the *AI_RandomWalk* script is programmed so that the `AI` moves around randomly by 2-10 units every 1-5 seconds and is able to detect `Food` during random movement (Figure 4.6A). No 'attractive areas' are specified in this example. Movement is permitted via the *AI_Movement* script and is temporarily disabled by the *AI_Controller* script whenever it would interfere with other behaviours such as item interactions.



AI_Random Walk (Script)

Script	AI_RandomWalk
Attractive Areas	
Size	0
Favour Unvisited Attractive Area	☐
Min Walk Distance	2
Max Walk Distance	10
Min Walk Delay	1
Max Walk Delay	5
Allow Food Detection During Walk	☑

AI_Item Interaction Controller (Script)

Script	AI_ItemInteractionController
Right Hand	RightHandMiddle1 (Transform)
Left Hand	LeftHandMiddle1 (Transform)
Potential Interactables	
Size	3
Element 0	
Interactable	**Stick (1)**
Interact Once	☑
Element 1	
Interactable	**Tree**
Interact Once	☐
Element 2	
Interactable	**FruitBreakable**
Interact Once	☐
Min Interaction Interval	2
Max Interaction Interval	20
Favour Closest Interactable	☐
Favour Most Recent Interactable	☐
Interact In Order	☑
Loop Through Interactables	☑
Skip Unavailable Interactables	☐
Add Interactable After Contact	☐
Drop Items On Timer	☐
Drop Items After Interaction Number	☐
Drop Item After Use	☐

Figure 4.6. Examples of the *AI_RandomWalk* and *AI_ItemInteractionController* scripts attached to one of the `AIs` in the example environment. **(A)** The *AI_RandomWalk* script, in this example, instructs the `AI` to move a random distance between 2 and 10 units every 1 to 5 seconds and allows `Food` detection during random movement. **(B)** The *AI_ItemInteractionController* script instructs the `AI` to interact with a specified set of `interactables` in a specified way. In this example, the `AI` has the potential `interactables`: 'Stick (1)', 'Tree' and 'FruitBreakable'. The `AI` is instructed to interact with the stick object only once, after which it will be removed, and can interact with the other two `interactables` any number of times. The `AI` is instructed to interact with the `interactables` every 2 to 20 seconds in the order they are specified in the list (i.e. the stick first, then the tree, then the fruit) and to loop back to the beginning once it reaches the end of the list. This script can therefore be used to make `AIs` behave in a way that provides social information about cumulative behaviours.

Within the *AI_ItemInteractionController* script (Figure 4.6B), each `AI` has a list of three potential `interactables`. `AIs` are instructed to interact with the `interactables` in this list in order (one interaction every 2-10 seconds) and loop back to the beginning when they reach the end of the list. The 'potential interactables' list for each `AI` consists of one of the sticks, one of the trees and the fruit hidden within the branches of the chosen tree. `AIs` are instructed to interact with their chosen stick `interactable` only once, but can interact with the tree and fruit multiple times. Overall, this means that an `AI` will first approach and pick up one of the sticks (after which the stick will be removed from its potential interactables list). It will then approach the tree and interact with it while holding the stick. Since this meets the tree's interaction requirements, the fruit will fall out of the tree, making it accessible. The `AI` will then approach and break open the fruit, thus gaining access to the seeds inside. The `AI` will then continue to loop through the `interactables` still remaining in its potential interactables list – interacting with the tree, then the fruit, then the tree again, and so on. Since it still has the stick in hand and has not been instructed to drop it, any future interactions with the tree will be successful and cause the fruit to drop. Each interaction occurs after a delay of 2-10 seconds, during which time the `AI`'s other behaviours, such as its random walk, will be in play.

Each `AI` is assigned their own stick, tree and fruit `interactables`. This means that, while both `AIs` will demonstrate to the `player` how to complete the task, each `AI` will provide slightly different sources of social information (i.e. the specific tree used to get the fruit will differ). Finally, the *AI_FoodInteraction* script is set so that each `AI` will detect and collect any `Food` item (in this case, the seeds released from the fruit) within a 2-unit radius and the *AI_RandomWalk* script is programmed to allow `Food` detection during random walks. Thus, when an `AI` breaks open a fruit (or happens to pass a broken fruit while it is moving from one place to another), it will collect any seeds released.

4.6. Discussion and Concluding Remarks

Here I have described a novel experimental tool, VERSE, which takes advantage of gaming technology to allow researchers to create realistic, immersive, open world environments for studying human social learning. VERSE offers a unique way to bring human research in the field of social learning out of the laboratory and into spatially and ecologically relevant scenarios. Where human research has previously lagged behind animal research in the field in terms of ecological validity, this technology offers huge potential for future work on human behavioural ecology and social evolution.

Researchers using VERSE should, however, bear in mind that, while VERSE may offer a more realistic methodology for studying human social behaviour than traditional lab studies, it is still a simplification of real-world social environments. For example, VERSE, in its current form, fails to account for one key component of human social behaviour – verbal communication – which could be an important aspect of our social learning experiences (Rawat, 2016) (although previous research has suggested that children given conflicting information will trust what they see over what they are told; Ma and Ganea, 2010). However, it could be argued, if humans are studied from a behavioural ecology perspective, that *not* including such complex communication gives us a clearer picture of foundational social learning processes (such as stimulus or local enhancement, direct observations and visual cues) that can be analysed in a similar way (and so be directly compared) to studies on animal populations – as demonstrated in Chapter 5. Indeed, much of the previous work in the field has focussed on how individuals choose to learn based on the decisions of others rather than via direct communications (e.g. Mesoudi, 2008; Morgan *et al.,* 2012; Toelch *et al.,* 2014; Caldwell and Eve, 2014). VERSE could, however, be feasibly extended to include verbal (or written) communication in order to establish its importance in our cultural evolution.

It is also possible, particularly if important aspects of social interaction such as verbal communication are missing, that the artificial intelligence (AI) agents used as social information sources in VERSE may not be viewed by players as truly social entities, but simply as a part of their environment. Evidence from online roleplaying games such as *World of Warcraft* and *Second Life* as to whether non-player characters (NPCs) are viewed as true social interactors is mixed. Often, the identities of NPCs, which generally exist to enrich gameplay and form narratives, are known to the players, which is likely to have a large impact on the extent to which they can be viewed as truly social entities. However, even so, players can form emotional connections with NPCs (Rapp, 2018) and actively collaborate with AI ‘teammates' (Zhang *et al.,* 2021). Some studies also show that the distinction between NPCs and real players isn’t necessarily clean cut. According to Crenshaw and Nardi (2015), for example, players treated researcher-controlled characters using scripted responses, which could easily be replaced with computer-controlled NPCs, as social cues. Similarly, during Banks and Martey’s (2016) attempts to create ‘transparent’ researcher presence in virtual research environments, a researcher-controlled NPC had to be largely de-humanised to prevent players communicating and interacting with it. In their current form, VERSE AIs are intended to provide pseudo-social cues to establish when and how players copy others – and how this is influenced by the physical form of those social cues. However, further research would be required to establish just how 'social' these AI entities are viewed as by players.

It is also important to remember that VERSE is a virtual platform, and this sort of methodology naturally comes with limitations. For example, since VERSE is game-like in its design, participants with different levels of gaming experience may respond differently to this type of methodology – e.g. 'gamers' may pick up the computer controls more quickly, thus allowing them to focus their attention on the task at hand more quickly than 'non-gamers', who may spend a greater proportion of time learning how to control their player. I would therefore recommend that researchers using VERSE in their experiments do the following to reduce any potential impact of prior gaming ability: (a) allow participants to learn the controls in an initial 'demo' environment prior to starting the official experiment, and (b) collect data from each participant concerning prior gaming experience to include in their statistical analysis. I follow these recommendations in Chapter 5 during an investigation into human social information use within several VERSE environments and find little evidence to suggest that participants' in-game behaviour was influenced by their prior gaming experience. Another limitation of VERSE is that participants control a virtual player using computer keys, and hence there is little scope for investigating the learning of motor skills. Despite this, VERSE offers much more flexibility and ecological realism than previous computer-based methods, for example by allowing exploration over large, three-dimensional environments. If future researchers wish to incorporate more realistic motor functions into their experiments, VERSE could feasibly be extended into a fully immersive VR environment, compatible with commercial VR headsets and controllers (e.g. Oculus Quest or HTC Vive), where participants can perform tasks and pick up virtual objects using actual hand movements as opposed to computer keys. In many respects, however, VERSE (or virtual environments in general) offers potential far beyond what is possible in the real world. For example, VERSE could be used to explore human behaviour in scenarios which are impossible to investigate in humans otherwise – such as our responses to dangerous environments, natural disasters and even predators.

Overall, VERSE offers a great deal of potential for researchers wishing to study human behaviour and learning within large, realistic virtual environments. By allowing humans to be studied in spatially explicit environments with the complete behavioural freedom to attempt tasks as they wish, including by observing or ignoring the actions of others, VERSE also offers researchers the opportunity to study humans within a common evolutionary framework alongside animal research. This may even include directly replicating animal experiments using human participants. Due to its modular design, a potentially unlimited number of experiments can be produced in VERSE, including completely novel tasks within completely novel environments, in order to investigate how human social behaviour aids us in realistic survival scenarios. I hope to see future work using VERSE to conduct innovative experiments into human social behaviour.

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Chapter 5 | Human social learning biases in immersive virtual environments

5.1. Abstract

‘Social learning strategies’ describe what, when and from whom individuals choose to learn. Evidence suggests that both humans and animals are capable of strategic social learning. However, human research, which generally consists of small, highly abstract laboratory experiments, tends to lack realism, making it difficult to understand the importance of our use of social information in an evolutionary context. In this study, I use virtual reality to simulate three novel tasks inspired by the animal literature (Container, Route Choice and Foraging task) within complex, three-dimensional environments. In each experiment, combinations of demonstrators with different characteristics gave opposing solutions to the task to determine from whom participants preferentially learned. Importantly, participants were able to freely navigate the environment and attempt the task in any way they chose by using or ignoring social information. I found that participants displayed an overall bias towards learning asocially (independently) rather than socially. Asocial learning was favoured more strongly during complex tasks that spanned larger spatial scales, potentially due to the difficulties in keeping track of social information in such scenarios. When learning from others, participants displayed a bias towards learning from the majority over the minority (positive frequency-dependent social learning) and towards learning from the most successful demonstrators (payoff-based social learning) – which supports the findings of previous, lab-based experiments. There was no apparent bias with respect to demonstrator dominance status, gender and body size. My findings are the first to show a variation in the use of social learning across task and environmental complexities in humans, to carry out a comprehensive evaluation of hypothetical human learning biases, and to provide a methodological link between non-human and human social learning experiments. As demonstrated here, immersive virtual environments have great potential for research into human social evolution and I strongly encourage future research to adopt a similar approach.

Keywords: Social learning; asocial learning; social learning strategies; model bias; virtual reality; artificial intelligence (AI)

5.2. Introduction

Across the animal kingdom, individuals are routinely faced with challenges to overcome, some of which they have experienced before and others that are completely novel. The ability to learn novel behaviours and use them adaptively is therefore highly advantageous. However, learning comes with a cost – trying out different behaviours to find the most successful in a given scenario is costly in terms of time and energy and may leave an individual vulnerable to predation or toxin ingestion. One way to overcome many of these costs is to learn from others – a process known as 'social learning' – thus gaining information from those who already have the knowledge, while reducing the time, risk and energy associated with asocial (independent) learning (Hoppitt and Laland, 2013). Social learning can be adaptive in a wide variety of biological contexts, including foraging, predator avoidance and mate choice (Galef and Laland, 2005). For humans in particular, social evolution has also been paramount to our development of culture. However, indiscriminately copying others rather than sampling directly from the environment can also result in the spread of maladaptive behaviours or the use of outdated information (Laland and Williams, 1998; Rogers, 1988). Evolutionary theory therefore predicts that individuals should be selective in terms of how they use social information (Laland, 2004; Boyd and Richerson, 1985; Schlag, 1998; Rendell *et al.,* 2010).

'Social learning strategies' describe how individuals choose to use social information - specifically when they favour social over asocial learning, what type of information or behaviour they learn, and from whom they learn (Laland, 2004; Rendell *et al.*, 2011). As discussed in Chapter 1, empirical research suggests that both humans and non-human animals are strategic in their use of social information. For example, humans and guppies both favour social learning when asocial learning is costly (Morgan *et al*., 2012; Webster and Laland, 2008; Coolen, *et al*. 2003); humans, sticklebacks and capuchins all copy successful and/or proficient individuals (Mesoudi, 2008; Mesoudi and O'Brien, 2008; Morgan *et al*., 2012; Kendal, Rendell, *et al.*, 2009; Pike *et al.*, 2010; Coelho *et al.* 2015); and humans, sticklebacks and primates tend to conform to the majority or group norms (Efferson *et al*., 2008; Morgan *et al*., 2012; Pike and Laland, 2010; Hopper *et al.* 2011; Van de Waal *et al.*, 2013). Additional evidence from humans suggests that people favour variants that are increasing in frequency (Toelch *et al*., 2010), and that they are more likely to make use of social information if payoffs are less predictable (Caldwell and Eve, 2014) or if the task is perceived as difficult (Flynn *et al.*, 2016) or unfamiliar (Morgan *et al*., 2012). Both humans and non-human animals also display 'model-based' biases towards learning from individuals with certain characteristics. For example, various species, including humans and certain primates, display biases towards copying high-ranking and/or older individuals (Henrich and Henrich, 2010; Horner *et al.*, 2010; Coelho *et al.* 2015; Kendal *et al.*, 2015), potentially because these characteristics act as an indicator of an individual's overall success. Similarly, individuals may display biases towards copying kin (Schwab *et al.*, 2008; Griesser and Suzuki, 2016) and/or familiar individuals (Swaney *et al.*, 2001; Corriveau and Harris, 2009; Guillette *et al.*, 2016), potentially because these individuals are more tolerant to being closely observed. There is also evidence for individual variation in the use of social information, including some individuals (known as 'mavericks') ignoring social information completely (Efferson *et al.*, 2008).

As discussed in Chapter 1, human social learning experiments are often highly abstract and restricted by laboratory environments, making it difficult to establish the validity of such generalisations across the human / non-human divide. In Chapter 4, I introduced the concept of using immersive virtual environments to conduct human social learning experiments in more 'natural' conditions and described a novel research tool – "Virtual Environments for Research into Social Evolution" (VERSE) – specifically designed for this purpose. In VERSE, participants take control of a virtual player and to move freely around large-scale, naturalistic terrain, while solving tasks in the presence of computer-controlled agents that provide them with specific social information controlled by the researcher. Thus, VERSE combats many of the issues associated with restrictive, lab-based social learning experiments, such as abstract tasks and a lack of spatial realism.

In this chapter, I use VERSE to replicate social learning experiments from the animal literature using human participants, thus providing a unique insight into human social information use within ecologically relevant scenarios. In particular, I focus on (a) whether participants preferentially learn socially or asocially when exposed to a series of novel tasks; (b) whether participants display biases towards learning from demonstrators with particular physical and/or behavioural characteristics and (c) whether participants are more prone to copying demonstrators that use more rewarding behaviours. I discuss these findings in relation to previous work on humans conducted in more restrictive laboratory settings and also in relation to the animal literature. By generating an experimental environment where participants have the freedom to navigate large scale landscapes and complete tasks as they wish, and where the use of social information requires the active observation of knowledged demonstrators, this study also aims to bridge the gap between animal and human research by demonstrating how virtual reality can offer a highly promising way of studying human social behaviour within an evolutionarily framework.

5.3. Methods

5.3.1. Virtual Environments for Research into Social Evolution (VERSE)

This study was conducted using VERSE (described in detail in Chapter 4) – a novel research tool for studying human social behaviour within immersive virtual environments. VERSE allows researchers to create realistic, large-scale three-dimensional environments containing ecologically relevant tasks that allow direct comparison to (or replication of) behavioural experiments on freely interacting animal populations. Within VERSE, participants take control of a virtual 'player' to explore and interact with the environment freely. Tasks can be created that require the player to make use of 'interactables' – objects that can be interacted with, subject to specific requirements, and that respond to interactions in different ways, e.g. by breaking open, releasing rewards or being held by the player. Artificial intelligence agents (AIs) can be added to the environment and programmed with specific behaviours such as random walks, route following and object interactions to provide realistic sources of social information. Crucially, if participants are to take advantage of this social information, they must observe AI behaviours and decide which aspects of those behaviours to copy – thus, VERSE immerses participants in a realistic social environment and avoids the oversimplification of social information that is often present in lab studies.

5.3.2. Participant recruitment

All participants were recruited from the Faculty of Biological Sciences, University of Leeds. Prior to the main experiment, 41 postgraduates and members of academic staff volunteered (in response to an email request) to complete a questionnaire regarding their perceptions of the AI models to be used in the main study. This was to explore whether the models to be used in the main experiment were perceived in the intended way (e.g. the 'female' AI as female, the 'dominant' AI as dominant to the 'subordinate' AI, etc.). This is discussed in more detail in the Supplementary Material (Tables 5.S4, 5.S5) – in general, people were found to perceive the AIs as intended. For the main experiment, a total of 143 undergraduates (51 males, 91 females; ages 18-31 years; mean age = 20.6 years) were recruited via a faculty-wide email advertisement. Participants were randomly divided into two 'reward groups', as discussed below. All participants who took part in the main experiment received a £15 Amazon voucher as compensation for their time. Ethical approval for this study was obtained by the Faculty of Biological Sciences Research Ethics Committee (LTSBIO-029).

5.3.3. General experimental design

Participants controlled a virtual human ‘player’ within a number of realistic, three-dimensional virtual environments (constructed using VERSE) in a series of three experiments inspired by the animal literature. Each experiment required participants to complete a novel task (detailed below) in the presence of computer-controlled AI ‘demonstrators’, which acted as realistic sources of social information. Each task was repeated across six ‘demonstrator conditions’ (detailed below) designed to investigate specific social learning biases. The order of presentation for both tasks and demonstrator conditions were randomised across participants according to a balanced Latin square design (Supplementary Material, Tables 5.S1- 5.S3).

The study was conducted remotely, with participants taking part on their own personal computers. Prior to starting the study, participants were given instructions on how to control the virtual player, including how to move the player, rotate the camera and interact with objects, and were then asked to practice this within a ‘demo’ environment. This demo ensured that all participants were comfortable with the game controls prior to starting the experiment, regardless of prior IT and/or gaming experience. Each participant was then given a reference number, used to anonymise their game data, and asked to complete each of the three tasks in order. At the beginning of each task, further instructions were given onscreen, detailing the aim of the specific task. Participants were notified of the presence of ‘other players’ within the game who they were not in competition with and who had prior knowledge of the task. They were not informed whether or not they were expected to use information supplied by these players. Game data was collected automatically during gameplay. After the completion of all three tasks, participants uploaded their game data anonymously to a file request link and filled in a post-experiment questionnaire, as detailed below.

5.3.4. Demonstrator conditions

Each of the three tasks (described below) was replicated across six demonstrator conditions (Table 5.1), designed to identify a number of potential social learning biases highlighted throughout the animal and human literature. For each demonstrator condition, two sets of humanoid AI ‘demonstrators’ with different physical and/or behavioural characteristics (hereon referred to as ‘demonstrator A’ and ‘demonstrator B’) were programmed to make opposing decisions about the given task. At all times during the experiment, participants were free to watch, copy or ignore demonstrators entirely.

Table 5.1. Descriptions of the two demonstrators displaying opposing solutions to tasks in each of the six demonstrator conditions used in the study. In scenarios where different options resulted in different payoffs, ‘demonstrator A’ always displayed a more profitable solution to the tasks than ‘demonstrator B’. In scenarios where payoffs did not differ, both demonstrators displayed equally profitable solutions.

	Demonstrators	
Condition	**Demonstrator A**	**Demonstrator B**
Asocial	None	None
Soc/Asoc	Single AI, with default appearance.	None
Dom/Sub	A single ‘dominant’ AI with muscular appearance. Programmed to display an aggressive behaviour (punching outwards) towards the subordinate AI at the beginning of the game level.	A single ‘subordinate’ AI with hunched, emaciated appearance. Programmed to display a submissive behaviour (shielding face and turning away) in response to the dominant AI at the beginning of the game level.
Three/One	Three AIs, all with default AI appearance.	Single AI, with default AI appearance.
Male/Female	A single ‘male’ AI, with default AI appearance.	A single ‘female’ AI, modified to enhance the waist-to-hip ratio and reduce muscle mass.
Large/Small	A single AI larger than the player. Otherwise has the default AI appearance.	A single AI smaller than the player. Otherwise has the default AI appearance.

5.3.5. Reward groups

Participants were assigned to one of two ‘reward groups’ designed to investigate how demonstrator success (in addition to their individual characteristics) influenced their likelihood of being copied. In the ‘Same Rewards’ group (*n* = 72), the choices made by both demonstrators in each demonstrator condition were equally profitable and so participants received the same in-game payoff regardless of which demonstrator they copied. This condition was used to investigate participants’ innate biases towards particular demonstrators when there was no direct benefit of choosing to learn from specific individuals. In the ‘Different Rewards’ group (*n* = 71), different solutions to a task resulted in a different payoff. For each demonstrator condition, demonstrator A always provided a higher payoff solution to each task compared demonstrator B, thus giving participants the opportunity to learn which demonstrators tended to be the most successful. Comparisons of the two reward groups were made to investigate whether participants tended to learn from more successful demonstrators, beyond any innate preferences they may hold for demonstrators with particular characteristics.

5.3.6. Tasks

5.3.6.1. Token task

This task (inspired by Horners *et al.*'s 2010 experiment on chimpanzees) was designed to test the influence of different demonstrators on participant choices when making simple, binary decisions. Participants were required to pick up and deposit a token into one of two possible containers – blue(/left) or yellow(/right) – over 10 rounds per demonstrator condition to receive food rewards (Figure 5.1). Participants were instructed to gather as many food rewards as they could. They were informed that the rewards varied between rounds and that the number of rewards they received would depend on their choice of container. This task was replicated once per demonstrator condition (i.e. six game levels in total).

At the start of each round, a black token for the player and a white token for each of the AIs were placed on the ground. Participants could pick up their own token using the '?' computer key (following instructions given prior to the experiment), but were unable to pick up the AIs' tokens in order to prevent players gaining access to additional rewards. At the start of each round, a 'reward number' was distributed to each of the two containers. The reward number varied between rounds in order to add uncertainty to a participant's choice. Demonstrators would then pick up their tokens and deposit them into opposing containers. The reward dispensed to demonstrators were not visible, thus encouraging the participant to make choices based on the characteristics of the demonstrators rather than the number of rewards they witnessed each receiving. Participants deposited their token into a container by approaching that container and pressing the '?' key. This caused a number of food rewards (equivalent to that container's reward number) to be released from the container, which the player could then collect by walking into them. Once all tokens were deposited (by both the participant and all the AIs present) during a particular round, they regenerated in their original positions. This was done (i) to make each round distinct and prevent overlap and (ii) to force the participant and AIs to move back to their original position before making their next choice. The current round number and the total number of food items collected during the current demonstrator condition were displayed onscreen. After 10 rounds of token deposits were completed, there was a 5 second delay to allow the player to finish collecting any dispensed food rewards. The participant was then given their ‘food collection score’ before moving to the next level / demonstrator condition. This score was the number of food items they had collected during the current level, as a percentage of the number of food items they could have collected if they would have chosen the ‘best’ container during each round.

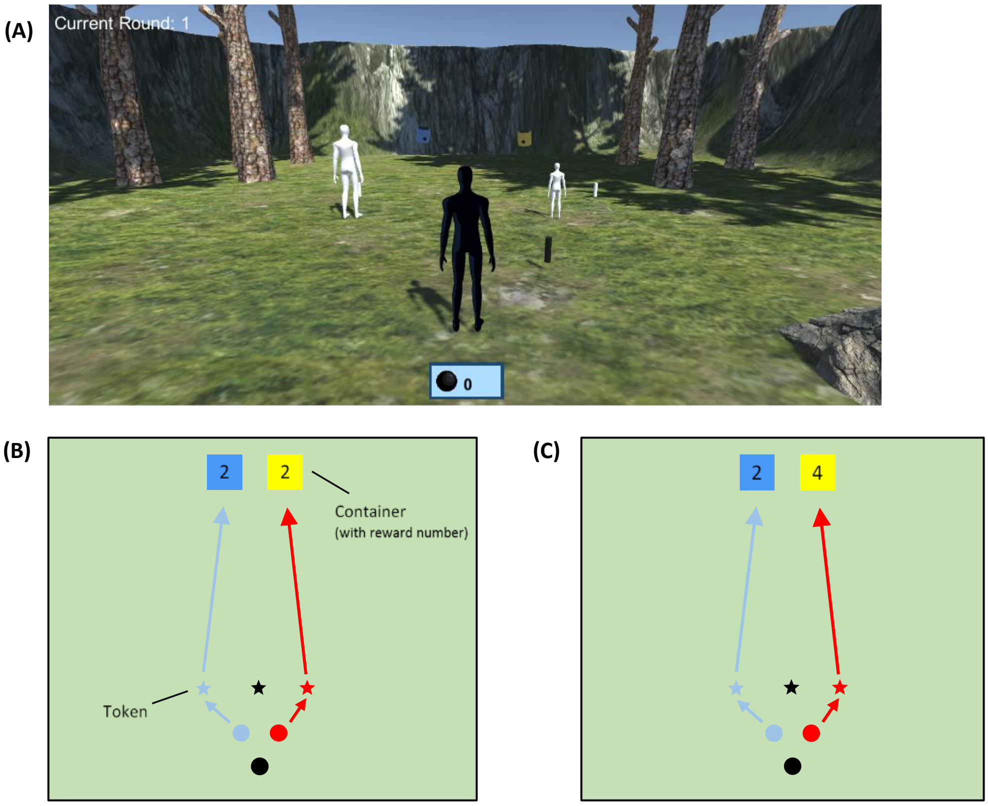

Figure 5.1. The Container task. **(A)** In-game representation. Participants control the player (black figure) to pick up a token (black cylinder) and deposit it in one of two possible containers (blue and yellow structures at the back of the environment) to receive food rewards. Two sets of demonstrator AIs (white figures) can be observed picking up their own tokens (white cylinders) and depositing them into one of the two containers. In this example, the participant is observing the choices made by a large demonstrator AI and a small demonstrator AI. The amount of food collected by the participant is displayed at the bottom of the screen and the current round is displayed at the top left. **(B-C)** Schematic representations of the task. The black circle represents the player, blue and red circles represent the demonstrator AIs, stars represent the tokens to be deposited into the containers, blue and yellow squares represent the containers (with the rewards contained within them shown as a number) and blue and red arrows represent AI choices. **(B)** In the ‘Same Rewards’ group, both containers hold equal rewards. **(C)** In the ‘Different Rewards’ group, containers hold different rewards and the highest reward is always chosen by demonstrator A.

For the Same Rewards group, the participant received the same number of food items regardless of which container they chose on a particular round, i.e. the reward number was equivalent for both containers (Figure 5.1B). The reward number varied between rounds and was always a random number between one and three. Each round, one demonstrator was randomly selected to deposit their token into the yellow container, while the other demonstrator chose the blue container. Demonstrator choices were randomised in this way so that a distinction could be made between participants favouring a particular demonstrator versus favouring a particular container. For the Different Rewards group, the number of food items dispensed differed between containers (Figure 5.1C). At the start of each round, one container was randomly selected as the 'best' choice and was allocated a random reward number between four and six. The other container was selected as the 'worst' choice and was allocated a random reward number between one and three. For each demonstrator condition, demonstrator A always chose the container with the best reward.

Data collection and preparation. The container chosen by the player and each demonstrator during each round were logged. A participant was said to have copied a particular demonstrator if they chose the same container as that demonstrator during a given round. Since there were only two possible choices in this task, participants were therefore forced to choose the same container as one of the demonstrators (with the exception of the *Soc/Asoc* condition, where one option was always undemonstrated). As such, there was no scope for asocial learning that was completely independent of demonstrator choices. For each participant, the total number of times each demonstrator was copied during each demonstrator condition was then calculated.

5.3.6.2. Route choice task

This task (inspired by Laland and Williams' 1998 experiment on guppies) was designed to test how human route choice preferences within naturalistic, large-scale environments were influenced by the choices of other individuals. Participants were placed in a series of forest environments and instructed to find their way through the forest to a hidden cave using as little energy as possible. In each environment, two clear, treeless paths were available (left or right), both of which led to the end point (Figure 5.2). Three replicates were used for each of the six demonstrator conditions (18 game levels in total). Each replicate consisted of a new, visually distinct environment, with the end point and two clear paths positioned differently. Participants began each level with an energy value of 100%. Movement caused this energy value to deplete. The player's current energy value was displayed as a bar at the bottom of the screen during gameplay and the final energy value for that level was additionally displayed as a numerical value onscreen once the player reached the cave.

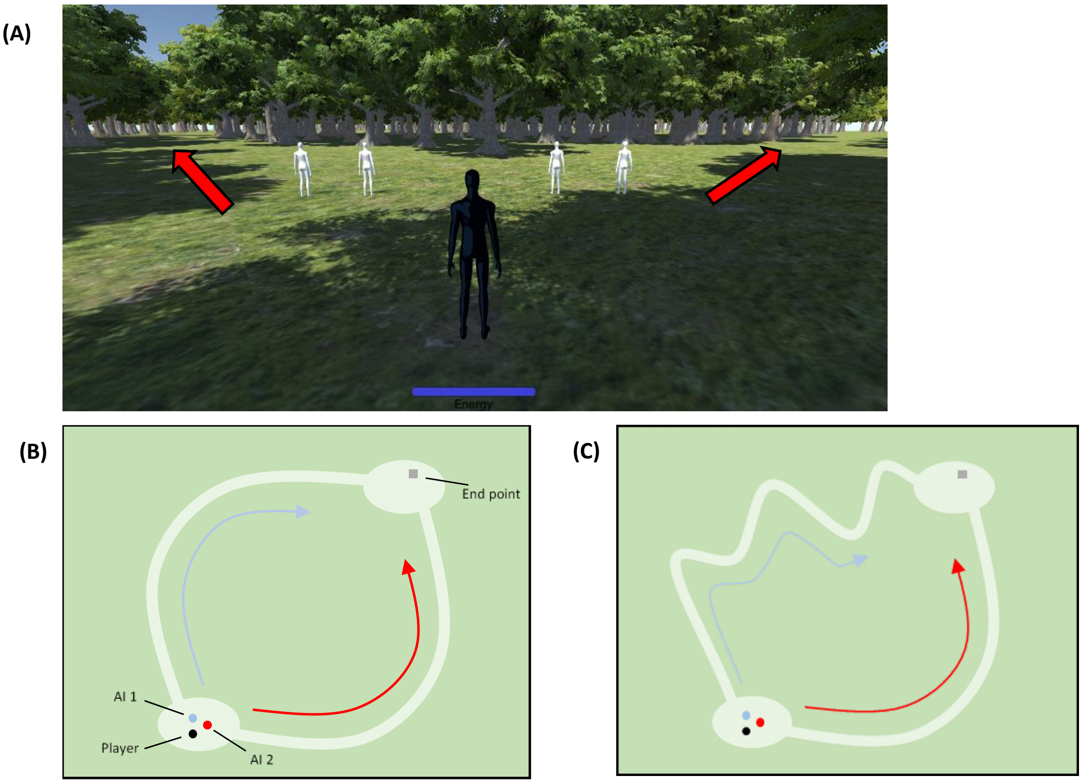

Figure 5.2. The Route Choice task. **(A)** In-game representation. Participants control the player (black figure) in a large, virtual forest environment. Two clear paths through the forest are located on the left and right-hand sides of the player's starting position (indicated by red arrows). Two sets of demonstrator AIs (white figures) make opposing decisions about which path to take. This example shows the *Three/One* demonstrator condition, where three AIs follow one of the clear paths to the end point and a single AI follows the alternative path. The remaining energy of the player is shown as a blue bar at the bottom of the screen and depletes as the player moves. **(B-C)** Schematic representations of the task. The black circle represents the player, blue and red circles represent the demonstrator AIs, the grey square represents the end point, light green areas represent the clear paths through the forest and blue and red arrows represent the paths chosen by the demonstrators. **(B)** In the 'Same Rewards' group, the two clear paths are of approximately the same length. **(C)** In the 'Different Rewards' group, one path is substantially longer than the other and the shortest path is always chosen by demonstrator A.

For the Same Rewards group, the length of each clear path, and so the energy required to navigate them, was approximately the same (Figure 5.2B). For each level, one demonstrator was randomly chosen to follow the left-hand path and the other demonstrator followed the right-hand path. For the Different Rewards group, one path was substantially longer than the other (Figure 5.2C) and so was more energetically costly to travel. Demonstrator A always followed the shorter path and demonstrator B always followed the longer path. The direction (left or right) of the shortest path was randomised between replicates to prevent participants basing their choices purely on direction. Participants were given complete freedom of movement – they could choose to follow the demonstrators, choose one of the paths independently, or ignore the clear paths entirely and attempt to navigate the trees instead. Thus, participants had the opportunity to use social information or make completely independent decisions.

Data collection and preparation. The locations of the player and all AIs were logged at one second intervals throughout gameplay and this data was used to map the exact routes taken by each character. For each level, a participant was said to have copied a particular demonstrator if their location fell within the demonstrator's path choice at least half the time. This was calculated in R (v.4.0.4). Using the *gBuffer* function from the *rgeos* package (Bivand and Rundel, 2020), a 15-unit buffer, which approximately matched the width of the clear paths, was created around each demonstrator's route. Using every fifth data point from the player's location data, the *point.in.polygon* function from the *sp* package (Pebesma and Bivand, 2005; Bivand *et al.,* 2013) was used to calculate how many of the player's location points fell within the buffer region of each demonstrator's route. If ≥50% of player's route was contained within the buffer region of a particular demonstrator's route, the participant was considered to have copied the route choice of that demonstrator. Otherwise, the participant was considered to have navigated the forest independently. For each participant, the total number of times each demonstrator was copied and the total number of times a route was chosen asocially were calculated.

5.3.6.3. Foraging task

This task (inspired generally by experiments on free-roaming animal populations) was designed to test the influence of different demonstrators on participant behaviour in a realistic foraging scenario. Participants were given 200 seconds to explore a large, open environment in search of food (Figure 5.3). There was one replicate per demonstrator condition (i.e. six game levels in total), each with a distinctly different environment. Within each environment, there were 8 randomly located food patches, each containing a total of 40 food items (two sets of 20, where each set was a different ‘food type’). Food items all looked like mushrooms, but different food types were coloured differently and, in some cases, had different nutritional values (Supplementary Material, Table 5.S7). The player was given a food score and health bar, which were displayed onscreen. When the player collected a food item, its nutritional value was added to their food score. Food could also be poisonous (i.e. have a negative nutritional value). Collecting poisonous food reduced the player’s food score and health. If the player’s health reached zero due to eating poisonous food items, the current level ended prematurely. Participants were informed of this prior to starting the task. Once 200 seconds had elapsed, participants were given their food score as a percentage of the maximum score that could have been obtained if they had collected all non-poisonous foods in the area, before proceeding to the next level.

For each demonstrator condition, three of the eight available food patches were visited by one demonstrator, another three were visited by the other demonstrator and the remaining two were not visited by any demonstrator (i.e. they could only be discovered independently). Each demonstrator visited their chosen food patches in a random order. Once they reached a food patch, demonstrators would ‘eat’ 10 food items from only one of the available food types located there, thus demonstrating food preferences to the participant while leaving the majority of food items for the player to collect.

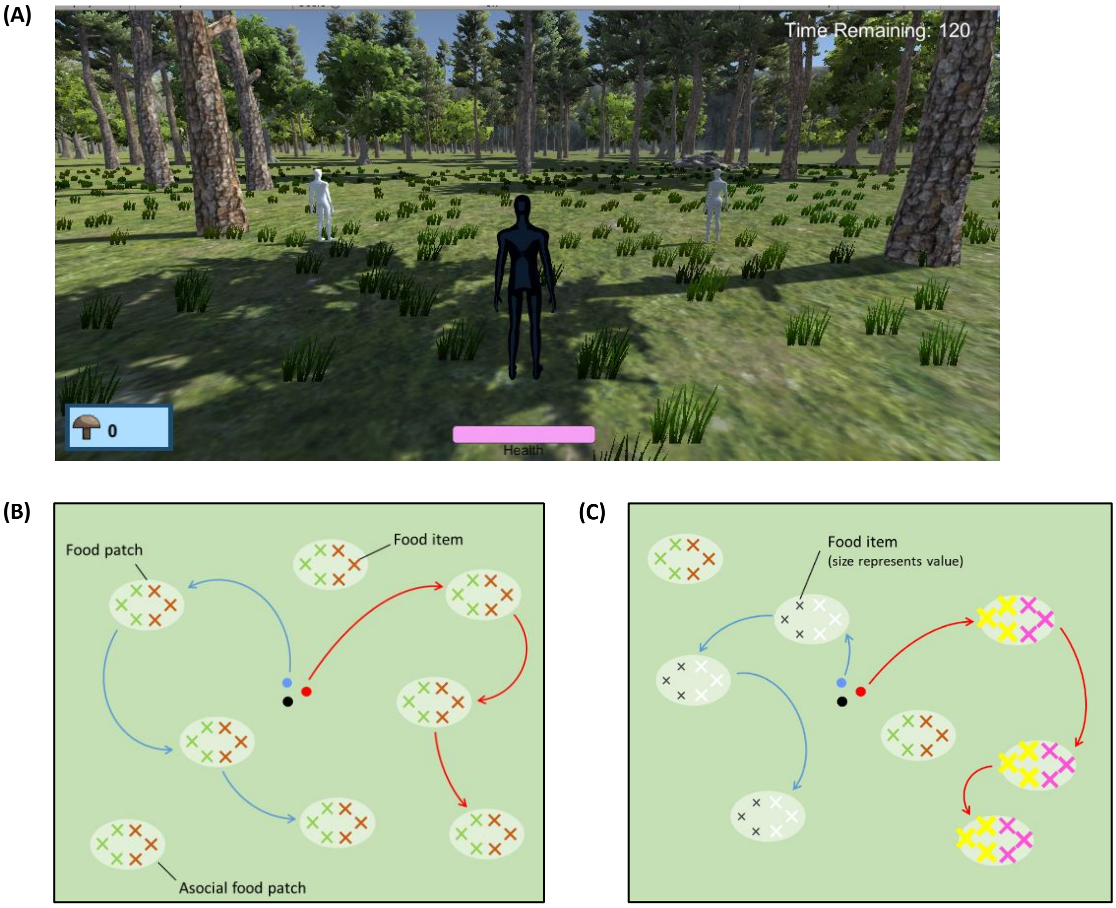

Figure 5.3. The foraging task. **(A)** In-game representation. Participants control their player to explore a large environment in search of patches of food. Demonstrator AIs convey social information about food patches by visiting them. In this example, a male and female demonstrator AI display this information. Participants are given 200 seconds to explore the environment. The remaining time is shown at the top right of the screen. On the bottom left of the screen, participants can see their current number of food items collected. At the bottom middle of the screen, participants are shown their remaining health, which depletes when they collect poisonous food. **(B-C)** Schematics of the task. The black circle represents the player, blue and red circles represent demonstrator AIs, light green areas represent food patches, different coloured crosses represent different food types (and their size represents their nutritional value) and red and blue arrows represent the food patch choices made by the demonstrators. Each set of demonstrator AIs visits three of the eight possible food patches and eats only one food type from it. Two 'asocial' food patches are not visited by any demonstrator. **(B)** In the 'Same Rewards' group, all food items have the same nutritional value. **(C)** In the 'Different Rewards' group, different food types have different nutritional values. Demonstrator A visits the three food patches containing the two most profitable food types and eats only the most profitable of these. Demonstrator B visits the food patches containing the two least profitable food types, but eats only the most profitable of these.

For the Same Rewards group, all food patches contained the same two food types, each of which had the same nutritional value of +1 (Figure 5.3B). For the Different Rewards group, each food patch contained different food types with different nutritional values (Figure 5.3C). The three food patches visited by demonstrator A contained two food types with the highest nutritional values, +5 and +3. The three food patches visited by demonstrator B contained two food types with the lowest nutritional values, +1 and -1. The latter was a poisonous food type which depleted the player's health and food score. In each case, the demonstrator only 'ate' the highest-value food type in their visited patches. The remaining two food patches that were visited by no demonstrators contained two food types, both with nutritional values of +1. Thus, demonstrator choices were arranged in such a way that copying the food patch choice of the best demonstrator would result in the most profitable food patches being found, and copying the exact food type preferences of demonstrators would result in the most nutritious foods being collected and poisonous foods being avoided. Here, I report findings for participant food patch choice only. For further details and analyses on specific food type preferences, please refer to the Supplementary Material (Tables 5.S7-S8; Figure 5.S2).

Data collection and preparation. Each time the player or one of the demonstrators entered a food patch, the location and time of the visit was logged. A player was considered have copied a demonstrator's food patch choice if they entered a food patch within 20 seconds before or after that demonstrator had entered the same food patch. This time window gave the player enough time to follow a distant demonstrator into a food patch and also gave the demonstrator enough time to catch up if the player had overtaken them *en route* to the food patch. If a player entered a food patch that was not visited by any demonstrators within this time window, this was considered an asocial food patch choice. For each participant, the total number of times each demonstrator was copied and the total number of times an asocial decision was made were calculated.

5.3.7. Post-study questionnaire

After the experiment, participants completed a post-study questionnaire. This questionnaire was used to gather information about individual characteristics that may influence social information use, including age and gender. As previous research has indicated a correlation between social information use and aggression levels (e.g. Chapter 3; Bandura, 1961), I also obtained self-assessed aggression scores for each participant, using Bryant and Smith's (2001) aggression questionnaire, to investigate whether aggression levels influenced the social information use in humans. Participants were given twelve statements (from Bryant and Smith, 2001) and asked to rate each on a six-point scale from 'Not at all characteristic of me' to 'Very much characteristic of me'. Statements related to different types of aggression (physical aggression, verbal aggression, anger and hostility) and were given in the randomised order suggested by Bryant and Smith (2001). I also considered that a participant's tendency to play video games may influence their general behaviour within VERSE – e.g. those who play video games often may have a tendency to be more exploratory. Participants were therefore asked how often they played video games in their everyday lives (on a 5-point Likert scale from 'never' to 'daily') and whether they found the game used in the experiment easy to control (yes/no).

5.3.8. Statistical analysis

All statistical analyses were conducted in R (v.4.0.4) (R Core Team, 2022). Using the data on the number of times each demonstrator and no demonstrator were copied for each task, a series of binomial Generalised Linear Models (GLMs) with a logit-link function were used to model the tendency of participants to favour certain types of learning over others. Unless stated otherwise, I used data from the Same Rewards group in order to model general social learning biases, irrespective of demonstrator success or any differences in payoff. Due to the large number of models tested for each hypothesis, p-values were corrected for multiple comparisons using the false discovery rate (FDR) method (Benjamini and Hochberg, 1995; Pike, 2011) via the *p.adjust* function in R (R Core Team, 2022). I tested several hypotheses concerning participants' use of social information within my environments, as detailed below.

(i) Do individuals show a preference towards learning socially or asocially?

Firstly, I used binomial GLMs to model the tendency of participants to learn socially (copy any demonstrator) or asocially (copy no demonstrator). This was modelled in two ways – first, as the tendency of participants to favour copying a single demonstrator over making an alternative, asocial decision in the *Soc/Asoc* condition and, second, as the tendency of participants to favour copying either demonstrator over making an independent choice across all demonstrator conditions. The latter was modelled for the Route Choice and Foraging tasks only, as the Container task permitted only binary choices that, when two demonstrators were present in the environment, did not allow participants to make decisions completely independently of demonstrator choice. This method was applied to data from the Same and Different Rewards groups to establish how variation in rewards influenced social information use.

(ii) Is the preference for social/asocial learning "adaptive" in the Route Choice and Foraging environments?

Secondly, based on the results of the above models, I asked whether participants' overall preference (if any) towards social versus asocial learning was beneficial within these virtual environments. The following analysis was conducted only for the Route Choice and Foraging tasks, i.e. the tasks in which participants had the freedom to choose their own solutions. The Container task is not included because it constrained participants to choosing one of two outcomes, each of which was equally profitable for participants in the Same Rewards group. For each task, I split participants into two groups – those who tended to learn socially (i.e. copied a demonstrator >50% of the time) and those who tended to learn asocially (i.e. copied a demonstrator <50% of the time) across all demonstrator conditions. I then compared the average success (measured as final food scores or final remaining energy values) of largely social versus largely asocial learners across all demonstrator conditions. Since scores could not always be transformed into a Normal distribution, Mann-Whitney U tests were used to determine whether one group was significantly more successful than the other.

(iii) Do participants vary in their use of social information?

Thirdly, based on previous research which has suggested that some individuals are mainly asocial learners while others are mainly social learners (Efferson *et al.,* 2008; Toelch *et al.,* 2014; Miu *et al.,* 2020) I investigated whether participants in the Same Rewards group varied in their reliance on social learning. I used a series of Spearman's rank-order correlation tests to determine whether participants were consistent in their use of social information across tasks – i.e. whether certain individuals could be categorised based on their overall reliance on social information across different contexts. Specifically, I obtained pairwise correlation measures for the proportion of times each participant learned socially within the *Soc/Asoc* demonstrator condition for all three tasks, and across all demonstrator conditions for the Route Choice and Foraging tasks.

(iv) When learning socially, do individuals display innate biases towards learning from specific types of demonstrators, irrespective of demonstrator success?

Fourthly, to investigate general social learning biases towards demonstrators with particular characteristics, binomial GLMs were used to model likelihood that participants in the Same Rewards group copied one demonstrator over the other in the *Dom/Sub, Three/One, Male/Female* and *Large/Small* demonstrator conditions. Since all demonstrators in the Same Rewards group displayed equally profitable behaviours, any biases towards copying particular demonstrators could not be due to differences in demonstrator success.

It is worth noting here that AIs were categorised based almost entirely on physical differences, and that each participant may have perceived these differences in different ways. For example, gender perceptions – which are culturally influenced – may not necessarily align with physical sex differences (although the pre-study questionnaire revealed that, on this occasion, participants unanimously identified the 'male' AI as male and the 'female' AI as female based on physical differences alone; Supplementary Material, Tables 5.S4-S5). Here, I use the term 'sex' when describing any biases toward AIs in the *Male/Female* demonstrator condition. The rationale for this choice of term is that I am interested in larger scale evolutionary patterns of sex bias in social learning. However, I recognise that in the context of humans there will be a considerable influence of social gender norms on those sex biases, such that the two are very difficult to disentangle. It should therefore be emphasised that this part of the experiment focussed on whether general biases towards certain categories of demonstrator – as defined by physical and, in the case of the dominant/subordinate pairing, behavioural differences – exist within the study group, rather than the underlying psychological processes dictating such biases.

(v) Do individuals preferentially copy more successful demonstrators?

Finally, I investigated whether participants were more likely to copy more successful demonstrators, beyond any innate preferences for those with particular characteristics. To do this, I combined data from the Same Rewards and Different Rewards groups and used binomial GLMs to model the tendency of participants to copy demonstrator A over demonstrator B across the *Dom/Sub, Three/One, Male/Female* and *Large/Small* conditions, with reward group as a predictor. In other words, I analysed whether participants copied demonstrator A significantly more when it displayed more profitable behaviours than demonstrator B, compared to when both demonstrators used equally profitable behaviours. An ANOVA test was then used to establish whether the model that included reward group as a predictor provided a better fit to the data than a corresponding null model.

For hypotheses *i, iv* and *v*, I additionally tested whether participants' individual characteristics (age, gender, aggression, etc) influenced their choices by running a series of binomial GLMs for each hypothesis, as described in the main analysis but with each individual characteristic added as predictors. The results of these additional analyses revealed no consistent or clear pattern. The results and further details on the analysis of individual characteristics are therefore reported in the Supplementary Material (Tables 5.S11-S13).

5.4. Results

(i) Do individuals show a preference towards learning socially or asocially?

In the *Soc/Asoc* demonstrator condition, where a single AI demonstrated one option and all other options remained undemonstrated, participants were equally likely to learn socially as asocially in the Container (50.0% of all learning events social) and Route Choice (47.1% social) tasks, but were significantly less likely to learn socially than asocially in the Foraging task, with only 21.4% of learning events involving copying others, when demonstrators displayed equally profitable solutions (i.e. in the Same Rewards group) (Figure 5.4A). This result held both in their initial responses and overall across all choices made (Table 5.2). In treatment conditions where multiple options were demonstrated by different AIs, participants still had the option to ignore all social information in the Route Choice and Foraging (but not the Container) tasks. Taken across all demonstrator conditions, social learning accounted for an estimated 41.6% of learning events in the Route Choice task and 33.2% of learning events in the Foraging task (Figure 5.4B) – a statistically significant preference for asocial learning in both cases (Table 5.2). In other words, across the duration of the experiment, participants generally chose to find their own route through the forest and visit food patches independently of demonstrators. Therefore, participants appeared to display a general bias towards learning asocially (e.g. through independent exploration of environments) rather than socially. Interestingly, in scenarios where rewards varied (i.e. in the Different Rewards group), there was an increased reliance on social learning compared to scenarios where rewards were equal. This resulted in a general preference towards social learning in the Container (71.8% social in the *Soc/Asoc* condition) and Route Choice (56.6% social across all demonstrator conditions) tasks, although a preference for asocial learning remained in the Foraging task (41.3% social across all demonstrator conditions) (Figure 5.4C-D) (Supplementary Material, Table 5.S6).

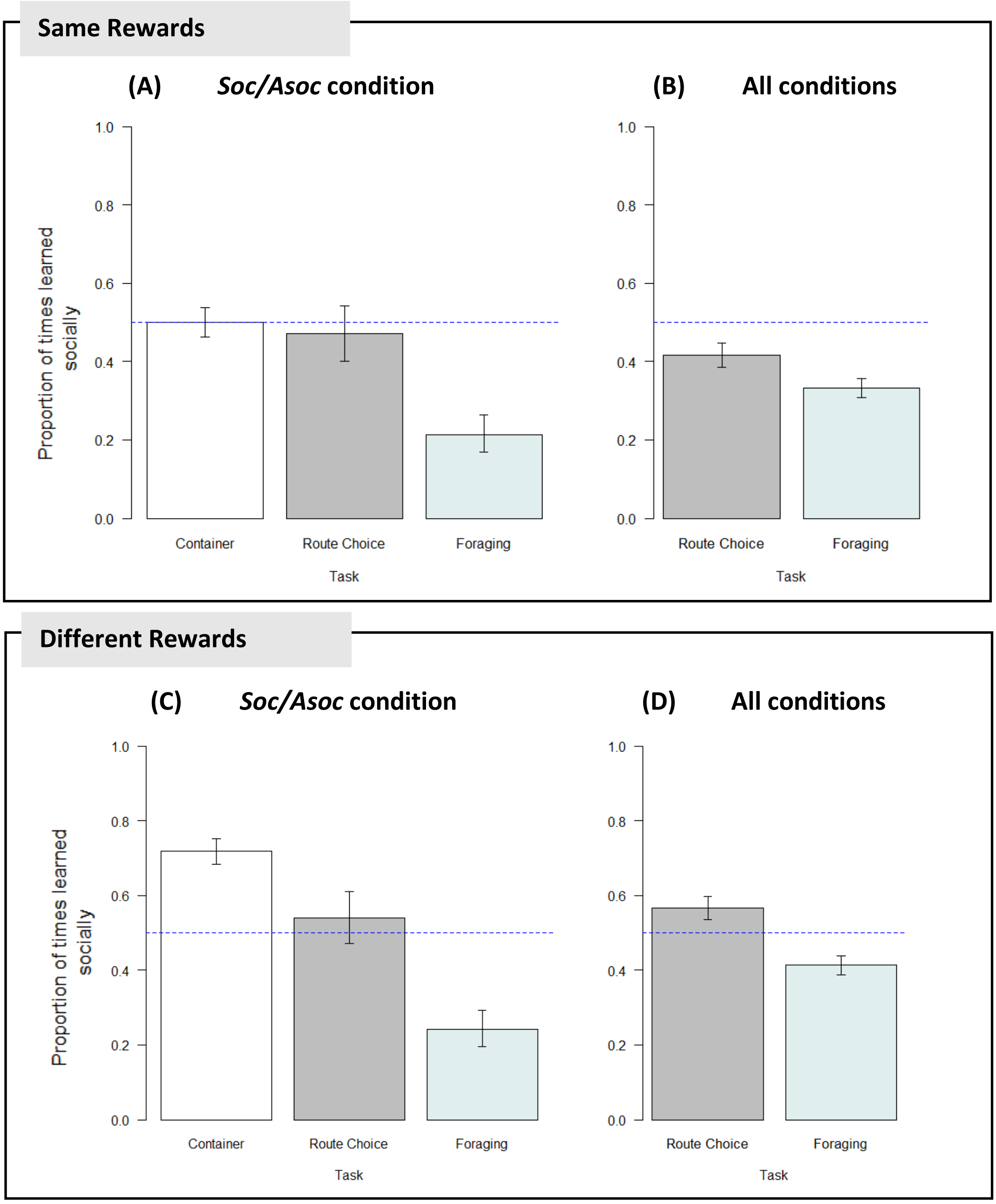

Figure 5.4. The proportion of times participants learned socially (rather than asocially) across three tasks, in **(A-B)** in scenarios where demonstrators displayed equally profitable behaviours, and **(C-D)** in scenarios where demonstrated behaviours received varying rewards. **(A, C)** In the *Soc/Asoc* demonstrator condition, only one option was demonstrated, thus social learning involved following the demonstrated option while asocial learning involved choosing an alternative, undemonstrated option. **(B, D)** Combined across all demonstrator conditions, for the Route Choice and Foraging tasks only. In this case, social learning involved choosing one of the demonstrated options and asocial learning involved choosing an option that

was not demonstrated (e.g. choosing a route that was different to both demonstrators). Error bars represent Clopper-Pearson 95% confidence intervals. Horizontal reference line (dashed blue) is at 0.5 and indicates equal amounts of social and asocial learning occurred.

(ii) Is the preference for social/asocial learning “adaptive” in the Route Choice and Foraging environments?

In section (*i*)*,* I demonstrated that participants in the Same Rewards group showed a general preference for learning asocially. When summed across all demonstrator conditions, participants in the Same Rewards group who favoured asocial learning, on average, completed the Route Choice task with significantly more energy remaining (social score: 73.3%; asocial score: 76.7%; Mann-Whitney U test; $U(1) = 191$, $p < 0.001$) and collected significantly more food in the Foraging tasks (social score: 35.0%; asocial score: 41.2%; Mann-Whitney U test; $U(1) = 213$, $p = 0.042$) than those who favoured social learning (Figure 5.5A-B). Thus, a preference for asocial learning did appear to be profitable. Results were qualitatively similar when the same analysis was carried out on data from the *Soc/Asoc* demonstrator condition only (Supplementary Material, Figure 5.S1). However, the adaptive value of favouring asocial learning was degraded when rewards (and demonstrator success) varied – in the Different Rewards group, participants tended to be equally successful regardless of whether they favoured social or asocial learning in both the Route Choice (social score: 74.5%; asocial score: 74.7%; Mann-Whitney U test; $U(1) = 498$, $p= 0.402$) and Foraging tasks (social: 43.4%; asocial: 40.2%; Mann-Whitney U test; $U(1) = 652$, $p = 0.221$) (Figure 5.5C-D). This coincided with the general drop in reliance on asocial learning, described above.

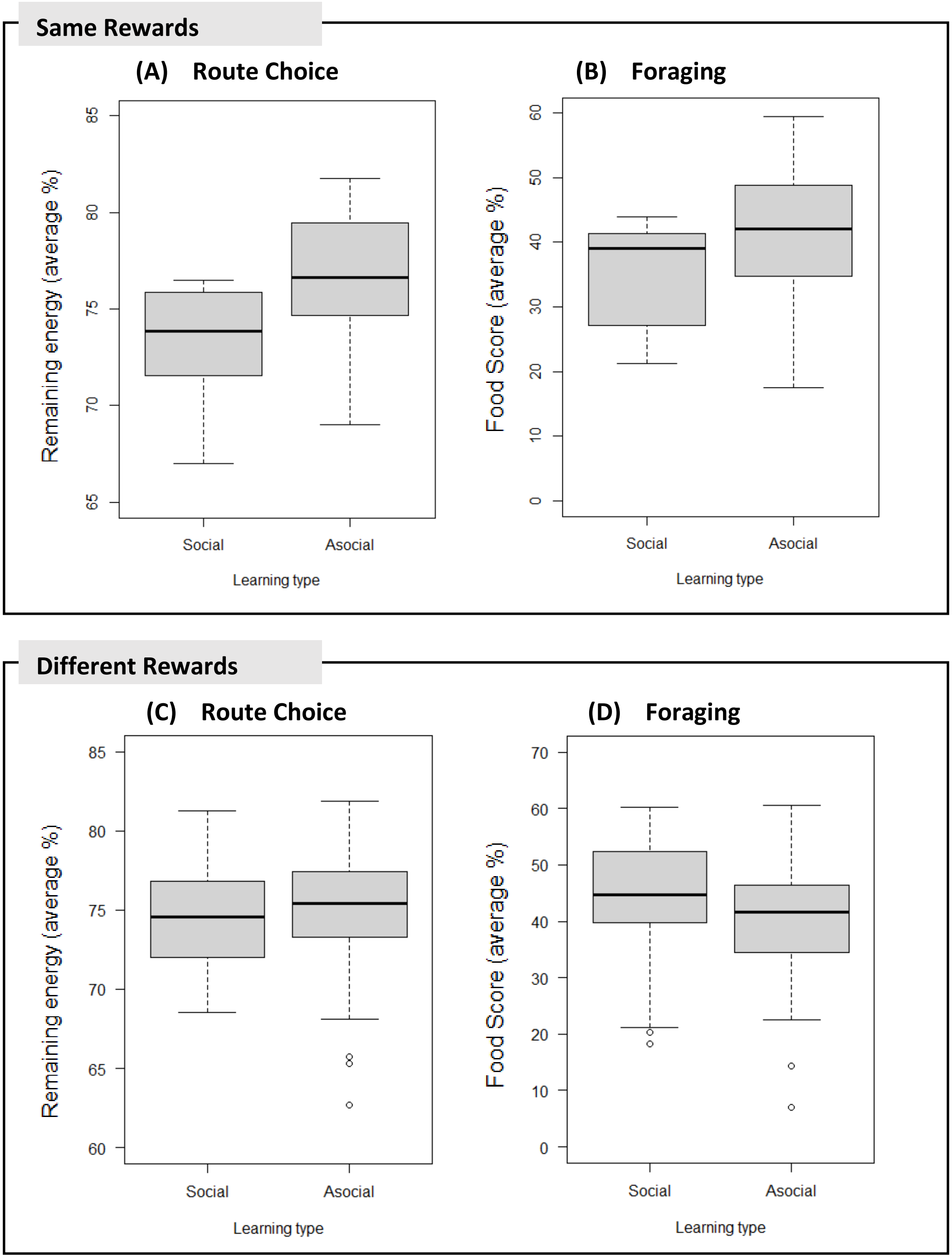

Figure 5.5. The average success rates of participants who favoured social and asocial learning, across all demonstrator conditions. The top box shows the success rates in **(A)** the Route Choice task, measured as the average percentage of energy remaining, and **(B)** the Foraging task, measured as the average food score as a percentage of the maximum possible food score, when all demonstrators displayed behaviours of equal payoff. The bottom box shows the success rates in **(C)** the Route Choice task and **(D)** the Foraging task when different demonstrated behaviours received different payoffs. Thick horizontal lines represent medians and boxes indicate the interquartile range. Whiskers extend to 1.5x the interquartile range.

Table 5.2. Intercept estimates, standard error, z-values and p-values for binomial GLMs modelling the likelihood of participants learning socially over asocially in the *Soc/Asoc* demonstrator condition and across all demonstrator conditions, during each of the three tasks. A significant positive term indicates that participants were more likely to learn socially, while a significant negative intercept term indicates that participants were more likely to learn asocially. Analyses were conducted using data on (i) all choices made and (ii) just the initial choices made during each demonstrator condition. P-values are adjusted for multiple comparisons using false discovery rates. Significant p-values (< 0.05) are highlighted in bold.

		Container				Route Choice				Foraging			
	Condition	Intercept	Std. Error	z	p	Intercept	Std. Error	z	p	Intercept	Std. Error	z	p
All choices	*Soc/Asoc*	0.000	0.076	0	1	-0.118	0.140	-0.840	0.446	-1.301	0.138	-9.439	**<0.001**
	All	-	-	-	-	-0.339	0.063	-5.367	**<0.001**	-0.700	0.054	-12.900	**<0.001**
Initial choices	*Soc/Asoc*	0.465	0.246	1.895	0.096	-0.357	0.246	-1.448	0.185	-0.847	0.261	-3.249	**0.003**
	All	-	-	-	-	-0.348	0.110	-3.170	**0.004**	-0.160	0.107	-1.495	0.185

Table 5.3. Intercept estimates, standard error, z-values and p-values for binomial GLMs modelling the likelihood of participants copying the choices of demonstrator A over demonstrator B when learning socially, across only the demonstrator conditions where two demonstrators were available, during each of the three tasks. A significant positive intercept term indicates that the participants were more likely to copy demonstrator A, while a significant negative term indicates that participants were more likely copy demonstrator B. Analyses were conducted using data on (i) all choices made and (ii) just the initial choices made during each demonstrator condition. P-values are adjusted for multiple comparisons using false discovery rates. Significant p-values (< 0.05) are highlighted in bold.

		Container				Route Choice				Foraging			
	Condition	Intercept	Std. Error	z	p	Intercept	Std. Error	z	p	Intercept	Std. Error	z	p
All choices	*Dom/Sub*	0.166	0.076	2.190	0.077	0.381	0.245	1.556	0.227	0.511	0.220	2.320	0.069
	Three/One	1.046	0.086	12.140	**<0.001**	1.235	0.284	4.347	**<0.001**	0.490	0.181	2.702	**0.034**
	Male/Female	0.006	0.076	0.076	0.981	-0.249	0.214	-1.163	0.420	0.497	0.189	2.631	**0.036**
	Large/Small	-0.023	0.076	-0.302	0.922	0.058	0.197	0.296	0.922	-0.019	0.195	-0.098	0.981
Initial choices	*Dom/Sub*	0.465	0.246	1.895	0.139	0.647	0.372	1.737	0.178	0.916	0.418	2.190	0.077
	Three/One	0.715	0.255	2.808	**0.030**	2.526	0.735	3.437	**0.005**	0.201	0.318	0.631	0.745
	Male/Female	-0.114	0.239	-0.478	0.844	-0.636	0.412	-1.543	0.227	0	0.324	0	1
	Large/Small	-0.057	0.239	-0.239	0.927	0.348	0.377	0.924	0.570	0.236	0.345	0.684	0.741

(iii) Did participants vary in their use of social information?

In section (*i*), I explored whether social or asocial learning was predominant in the different tasks. Here, I test whether individual participants were consistent in their use of social information across tasks. For each task, participants in the Same Rewards group varied substantially in the proportion of times they chose to learn socially. This ranged from a complete ignorance of to a complete reliance on social information, depending on the task and participant in question. In the *Soc/Asoc* condition, the proportion of times a participant copied the single AI ranged from 0 to 1 in all three tasks (Container average: 0.5 ± 0.21 SD; Route Choice average: 0.47 ± 0.38 SD; Foraging task average: 0.22 ± 0.29 SD). There was no significant correlation between a participant's tendency to copy versus ignore the single AI across the three tasks in the *Soc/Asoc* condition (Spearman's rank tests: Container—Route, $r_s(65) = -0.02$; $p = 0.87$; Container—Foraging, $r_s(67) = -0.03$; $p = 0.81$; Route—Foraging, $r_s(66) = 0.17$; $p = 0.18$) (Figure 5.6A-C). When taken across all demonstrator conditions, the proportion of times a participant copied either demonstrator rather than opting for an alternative, asocial option ranged from 0.07 to 1 for the Route Choice task (average: 0.41 ± 0.27 SD) and from 0 to 0.83 for the Foraging task (average: 0.34 ± 0.20 SD). There was a moderate, statistically significant correlation in each participant's tendency to copy rather than find an alternative solution across the Route Choice and Foraging tasks when data was combined across demonstrator conditions (Spearman's rank test: $r_s(67) = 0.30$; $p = 0.01$) (Figure 5.6D). Note that combining participant choices across all demonstrator conditions may give a more precise measure of social learning tendency due to the larger number of replicates the data is taken over (5 replicates for each participant when taken across all demonstrator conditions, compared to 1 replicate for the *Soc/Asoc* condition only). Overall, this suggests that participants displayed some consistency in their inclination towards using social information across different tasks and demonstrator conditions, but not to the extent that they could be categorised as solely social or asocial learners.

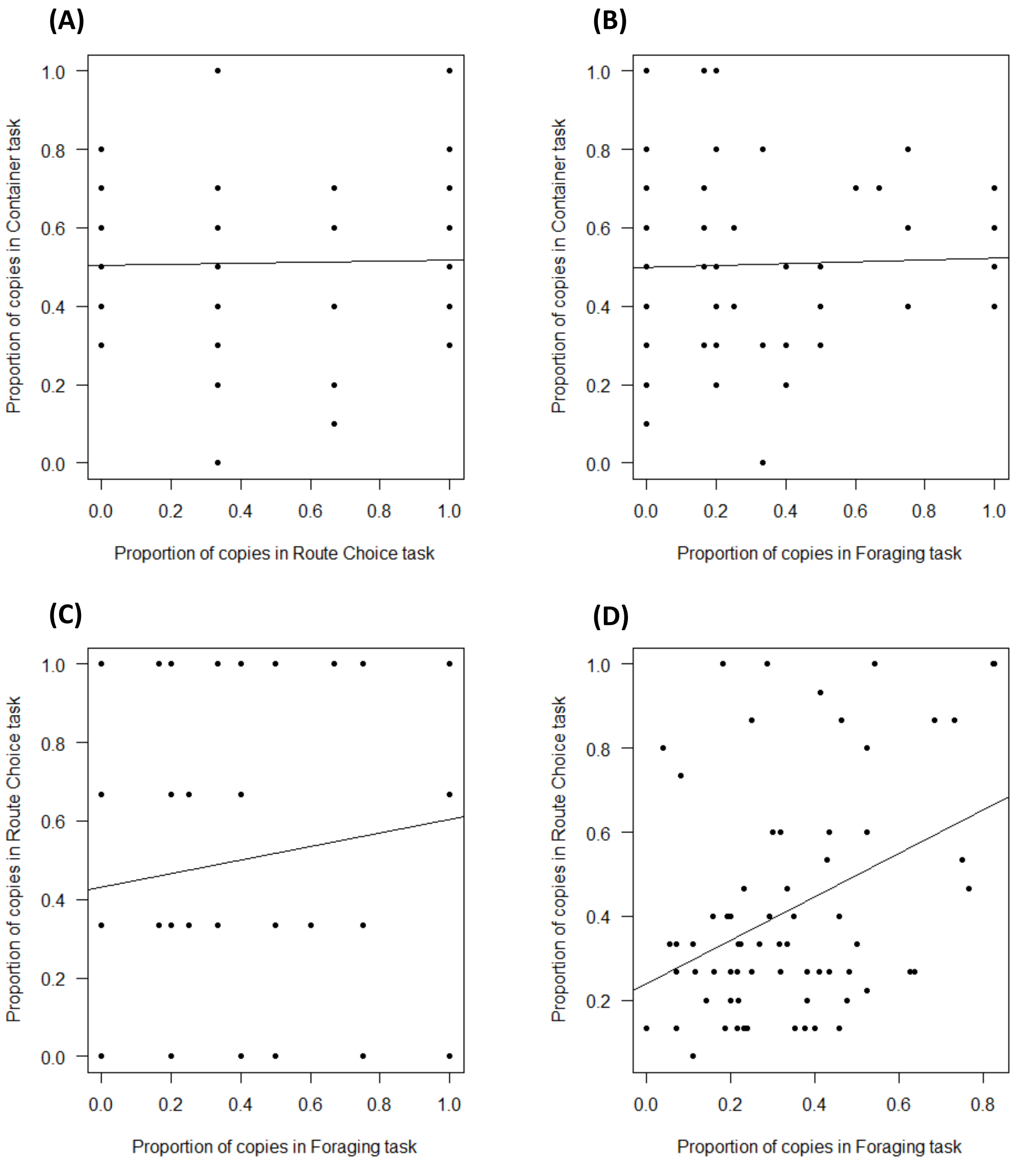

Figure 5.6. Correlations between the proportion of times each participant used social information in each pair of tasks. **(A-C)** For the *Soc/Asoc* condition only (i.e. when only one demonstrator was present and all other choices were considered asocial learning): **(A)** Container ~ Route Choice. **(B)** Container ~ Foraging. **(C)** Route Choice ~ Foraging. **(D)** Across all demonstrator conditions (i.e. the proportion of times any available demonstrator was copied as opposed to making a completely independent decision): Route Choice ~ Foraging. In all cases, each data point represents an individual participant. Regression lines are also shown.

(iv) When learning socially, do individuals display innate biases towards learning from specific types of demonstrators, irrespective of demonstrator success?

Dominance bias. When both dominant and subordinate demonstrators were equally successful, participants copied the dominant demonstrator more often than the subordinate in the Container (54.1% of social learning events copied dominant), Route Choice (59.4% dominant) and Foraging (62.5% dominant) tasks (Figure 5.7A). After FDR corrections, this bias towards copying the dominant demonstrator was only statistically significant in the Foraging task (Table 5.3). Participants also demonstrated a significant initial bias towards copying the dominant demonstrator in the Foraging task (Table 5.3).

Frequency bias. Participants copied the majority more often than the minority in the Container (74.0% majority), Route Choice (77.5% majority) and Foraging (62.0% majority) tasks (Figure 5.7B). This bias towards the majority was statistically significant across all tasks (Table 5.3). Participants also displayed a significant initial bias towards copying the majority in the Container and Route Choice tasks (Table 5.3).

Sex bias. Participants did not display any sex-based bias in the Container task (50.1% male). The female demonstrator was copied more often in the Route Choice task (56.2% female) but this was not statistically significant (Table 5.3). The male demonstrator, however, was copied significantly more often in the Foraging task (62.2% male) (Table 5.3) (Figure 5.7C).

Size bias. Participants did not display any significant bias towards demonstrators of different sizes in either the Container (49.4% large), Route Choice (51.5% large) or Foraging (49.5% large) tasks (Table 5.3; Figure 5.7D).

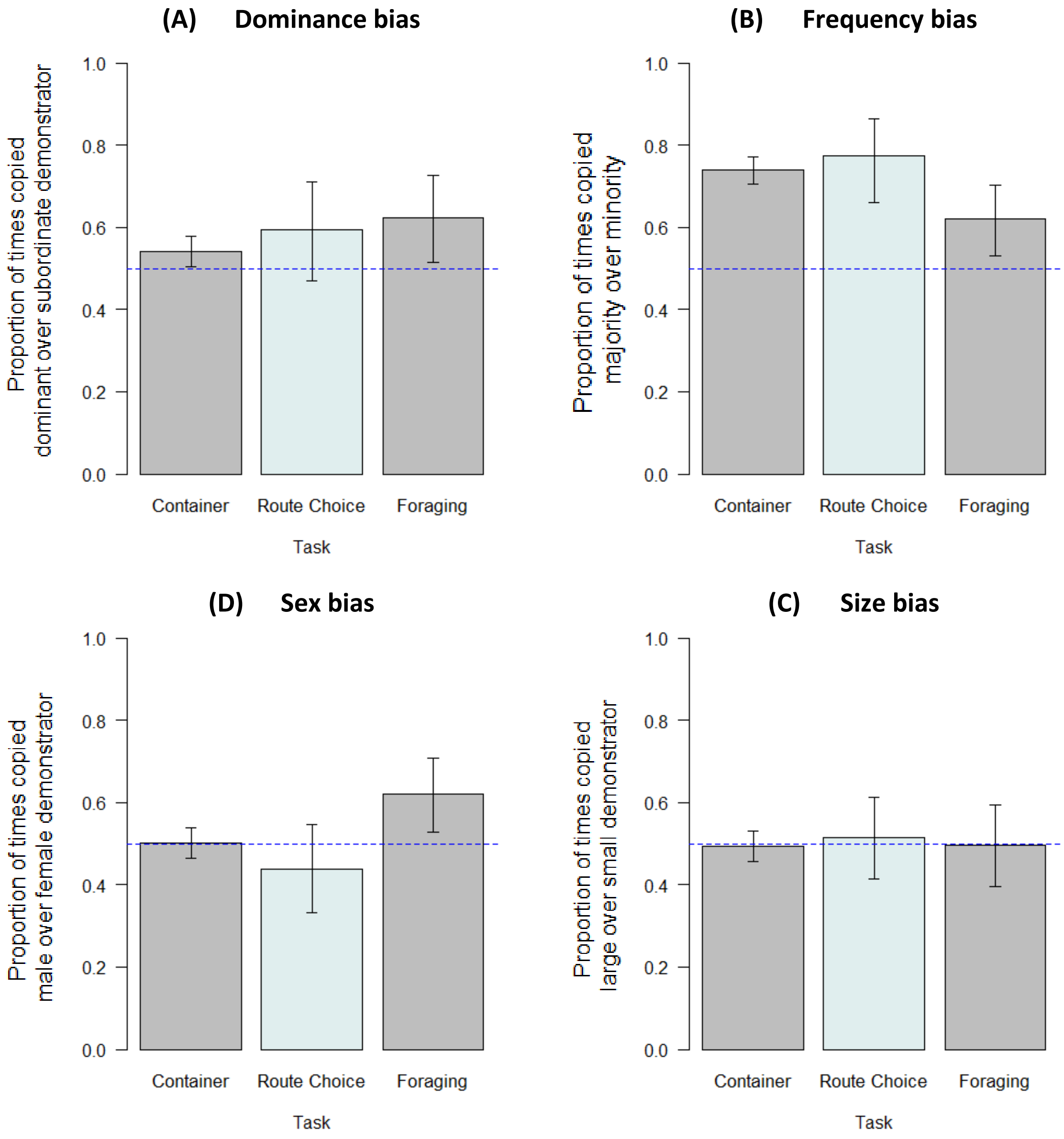

Figure 5.7. Preferences based on demonstrator characteristics. The proportion of times participants copied **(A)** the dominant over the subordinate demonstrator, **(B)** the majority (three demonstrators) over the minority (one demonstrator), **(C)** the male over the female demonstrator and **(D)** the large over the small demonstrator, during the Container, Route Choice and Foraging tasks. In all cases, each demonstrator displayed equally profitable behaviours. Error bars represent Clopper-Pearson 95% confidence intervals. Horizontal reference line (dashed blue) is at 0.5 and indicates no preference for either demonstrator.

(v) Do individuals preferentially copy more successful demonstrators?

When learning socially, participants in the Different Rewards group displayed a strong, statistically significant bias towards copying the more successful demonstrator (demonstrator A) over the less successful demonstrator (demonstrator B) in the Container (75.7% of social learning events copied the successful demonstrator), Route Choice (74.2% successful) and Foraging (72.8% successful) tasks (Table 5.4; Figure 5.8). This pattern was consistent across almost all demonstrator condition/task combinations (Supplementary Material, Table 5.S9), suggesting that a preference for copying the most successful demonstrators was not influenced by context or the specific demonstrators involved.

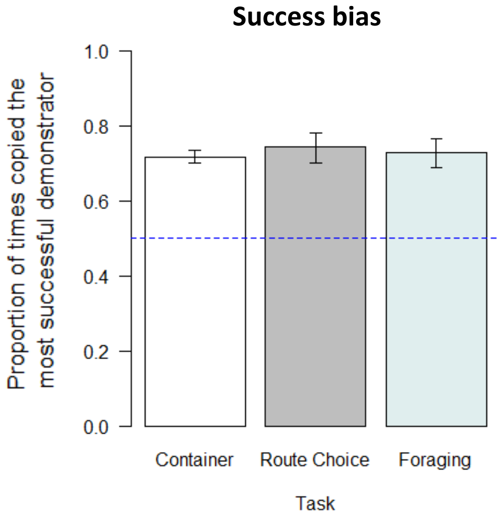

Figure 5.8. The proportion of times participants copied the most successful over the least successful demonstrator (i.e. the proportion of times demonstrator A was copied over demonstrator B in scenarios where rewards varied) across the three tasks. Data is collated across the *Dom/Sub, Three/One, Male/Female* and *Large/Small* demonstrator conditions, i.e. conditions in which two demonstrators were present. Error bars represent Clopper-Pearson 95% confidence intervals. Horizontal reference line (dashed blue) is at 0.5 and indicates no preference for either demonstrator.

As demonstrators A and B varied in their characteristics – which, as discussed above, influenced their likelihood of being copied – any innate preferences for the demonstrators themselves may have contributed to participants' general inclination to copy the more successful demonstrators. For example, the tendency of participants in the Different Rewards group to copy the majority in the *Three/One* condition (Supplementary Material, Table 5.S9) may have been because the majority displayed more profitable behaviours, but may have also been influenced by an innate bias towards copying the majority, regardless of direct payoffs, as discussed above. Indeed, demonstrator A was, on average, copied more often even in the Same Rewards group, when they did not display more profitable behaviours (Supplementary Material, Figure 5.S3) – although this tendency was less pronounced than when demonstrator success did vary.

To investigate success-based biases more thoroughly, I therefore compared participants' tendency to copy demonstrator A over demonstrator B in the Different Rewards group to that of participants in the Same Rewards group. Demonstrator A was significantly more likely to be copied in the Different Rewards group (i.e. when they displayed more profitable behaviours) than the Same Rewards group (i.e. when their behaviours were no more profitable than the alternative demonstrator) (Table 5.4) and GLMs predicting the likelihood of demonstrator A being copied performed significantly better when reward group was included as an independent factor (Table 5.S10). In other words, participants' tendency to copy particular demonstrators was significantly enhanced beyond any innate preferences when those demonstrators displayed higher-payoff behaviours. This strongly suggests that participants were strategic in their social information use, favouring the behaviours of more successful demonstrators when learning socially.

Table 5.4. Parameter estimates, standard error, z-values and p-values for binomial GLMs modelling the likelihood that participants copied demonstrator A over demonstrator B in scenarios where rewards were either the same or different, as measured by the RewardGroup factor, across the three tasks. The intercept is taken as RewardGroup = Same. The estimate for the RewardGroup (Different) parameter therefore represents the increase in likelihood of copying demonstrator A when demonstrator A was more successful than demonstrator B. Data was collated across the *Dom/Sub, Three/One, Male/Female* and *Large/Small* demonstrator conditions. P-values are adjusted for multiple comparisons using false discovery rates. Significant p-values (< 0.05) are highlighted in bold.

Task	Parameter	Estimate	Std. Error	Z	p
Container	*Intercept*	0.279	0.038	7.309	**<0.001**
	RewardGroup (Different)	0.648	0.057	11.427	**<0.001**
Route Choice	*Intercept*	0.267	0.111	2.408	**0.016**
	RewardGroup (Different)	0.790	0.153	5.163	**<0.001**
Foraging	*Intercept*	0.372	0.097	3.835	**<0.001**
	RewardGroup (Different)	0.612	0.139	4.400	**<0.001**

5.5. Discussion

In this experiment, I have demonstrated a novel approach to studying human social learning behaviour, through the use of specially designed, three-dimensional virtual environments that allow participants to express more natural behaviours, across more realistic scenarios and spatial scales, than is often possible in laboratory conditions. Using this technology, I explored the strategic use of social information by participants completing novel tasks inspired by the animal literature – thus allowing direct generalisations to be made across the human / non-human divide. Overall, I found that participants generally preferred to learn asocially (although reliance on social information did vary between individuals and contexts) and that, in certain environments, asocial learning allowed participants to exploit more profitable, undemonstrated solutions. I also found that participants were strongly biased towards copying the majority over the minority and towards copying more successful demonstrators. Below, I discuss my findings in detail, including how they compare to previous research from more restrictive laboratory experiments and evidence for similarities in social information use across other, unrelated taxa.

Participants displayed a strong overall preference for independent learning.

Perhaps my most striking finding concerned the way in which participants used social versus asocial information. Namely, participants displayed a general preference for learning a task independently rather than learning socially. It is widely accepted that social learning and the development of cultural norms has been paramount to human survival, enabling us, across our evolutionary past, to adapt to many habitats across the globe, beyond what we could have accomplished using individual knowledge alone (Herrmann *et al.,* 2007; Tomasello, 2009; Boyd *et al.*, 2011; Whiten and Erdal, 2012; Marean, 2015). The fact that humans are highly cultural creatures – and culture is, by definition, the product of social transmission of behaviours through a population (Laland and Hoppitt, 2003) – suggests that our decisions are highly influenced by the decisions of those around us. Theoretical analyses also agree that social learning, provided it is strategic, tends to outcompete asocial learning (Rendell *et al.,* 2010; Boyd and Richerson, 1985). Despite this, several empirical studies have demonstrated, in agreement with my own findings, that adult humans are often biased towards using information they have gained independently (Yaniv and Kleinberger, 2000; Eriksson and Strimling, 2009; Weizsäcker, 2010). This has previously been attributed to the relatively simple, two-option tasks used in such studies, which allow participants to be confident enough in their own decisions to avoid the use of social information (Morgan *et al.,* 2012; Muthukrishna *et al.,* 2016). On the contrary, I found that participants demonstrated a general bias towards asocial learning when presented with relatively complex tasks within complex, spatially explicit, three-dimensional environments.

This is comparable to the information use strategies of various species, including birds, fish and ants, which tend to favour independently acquired over social information unless there is a good reason for following others, e.g. asocial information is costly or out of date (Templeton and Giraldeau, 1996; Kendal *et al.,* 2004; van Bergen *et al.,* 2004; Czaczkes *et al.,* 2019). It is important to note, however, that, in many of these studies, individuals are already in possession of asocial information prior to acquiring social information, rather than making a decision to *learn* either socially or asocially, which differs from the methodology used here. It is therefore possible that individuals in these studies are favouring information already in their behavioural repertoire over conflicting social information, rather than favouring asocial learning *per se* – whereas here, I have demonstrated a general bias for exploring and learning independently rather than actively observing and copying others. A general bias for acquiring information independently could additionally suggest hierarchical decision making in the way participants chose to learn, as suggested by Laland (2004) – i.e. participants first decide whether to learn socially or asocially and only if a decision to learn socially is made do they then decide *who* to learn from.

Participants varied, somewhat consistently, in their reliance on social information.

While participants were generally inclined towards learning asocially, I also found substantial inter-individual variation in social information use, which correlated to some degree across different tasks. This could not be attributed to any of the individual characteristics tested here; namely a participant’s age, gender or aggression levels. In line with my findings, previous research on humans typically reports no influence of an individual’s sex on their social information use (Mesoudi *et al.,* 2016) – in contrast with animals such as songbirds and chimpanzees, for which sex-specific social learning has been demonstrated (Aplin *et al.,* 2013; Mesoudi *et al.,* 2016). The influence of age on human social information use, however, is less clear. In traditional hunter-gatherer communities, children show a higher reliance on social information, while adults are more prone to independent learning (Hewlett *et al.*, 2011; Demps *et al.*, 2012). This is comparable to work on other species, including songbirds and otters, which also demonstrate higher rates of social learning in juveniles than adults (Langen, 1996; Aplin *et* *al.,* 2013; Farine *et al.,* 2015*;* Ladds *et al.,* 2017). While I found no obvious influence of age on social information use, it is important to note that the study group used in this experiment were all young adults and thus had a very narrow age range. A high reliance on social learning over an extended juvenile period in humans may result in an extensive behavioural repertoire by the time individuals reach adulthood – which may offer an additional explanation as to why the adult individuals in my study group tended to learn independently. However, Whiten *et al.* (2016) demonstrated that western adults and children were equally likely to imitate a knowledged individual in a real-world situation; thus, the choice of whether to learn socially or asocially – and the influence of age on social information use – may be context specific.

The role of aggression on an individual's use of social information has received little attention in previous studies. Research on birds has demonstrated that aggression is correlated with other individual traits relating to exploratory behaviour, which have been linked to social information use. Specifically, less neophobic, more aggressive birds that explore an environment quickly and with little attention to detail are more likely to copy the behaviour of tutors than their slower, more thorough counterparts (Marchetti and Drent, 2000). Boldness has also been linked to social information use in guppies, but with the opposite result – 'shy' fish were more likely to follow 'bold' fish to a novel feeder (Dyer *et al.,* 2009). In the present study, I found no correlation between human individuals' use of social information or preferences towards particular demonstrators and their score on Bryant and Smith's (2001) aggression scale. While I did not explore the influence of traits such as boldness or exploratory behaviour on social information use in my study, the VERSE system offers a perfect environment for investigating these individual influences in humans. Other individual characteristics have been demonstrated to influence social information use in both the animal and human literature, including developmental stress, reproductive state, past experience (Mesoudi *et al.,* 2016), self-confidence (Morgan *et al.,* 2012), and ethnicity / cultural background (Karunanayake and Nauta, 2004; Corriveau *et al*., 2013, 2017; DiYanni *et al.,* 2015; Van Leeuwen *et al*., 2018). It is therefore possible that some other, untested traits correlated with social information use in my study group – especially as the social learning environments used in this experiment offered a high level of freedom in the way participants could behave, thus allowing plenty of opportunity for factors such as an individual's prior knowledge, motivation and general skill level to aid them in completing their objectives.

Individual variation in social information use has been highlighted in human social learning research before. Toelch and colleagues (2014), for example, demonstrated consistent, context-independent individual differences in reliance on social information. Similarly, Kameda and Nakanishi (2002) found that information producer-scrounger dynamics emerged in groups completing computer-based tasks; Eriksson and Strimling (2009) demonstrated variation in people's exploration of additional options, which was linked to gender and cooperativeness; and Miu (2017) found that individuals demonstrated flexibility in their use of social information when completing a series of computer science problems. Efferson and colleagues (2008) even demonstrated the existence of two distinctly different groups of learners in their study group – 'conformists', who show an exaggerated tendency to follow the majority, and 'mavericks' who ignore social information altogether. In the present study, I did not find evidence that participants could be categorised as explicitly as suggested by Efferson and colleagues, but I did find a correlation in participants' reliance on social information between tasks which was comparable to Toelch and colleagues' results, despite the very different methodologies used.

In addition, as in Miu (2017) and Toelch *et al.* (2014), I found that individuals fell on a continuous spectrum between complete ignorance of and complete reliance on social information and that, despite individual preferences for learning socially or asocially, the vast majority of participants used some combination of socially and asocially acquired information – and thus, seemed to explore both options rather than relying solely on one type of learning. According to Campbell *et al.* (2020), such 'partial copying' plays a potentially important role in adaptive information transfer. Relying too heavily on social information diminishes opportunities to find alternative solutions, while partial copying allows individuals to balance the benefits of exploiting existing solutions and exploring new ones. In addition, flexibility in social information use is thought to be an important driver of the development of cumulative culture (Miu *et al.,* 2020). Empirical work generally considers only when, how and who individuals copy, rather than how much they copy – although there is evidence that human children will incorporate both socially and asocially learned solutions into their repertoire when solving novel puzzles (Wood *et al.,* 2013a). While it was not necessarily my intention to do so, I have demonstrated here that adult humans will combine both socially and asocially acquired information when learning novel, complex tasks in realistic environments. According to Campbell *et al.* (2020), such behaviour at the individual level should allow whole populations to maintain a diversity of possible solutions – including the most optimal solutions – thus offering an adaptive advantage over populations that copy too often or too quickly and so risk becoming fixed on sub-optimal behaviours. Therefore, it may be more important that a range of degrees of social learning exists at the population level to balance innovation and information spread, than that individuals themselves are consistent in their degree of social learning.

Participants altered their reliance on social information depending on the context.

I found that participants' tendency to learn socially varied in several ways depending on the scenario they were faced with. Firstly, participants displayed an increased reliance on asocial learning as the tasks became more complex. This is somewhat surprising – one might expect that, when faced with more complex tasks, it would become more difficult to find solutions independently (e.g. require more random searches of the environment) and so informed demonstrators would become more valuable sources of information. Previous work tends to agree that both human and non-human animals are more prone to copying others when tasks are more difficult (Baron *et al.,* 1996; Laland, 2004; Kendal, Kendal, *et al*., 2009; Morgan *et al.*, 2012) – although this is not the case for all species (e.g. task difficulty does not appear to influence social information use in otters; Ladds *et al.,* 2017). Nevertheless, in scenarios where demonstrators displayed equally profitable behaviours, I found that participants who were prone to learning asocially tended to be more successful, suggesting that a reliance on asocial learning was beneficial even when tasks were complex. I therefore suggest that this pattern of behaviour may not be due to task complexity *per se*, but due to a combination of greater opportunities for asocial learning and increased difficulty in acquiring social information due to spatial factors as task complexity increased.

The tasks used in my study essentially formed a continuum in both spatial scale and the variety of alternative, undemonstrated solutions that could be explored. The Container task involved making simple, binary decisions in a small environment where demonstrators were always in close proximity and where there was little to no opportunity for purely independent decisions to be made. The Route Choice task involved an initial decision in a localised area in the presence of demonstrators and required participants to locate a single end point – but ultimately required navigating longer distances, over which demonstrators quickly moved out of view if they were not closely followed, and offered more flexibility in the sense that participants could deviate from demonstrated paths. The Foraging task, by comparison, required participants to form search patterns across larger landscapes, over which demonstrators quickly became scattered, and offered participants a high level of flexibility in the way the task could be solved, in the sense that they could navigate the environment with complete freedom and could visit any of the food patches, in any order.

Muthukrishna and colleagues (2016) have previously demonstrated that people are more likely to change their decisions in favour of demonstrated solutions as the number of possible options increases, which at first glance appears to contradict my results. However, in Muthukrishna and colleagues' experiment, social information was presented for all options, thus there were no options that could be discovered via purely independent exploration. I have, in contrast, demonstrated that participants will independently explore complex environments in search of more profitable alternative solutions (e.g. shorter routes or undiscovered food patches) than are currently available in the social information pool – which has clear adaptive value if it prevents individuals from becoming fixed on less profitable behaviours by constant copying. In addition, from the Container to the Foraging task, demonstrators became more scattered across larger spatial scales, which may have effectively increased the cost of acquiring social information by making it more difficult to determine what everyone is doing at a particular time. This may have further increased participants' reliance on asocial learning within these larger, more complex environments. Social learning is often assumed to be less costly than asocial learning, however an increase in the cost of acquiring social information reduces its adaptive value (Mesoudi, 2008). Taken together, this would explain the increased reliance on asocial learning as task complexity increased. Due to the restrictions of laboratory conditions that more closely resemble my Container task, previous research has not fully considered the influence of spatial asynchrony of demonstrators on a participant's ability to use social information and I suggest that this may lead to overestimations of human reliance on social information in more realistic scenarios.

I also reported an increase in social learning when rewards and demonstrator success varied compared to scenarios where demonstrated behaviours received equal payoffs. Participants who relied more heavily on social learning were no more successful than largely asocial learners in these scenarios and so there appeared to be no direct benefit to this increase in social learning. Therefore, it may be that participants were instead responding to greater uncertainty about their own independent choices caused by variability in potential rewards. This result is indicative of a number of potential social learning strategies, including *copy-when-uncertain, copy-if-dissatisfied* and – since asocial learning was less profitable and therefore more costly to acquire in terms of time and energy when the environment contained varying payoffs – *copy-when-asocial-learning-is-costly* strategies (Laland, 2004; Boyd and Richerson, 1985). Theoretical analyses predict that individuals will increase their reliance on social information, which is cheaper but less reliable than sampling directly from the environment, when asocial learning is too costly to acquire or when it is difficult to determine the best behaviour to use by oneself – e.g. due to variation in yield (Boyd and Richerson, 1985) or delayed rewards (Caldwell and Eve, 2014) – which appears consistent with the results reported here.

Taken together, my findings indicate that a person's tendency to favour social over asocial learning was dependent on a trade-off between (a) the reliability / predictability of information gathered asocially, (b) the additional opportunities provided by asocial learning and (c) the difficulty in acquiring social information. Specifically, participants only displayed a bias towards learning socially when social information was relatively easy to acquire *and* when the benefits of learning asocially were less pronounced, otherwise an inclination towards independent learning was found. In other words, participants appeared to be adaptively weighting their perceived importance of social information – sampling directly from the environment rather than gaining potentially outdated information from others is ultimately going to be more profitable, provided this information is reliable, but social information may act as a cheap alternative if it is relatively easy to acquire. In line with each of these interpretations, previous studies have demonstrated that (a) people increase their use of social information when uncertain about their own choices (Morgan *et al.*, 2012; Toelch *et al.,* 2014), (b) allowing independent interaction with a task prior to receiving social information results in children exploring a greater combination of solutions to a task (Wood *et al.,* 2013a) and (c) explicit, numerical costs associated with gaining information independently (Kameda and Nakanishi, 2002; Mesoudi and O'Brien, 2008; Morgan *et al.*, 2012) or socially (Mesoudi, 2008) increases a participant's reliance on the alternative.

I have additionally demonstrated that participants will respond in such a way not only to explicit costs of using information (as is used in most studies), but also to indirect costs, such as difficulties in obtaining social information due to spatial asynchrony of demonstrators or variation in payoffs rendering independent learning less profitable and thus more costly to implement. My findings are surprisingly comparable to work on starlings (*Sturnus vulgaris*) and nine-spined sticklebacks (*Pungitius pungitius*). Evidence from both species suggest that individuals prefer to tackle foraging problems independently, but will weight their use of social and asocial information depending on their reliability and how difficult they are to acquire (Templeton and Giraldeau, 1996; van Bergen *et al.*, 2004). Thus, this is an excellent example of how studying human behaviour using the VERSE system can allow direct comparisons to the animal literature through the creation of more realistic, spatially complex social learning environments.

> *Demonstrator physical and/or behavioural characteristics had little influence on their likelihood of being copied.*

Learning from individuals with particular physical and/or behavioural characteristics may be adaptive if those characteristics can be used as an indicator of that individual's likelihood of success. An individual’s size, for example, may be an indicator of its ability to gain nutrients and avoid toxins, thus making larger individuals worth copying. Size-based social learning has been demonstrated in nine-spined sticklebacks (Duffy *et al.*, 2009) and there is some evidence that taller human individuals have more social influence and are perceived as stronger leaders (Blaker *et al.,* 2013). However, I found no evidence to suggest that, in the contexts explored here, participants were any more likely to copy large over small demonstrators. A person’s height may also be linked to their perceived dominance (Lourenco *et al.,* 2016) and it may be this that increases their influence over others, particularly if an individual’s dominance status can be linked to their general success and thus their likelihood of using profitable behaviours.

A tendency to copy dominant individuals has been demonstrated in some species, most notably domestic hens (*Gallus gallus domesticus*) (Nicol and Pope, 1994; Nicol and Pope, 1999) and chimpanzees (*Pan troglodytes*) (Kendal *et al.,* 2015); however in some cases it is unclear whether this is due to a genuine observer bias or whether dominant individuals simply restrict subordinates’ access to novel task, thus making them less effective as demonstrators (Watson *et al.,* 2017). A study by Wood *et al.* (2013b) demonstrated that human children do selectively watch more dominant demonstrators in an open diffusion experiment, even when dominant individuals do not monopolise the novel task. I found a weak tendency to copy dominant over subordinate individuals – although not statistically significant when corrected for multiple comparisons. Thus, demonstrator dominance appeared to have little influence over the decisions of observers. However, the slight bias I detected could warrant further investigation, perhaps with a more complex dominance system. Dominance hierarchies are the product of many pairwise interactions and, as such, the way I represented dominance in my study was relatively simplistic. For example, aggressive displays gave participants information about the relative dominance levels of two demonstrators, but gave no information about how dominant each demonstrator was to the participant themselves. The effect of dominance on a demonstrator’s tendency to be copied could be further explored within environments where larger populations of individuals with stable dominance hierarchies exist – and the VERSE system certainly offers a lot of potential to do this.

I also investigated whether the sex of demonstrators – as determined by their physical characteristics – influenced their likelihood of being copied. Sex-based model biases have received little attention in the social learning literature, but where these biases have been identified, they usually come with clear adaptive value. For example, wild vervet monkeys (*Chlorocebus aethiops*) tend to copy female conspecifics, potentially because males disperse from their natal territory, while females are philopatric and so likely have more knowledge about food resources in their territory (Van de Waal *et al.,* 2010). In human hunter-gatherer communities, individuals display strong sex-based biases when there is sexual division of labour – exclusively learning about fishing and yam growing from males and exclusively learning about medicinal plants from females (Henrich and Broesch, 2011). The only statistically significant evidence I found for a sex-based bias in my study group was a slight tendency to copy male demonstrators in the Foraging task. This may have been a chance occurrence, or could suggest that males were assumed to be better foragers, perhaps because they are perceived as more 'typical' hunter-gatherer figures. It has been traditionally reported that men in hunter-gatherer populations are more mobile, display a significant advantage at tasks relating to spatial ability (Cashdan *et al.*, 2012) and, as a result, are more productive than women in terms of food acquisition (Kaplan *et al.*, 2000) than women, who are often assumed to be restricted in their foraging abilities by childcare responsibilities (Kaplan *et al.*, 2000; Lloyd and Bunch, 2005; Gurven and Hill, 2009). It is possible that this perception influenced the effect of demonstrator sex on their likelihood of being followed in the Foraging task – although further investigation would be necessary to test this explanation more thoroughly. Interestingly, in actuality, men and women in traditional hunter-gatherer societies simply differ in their foraging roles and it appears to be this division of labour that has resulted in sex differences in spatial abilities. Male foraging (primarily hunting) is often associated with longer travel distances and a necessity to track mobile prey, while female foraging (primarily gathering) is associated with the exploitation of reliable food patches containing immobile plant resources (Hilton and Greaves, 2008; Pacheco-Cobos *et al.*, 2010; Kaplan *et al.*, 2000). In this sense, if this would have been a real-life foraging situation, the female may have actually provided the most reliable information about food patch location.

Overall, however, I found very little evidence that demonstrator characteristics influenced their likelihood of being copied – where a statistically significant bias was found, the bias was only weak. Further investigation into the correlation between a demonstrator's characteristics and their social influence, perhaps using larger populations with mixed pools of characteristics more representative of real social groups, could provide further insight – and VERSE offers an ideal platform to conduct such an experiment.

Participants copied the majority over the minority.

While demonstrator characteristics appeared not to influence participants' use of social information, their frequency did. When participants chose to use social information rather than attempt a task independently, there was strong evidence of an innate bias towards copying the majority, even when it was no more profitable to do so. This occurred across all tasks and is in agreement with previous, lab-based human experiments (Morgan *et al.,* 2012; Haun *et al*., 2012; Muthukrishna *et al.,* 2016; Deffner *et al*., 2020), suggesting that humans possess a majority bias in a wide range of contexts and task complexities. An innate tendency to copy the majority (also known as a 'positive frequency-dependent' bias) is likely to be an adaptive strategy when learning to survive in a novel environment because, if many individuals already use a specific behaviour within that environment, it is likely to be an adaptive behaviour that receives adequate payoff to sustain those individuals. In addition, such a strategy is fairly easy to implement as it does not require different demonstrators to be assessed based on their individual characteristics or success rates. It is therefore unsurprising that a bias towards copying the majority strategy has been identified across a number of taxa, from humans and other primates to birds to fish (Morgan *et al.,* 2012; Van de Waal *et al.*, 2013; Aplin *et al,* 2015; Day *et al.,* 2001) and that theoretical analyses agree on its adaptive value (Boyd and Richerson, 1985).

In some cases, a tendency to copy the majority may occur simply because an individual is exposed more often to a behaviour used by a greater number of demonstrators, thus offering more opportunities to learn said behaviour; while in other cases, a disproportionate tendency to adopt the majority decision is found (Laland, 2004). I argue that I have demonstrated the latter here. While participants were approximately three times as likely to copy the behaviour of three demonstrators over a single demonstrator – which initially appears to be a linear relationship between demonstrator number and likelihood of copying – my experimental design meant that all three demonstrators displayed the same behaviour at the same time, essentially acting as a single unit. Therefore, a greater number of demonstrators should have had little influence on learning opportunities, suggesting that participants were indeed responding to differences in the frequency of demonstrator using the same behaviour. Despite this, it is important to note that, while participants did strongly favour the majority over the minority, demonstrator consensus still did not cause participants to favour social information over independently acquired information. This may not have been the case had I used a greater number of demonstrators, as it has previously been shown that an increase in demonstrator number as well as the consensus between them increases participants' tendency to copy (Morgan *et al.,* 2012). It would therefore be interesting to see if increasing the size of the demonstrator population within the VERSE system affects the likelihood of participants using social information over their own independent exploration.

Participants copied the most successful demonstrators.

While participants did not appear to use indirect indicators of demonstrator success, such as size and dominance status, in their social learning decisions, they did preferentially copy the behaviours of demonstrators who consistently received higher direct payoffs. This was coupled with an increase in reliance on social over asocial information, as discussed above. Payoff-based social learning has been reported in human lab studies before (Mesoudi and O'Brien, 2008; Mesoudi, 2011; Atkisson *et al.,* 2012; Molleman *et al.,* 2014; Miu *et al.,* 2018), but using comparatively simple sources of social information that have disregarded the potential difficulties in assessing multiple behaviours being performed asynchronously in both space and time. Copying the most successful individuals has obvious adaptive benefits, as confirmed by theoretical analyses (Schlag, 1998; Grove, 2018); however, gaining this information in real world situations comes with the time and energy costs of tracking and comparing the success rates of multiple individuals for a given task, which is likely to become more difficult across larger spatial scales. My findings show that human participants were, within spatially complex environments and across multiple sets of demonstrators, able to learn which demonstrators were more successful at the tasks in question and selectively copy their behaviours. Interestingly, Mesoudi (2011) reported that participants were more likely to attempt a task independently than copy others even when provided with the opportunity for payoff-based social learning, which is comparable to the behaviour found in my Foraging task. This is despite social information being relatively more difficult to collect in my experiment, owing to the fact that participants had to actively follow, observe and compare the behaviours of multiple demonstrators, while in Mesoudi's (2011) experiment, participants had only to click a button to copy the arrowhead design of the most successful individual. By comparison, in my Container and Route Choice tasks, in which social information was easier to obtain, participants preferred to make use of social information when the environment contained varying payoffs.

Strategically copying the most successful individuals is certainly not a solely human trait, and has been demonstrated in a number of other species, both in the lab and in open environments. Nine-spined sticklebacks, for example, use public information to assess the profitability of food patches and appear to deploy a 'hill-climbing' strategy when deciding where to feed, favouring the choices of individuals more successful than themselves until an optimal behaviour is reached (Coolen *et al.*, 2003; Kendal, Rendell, *et al.*, 2009). Similarly, field experiments on wild white-faced capuchins (*Cebus capucinus*) and vervet monkeys show that both species preferentially learn the food extraction techniques of conspecifics who receive the highest yield (Barrett *et al.,* 2017; Canteloup *et al.,* 2021). This strategic use of social information essentially allows individuals to reap the benefits associated with both social and asocial learning – reducing the time and risk associated with independent learning while ensuring that social information is accurate and profitable. Thus, despite the additional time and effort required to establish who receives a higher payoff during a given task compared to other forms of social learning, such a strategy clearly provides a substantial enough reward to be worthwhile and appears to be an adaptive social learning strategy across multiple taxa.

5.6. Summary and conclusions

In this study I have demonstrated a novel approach to studying human social learning behaviour, through the use of specially designed, three-dimensional virtual environments, developed using gaming technology, that allow participants to express more natural behaviours, across more realistic spatial scales, than is often possible in laboratory conditions. Using this technology, I explored human social learning strategies in a series of experiments inspired by the animal literature – thus allowing direct generalisations to be made across the human / non-human divide. In general, participants displayed an innate bias towards learning independently rather than socially in these complex environments, although this almost always involved at least some degree of partial copying. I also found substantial variation in social information use between individuals. Individuals additionally balanced their reliance on socially and asocially acquired information depending on their reliability and ease of acquiring. While I found little evidence to suggest that participants were biased towards copying demonstrators with particular individual characteristics, I did find clear evidence for two social learning biases previously highlighted in both the human and animal literature – namely a tendency to copy the majority and a tendency to copy successful individuals. These happen to be the two of the most extensively studied social learning strategies, demonstrated before both in humans and across other taxa, and there is evidence to suggest that both strategies are adaptive ways of gaining the most profitable social information. Overall, my novel approach to studying human social learning allowed me to study how people learn in novel, realistic environments, taking into account the real-life complexities of gathering information both socially and asocially. With a good foundation of human social learning research already present in the literature, I encourage future researchers to focus on testing these foundations against more realistic scenarios in order to better understand the evolutionary importance of the way in which we learn from one another.

Data accessibility. All raw data, organised datasets and R code required to reproduce the results of this study are available in the FigShare repository (doi: 10.6084/m9.figshare.19196600) (Easter, 2022). Additional supplementary analyses and results are provided in the Supplementary Material.

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Ethical approval. Ethical approval for this study was obtained by the Faculty of Biological Sciences Research Ethics Committee, University of Leeds (LTSBIO-029).

5.7. Supplementary Material

5.7.1. Presentation order of tasks and demonstrator conditions across participants

Both the order of task presentation and the order of demonstrator condition presentation were randomised across participants to reduce the impact of presentation order on social information use (Tables 5.S1, 5.S2). The order of presentation for both the tasks and the demonstrator conditions within each task followed a balanced Latin square design where possible. For the Route Choice and Foraging tasks, where several replicates were produced for each demonstrator condition, each with a distinctly different environment, the replicates used were also randomised across participants (Table 5.S3).

Table 5.S1. The randomised order of tasks and demonstrator conditions for each participant. Demonstrator orders are represented by letters, which correspond to the appropriate rows in Table 5.S2.

	Task 1		**Task 2**		**Task 3**	
Participant	Task	Demonstrator order	Task	Demonstrator order	Task	Demonstrator order
1	Route finding	A	Tokens	B	Foraging	F
2	Route finding	B	Tokens	C	Foraging	A
3	Route finding	C	Tokens	D	Foraging	B
4	Route finding	D	Tokens	E	Foraging	C
5	Route finding	E	Tokens	F	Foraging	D
6	Route finding	F	Tokens	A	Foraging	E
7	Route finding	A	Foraging	B	Tokens	F
8	Route finding	B	Foraging	C	Tokens	A
9	Route finding	C	Foraging	D	Tokens	B
10	Route finding	D	Foraging	E	Tokens	C
11	Route finding	E	Foraging	F	Tokens	D
12	Route finding	F	Foraging	A	Tokens	E
13	Tokens	A	Foraging	B	Route finding	F
14	Tokens	B	Foraging	C	Route finding	A
15	Tokens	C	Foraging	D	Route finding	B
16	Tokens	D	Foraging	E	Route finding	C

17	Tokens	E	Foraging	F	Route finding	D
18	Tokens	F	Foraging	A	Route finding	E
19	Tokens	A	Route finding	B	Foraging	F
20	Tokens	B	Route finding	C	Foraging	A
21	Tokens	C	Route finding	D	Foraging	B
22	Tokens	D	Route finding	E	Foraging	C
23	Tokens	E	Route finding	F	Foraging	D
24	Tokens	F	Route finding	A	Foraging	E
25	Foraging	A	Route finding	B	Tokens	F
26	Foraging	B	Route finding	C	Tokens	A
27	Foraging	C	Route finding	D	Tokens	B
28	Foraging	D	Route finding	E	Tokens	C
29	Foraging	E	Route finding	F	Tokens	D
30	Foraging	F	Route finding	A	Tokens	E
31	Foraging	A	Tokens	B	Route finding	F
32	Foraging	B	Tokens	C	Route finding	A
33	Foraging	C	Tokens	D	Route finding	B
34	Foraging	D	Tokens	E	Route finding	C
35	Foraging	E	Tokens	F	Route finding	D
36	Foraging	F	Tokens	A	Route finding	E

Table 5.S2. The six demonstrator condition orders, randomised across participants.

	Order					
	1st	**2nd**	**3rd**	**4th**	**5th**	**6th**
A	*Asocial*	*Soc/Asoc*	*Dom/Sub*	*Three/One*	*Male/Female*	*Large/Small*
B	*Soc/Asoc*	*Three/One*	*Asocial*	*Large/Small*	*Dom/Sub*	*Male/Female*
C	*Three/One*	*Large/Small*	*Soc/Asoc*	*Male/Female*	*Asocial*	*Dom/Sub*
D	*Large/Small*	*Male/Female*	*Three/One*	*Dom/Sub*	*Soc/Asoc*	*Asocial*
E	*Male/Female*	*Dom/Sub*	*Large/Small*	*Asocial*	*Three/One*	*Soc/Asoc*
F	*Dom/Sub*	*Asocial*	*Male/Female*	*Soc/Asoc*	*Large/Small*	*Three/One*

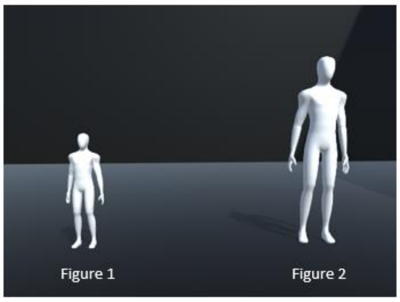
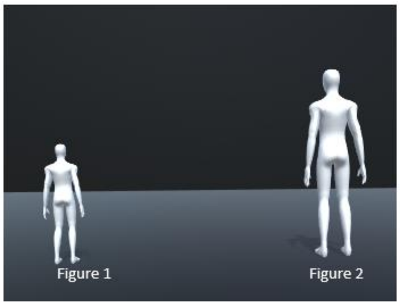
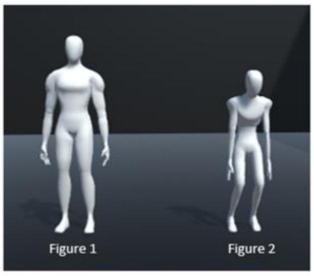
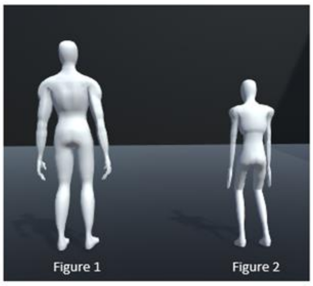
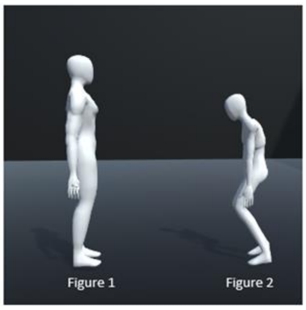
Table 5.S3. The replicates used and their order of presentation for the Route Choice and Foraging tasks, for each of the demonstrator orders shown in Table 5.S2.

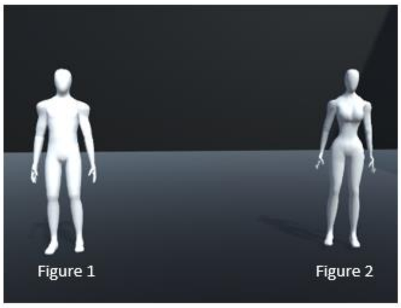
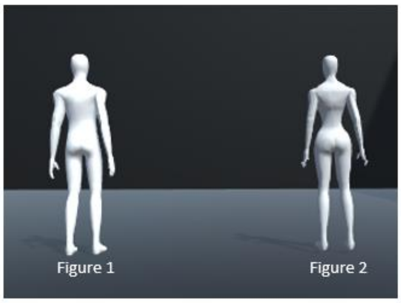
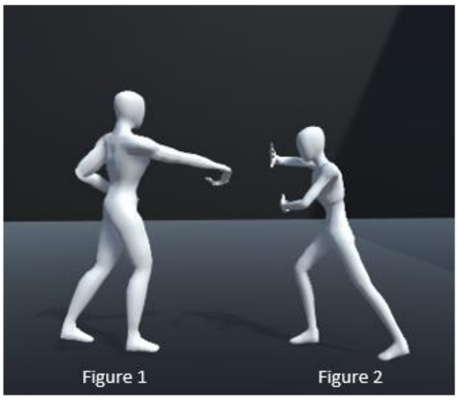
Demonstrator condition order	Route Choice (three of a possible five)	Foraging (one of a possible three)
A	1, 2, 3	1
B	4, 5, 1	2
C	3, 4, 2	3
D	2, 1, 5	1
E	5, 3, 4	2
F	1, 4, 3	3

5.7.2. Perceptions of the AI models used.

Prior to commencing the experiment, it was important to understand whether people, in general, perceived the AI models in the way intended by the researchers – e.g. viewed the ‘female’ AI as female, the ‘dominant’ AI as dominant to the ‘subordinate’ AI, etc. A group of 41 University of Leeds postgraduate students and academic staff volunteered, in response to an email request, to complete an online questionnaire using Microsoft Forms, in which they gave their perceptions of the AI models to be used in the main experiment. In this questionnaire, participants were presented with four sets of images, each displaying a pair of AI models (Table 5.S4). For each set, the following questions were asked: (i) In your opinion, what gender(s) are the two figures? (ii) In your opinion, does one figure appear to be more dominant than the other? (iii) In your opinion, which figure appears friendlier or more approachable? (iv) In your opinion, which figure appears more aggressive?

Table 5.S4. Images presented to a group of participants prior to the main experiment, showing four sets of two AI models. These AI models were to be used in the main experiment to detect biases towards learning from individuals with certain characteristics. This questionnaire was therefore used to establish whether people generally perceived the AIs in the intended way.

Set	Description	Image displayed
1	Figure 1 is a small AI, Figure 2 is a large AI. Both figures are the 'default' body shape used in the experiment. Other than overall size, all proportions are the same.	 *Front view*  *Back view*
2	Figure 1 is a 'dominant' AI, which is more muscular and stands upright. Figure 2 is a 'subordinate' AI, which is emaciated in appearance and stands hunched. An additional side view was given to make this difference in posture clear.	 *Front view*  *Back view*  *Side view*

3	Figure 1 is a ‘male’ AI (which was also used as the default AI in the *Three/One* and *Large/Small* demonstrator conditions). Figure 2 is a ‘female’ AI.	 *Front view*  *Back view*
4	‘Dominant’ and ‘subordinate’ AIs with interaction. Figures are the same as in set 2, but now display the character interactions that will be displayed at the beginning of each *Dom/Sub* demonstrator condition in the main experiment.	

The results of the questionnaire are displayed in Table 5.S5. In response to AIs of different sizes, 92% of participants agreed that both AIs were male. Both AIs were viewed as equally dominant by 48% of participants, and the larger AI was viewed as dominant to the smaller AI by 43% of participants. This suggests that any bias towards learning from larger AIs in the main experiment could be, in part, due to a dominance bias. Aggressiveness and approachability of AIs based on their size varied between participants.

In response to a ‘male’ and a ‘female’ AI, 100% of participants agreed that the ‘male’ AI was male and the ‘female’ AI was female. Gender was therefore an easily distinguishable trait and participants perceived AI genders in the intended way. Interestingly, this consensus suggests that participants’ perception of ‘gender’ aligned with stereotypical physical sex differences. In general, both male and female AIs were viewed as equally dominant, approachable and aggressive. Thus, I can be confident that that any learning biases detected in the *Male/Female* demonstrator condition will be due to their perceived gender differences and not due to any of the alternate characteristics considered here. It is also worth noting that the ‘male’ AI displayed here was the default AI used across demonstrator conditions that did not require physical characteristics to be altered (namely the *Soc/Asoc* and *Three/One* conditions), and so participants will likely view all AIs as male in these conditions as well.

In response to the ‘dominant’ and ‘subordinate’ AIs, 95% of participants agreed that the ‘dominant’ AI was dominant to the ‘subordinate’ (which dropped slightly to 87% when actions were added), and the ‘subordinate’ AI was never viewed as dominant to the ‘dominant’ AI. Thus, participants perceived the dominance status of these AIs in the intended way. When the two AIs were displayed with no actions, there was variation in the genders they were both perceived as, but the majority of participants agreed that the ‘subordinate’ was female. When actions were included in the image, the ‘dominant’ AI was viewed as male by 80% of participants and the ‘subordinate’ AI was viewed as female by 72% of participants. Any dominance-based learning biases detected in the main experiment could therefore be due, at least in part, to perceived differences in their gender. Interestingly, when the AIs were displayed without associated actions, the majority of participants found the ‘dominant’ AI to be more approachable, despite a general consensus that the ‘dominant’ AI was either equally or more aggressive-looking than the ‘subordinate’ AI. When the AIs were shown again with their associated actions, however, perceptions on approachability and aggression were altered, with the ‘dominant’ AI generally viewed as more aggressive-looking than the ‘subordinate’ AI, and the majority of participants now perceiving the ‘subordinate’ AI as more or equally approachable compared to the ‘dominant’ AI. Perceptions of aggressiveness and, in particular, approachability therefore appear independent of perceptions of dominance – with participants generally finding the AI dominant in appearance alone more approachable. This may be because the hunched, emaciated appearance of the ‘subordinate’ AI was viewed as intimidating. However, when the AIs displayed dominance-related actions, the relatively aggressive action of the ‘dominant’ AI made them appear less approachable. As dominance is often directly linked to aggression, including the dominance-related interactions between these two AIs thus seems an important factor to reinforce their perceived relationship.

Table 5.S5. Results of the pre-study questionnaire on the perceptions of different AI models, showing participants' perceptions of the gender, dominance, approachability and aggressiveness of the two AIs in each pair. Values represent the proportion of participants expressing a particular opinion about the characteristics of each AI pair.

		AI pair			
Characteristic	**Opinion**	**Small/Large**	**Male/Female**	**Dom/Sub**	**Dom/Sub (with actions)**
Gender	Fig 1 male, fig 2 female.	0.04	1.00	0.38	0.54
	Fig 1 female, fig 2 male.	0.04	0	0.05	0.03
	Both male.	0.91	0	0.23	0.26
	Both female.	0	0	0.35	0.18
Dominance	Fig 1 is dominant.	0.09	0.03	0.95	0.87
	Fig 2 is dominant.	0.43	0.08	0	0
	Both equally dominant.	0.48	0.90	0.05	0.13
Approachability	Fig 1 is more approachable.	0.30	0.08	0.68	0.08
	Fig 2 is more approachable.	0.22	0.15	0.13	0.51
	Both equally approachable.	0.48	0.78	0.20	0.41
Aggressiveness	Fig 1 is more aggressive.	0.13	0.03	0.40	0.84
	Fig 2 is more aggressive.	0.35	0.13	0.08	0.03
	Both equally aggressive.	0.52	0.85	0.52	0.13

5.7.3. Additional analysis: How was participants' tendency to use social over asocial information influenced by differences in rewards?

To establish whether variable rewards had an influence on participants' tendency to use social over asocial information, a set of binomial GLMs were run using data from both reward groups, using reward group as a predictor – firstly for the *Soc/Asoc* demonstrator condition, then (for the Route Choice and Foraging tasks only) across all demonstrator conditions where participants were able to make decisions completely independently of demonstrator choice. In the Container task, participants in the Different Rewards group were significantly more likely to copy the single AI rather than make opposing decisions than those in the Same Rewards group (Table 5.S6) (Figure 5.4, main text). As the single AI always demonstrated the most profitable option in this scenario, this reflects an example where using rather than opposing social information also amounts to copying the most successful demonstrator. Participants therefore seemed to be aware that the demonstrated option in this scenario would result in the highest payoffs, and responded by copying the single AI more often.

In the Route Choice and Foraging tasks, participants were offered a much greater degree of flexibility in their choices, beyond simple binary decisions, and so copying did not necessarily result in the most profitable behaviours being learned. In these tasks, participants in the Different Rewards group were no more likely, compared to participants in the Same Rewards group, to use social over asocial information when presented with only a single demonstrator (Table 5.S6). However, participants in the Different Rewards group did use social information significantly more often than participants in the Same Reward group on average across all demonstrator conditions (Table 5.S6). For the Route Choice task, this amounted to a favouring of social over asocial learning when there was variation in demonstrated route length, compared to a favouring of asocial learning when demonstrated route lengths were equal (Figure 5.4, main text). For the Foraging task, while participants were more likely to learn socially when foods of differing values were present in the environment than when those foods were of equal value, participants still favoured asocial learning overall (Figure 5.4, main text). Interestingly, in both Route Choice and Foraging tasks, the initial choice made during each demonstrator condition tended to involve copying (Table 5.S6). Overall, this suggests that an awareness of reward variation, probably accumulated over previous demonstrator conditions, made participants more prone to copying. However, in the Foraging task, after an initial bias towards copying, participants then started to engage in independent exploration.

Table 5.S6. Parameter estimates, standard error, z values and p-values for the intercept and the effect of variation in rewards on participants likelihood of using social over asocial information, in their initial choices and overall, in the *Soc/Asoc* demonstrator condition and as a whole over all demonstrator conditions. Intercept is taken as RewardGroup = Same. P-values are adjusted for multiple comparisons using false discovery rates. Significant p-values (< 0.05) are highlighted in bold.

		Parameter	Container				Route Choice				Foraging			
Condition			Estimate	Std. Error	z	p	Estimate	Std. Error	z	p	Estimate	Std. Error	z	p
All choices	*Soc/Asoc*	Intercept	0.000	0.076	0	1	-0.118	0.140	-0.840	0.452	-1.301	0.138	-9.439	**<0.001**
		RewardGroup (Different)	0.937	0.113	8.292	**<0.001**	0.282	0.198	1.428	0.191	0.159	0.191	0.829	0.452
	All	Intercept	-	-	-	-	-0.339	0.063	-5.367	**<0.001**	-0.700	0.054	-12.900	**<0.001**
		RewardGroup (Different)	-	-	-	-	0.606	0.089	6.790	**<0.001**	0.349	0.077	4.550	**<0.001**
Initial choices	*Soc/Asoc*	Intercept	0.465	0.246	1.895	0.089	-0.357	0.246	-1.448	0.191	-0.847	0.261	-3.249	**0.002**
		RewardGroup (Different)	-0.036	0.345	-0.105	0.964	0.738	0.348	2.123	0.060	0.702	0.355	1.976	**0.080**
	All	Intercept	-	-	-	-	-0.348	0.110	-3.170	**0.004**	-0.160	0.107	-1.495	0.191
		RewardGroup (Different)	-	-	-	-	0.731	0.155	4.708	**<0.001**	0.610	0.154	3.958	**<0.001**

5.7.4. Additional analysis: Success rates of social versus asocial learners in the *Soc/Asoc* condition.

In the main text, I compared the average success rates of participants who tended to learn socially versus those who tended to learn asocially, across all demonstrator conditions. Here, I present the same analysis, but using the *Soc/Asoc* demonstrator condition only – thus comparing the relative successes of participants who tended to copy or ignore a single demonstrator. These results were qualitatively the same as those presented in the main text. In the Same Rewards group, those who tended to learn asocially were significantly more successful than those who favoured social learning in both the Route Choice (Mann-Whitney U test; $U(1) = 265$, $p < 0.001$) and Foraging Tasks (Mann-Whitney U test; $U(1) = 119.5$, $p = 0.012$); whereas in the Different Rewards group, participants who learned largely asocially had similar success rates to those who learned largely socially (Mann-Whitney U tests; Route Choice: $U(1) = 493$, $p = 0.295$; Foraging: $U(1) = 380$; $p = 0.423$) (Figure 5.S1).

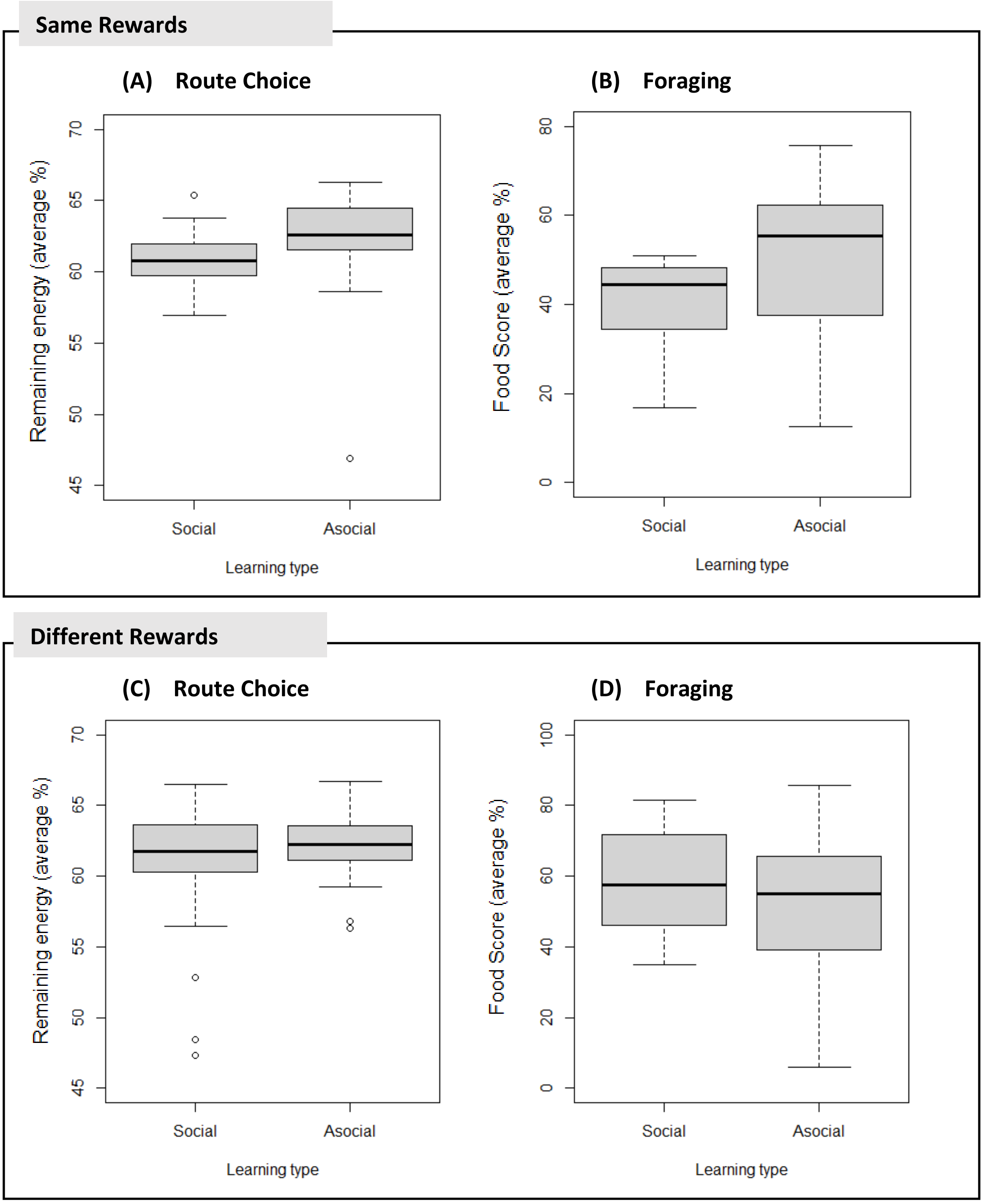


Figure 5.S1. The average success rates of participants who favoured social and asocial learning, in the *Soc/Asoc* condition only, in scenarios where demonstrators received equal rewards for their choices. The top box shows the success rates in **(A)** the Route Choice task, measured as the average percentage of energy remaining, and **(B)** the Foraging task, measured as the average food score as a percentage of the maximum possible food score, when all demonstrators displayed behaviours of equal payoff. The bottom box shows the success rates in **(C)** the Route Choice task and **(D)** the Foraging task when different demonstrated behaviours received different payoffs. Thick horizontal lines represent medians and boxes indicate the interquartile range. Whiskers extend to 1.5x the interquartile range.

5.7.5. Additional analyses of the Foraging task: Did participants learn the specific food type preferences of demonstrators?

In addition to food patch choices, the influence of demonstrator food type choices on participant food collection behaviour was analysed for the Foraging task. For each environment in the Foraging task, food patches were divided into two sections, each containing twenty items of a different food type. Different food types were coloured differently and, in some cases, had different nutritional values. All food types used in the study are given in Table 5.S7. Each demonstrator visited three food patches and 'ate' only one food type from that patch, thus allowing participants to learn preferences for specific food types.

Table 5.S7. The food types used in the foraging task, along with their nutritional values.

Food item name	**Appearance**	**Nutritional value**
YellowMushroom		+5
PinkMushroom		+3
BrownMushroom		+1
GreenMushroom		+1
WhiteMushroom		+1
DarkMushroom		-5

For the Same Rewards group, all eight food patches contained a set of twenty *BrownMushrooms* and a set of twenty *GreenMushrooms* (Table 5.S7). All food items therefore had the same nutritional value of +1. Both demonstrators only ate the *GreenMushrooms* located in their chosen food patches. Thus, if participants were prone to copying the food preferences of certain demonstrators, they should be disproportionately more likely to collect the *GreenMushrooms* over the *BrownMushrooms*. A binomial GLM was run predicting the initial choice made by participants (i.e. the first food item collected during the first demonstrator condition they were subjected to) (*n* = 57). The reason that initial choices were considered here, rather than the total number of each food type collected by participants, is because AI demonstrators depleted the *GreenMushrooms,* leaving fewer for the player to collect and making it more likely that a GLM would detect a tendency to collect the *BrownMushrooms* more often. According to this model, participants did not show an initial preference towards the demonstrated food type, the *GreenMushrooms* (Table 5.S8).

Table 5.S8. Intercept estimates, standard errors, Z values and p-values for GLMs predicting the likelihood that (i) participants in the Same Rewards group would display an initial preference for the demonstrated *GreenMushroom* food type; (ii) participants in the Different Reward group who initially visited the best food patch would display an initial preference for the demonstrated *YellowMushroom* food type; and (iii) participants in the Different Reward group who initially visited the worst food patch would display an initial preference for the demonstrated *WhiteMushroom* food type.

Reward group	Food patch type	Intercept	Std. Error	Z value	p-value
Same Rewards	All	-0.391	0.2700	-1.448	0.148
Different Rewards	Best food patch	-0.201	0.318	-0.631	0.528
	Worst food patch	0.154	0.556	0.277	0.782

For the Different Rewards group, food patches contained food items of differing nutritional values as follows: Three food patches contained a set of twenty *PinkMushrooms* and a set of twenty *YellowMushrooms* – these were visited by demonstrator A, who ‘ate’ only the *YellowMushrooms* from these patches. Three food patches contained a set of twenty *WhiteMushrooms* and a set of twenty *DarkMushrooms* – these were visited by demonstrator B, who ‘ate’ only the *WhiteMushrooms*. The remaining two (asocial) food patches contained a set of twenty *BrownMushrooms* and a set of twenty *GreenMushrooms*. Thus, demonstrator choices were arranged in such a way that (*i*) copying demonstrator A would result in participants finding the most profitable food patches and (*ii*) copying the food type preference of any demonstrator would result in participants collecting the most profitable food types within a given food patch (and would allow participants to avoid collecting poisonous foods when foraging on the 'worst' food patches). To determine whether participants were more likely to copy the food type preferences of demonstrators in these environments, where rewards were uncertain and potentially maladaptive decisions could be made, two binomial GLMs were run, again using data concerning the initial choice made by each participant. The first model predicted the likelihood that participants who visited the best food patch first (*n* = 40) also displayed an initial preference towards the food type demonstrated by demonstrator A, i.e. collected the *YellowMushroom* first. The second model predicted the likelihood that participants who visited the worst food patch first (*n* = 13) also displayed an initial preference towards the food type demonstrated by demonstrator B, i.e. collected the *WhiteMushroom* first. These models revealed that, again, participants were not influenced by the specific food preferences of demonstrators (Table 5.S8). Once they had followed a demonstrator into a food patch, they were equally likely to collect either food type first.

Overall, these analyses suggests that, while certain demonstrators influenced participants' food patch choices, as discussed in the main text, the individual food type preferences of demonstrators were not copied. However, despite this, participants were adaptive in the way they collected food items. When visiting the best food patches, participants collected approximately equal proportions of *PinkMushrooms* and *YellowMushrooms* (Figure 5.S2A). However, when visiting the worst food patches, they disproportionately collected the *WhiteMushrooms* and avoided the poisonous *DarkMushrooms* (Figure 5.S2B). As participants' initial food preferences were unaffected by demonstrator choice, it is likely that participants learned asocially to avoid poisonous foods, probably by sampling them first and learning that this food type lowered the player's health and food score. Participants were therefore adaptive in the way in which they collected food from patches, collecting all food types with a positive nutritional score and ignoring demonstrator food preferences (which would have been maladaptive to copy, since participants would have avoided collecting alternative food types with positive nutritional values in the best food patches), while also avoiding poisonous foods.

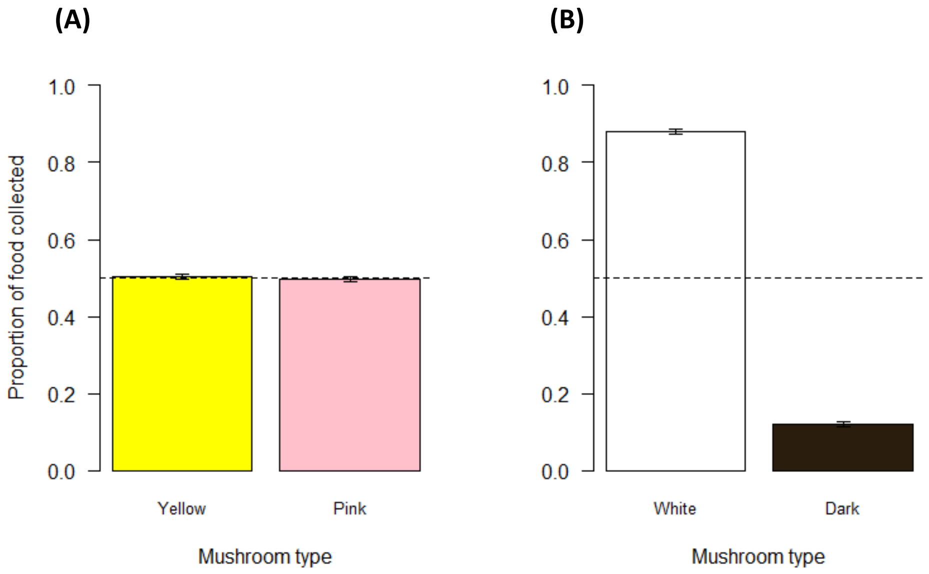


Figure 5.S2. (A) The proportion of *YellowMushrooms* (nutritional value: +5) and *PinkMushrooms* (nutritional value: +3) collected by participants when visiting the best food patches. **(B)** The proportion of *WhiteMushrooms* (nutritional value: +1) and *DarkMushrooms* (poisonous; nutritional value: -3) collected when visiting the worst food patches. Proportions are taken from the total number of food items collected across all demonstrator conditions, within the Different Rewards group. Horizontal (dashed) reference line is at 0.5 and indicates no preference for either food type.

5.7.6. Additional analyses concerning participant choices of demonstrator A vs demonstrator B based on their relative success rates

Table 5.S9. Intercept estimates, standard error, z-values and p-values for binomial GLMs modelling the likelihood that participants copied demonstrator A over demonstrator B in the *Dom/Sub, Three/One, Male/Female* and *Large/Small* demonstrator conditions, and overall across all four demonstrator conditions, for each of the three tasks, in scenarios where payoffs differed depending on which demonstrator was copied. P-values are adjusted for multiple comparisons using false discovery rates. Significant p-values (< 0.05) are highlighted in bold.

Task	**Demonstrator Condition**	**Intercept Estimate**	**Std. Error**	**Z value**	**p-value**
Container	*Dom/Sub*	0.930	0.083	11.090	**<0.001**
	Three/One	1.266	0.091	13.870	**<0.001**
	Male/Female	0.557	0.079	7.089	**<0.001**
	Large/Small	1.009	0.085	11.810	**<0.001**
	All (A/B)	0.927	0.042	22.110	**<0.001**
Route Choice	*Dom/Sub*	1.263	0.214	5.900	**<0.001**
	Three/One	1.936	0.276	7.011	**<0.001**
	Male/Female	0.177	0.180	0.983	0.326
	Large/Small	1.299	0.246	5.278	**<0.001**
	All (A/B)	1.056	0.106	10.010	**<0.001**
Foraging	*Dom/Sub*	0.922	0.206	4.482	**<0.001**
	Three/One	1.266	0.197	6.421	**<0.001**
	Male/Female	0.786	0.188	4.173	**<0.001**
	Large/Small	0.936	0.212	4.414	**<0.001**
	All (A/B)	0.984	0.100	9.857	**<0.001**

Table 5.S10. ANOVA results for GLMs modelling the likelihood of copying demonstrator A over demonstrator B across participants in two different groups – one where rewards were equal regardless of the demonstrator copied, and one where copying demonstrator A over demonstrator B resulted in higher payoffs (as measured by the 'RewardGroup' factor). For each of the three tasks, a null, intercept-only model (representing the likelihood that demonstrator A is copied over B overall, across both reward groups) is compared with a model in which reward group was included as a factor. Significant p-values (< 0.05) are highlighted in bold and indicate significant differences in demonstrator choice across the two reward groups.

Task	Model	Deviance	Residual Deviance	p-value
Container	*NULL*		603.1	
	RewardGroup	129.9	138.0	**< 0.001**
Route Choice	*NULL*		245.5	
	RewardGroup	26.9	218.5	**< 0.001**
Foraging	*NULL*		433.3	
	RewardGroup	19.6	135.0	**< 0.001**

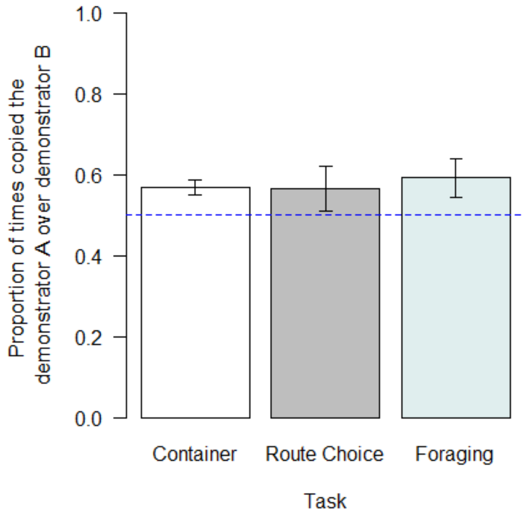


Figure 5.S3. The proportion of times participants copied demonstrator A and demonstrator B overall, across the *Dom/Sub, Three/One, Male/Female* and *Large/Small* demonstrator conditions, for each of three tasks, in scenarios where both demonstrators displayed behaviours of equal payoff. Error bars represent Clopper-Pearson 95% confidence intervals. Horizontal reference line (dashed blue) is at 0.5 and indicates no preference for either demonstrator.

5.7.7. Additional analysis – the influence of individual characteristics on their use of social information

A series of binomial GLMs were run to investigate whether participants' individual characteristics influenced their tendency to learn socially over asocially (hypothesis *i* in the *Statistical Analysis,* section 5.3.8, of the main text), their tendency to copy demonstrators with certain characteristics (hypothesis *iv*) and their tendency to copy the most over the least successful demonstrators (hypothesis *v*). The individual characteristics tested were age, gender, aggression score and time spent playing video games. As recommended by Bryant and Smith (2001), the four subcategories of aggression – physical aggression, verbal aggression, hostility and anger – were modelled separately, as these describe different types of aggression that are not necessarily correlated. In addition, the overall aggression score, summed across each of the four categories, was modelled as a measure of general aggression. To avoid issues of collinearity, overall aggression was never included in the same model as any of the four subcategories. For each type of aggression, a participant's score was averaged across all questions in the particular aggression category, and then scaled between 0 and 1.

Time spent playing video games was included in this analysis to assess whether familiarity with video game play influenced participants' general behaviour in VERSE, thus affecting social information use – e.g. if those who play video games often are more exploratory due to higher levels of confidence with video game controls, this may result in a higher tendency to learn asocially. Participants were asked to rate their usual video game usage as either "Never", "Now and again", "A few times a month", "A few times a week" or "Daily". For ease of analysis, these options were then collated into two categories, with the first three options classed as "Rarely" and the remaining two classes as "Often", before insertion into the GLM.

The influence of each individual variable was modelled separately. For each hypothesis to be tested, a binomial GLM was run for each individual variable (age, gender, aggression score, video game play), with said variable as a predictor. Where more than one individual variable was found to have a significant influence on the use of social information, each combination of individual variables were modelled and ANOVA tests and AIC values were used to establish which model provided the best fit to the data.

Overall, there was no clear pattern observed for an influence of the tested individual characteristics on either social information use (Table 5.S11), biases towards certain demonstrator characteristics (Table 5.S12) or tendency to copy more successful demonstrators (Table 5.S13). Most of the models tested were not statistically significant after FDR corrections were performed. However, regarding the influence of age on social learning, it is important to note the relatively narrow age range of the participants (mean: 21; range: 18-31). Different results may have been obtained if a wider age range would have been considered.

Video game play did not appear to have a significant influence on participants' behaviour within VERSE, with one exception: participants who played video games more often were more likely to copy the most successful demonstrators across demonstrator conditions – however this was significant in the Container task only. This could suggest that 'gamers' displayed some different behaviours to 'non-gamers' (e.g. a greater capacity to track the success rates of AIs) during relatively simple, two-option tasks, but not when exposed to more complex, exploratory tasks. All in all, this suggests that, in general, VERSE is well suited to studying human social behaviour in complex, immersive environments irrespective of whether participants are 'gamers' or not, despite VERSE being game-like in its nature.

Table 5.S11. Estimates, standard error, z values and p-values obtained from a series of binomial GLMs modelling the influence of each individual characteristic on participants' tendency to use favour social over asocial learning across three tasks, during the *Soc/Asoc* demonstrator condition (where a single demonstrator displayed one option and all other options were undemonstrated) and altogether across all demonstrator conditions. Each individual variable was modelled separately in its own GLM. P-values are adjusted for multiple comparisons using false discovery rates, after which none of the tested models were found to be statistically significant ($p < 0.05$).

		Container				**Route Choice**				**Foraging**			
Individual characteristic	**Demonstrator condition**	**Estimate**	**Std Error**	**z**	**p**	**Estimate**	**Std Error**	**z**	**p**	**Estimate**	**Std Error**	**z**	**p**
Age	*Soc/Asoc*	0.034	0.042	0.823	0.888	0.043	0.068	0.640	0.908	0.147	0.059	2.505	0.160
Gender (male)	*Soc/Asoc*	-0.352	0.159	-2.214	0.270	-0.070	0.292	-0.240	0.971	0.164	0.281	0.585	0.932
Aggression (overall)	*Soc/Asoc*	0.449	0.603	0.744	0.888	0.351	1.198	0.293	0.971	0.999	1.074	0.930	0.888
Aggression-physical	*Soc/Asoc*	-0.063	0.616	-0.103	0.988	0.098	1.222	0.080	0.988	-0.236	1.111	-0.212	0.971
Aggression-verbal	*Soc/Asoc*	0.079	0.397	0.198	0.971	0.005	0.751	0.007	0.995	1.958	0.697	2.809	0.100
Aggression-anger	*Soc/Asoc*	0.933	0.447	2.085	0.296	0.269	0.863	0.312	0.971	-0.313	0.820	-0.382	0.971
Aggression-hostility	*Soc/Asoc*	-0.019	0.419	-0.047	0.988	0.351	0.804	0.436	0.971	0.039	0.763	0.051	0.988
Video game play (often)	*Soc/Asoc*	-0.454	0.160	-2.844	0.100	-0.320	0.303	-1.058	0.829	0.253	0.282	0.897	0.888
Age	*All (soc/asoc)*	-	-	-	-	0.081	0.061	1.329	0.640	0.013	0.042	0.299	0.971
Gender (male)	*All (soc/asoc)*	-	-	-	-	-0.146	0.219	-0.667	0.908	0.340	0.202	1.682	0.531
Aggression (overall)	*All (soc/asoc)*	-	-	-	-	-1.168	0.894	-1.306	0.640	-0.374	0.768	-0.487	0.971
Aggression-physical	*All (soc/asoc)*	-	-	-	-	-0.172	0.907	-0.189	0.971	-1.037	0.775	-1.338	0.640
Aggression-verbal	*All (soc/asoc)*	-	-	-	-	-0.418	0.553	-0.757	0.888	0.748	0.497	1.507	0.640
Aggression-anger	*All (soc/asoc)*	-	-	-	-	-0.904	0.625	-1.447	0.640	-0.174	0.564	-0.308	0.971
Aggression-hostility	*All (soc/asoc)*	-	-	-	-	-0.718	0.604	-1.189	0.720	-0.983	0.541	-1.818	0.460
Video game play (often)	*All (soc/asoc)*	-	-	-	-	-0.170	0.234	-0.729	0.888	0.175	0.203	0.862	0.888

Table 5.S12. Estimates, standard error, z values and p-values obtained from a series of binomial GLMs modelling the influence of each individual characteristic on participants' tendency to copy the dominant demonstrator over the subordinate in the *Dom/Sub* condition, three over one demonstrator in the *Three/One* condition, the male over the female demonstrator in the *Male/Female* condition and the large over the small demonstrator in the *Large/Small* condition, across the three tasks, in conditions where both demonstrator displayed equally profitable behaviours. Each individual variable was modelled separately in its own GLM. P-values are adjusted for multiple comparisons using false discovery rates, after which none of the tested models were found to be statistically significant ($p < 0.05$).

		Container				**Route Choice**				**Foraging**			
Individual characteristic	**Demonstrator condition**	**Estimate**	**Std Error**	**z**	**p**	**Estimate**	**Std Error**	**z**	**p**	**Estimate**	**Std Error**	**z**	**p**
Age	*Dom/Sub*	0.024	0.042	0.587	0.945	-0.089	0.132	-0.673	0.945	0.021	0.091	0.234	0.945
Gender (male)	*Dom/Sub*	-0.043	0.159	-0.269	0.945	-0.237	0.521	-0.454	0.945	2.266	0.663	3.419	0.096
Aggression (overall)	*Dom/Sub*	0.553	0.605	0.914	0.812	0.097	2.044	0.048	0.945	-4.428	2.013	-2.200	0.384
Aggression-physical	*Dom/Sub*	-0.243	0.617	-0.394	0.945	0.593	1.824	0.325	0.945	-4.761	2.036	-2.339	0.365
Aggression-verbal	*Dom/Sub*	-0.083	0.398	-0.210	0.945	0.639	1.348	0.474	0.945	-0.064	1.360	-0.047	0.995
Aggression-anger	*Dom/Sub*	0.628	0.448	1.403	0.773	-0.545	1.476	-0.369	0.945	-3.744	1.334	-2.807	0.168
Aggression-hostility	*Dom/Sub*	0.720	0.423	1.702	0.534	-0.406	1.434	-0.283	0.945	-1.653	1.298	-1.273	0.812
Video game play (often)	*Dom/Sub*	-0.043	0.159	-0.269	0.945	-0.219	0.579	-0.378	0.945	0.288	0.461	0.625	0.945
Age	*Three/One*	0.105	0.055	1.901	0.421	0.231	0.239	0.963	0.812	-0.043	0.078	-0.548	0.945
Gender (male)	*Three/One*	-0.186	0.179	-1.042	0.812	0.318	0.715	0.444	0.945	-0.441	0.387	-1.139	0.812
Aggression (overall)	*Three/One*	0.697	0.694	1.004	0.812	-2.182	2.649	-0.824	0.856	3.170	1.604	1.976	0.400
Aggression-physical	*Three/One*	-1.034	0.668	-1.549	0.645	-2.552	2.670	-0.956	0.812	-0.109	1.512	-0.072	0.995
Aggression-verbal	*Three/One*	0.460	0.458	1.006	0.812	-0.713	1.544	-0.462	0.945	1.564	0.961	1.628	0.582
Aggression-anger	*Three/One*	0.312	0.511	0.612	0.945	-2.256	1.694	-1.331	0.793	3.458	1.277	2.708	0.168
Aggression-hostility	*Three/One*	1.091	0.495	2.204	0.384	0.473	1.746	0.271	0.945	1.265	1.089	1.161	0.812
Video game play (often)	*Three/One*	0.172	0.183	0.940	0.812	0.337	0.840	0.401	0.945	0.096	0.422	0.228	0.945

Age	*Male/Female*	0.002	0.041	0.041	0.995	0.200	0.180	1.113	0.811	0.050	0.103	0.489	0.945
Gender (male)	*Male/Female*	0.000	0.158	0.000	1.000	-0.309	0.511	-0.604	0.945	-0.388	0.402	-0.965	0.812
Aggression (overall)	*Male/Female*	0.874	0.605	1.445	0.748	-2.077	1.947	-1.066	0.812	-1.352	1.573	-0.859	0.832
Aggression-physical	*Male/Female*	0.127	0.616	0.205	0.945	-0.027	1.810	-0.015	0.998	0.095	1.575	0.060	0.995
Aggression-verbal	*Male/Female*	-0.263	0.397	-0.661	0.945	-1.595	1.209	-1.320	0.793	-0.285	1.027	-0.277	0.945
Aggression-anger	*Male/Female*	0.878	0.447	1.963	0.400	-1.375	1.466	-0.938	0.812	-0.286	1.155	-0.248	0.945
Aggression-hostility	*Male/Female*	1.151	0.425	2.708	0.168	-0.810	1.337	-0.606	0.945	-2.512	1.236	-2.033	0.400
Video game play (often)	*Male/Female*	-0.050	0.158	-0.317	0.995	-0.474	0.527	-0.899	0.812	0.013	0.419	0.032	0.995
Age	*Large/Small*	0.002	0.041	0.043	0.995	0.081	0.102	0.798	0.868	-0.280	0.140	-2.001	0.400
Gender (male)	*Large/Small*	-0.270	0.159	-1.700	0.534	-0.509	0.410	-1.243	0.812	0.507	0.442	1.147	0.812
Aggression (overall)	*Large/Small*	0.792	0.604	1.311	0.793	-0.725	1.701	-0.426	0.945	-1.432	1.575	-0.909	0.812
Aggression-physical	*Large/Small*	0.344	0.617	0.558	0.945	-1.329	2.196	-0.605	0.945	-1.612	1.805	-0.893	0.812
Aggression-verbal	*Large/Small*	0.423	0.398	1.065	0.812	0.548	1.083	0.506	0.945	-0.061	1.037	-0.059	0.995
Aggression-anger	*Large/Small*	0.914	0.447	2.047	0.400	-0.500	1.249	-0.400	0.945	-0.087	1.133	-0.077	0.995
Aggression-hostility	*Large/Small*	0.086	0.419	0.205	0.945	-1.088	1.125	-0.967	0.812	-2.015	1.118	-1.802	0.494
Video game play (often)	*Large/Small*	-0.019	0.158	-0.117	0.995	-0.266	0.427	-0.624	0.945	-0.160	0.433	-0.370	0.945

Table 5.S13. Estimates, standard error, z values and p-values for the interaction between the individual characteristics of participants and the 'reward group' they were assigned to, produced from binomial GLMs modelling the likelihood that participants copied demonstrator A over demonstrator B across all demonstrator conditions. Reward group is a binomial factor describing whether demonstrators received the same or different rewards for their actions (reference group = same). The interaction term therefore describes how much more likely participants with particular characteristics were to copy more successful demonstrators, relative to any innate preferences for the individual characteristics of those demonstrators. P-values are adjusted for multiple comparisons using false discovery rates. Statistically significant estimates ($p < 0.05$) are highlighted in bold and significant models are additionally highlighted in green.

	Container				**Route Choice**				**Foraging**			
Individual characteristic	**Estimate**	**Std Error**	**z**	**p**	**Estimate**	**Std Error**	**z**	**p**	**Estimate**	**Std Error**	**z**	**p**
Age	-0.095	0.035	-2.688	0.084	-0.053	0.103	-0.512	0.745	-0.071	0.077	-0.911	0.579
Gender (male)	0.254	0.120	2.114	0.202	0.445	0.344	1.293	0.465	-0.667	0.295	-2.260	0.192
Aggression (overall)	-0.086	0.451	-0.192	0.885	-0.140	1.293	-0.108	0.914	1.781	1.119	1.592	0.331
Aggression-physical	0.507	0.442	1.146	0.465	-0.658	1.334	-0.493	0.746	1.613	1.048	1.540	0.331
Aggression-verbal	0.479	0.307	1.562	0.331	-0.985	0.845	-1.166	0.465	0.188	0.758	0.248	0.877
Aggression-anger	-0.254	0.327	-0.778	0.656	0.403	0.906	0.445	0.750	0.985	0.793	1.242	0.465
Aggression-hostility	-0.664	0.327	-2.030	0.202	0.571	0.916	0.624	0.711	1.538	0.800	1.923	0.216
Video game play (often)	0.501	0.127	3.934	**0.002**	0.206	0.347	0.594	0.711	0.310	0.305	1.015	0.531

5.8. References

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Chapter 6 | General Discussion

The fitness of an individual is driven by that individual's adaptations to abiotic and biotic environments. Biotic drivers may include trophic interactions, where a species evolves an ability to capture prey or avoid becoming prey of another species. Interspecific interactions may also involve competition for shared resources, where greater efficiency in finding or using resources may confer an adaptive advantage. However, species need not rely on genetic change to enhance fitness. Cognitive flexibility can lead to the accumulation of adaptive behaviours through exploiting the individual learning of others - a process known as "social learning" - which can result in the transmission of novel information or behaviours through entire populations (Hoppitt *et al.,* 2010). An understanding of population-level social transmission patterns requires an understanding of how individuals are connected within their social network and of the behavioural, social and physical factors that permit, promote or prevent information transfer from one individual to another. Examining such factors and their influence on social learning and information transmission across different study systems – plus the development of novel methodologies that allow these processes to be represented more realistically during both theoretical and empirical behavioural experiments – has been a major focus of this thesis.

In this thesis, I have approached the study of social learning from a novel perspective by considering how individual behaviours (from simple movement patterns to complex cognitive processes), the underlying connections between individuals and the physical properties of their environment can all work together to ultimately determine how information is propagated through a population. What follows is an overview of the literature and hypotheses described in Chapter 1 and the empirical research described in Chapters 2-5, followed by a synthesis of some key themes drawn from across those chapters (most notably the importance of individual variation in driving population-level information transmission patterns) and an explanation of the novel methodologies explored and produced throughout this thesis. I will then conclude with a discussion of the potential applications for this research in fields outside of ecology and evolution.

6.1. Chapter overview

In Chapter 1, I introduced the concept of social information transfer between two individuals occurring over three key stages (Figure 1.1) – requiring firstly an appropriate connection to form between two individuals to permit information transfer (as discussed in Chapter 1, the definition of a ‘connection’ here will depend on the particular social system and on the behaviour being learned); secondly, the ability and inclination of the ‘demonstrator’ to pass on novel information or behaviours to others; and thirdly, the ability and inclination of the ‘observer’ to learn this information from the demonstrator in question. I also introduced three key factors which I hypothesised to influence social transmission through populations – the spatial movements of individuals, the types of connections between those individuals and the characteristics of the demonstrators in question (Figure 1.2). The literature is dominated by research into social learning strategies, taken from the observer’s perspective, while investigations into the importance of spatial factors, social bonds and the information transfer capabilities of demonstrators are comparatively rare. As such, I have focussed on incorporating these factors into the social learning research to gain a more comprehensive insight into the individual-level factors that influence information processing at the population level. Through Chapters 2-5, I have explored the behavioural, physical and social factors influencing social information transmission across the three stages of information transfer introduced in Chapter 1. In each chapter, I focussed on different model systems and different methodologies, thus taking a comparative approach to the study of social learning.

In Chapter 2, using a spatially explicit, agent-based simulation model, I explored how among-individual behavioural variations influenced the population-level patterning of interactions. I found that among-individual differences in space-use behaviour resulted in faster, more efficient information transfer through the production of long-distance travellers which linked together spatially separate clusters of inactive individuals, while limiting the number of ‘unnecessary’ connections that form as a result of homogeneous mixing. This finding illustrates how the connections between individuals necessary for information transfer to occur (Figure 1.1, stage 1) can be broken and reformed depending on the spatial movements of those individuals (as hypothesised in Figure 1.2A). I also found that variation in activity (when activity influenced an individual’s tendency to transmit or receive information – i.e. Figure 1.1, stages 2 and 3) altered the structure of the population social network, resulting in the overproduction of regulatory network motifs known as ‘feed-forward loops’ (Mangan and Alon, 2003; Waters and Fewell, 2012).

In Chapter 3, using multi-network NBDA, I investigated how the social relationships connecting individuals (Figure 1.2B) drove the transfer of information in a population of zebra finches (*Taeniopygia guttata*). I found strong evidence that individuals learned largely from those they shared aggressive encounters with and, to a lesser degree, from their mates. I also found that a minority of highly connected individuals acted as ‘hubs’ of information for their connected conspecifics by learning the solution to a foraging task quickly and solving the task often. The comparative multi-network approach used in this chapter allowed me to assess how different social bonds connected birds together within the larger social network and the relative importance of these bonds for driving behavioural changes throughout the social group.

In Chapter 4, I described a novel tool – "Virtual Environments for Research into Social Evolution" (VERSE) – which uses gaming technology to allow the study of human social learning and behaviour within immersive, three-dimensional virtual environments and aims to overcome many of the limitations of previous research conducted in more restrictive laboratory settings (as discussed in Chapter 1). I gave space in the thesis for a detailed description of this methodology because of the clear but unexploited value of virtual reality software for the development of behavioural experiments. Within this chapter, I illustrated how gaming technology can offer researchers a way of building behavioural science experiments that parallel the naturalistic experiments found in the animal literature, while still offering a reasonable degree of experimental control. While my system may or may not be used more widely following publication, I hope that my illustration of what is possible using gaming environments will encourage others to explore this area in greater depth. The exciting findings from Chapter 5, in particular, demonstrate the value of such a tool very clearly.

In Chapter 5, I used VERSE to explore human social learning biases (Figure 1.2C) within complex, large-scale, three-dimensional environments in a series of experiments directly inspired by the animal literature. I found that, in these environments, humans used a mixture of social and asocial learning, but tended to rely on asocial information to a greater degree, unless there was a clear benefit of learning from others. Reliance on social information was influenced by the reliability of asocial learning, extra opportunities provided by asocial learning, variation in possible rewards and the difficulty in acquiring social information (potentially caused by the spatial distribution of demonstrators, as hypothesised in Chapter 1, Figure 1.2A). This balancing of social and asocial information is similar to findings in unrelated taxa, e.g. starlings (*Sturnus vulgaris*) (Templeton and Giraldeau, 1996) and nine-spined sticklebacks (*Pungitius pungitius*) (van Bergen *et al*., 2004). I also found strong evidence to suggest that, when learning from others, humans will favour the decisions of the majority and of the most successful demonstrators. Again, this aligns with findings in unrelated taxa (e.g. fish, Day *et al.,* 2001; Coolen *et al*., 2003; Kendal *et al*., 2009; birds, Aplin *et al,* 2015; and primates, Barrett *et al*., 2017; Canteloup *et al*., 2021; Van de Waal *et al.*, 2013), suggesting similar patterns of social information use across the human / non-human divide. Furthermore, this finding is in agreement with research conducted in more restrictive laboratory settings (Morgan *et al.*, 2012; Mesoudi, 2011; Molleman *et al.*, 2014), suggesting that human social learning biases can be generalised across contexts of different complexities.

In the following section, I outline some of the key themes that have emerged across the chapters that I have described above.

6.2. The importance of individual variation in determining the pathways of social information transmission

A particularly striking concept evident throughout this thesis is the existence of substantial behavioural variation at the individual level and its importance in determining information transmission dynamics at the population level. Within a social group, individuals are not all the same. They vary in their physical and behavioural characteristics, in their individual preferences, in their cognitive abilities, in the relationships they share with one another. Even the same individual will vary over time in their spatial movements, knowledge and experience, connectivity to and communications with other individuals. All of these factors and more will have a collective influence on who learns when, how and from whom.

In Chapter 1, I hypothesised three key individual-level factors that would have a profound effect on social information transmission at the group level – namely spatial movements, social connections and demonstrator characteristics (Figure 1.2). For each of these factors, among-individual variations are likely to play a key role. In the following sections, I expand on these earlier hypotheses and identify, based on the evidence throughout this thesis and in previous literature, five areas (illustrated in Figure 6.1) in which individual variation appears to play a key role in dictating how novel information enters and is subsequently transmitted through a population.

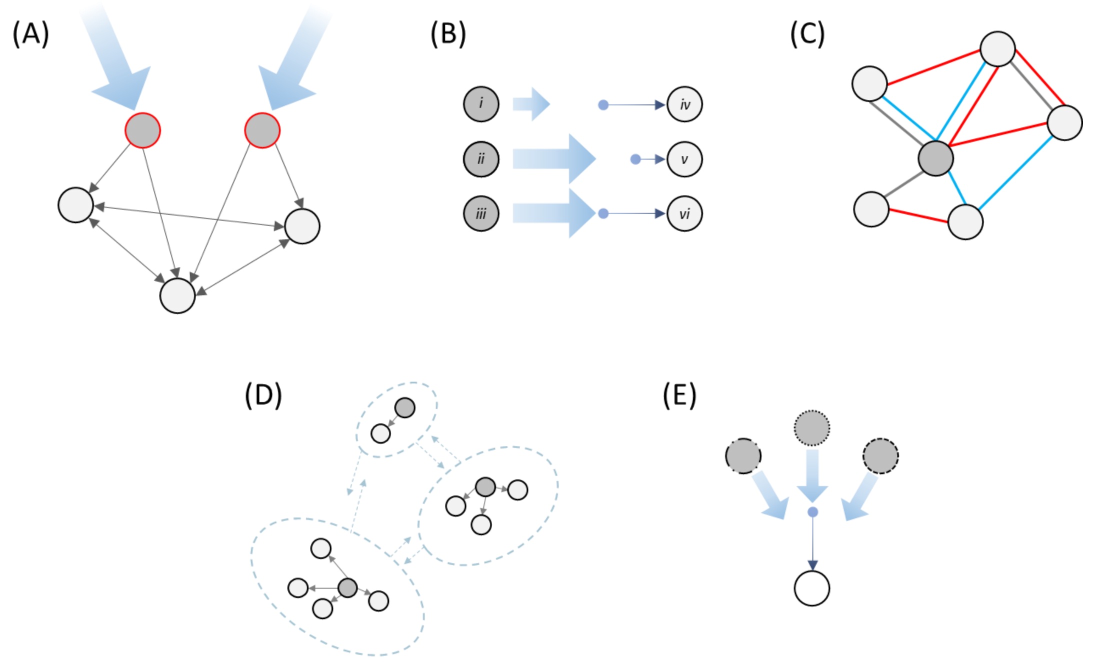

Figure 6.1. Five ways in which individual variation can dictate the pathways of social transmission through the population, from informed demonstrators (grey circles) to uninformed observers (white circles). **(A)** Some individuals may favour asocial learning (red outline) while others favour social learning (black outline) (as found in Chapter 5). Asocial learners allow up-to-date information, gathered directly from the environment, to enter the population. This information can then spread more rapidly through the population via social learners. **(B)** The tendency (indicated by the length of arrows) of individuals to transmit information to (thick arrows) and receive information from (thin arrows) others influences who learns from whom and thus the direction of social transmission (Chapter 2). A 'successful' exchange of information is represented by the two arrows meeting in the middle. Thus, in this example, information is only successfully transmitted from individual *iii* to individual *vi*. Individuals *ii* and *iii* have the potential to transmit information to individuals *iv* and *vi*, should they interact. However, individual *i* is unlikely to transmit information to others, while individual *v* is unlikely to receive it. **(C)** The types of connections shared by individuals (Chapter 3). These may represent, for example, different social relationships. Information may be transmitted through different connections at different rates. **(D)** The spatial locations of individuals (Chapter 2). Depending on the type of information being transmitted, individuals may be more likely to learn from those who are in close physical proximity. In this case, information is likely to transmit within clusters of local individuals (bounded by dashed lines) often or at a relatively fast rate (solid grey arrows), while social transmission between individuals who are more spatially isolated will be comparatively slower or occur less often (dashed blue arrows). **(E)** Characteristics of informed demonstrators (Chapter 5). An uninformed observer may choose to learn from specific demonstrators based on their individual characteristics (different patterned borders), even when they are equally connected to all possible demonstrators (e.g. all within close spatial proximity). Such preferences from the observer's perspective can promote information transfer along one pathway while blocking it in other potential pathways.

6.2.1. Variation in the tendency to learn socially dictates how novel information enters the population

First of all, individual variation in the tendency to learn socially versus asocially appears to be key in determining how novel behaviours initially enter and subsequently spread through the social network. Social learning is a relatively cheap and effective way of gaining information (Boyd and Richerson, 1985; Rendell, Boyd *et al.,* 2010), but a population of entirely social learners who never sample directly from the environment would be incapable of innovation and so would risk becoming fixed on behaviours that are suboptimal, outdated or even maladaptive. Similarly, populations that rely entirely on relatively costly asocial learning are likely to be outcompeted by those capable of at least some level of social learning (Enquist *et al.,* 2007; Rendell, Fogarty, *et al.,* 2010). Therefore, a mixture of both social and asocial learning is necessary for allowing populations to maintain a steady influx of information sampled directly from the environment, which can then spread more rapidly and efficiently through the population via social transmission (Figure 6.1A). This was demonstrated in Rendell, Boyd, *et al.*'s (2010) 'social learning strategies tournament' where, in a population of agents programmed with different social learning strategies, exclusive social learners were only successful due to their ability to 'parasitise' optimal information from asocial learners. Such variations in social information use may be particularly important in fluctuating environments, where populations must respond quickly and efficiently to up-to-date external cues. Again, this idea is well illustrated by Rendell and colleagues' social learning strategies tournament, where high levels of social learning combined with comparatively rare rates of innovation allowed the population to respond more effectively to changing environments through the development of a more extensive behavioural repertoire (Rendell, Boyd, *et al.,* 2011).

In line with this prediction, I demonstrated a mixture of social and asocial learning in two unrelated species. In Chapter 3, I estimated that around half of the learning events in a population of zebra finches involved social learning via a series of hypothesised pathways, indicating a mixture of both asocial and social learning within the population. While some of the remaining learning events may have involved alternative social learning pathways not included in the analysis, the task was introduced to a completely naïve population with no trained demonstrators and so at least some level of innovation must have occurred for the task solutions to initially enter the population. Similarly, in Chapter 5, I demonstrated considerable individual variation in reliance on social information in humans, ranging from complete reliance on to complete ignorance to the behaviours of demonstrators, depending on the individual and context. I also found that there were human participants who showed some consistency in their use of social information. This has been demonstrated in humans before (Toelch *et al.,* 2014), with some studies even categorising individuals into ‘conformists’, who disproportionately copy the majority, and ‘mavericks’, who ignore social information completely (Efferson *et al.,* 2008). As demonstrated in Chapter 5, those with a heavier reliance on asocial learning were able to exploit alternative solutions to a task that proved to be more profitable than those demonstrated by others (i.e. shorter navigation routes and additional food resources). By introducing these more profitable behaviours into the population, asocial learners have the potential to act as important sources of information to those who rely more heavily on social learning. At the individual level, being a largely asocial learner in a population of largely social learners may be disadvantageous, allowing others to ‘scrounge’ resources from you that you have expended time and energy in gaining (e.g. Barnard and Sibly, 1981; Giraldeau and Lefebvre, 1986; Rendell, Boyd, *et al.*, 2010). However, for highly social species, in which an individual’s survival is linked to that of the social group, the benefits to the population as a whole may outweigh the costs to the individual. This is perhaps most evident in eusocial insect species such as honeybees (*Apis mellifera*), in which some individuals act as ‘scouts’, specialising in searching independently for resources so that this information can be transmitted to the rest of the worker population (Dreller, 1998).

Once a novel behaviour has entered the population, it can then be propagated through the population via social learning. The specific route the information takes through the population will be determined by the available learning pathways between individuals. Individuals within a population are not connected homogeneously, and various factors can influence who is connected to whom within the larger social network and the direction of information transfer between those individuals. These factors can be as simple as variation in individual activity and movement patterns (Chapter 2) or as complex as variation in the social relationships between individuals (Chapter 3) or social learning biases towards particular demonstrators (Chapter 5) – and may have important implications for the development of culture by resulting in different behaviours being learned by different subsets of the population.

6.2.2. Variation in tendency to transmit and receive social information dictates the direction of information transfer along transmission pathways

Among-individual variation in personality traits that correlate with social information use as part of a 'behavioural syndrome' can result in directed information transfer along particular behavioural axes by influencing who transmits information to (and who receives it from) others (Figure 6.1B). This was demonstrated in Chapter 2, where the behavioural axis in question was activity – with higher-activity individuals passing information on to lower-activity individuals in a directional manner. Activity-related information transfer is most notable in honeybees, which vary greatly in their propensity to transmit information to others, with highly active foragers being more likely to recruit less active individuals to novel resources via 'waggle dancing' behaviour (Seeley, 1994; George *et al.*, 2020). In other species, personality traits such as boldness and/or exploratory behaviour can determine who transmits information to whom. For example, Dyer *et al.'*s (2009) experiment on guppies (*Poecilia reticulata*) demonstrated a tendency for 'shy' fish to follow 'bold' fish to novel feeders. Similarly, according to Marchetti and Drent (2000), exploratory behaviour is linked to social information use in great tits (*Parus major*). Specifically, 'slow' foragers, who were more thorough in their exploratory behaviour, were more likely to visit novel feeders when exploring alone, but less likely to visit feeders demonstrated by a tutor; while 'fast' foragers, who were less thorough, were much more likely to visit novel food sources that were demonstrated by a tutor than find them independently. Individuals may also vary in their tolerance to close – and potentially intrusive – observations by naïve conspecifics, in which case, more tolerant individuals are more likely than less tolerant individuals to transmit information to others (Kline, 2015).

In some cases, variation in reliance on social versus asocial learning, as discussed above, may, in addition to dictating how information initially enters the population, drive the direction of information flow between individuals. Often, individuals will not rely solely on either social or asocial information and will instead use a mixture of the two, but may do so to different degrees. For example, in Chapter 5, individuals varied considerably in their use of social information, forming a behavioural axis ranging from complete ignorance to complete reliance on social information, depending on the context. Largely social learners will seek information from their conspecifics more readily than largely asocial learners. This may result in the kind of transitive network substructures and directed information transfer demonstrated in Chapter 2, with those who rely more heavily on asocial learning transmitting information to those who rely more heavily on social learning. In other cases, individuals may even specialise in information transmission by actively facilitating learning in others. For example, helper meerkats (*Suricata suricatta*) ‘teach’ pups to interact with dangerous prey by disarming and introducing this prey to them, thus providing them with opportunities to learn prey-handling skills that would be potentially lethal for them to learn independently (Thornton and McAuliffe, 2006). Similarly, various species of ant engage in ‘tandem runs’, where a knowledged individual leads a naïve individual to a novel resource (Franks and Richardson, 2006). The waggle dances of informed honeybees also act specifically to transmit knowledge of novel floral resources to uninformed workers (von Frisch, 1967). In some cases, there may even be temporal variation in an individual’s tendency to transmit information that can act to boost information transfer through the population at crucial stages. Grass-cutting ants (*Acromyrmex heyeri*), for example, gather fewer resources at the beginning of their foraging bout, allowing them to return to the nest more quickly and inform nestmates about the location of novel resources (Bollazzi and Roces, 2011).

6.2.3. Variation in the social relationships between individuals can determine the possible pathways of information transmission through social groups

Social groups can be complex and individuals can vary in the relationships or social bonds they share with others (Figure 6.1C). A population may, for example, be composed of kin and non-kin, individuals who share positive associations and others who respond agonistically to each other, those who form mated pairs, and so on. If individuals who share specific relationships are more likely to associate with one another, display biases towards learning from one another, or actively transmit information to one another, specific relationship-based social learning pathways may form (as demonstrated in zebra finches in Chapter 3). By influencing the pattern of information transmission within the social group, relationship-based social learning may, in turn, result in among-individual variation in learned behaviours, e.g. knowledge / behavioural traits shared by friends or family. As discussed below, there are various examples of social relationships that can dictate information transmission through populations – some of which were explored in Chapter 3.

In populations containing individuals of mixed relatedness, for example, individuals may be more likely to learn from kin than non-kin. Due to their shared genetics, demonstrators should gain indirect fitness benefits from helping relatives to learn adaptive behaviours and so may be more tolerable to (or even encourage) observations from kin. Within a larger population, relatives may therefore be more likely to associate with one another, thus making social transmission within family units more likely. This is well illustrated by African elephant (*Loxodonta africana*) societies, in which females associate strongly within 'core groups' of related individuals (Archie and Chiyo, 2012). Information transmission between kin may come with additional benefits if relatives are more likely to occupy the same ecological niche or share similar behavioural capacities that make their behaviours more advantageous or easier for the observer to learn. Thus, individuals may develop biases towards learning from kin over non-kin. For example, Schwab *et al.* (2008) demonstrated that common ravens (*Corvus corax*) were more likely to copy the object manipulation and caching behaviour of siblings over non-siblings. Similarly, Siberian jay (*Perisoreus infaustus*) juveniles pay more attention to and are more likely to copy the predator mobbing behaviour of their parents over unrelated adults (Griesser and Suzuki, 2016), juvenile zebra finches learn foraging skills almost exclusively from their parents (Farine *et al.*, 2015) and bottlenose dolphins (*Tursiops aduncus*) learn from their mothers how to use sponges as 'tools' (Wild *et al.,* 2019).

'Vertical transmission' from parent to offspring is likely to be particularly prevalent across the animal kingdom due to the clear adaptive benefits for both parties. Individuals who have successfully raised offspring are likely to be in possession of behaviours that are adaptive in the offspring's natal environment, and so parent-to-offspring information transfer will allow juveniles to learn these important survival skills from more experienced adults, while also allowing parents to increase their offspring's chances of survival. In some cases, parents may provide their offspring with learning opportunities passively, for example, by providing them with partly processed foods or by remaining in close proximity and thus permitting close observations of their behaviour (van Schaik, 2010). In other cases, parents may actively encourage their offspring to learn specific skills. Active teaching of skills to offspring by parents occurs routinely in many human societies – although is comparatively rare in traditional hunter-gatherer communities (Boyette and Hewlett, 2018) – and has also been documented in some animal species. In some chimpanzee (*Pan troglodytes*) populations, for example, adult females help their offspring to learn how to foraging using tools by dropping or actively provisioning them with their own tools (Boesch, 1991; Musgrave *et al.*, 2016). Similarly, rhesus macaque (*Macaca mulatta*) mothers appear to actively encourage independent locomotion skills in their infants (Maestripieri, 1995). Pied babblers (*Turdoides bicolor*) appear to teach their chicks to associate specific "purr" calls with food, which they later use to direct their offspring towards food and away from predators (Raihani and Ridley, 2008). Similarly, the Australian superb fairy-wren (*Malurus cyaneus*) teaches its offspring particular identification calls while still in the egg, allowing parents to distinguish their own young from parasitic cuckoos once the chicks have hatched (Colombelli-Négrel *et al.*, 2012).

Unrelated individuals within a social group may also be connected by shared characteristics or particular social bonds. In populations where sexual division of labour exists, for example, same-sex social networks may become the dominant pathways of social learning. This is the case in some hunter-gatherer communities, where information about hunting and crop-growing is transmitted between males, while information about medicinal plants is transmitted between females (Henrich and Broesch, 2011). Individuals may share both positive (e.g. grooming, huddling) and negative (e.g. aggressive encounters) relationships with their conspecifics and, as demonstrated in Chapter 3, such relationships can dictate the pathways of social transmission through the population. Social learning pathways may form between individuals who associate positively as a direct result of these individuals being in close proximity more often, making them more likely to observe each other performing novel behaviours. For example, network-based analyses have revealed that information about novel tasks transmit along affiliative interaction networks in populations of starlings (*Sturnus vulgaris*) (Boogert *et al.,* 2014), ravens (Kulahci *et al.,* 2016) and redfronted lemurs (*Eulemur rufifrons*) (Schnoell and Fichtel, 2012). Similarly, familiarity facilitates social learning of foraging routes in guppies (Swaney *et al.,* 2001) and nest building in zebra finches (Guillette *et al.,* 2016). On the other hand, some species show the opposite tendency and pay more attention to unfamiliar individuals, thus essentially seeking information from outside their particular social group. This has been most notably demonstrated in Norway rats (*Rattus norvegicus*) (Galef and Whiskin, 2008) and may offer alternative benefits, such as the introduction of knowledge not already shared by closely affiliated individuals.

One might expect aggressive interactions to hamper social learning by causing individuals to actively avoid each other. However, as demonstrated in zebra finches Chapter 3, aggression may act as an important facilitator of social transmission. Learning from aggressors has been demonstrated before in zebra finches (Clayton, 1987; Jones and Slater, 1996) and, more anecdotally, in several other bird species, including indigo buntings (*Passerina cyanea*) (Payne, 1981) and white-crowned sparrows (*Zonotrichia leucophrys nuttalli*) (Baptista and Petrinovich, 1984). The reasons for individuals learning from their aggressors are unclear. I speculated that it may be a result of aggressors paying more attention to one another in order to avoid unnecessary conflict – or that the aggressive interaction itself is an indicator of close association – although other explanations were also discussed in Chapter 3.

Similarly, dominant-subordinate relationships have been linked to social transmission in various species. The direction of social transmission along dominant-subordinate pathways, however, varies between studies, and a case can be made for the adaptive value of either. On the one hand, routinely soliciting information from subordinates can provide dominants with cheap access to novel behaviours, allowing them to avoid the relatively costly process of independent learning and innovation. For example, trophallaxis in several ant species, during which nutritional information is transferred, tends to be directed from subordinates to dominants (Jeanson and Weidenmüller, 2014). On the other hand, dominant individuals may drive information transfer through the rest of the population by gaining early access to novel resources through their status, allowing them to inadvertently provide more subordinate individuals with increased opportunities for learning. This has been demonstrated in chimpanzees and vervet monkeys (*Chlorocebus aethiops*), where dominant-to-subordinate information transmission can be explained by the dominant individuals' tendency to monopolise a novel task (Kendal *et al.,* 2015; Watson *et al.*, 2017; Canteloup *et al.,* 2020). Similarly, in Chapter 3, I demonstrated that the majority of social learning events involved fight losers learning from fight winners, which appeared to be due to a subset of fight winners who were highly connected within the social network solving the task early and often. Even within the same population, the direction of information transfer through dominant-subordinate networks can reverse depending on the context, as has been demonstrated before in Arabian babblers (*Turdoides squamiceps*). This was attributed to context-specific variations in who tended to innovate, with subordinates being more likely to innovate when given completely novel tasks (Keynan *et al.*, 2015) and dominants being more likely to generalise previously-learned behaviours to new situations (Keynan, 2015, pp.69-94). This emphasises how individual behavioural variation within the same social group can drive information flow in a particular direction along specific social learning pathways.

Individuals may also share information with their mates – as demonstrated in zebra finches in Chapter 3. In species that form strong pair bonds, selective learning from mates may occur, particularly if mates tend to associate with each other for prolonged periods, thus increasing the likelihood that they will observe each other using novel behaviours. In social groups where mate-mate information transmission does occur, this may lead to the development of pair-specific behavioural preferences (Avital and Jablonka, 2000), which may, in turn, be passed on to offspring. In species where both parents contribute to the upbringing of offspring, the transmission of information between mates may also be an essential component of parental cooperation necessary to increase their offspring's survival (Avital and Jablonka, 2000). Learning from mates and the subsequent development of pair-specific behaviours may also have important social benefits. For example, there is evidence that certain bird species imitate the calls of their mates, which may contribute to pair bond formation and mate recognition (Hile *et al.,* 2000; Keenan and Benkman, 2008; Sewall, 2009; Luef *et al.,* 2017). Evidence from Chapter 3 contributes to the relatively understudied area of mate-biased social learning by revealing mate-mate social transmission of novel foraging skills in the highly social zebra finch. As discussed in Chapter 3, mate-mate information transfer is unlikely to form a primary pathway of social learning through large social groups due to the sparseness of such social networks. However, the multi-network approached used in Chapter 3 revealed how even sporadic mate-mate links can contribute to the flow of information through less sparse networks – potentially by linking together disconnected sections of the larger social network in a similar fashion to the long-distance travellers discussed in Chapter 2. In addition, mate-biased social learning may be an important precursor of family norms and traditions, and so the importance of these social bonds on learning should not be overlooked. Further research is required to establish how important mate-mate relationships are in dictating the patterns of social transmission in different contexts, how this differs for species with and without strong pair bonds and the ultimate consequences of mate-biased social learning in the development of pair- or family-specific behavioural traditions.

6.2.4. Spatial variation promotes information exchange within, while slowing it between, local sub-clusters of individuals

One factor that can have a profound effect on who learns from whom, but is often not taken into account in more restrictive, lab-based experiments, is individual variation in space (Figure 6.1D). The influence of spatial variation on social learning is easy to picture – in order for an individual to learn socially, it must be close enough to the demonstrator (or the cue left behind by the demonstrator) to observe a novel behaviour being performed or to receive communicated information. Exactly how close is 'close enough' is likely to be determined by the type of behaviour being learned and the mechanism of learning occurring. Learning via 'local enhancement', for example, which involves being attracted only to the location of a novel stimulus, is likely to be possible over much greater distances than imitation, which requires direct observation and copying of potentially complex behaviours (Hoppitt and Laland, 2013). Similarly, information transmitted via tactile cues (e.g. trophallaxis or antennation in social insect species) will require much closer contact than information transmitted via visual cues (e.g.

food processing skills), which will, in turn, require closer proximity than information transmitted via audio cues (e.g. song learning in birds). In addition, some types of social information (e.g. insect pheromones, food left behind by successful foragers) will last longer in the environment than information that can only be received instantaneously (e.g. observations of motor skills), thus giving distant individuals the opportunity to find and receive such information and potentially making social learning less susceptible to the influences of an individual's location at the time a signal is transmitted.

Variations in individual location are likely to result in dynamic social learning pathways, with individuals breaking and re-establishing connections over time. Even in populations where certain individuals display strong associations, such as the 'core groups' of female African elephants in Archie and Chiyo's (2012) study, these groups may become divided and reorganised over time. At an even finer scale, small-scale movements and/or aversion of gaze may temporarily disconnect even two closely associating individuals at the time a particular behaviour is being performed, which could prevent information from being exchanged. Information transmission patterns within populations of mobile individuals will therefore depend on how this information is communicated (i.e. whether close proximity and/or active observation is required) and the balance between association dynamics and the rate of social transmission (i.e. whether information is likely to be communicated while demonstrator and observer are in close enough proximity for the exchange to occur). The importance of considering animal social networks as dynamic entities was briefly highlighted in Chapter 2, where analyses of time-ordered social networks from populations with moving individuals yielded different results to those performed on static networks.

Where individuals vary in space, some individuals or groups of individuals may even become isolated from the rest of the social group. Spatial isolation may result in individuals struggling to gain access to social information, essentially breaking the social learning pathway. This may result in isolated individuals becoming more reliant on independent learning. This appeared to be the case in Chapter 5, where human participants were less likely to use social information in environments where demonstrators were spatially scattered. However, in some cases, spatial separation of clusters of individuals may be beneficial to the population – e.g. by helping to regulate information flow or hamper the spread of pathogens through a population. *Lasius niger* ants, for example, actively isolate themselves from other workers when exposed to pathogens (Stroeymeyt *et al.*, 2018).

The experiment described in Chapter 2 revealed that among-individual variations in space use can result in faster, more efficient information transfer between local clusters of otherwise spatially isolated individuals by connecting them with few, wider roaming individuals. This ties in well with previous findings in hunter-gatherer communities, where few, strong connections between households provided by unrelated 'friends' were found to improve the efficiency of information transfer (Migliano *et al.,* 2017). Similar clustering of individuals may also be an important precursor of local traditions and cumulative culture. By slowing information transfer through the population as a whole while encouraging localised innovations and information exchange, spatial separation of social groups can lead to the development of local behavioural traditions. For example, for species such as white-crowned sparrow (*Zonotrichia leucophrys*), corn buntings (*Emberiza calandra*) and sperm whales (*Physeter microcephalus*), spatially distant social groups have been known to develop local dialects (Slater, 1986; Rendell and Whitehead, 2005), most likely because individuals learn their vocalisations from those they are in closer spatial proximity to. Where spatially separated groups of individuals have developed contrasting solutions to the same problem, loose interconnections between these local groups (e.g. through the movements of highly mobile individuals, as illustrated in Chapter 2) can lead to recombination events, where aspects of two or more local traditions are combined to produce a potentially more effective overall solution (Migliano *et al.*, 2020).

It is therefore highly important that future research takes into account the influence of spatial locations on learning opportunities. This is particularly the case for experiments that tend to be conducted in small-scale laboratory environments – e.g. many studies on social learning strategies in humans, as discussed in Chapter 1. I discuss opportunities for novel methodologies to address these deficiencies and allow the incorporation of potentially important spatial factors into previously restrictive behavioural experiments in section 6.3, below.

6.2.5. Variation in demonstrator characteristics and observer biases determine which individuals are the most influential sources of information.

The pathways of social transmission can also be dictated from the observer's perspective by biases towards particular sources of information. When met with multiple information sources, such as incoming information from multiple social learning pathways, the observer must make a decision about which information to make use of. It may be possible to combine multiple sources of information, however this is costly in terms of time and energy, and may become problematic if multiple demonstrators perform behaviours asynchronously across time and space. In which case, it may be more beneficial to rely on innate, potentially context-specific, biases towards acquiring specific types of information or learning from specific types of demonstrator (Figure 6.1E). Where model-based biases exist, particularly if they are shared by many individuals within the population, demonstrators with specific physical and/or behavioural characteristics may become particularly influential sources of information within their social networks. This may have important effects on population-level information transmission patterns, as there may be an extent to which the potential social learning pathways are constrained by the pool of traits within that population. In a population where observers preferentially learn from large, dominant demonstrators, for example, a small, subordinate individual – spatially and socially connected to others and in possession of adaptive information – may become an overlooked opportunity for learning.

At the individual level and from the observer's perspective, model-based social learning biases (Rendell, Fogarty, *et al.*, 2011) can be beneficial if demonstrator characteristics can be used as a proxy for their likelihood of producing profitable behaviours. For example, in species where body size indicates an ability to gain adequate nutrition, we may expect a bias towards learning from larger individuals to develop. This has been most notably demonstrated in nine-spined sticklebacks (Duffy *et al.*, 2009). There is also some evidence that taller humans are more influential (Blaker *et al.,* 2013); although I found no evidence to suggest humans copied larger over smaller demonstrators in the virtual reality experiment in Chapter 5. Individuals may also display biases towards learning from the most dominant individuals in the social group, since dominance status is indicative of an individual's overall success. Domestic hens (*Gallus gallus domesticus*), for example, tend to copy the behaviour of dominant over subordinate demonstrators in a foraging task (Nicol and Pope, 1994; 1999). Similarly, in Chapter 5, I found a marginal effect of demonstrator dominance on social influence in humans – plus, the bias towards taller individuals in Blaker and colleagues' study may reflect a dominance-related bias in humans if participants perceived taller individuals as more dominant (as in Lourenco *et al.,* 2016). However, dominant individuals may not always make the best demonstrators if their ability to solicit information from their subordinates, as discussed above, makes them unmotivated to attempt novel tasks. Subordinates may therefore be more innovative than dominants – as demonstrated in meerkats (Thornton and Samson, 2012). In addition, if joint interaction with a knowledged demonstrator is required for effective social learning to occur, dominant individuals limiting observer access to a novel task may also limit their ability to act as demonstrators of information – as demonstrated in olive baboons (*Papio hamadrycis anubis*) (Caldwell, 2003). If subordinates prove to be more innovative and also more tolerant to close observations, a bias towards copying subordinates may offer a more effective way of gaining access to novel solutions. In line with this, novel behaviours have been shown to transmit more effectively through chimpanzee groups when seeded with a subordinate demonstrator than with a dominant demonstrator (Watson *et al.*, 2017). Biases towards learning from subordinates may, however, be masked by a dominant individual's ability to monopolise novel objects (Watson *et al.*, 2017).

Sex-based biases are relatively understudied but appear more likely to develop when there is sex-specific knowledge of a particular environment or task. If one sex is philopatric while the other migrates away from the natal environment, for example, s/he who remains is more likely to possess useful knowledge about the natal environment, as demonstrated in vervet monkeys (Van de Waal *et al.,* 2012). The dispersive sex, on the other hand, is more likely to encounter novel problems and this may be reflected in a tendency to be more persistent in their asocial learning efforts – as demonstrated in meerkats, where males (the dispersive sex) are more innovative than females (Thornton and Samson, 2012). Similarly, if one sex dominates a particular task, context-specific sex biases are likely to develop, as demonstrated in hunter-gatherer communities, where individuals are more likely to seek advice about hunting or crop-growing (male-dominated activities) from males and about medicinal plants (female-dominated activities) from females (Henrich and Broesch, 2011). When subjected to a series of virtual tasks, I found little evidence of any sex-based biases in humans, with the exception of a slight male bias in the foraging task, which could suggest that males are viewed as possessing greater foraging skills (Chapter 5).

A demonstrator's age may also mediate their social influence over others. The oldest individuals in the population may act as important sources of information, as these individuals must have developed a repertoire of behaviours profitable enough to allow them to survive to an old age. In support of this, preferences for observing and copying older individuals have been demonstrated in chimpanzees (Biro *et al.,* 2003; Horner *et al.*, 2010), capuchins (Coelho *et al.,* 2015), indigobirds (Payne, 1985) and humans (Henrich and Henrich, 2010; Wood *et al.,* 2013). Similarly, older African elephant matriarchs have a greater influence over the behaviours of their herd than younger matriarchs, as discussed in more detail below.

In Chapter 5, I found the strongest evidence for success-based and positive frequency-dependent social learning biases in humans – both of which have been demonstrated in humans before (Morgan *et al.,* 2012; Mesoudi, 2008; Mesoudi, 2011; Molleman *et al.,* 2014; Miu *et al.,* 2018). Both strategies have clear adaptive value and may be more reliable than the model-based biases discussed above, which are reliant on an individual's characteristics acting as a reliable indicator of its tendency to perform more profitable behaviours. As discussed above, even individuals with characteristics indicative of success may vary in their willingness or ability to transmit information to others (demonstrated in Chapter 2 to have a profound effect on information transmission patterns) or in the contexts in which they tend to perform better. Copying the demonstrator who receives the highest payoff in a given context comes with the time and energy constraints of observing and comparing the actions of multiple individuals, but ensures that naïve individuals learn only the most profitable behaviours. Thus, it is easy to envisage why a tendency to copy successful individuals has been documented in a wide range of taxa, including insects (Czaczkes *et al.,* 2019), fish (Coolen *et al.,* 2005; Kendal *et al.,* 2009), birds (Payne, 1985; Seppänen *et al.,* 2011), bats (Wilkinson, 1992), humans (Mesoudi, 2008; Mesoudi, 2011; Wood *et al.,* 2013; Chapter 5) and other primates (Barrett *et al.,* 2017).

Similarly, if a behaviour has accumulated in a population to a point where it is now used by the majority, said behaviour must be not only profitable, but also able to sustain use by a large number of individuals, making it a behaviour that is probably worth learning. This likely explains why a tendency to conform to local norms has been documented in a variety of different species and contexts, e.g. mate choice in fruitflies (*Drosophila melanogaster*) (Danchin *et al.,* 2018), foraging in nine-spined sticklebacks (Coolen *et al.,* 2005; Pike and Laland, 2010), great tits (Aplin *et al.,* 2015) and chimpanzees (Haun *et al.,* 2012), and problem-solving in humans (Morgan *et al.,* 2012; Haun *et al.,* 2012; Chapter 5). Positive frequency-dependent social learning biases are also important for the development of culture – if individuals tend to conform to a solution already prevalent in the population, rather than copying rarer variants or innovating novel solutions, stable traditions are much more likely to form (Claidière and Whiten, 2012). Both success- and frequency-based social learning biases can allow observers to filter out the most profitable behaviours to learn – and may also have important impacts on information transmission through the population as a whole, especially when both exist together. Individuals who are prone to copying only the most successful demonstrators can curb the transmission of suboptimal behaviours that have found their way into the population; while individuals who are prone to copying the majority allow the spread of these profitable behaviours to the remainder of the population, resulting in the formation of group-level decisions and behaviours.

6.2.6. Keystone information transmitters

Where individuals in a population vary in their tendency to acquire and transmit information to others, a select few 'keystone' individuals may exist who disproportionately drive information transfer through their social group (Figure 6.2). In previous literature, the existence of such key individuals has been most notably demonstrated in ant societies, where few select individuals can play key roles in colony organisation and functioning. This includes 'catalysts', which serve to increase worker activity, and 'organisers', which initiate and maintain collective colony processes (Robson and Traniello, 1999). Often, insect colonies rely on a very small proportion of individuals to carry out most of the colony's work (Charbonneau *et al.*, 2017) and the work of these key individuals can drastically impact the efficiency of colony processes (Dornhaus *et al.* 2008). The removal of 'organisers' from ant colonies, for example, can result in a collective task not being performed at all (Robson and Traniello, 1999).

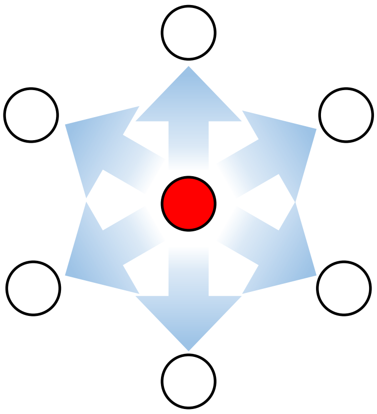

Figure 6.2. Keystone information transmitters. Within a population, certain 'key' individuals (red circle) can have a disproportionate influence over the behaviours of others. This may be due to a number of individual characteristics, including their connectedness within the social network, their ability to gain novel information more rapidly than their peers, their tendency to transmit this information to others and/or any behavioural or physical characteristics that make them more appealing as demonstrators of information.

In some animal populations, even a single individual may act as an essential communicator to the whole population and their individual characteristics may impact on their ability to coordinate group activities. For example, in African elephant communities, the vocal discrimination abilities of the herd is significantly influenced by the age of its matriarch. Herds led by older matriarchs show enhanced defensive responses (e.g. attentiveness, bunching together) towards the calls of unfamiliar individuals (McComb *et al.,* 2001) and dangerous predators (McComb *et al.,* 2011). This is believed to be a direct result of older individuals, with a more extensive ecological knowledge built up over a longer period of time, communicating the most appropriate responses to the rest of the herd – thus demonstrating how a single individual can act as a crucial repository of social information.

There are various reasons why a single individual (or set of individuals) may be disproportionately influential over the behaviours of their peers – several of which can be found within the chapters of this thesis. As discussed by Krause *et al.* (2010), a high level of connectivity within the social network is one reason why an individual may play a key role in information (or disease) transmission. I found such a pattern in zebra finches, where a select few highly connected individuals acted as 'hubs' of information about a novel foraging task (Chapter 3). However, high levels of connectivity is not the only reason why an individual may have a disproportionate influence over the behaviour of others. If a highly connected individual never gains access to a particular piece of information, for example, it will be unable to transmit this information to others. Individuals who gain early access to novel information (e.g. due to higher cognitive abilities, greater exploratory tendencies, a greater capacity to innovate or an ability to monopolise novel objects over its conspecifics) will have more opportunity to demonstrate this information to others and may therefore act as key sources of novel information. For example, the highly connected individuals in Chapter 3 also learned how to solve the novel foraging task early on in the study. As these individuals also tended to win aggressive encounters against their conspecifics, I concluded that their early solving of the task was an important driver of information in the fight winner to fight loser direction. In addition, as discussed above and in Chapter 2, where some individuals are more prone to passing on information to (or even promoting learning in) others, these individuals can act as key sources of social information within the population. Similarly, those individuals who provide a ‘link’ or ‘bridge’ between spatially or socially isolated subgroups may play a key role in information transmission. This was demonstrated by the long-distance travellers in Chapter 2 and in the hunter-gatherer example above, where friends provided important links between unrelated households (Migliano *et al*., 2017). Similarly, in school organisations, individuals who serve as communication channels between different departments play important roles in coordination and school-wide decision making (Bakkenes *et al.,* 1999).

In addition to the behavioural characteristics of the demonstrators themselves, the identity of such key information transmitters may be determined by where observers choose to focus their attention. If many observers share a bias towards learning from the same demonstrators, for example, the behaviours of these demonstrators will have a larger impact on the population than those who receive comparatively little attention. In some social societies, demonstrators who have, in the past, proved themselves in terms of skill and knowledge can gain respect and trust from their peers, giving them a prestigious status which can further boost their social influence in the future (Henrich and Gil-White, 2001; Atkisson *et al.,* 2012; Jiménez and Mesoudi, 2019; Brand *et al.*, 2020; Bond and Gaoue, 2020). In addition, because prestige is maintained through the respect and admiration of one's peers, prestigious individuals are highly motivated to build and maintain positive relationships, which may further increase their level of connectivity within the social network (Case *et al.,* 2018; Ketterman and Maner, 2021). However, if an individual's popularity is determined by characteristics unrelated to their ability to perform well in a particular task (e.g. their attractiveness or likability; Kim and Kim, 2022), then these influential individuals may not necessarily be in possession of the most beneficial information – and so learning selectively from popular individuals may come at the expense of ignoring less popular, but potentially more skilled, individuals. In some cases, the maintenance of such popularity is actually at the expense of task performance (Case *et al.,* 2018), which highlights how the presence of keystone information transmitters can easily become disadvantageous to the population if these individuals are not in the possession of the best knowledge. Thus, due to their disproportionate influence over the rest of the population, the actions of these keystone individuals – whether adaptive or maladaptive – can have a profound impact on the functioning and overall survival of the entire social group, and, if their conspecifics are particularly dependent on these individuals as sources of information, their removal from the population could theoretically lead to a complete breakdown of communication.

6.3. Novel methodologies for studying social learning and information transmission in realistic, spatially explicit environments

A major contribution of the research described in this thesis is through the development of novel methodologies that permit social learning, behaviour and information transmission to be studied in more realistic scenarios than current methodologies often permit. The most notable of these is the virtual platform for studying human social learning, VERSE, presented in Chapter 4. A major point of discussion throughout this thesis has been the lack of realism and ecological validity of human social learning experiments – including abstract tasks, unrealistic sources of social information and localised spatial scales. The potential for open-world virtual games for studying human behaviour has been highlighted before (Bainbridge, 2007; Lofgren and

Fefferman, 2007; Balicer, 2007; Johnson and Levine, 2008; Hou, 2012; Lakkaraju *et al.,* 2018; Brookes *et al.,* 2020) and an increasing body of evidence indicates that the social interactions and behaviours occurring within such virtual environments offer a realistic representation of real-life behaviours (Williams *et al.,* 2006; Cole and Griffiths, 2007). Despite this, no tool has previously been built specifically for the purpose of conducting realistic social learning experiments in the way suggested here, within an ecology and evolution framework. VERSE has exciting potential to contribute greatly to social learning research by offering a novel way to study human behaviour in realistic scenarios, within naturalistic, large-scale, immersive environments – particularly if combined the experimental framework recently described by Brookes *et al.* (2020) which is specifically designed to aid researchers in creating behavioural experiments within Unity, the platform in which VERSE was built. As demonstrated in Chapter 5, VERSE also offers a unique way of replicating animal behavioural experiments using human participants.

In Chapter 2, I introduced an agent-based, spatially explicit model designed to investigate the effects of individual behaviours on social network structure in a population of mobile individuals. These types of models are being increasingly used as a way of investigating how fine-scale individual processes produce emergent, larger-scale outcomes such as habitat use patterns (McLane *et al.,* 2011), disease transmission (Pie *et al.,* 2004; Bonnell *et al.,* 2010) and collective decision-making (Strandburg-Peshkin *et al.,* 2013; Yang *et al.,* 2019; Watzek *et al.,* 2021). My model allows factors such as individual behavioural variation, temporal changes in spatial location, interaction / communication distances and population size to be incorporated into social learning models, either as variables of interest or as a way of improving model realism through the incorporation of stochastic or partly stochastic processes.

The zebra finch experiment described in Chapter 3 expanded on a relatively recent method of detecting social transmission through several potential social learning pathways, known as multi-network NBDA (Farine *et al.,* 2015; Hoppitt, 2017), to study social transmission using a novel approach. While most social learning experiments consider how social information is transmitted through association or proximity networks, under the assumption that closely associating individuals are more likely to learn from one another (e.g. Allen *et al.,* 2013; Boogert *et al.,* 2014; Aplin *et al*., 2015), I investigated the possibility that the social relationships connecting pairs of individuals within the social network determined the pathways of social transmission through the group. So far, this has only been done in a handful of other studies – most notably Farine *et al.*'s (2015) work on zebra finches, which focussed on the connections between adults and juveniles, Kulahci *et al.*'s (2016) study on ravens, which focussed on affiliative and agonistic relationships, and Wild *et al.*'s (2019) recent work on parent-offspring social transmission in bottlenose dolphins. Chapter 3 expands on this methodology even further by taking a greater number of social relationships, considering each as a potential social transmission pathway and treating every possible combination of these pathways as a hypothesis as to the overall pattern of learning in the population. While this method may be more time-consuming and computationally intensive than examining the influence of each relationship separately, it is certainly a worthwhile method to consider – particularly because the influence of comparatively sparse networks may not be detectable unless combined with denser networks. This was demonstrated in Chapter 3, where networks connecting mated pairs (and therefore consisting of only a few sporadic connections) did not explain the observed patterns of information exchange, but did add to the explanatory power of alternative networks.

6.4. Future research

Throughout this summary chapter, I have pointed out various areas for potential novel research. In the following paragraphs, I lay out some more specific ideas in relation to the findings discussed throughout this thesis.

Social transmission of novel behaviours is a complex process which, as discussed extensively throughout this thesis, is dependent on a number of social, spatial and behavioural factors. First and foremost, future social learning research – both theoretical and empirical – should aim to incorporate these factors in order to gain a more realistic picture of social learning processes. Theoretical models should particularly aim to incorporate spatial factors and individual behavioural variations which, as discussed in Chapter 2, can have pronounced effects on group-level interaction patterns compared to analyses of fixed social networks. An interesting next step would be to expand the model in Chapter 2 to incorporate resources external to the nest and pit colonies with different pools of individual-level characteristics against each other to determine which characteristics contribute to colony success. For example, do individual variations in spatial movements, shown in Chapter 2 to increase the efficiency of information transfer, improve colony responses to varying resources?

Agent-based models have a lot of potential to investigate how individual-level behaviours can dictate population-level information transmission. Depending on the system and type of information being modelled, the realism of simulations such as that presented in Chapter 2 could be improved further by having agents base their decisions on visual sensing (as in Strandburg-

Peshkin *et al.,* 2013). The incorporation of environmental structuring (similar to Pie *et al.*, 2004) would allow more in-depth investigations into the importance of physical barriers for information transmission. In addition to modelling information flow, models such as these could offer important insights into the factors influencing disease dynamics and gene flow. Interestingly, a recent paper unearthed an additional potential application for agent-based, spatially explicit simulation models, such as that described in Chapter 2, in the production of biologically relevant null models for network motif analyses. Traditionally, when determining the significance of particular substructures within population social networks, researchers compare their relative abundances to those of randomly-generated networks (e.g. Waters and Fewell, 2012). Hart and colleagues (2021), however, argue that random networks do not account for the non-independence commonly seen in natural systems – for example, it is assumed that any two nodes, regardless of their individual characteristics, spatial location and so on, are equally likely to be connected to one another. In Chapter 2, my approach was to compare population social networks generated by simulations with inter-individual behavioural variations to a null 'Uniform' condition where these variations did not exist. Thus, the null model was able to incorporate the influences of individual movements and interactions on social network structure. This highlights the potential for such models in the development of more biologically and physically realistic null models, which account for the natural non-independence of interactions, for comparison with empirical data. Since the study described in Chapter 2 was conducted prior to the publication of Hart *et al.* (2021), this potential application was not explored in its entirety in this thesis, however the concept is briefly illustrated at the end of Chapter 2.

Empirical studies should aim to promote natural interactions and learning processes. Animal studies have already taken great steps in this direction through the use of statistical approaches such as NBDA which allow populations of individuals to navigate their environment and interact with each other naturally. NBDA offers a way of analysing the importance of social bonds (e.g. Chapter 3; Wild *et al.,* 2013; Farine *et al.,* 2015), spatial proximity (e.g. Boogert *et al.,* 2014; Kulahci *et al.,* 2016; van Leeuwen *et al.,* 2020) and individual personalities (e.g. Hasenjager *et al.,* 2020) for information transmission through networks of individuals. Multi-network NBDA has been particularly productive in allowing the transmission of behaviours along multiple pathways to be identified. By building comprehensive models of social transmission through multiple social learning pathways, multi-network NBDA also allows the additive effects of sparse networks to be identified by combining them with more highly connected networks, as illustrated by the *Mates* network in Chapter 3. Based on my work in Chapter 3, I suggest that future work should delve deeper into the importance of social relationships on learning processes. Social transmission between mates is particularly understudied – despite the potential adaptive benefits of pair specific preferences due to a mated pair's shared goal of producing surviving offspring and, in some species, their dependence on each other for their own survival (Avital and Jablonka, 2000). I therefore hope that my detection of (albeit relatively weak) mate-mate social transmission in zebra finches will encourage further study in this area – with the aforementioned caveat that the influence of sporadic mate-mate connections may be difficult to detect using network-based approaches if not viewed as a small part of a larger, more highly connected social network.

Human studies, on the other hand, are often limited to restrictive, unnatural laboratory environments. Therefore, future work on humans should focus on investigating our social behaviour in more realistic, open environments. Open diffusion experiments, for example, have only been used in a limited number of studies (e.g. Whiten and Flynn, 2010; Flynn and Whiten, 2012) and network-based analyses such as NDBA (Franz and Nunn, 2009; Hoppitt *et al.,* 2010; Hoppitt, 2017), to the best of my knowledge, have not been applied to human populations. In this thesis, I have explored the use of virtual reality as a way of studying human social learning within more realistic, three-dimensional environments and have developed VERSE specifically for this function. I strongly encourage future researchers to use VERSE to create more naturalistic experiments than is often possible in the lab.

VERSE is designed as a highly flexible tool which harnesses the benefits of gaming technology in order to produce experimental environments not easily created within laboratory conditions. As such, its potential applications are vast. Just a few examples of how VERSE could be used within the social learning research are: replicating human experiments formerly conducted in more restrictive laboratory conditions, replicating studies from the animal literature using human subjects (as I did in Chapter 5) and creating completely novel survival scenarios (e.g. foraging, predator avoidance, toxin aversion) not usually possible with human subjects. As suggested in Chapter 4 (section 4.6), research could also focus on VERSE's AI system to establish whether computer-controlled entities are viewed as true social cues, and what behavioural characteristics makes them integrate more realistically into a player's social landscape. If expanded to support multiple players, VERSE could also offer a unique, real-time perspective into human population-level information transmission patterns – including the use of specialised statistical methods, such as NBDA (Franz and Nunn, 2009; Hoppitt *et al.,* 2010; Hoppitt, 2017), which are frequently used on animal populations (e.g. Chapter 3) but, so far, have not been applied to human groups – as well as allowing investigations into the behavioural, physical and environmental factors that influence social processes at the population level, some of which have been discussed throughout this thesis. Social groups could even be studied over prolonged periods to allow investigations into human behavioural evolution and the development of group-specific cultural traditions (in small-scale versions of the often decades-long observations of animal populations, e.g. Allen *et al.,* 2013).

6.5. Potential applications

An understanding of the factors that influence population social networks, social learning, and the subsequent patterns of information transmission through groups of individuals is important not only within the fields of behavioural ecology, sociobiology and evolution, but could also have wider reaching consequences in various fields outside of academic research. Some examples are discussed below.

6.5.1. Conservation, translocation and reintroduction: the importance of social factors

Increasingly, the importance of integrating behavioural ecology with conservation is being recognised (Angeloni *et al.,* 2008; Merrick and Koprowski, 2017; de Azevedo and Young, 2021). Individual behaviours and personality traits can impact on a number of factors relating to the conservation, translocation and reintroduction of different species – including habitat use patterns, migration patterns, stress levels in response to disturbance, translocation and human handling, breeding success in captivity, responses to novel environments and the impact of anthropogenic disturbances (Merrick and Koprowski, 2017; de Azevedo and Young, 2021). An understanding of individual habitat preferences and movement patterns is also crucial for the identification of areas in need of protective status (Caro and Berger, 2019).

One of the key concepts discussed in this summary chapter is individual behavioural variability. In conservation science, failing to account for such variability can result in inaccurate predictions of population-level patterns. For example, Lesmerises and St-Laurent (2017) demonstrated that using population-level averages resulted in weak models of habitat use in black bears (*Ursus americanus*) by masking important individual differences. One could also argue that behavioural variants are themselves an important component of biodiversity – especially if these variants are socially transmitted to others in a form of behavioural inheritance that can drive changes in whole populations – and that conservationists should be seeking to maintain behavioural diversity (or even focus on particular behavioural variants) just as much as genetic diversity (Whitehead, 2010; Cordero-Rivera, 2017; Greggor *et al.*, 2017; Brakes and Rendell, 2022). Despite this, a large proportion of conservation research still fails to consider behaviour and personality traits at the individual level (Angeloni *et al.,* 2008) – and even fewer consider the importance of social factors.

Social species are particularly sensitive to rapid human-induced environmental changes, partially because human activities can disrupt the transmission of crucial information through the population, but also because reliance on social learning and the establishment of local traditions can impede rapid responses to anthropogenic forces if these forces cause local norms to become maladaptive (Whitehead and Richerson, 2009; Barrett *et al.,* 2019). Social species also pose additional conservation challenges because they are reliant on each other for their survival. In particularly close-knit groups, social bonds may be so strong that Individuals act collectively as one, potentially leading one another into dangerous, human-induced situations. For example, social organisation may be an important factor influencing the mass stranding events of Gray's beaked whales (*Mesoplodon grayi*), which strand in large, unrelated groups in response to anthropogenic noise (Hooker *et al.,* 2019; Brakes and Rendell, 2022). Conservation efforts for social species should therefore view the social group as a unit of conservation and focus not only on the conservation of populations and their habitats, but also on the preservation and understanding of important social bonds within those populations. How individuals interact with one another, how the social upbringing of an individual impacts on its future prospects, how adaptive and maladaptive information transmits through populations, the contexts that alter the pathways of social transmission and the role of cultural traditions for the survival of species are all important considerations in the conservation management of social species (Whitehead, 2010; Brakes *et al.,* 2019; Brakes *et al.,* 2021). Considering these often overlooked social aspects of animal behaviour may make us better able predict, and potentially mitigate against, the impacts of anthropogenic disturbances on animal populations, as discussed in more detail below.

A wide variety of human activities can reduce behavioural diversity and interrupt essential social interactions and communication channels in animal populations, thus impacting on the transmission and maintenance of adaptive behaviours in the face of population disturbances (Laiolo 2010; Greggor *et al.*, 2017). Chemical pollution, for example, can impede learning of antipredator behaviour in fish by impairing their ability to respond to the olfactory alarm cues of conspecifics (Mirza *et al.,* 2009). Anthropogenic noise pollution can have very similar effects.

Boat noise, for example, reduces the survival of juvenile coral reef fish by impacting on their ability to learn socially about novel predators (Ferrari *et al.,* 2018). For marine mammals, fishing, hunting and anthropogenic noise can all impact social dynamics and important dyadic relationships (e.g. the mother-calf bond), sometimes resulting in the fragmentation of entire social groups (Brakes, 2019; Brakes and Rendell, 2022). Similarly, noise pollution has been shown to erode male-female pair bonds in zebra finches, possibly due to masking of bond-maintaining calls (Swaddle and Page, 2007), which, given the potential importance of mate-mate communication for the social learning of foraging techniques in this species (Chapter 3), could result in disrupted population-level social transmission pathways. In the face of anthropogenic noise, some species are able to adaptively alter their vocalisations (e.g. by changing the timing, amplitude and frequency) in order to stay heard; however, these alterations may come with other fitness costs, such as a reduction in attractiveness to potential mates, and species that are unable to alter their vocalisations in such a way may be forced to either avoid noisy environments entirely or suffer the fitness disadvantages of settling there (Laiolo 2010). The direct removal of individuals from the population can also significantly impact social transmission of crucial information through populations, particularly if the individual that is removed happens to be a keystone information transmitter. For example, in species such as elephants, older individuals are often the targets of hunting and, as older individuals also act as essential sources of social knowledge due to their accumulated experience over time, their removal from the population can have disproportionate effects on the survival of their group (McComb *et al.,* 2001).

Habitat loss and fragmentation can have profound consequences not only on genetic diversity, species richness and population sizes (Fahrig, 2003), but also on animal behaviour, including their social behaviour (Yahner and Mahan, 2002). Anthropogenically driven changes to habitats can result in changes to population social structure and organisation, including the type and frequency of social interactions (Yahner and Mahan, 2002). For example, Arroyo-Rodríguez *et al.* (2010) reported that habitat fragmentation and disturbance led to increased fission-fusion dynamics, changes in the composition of social groups and overall reduced rates of social interaction and activities in howler monkeys (*Alouatta* spp.). Where changes in land use alter the spatial distributions of groups of individuals (e.g. due to the production of heterogeneous, patchy landscapes), the patterning of social interactions at the population level can be substantially altered, as indicated by the results of Chapter 2. In addition to its influence on social transmission, the spatial distribution of individuals can have important impacts on disease dynamics. For example, differences in the number and size of habitable patches in fragmented landscapes, combined with inter-patch distance, can determine whether individuals tend to remain in the same patch for prolonged periods or frequently move between them, which subsequently influences both within- and between-patch disease transmission (Tracey *et al.,* 2014). Similarly, the presence of few, isolated high resource patches within heterogeneous environments can result in 'hot spots' of disease transmission by encouraging high densities of social interaction at the high resource sites (Bonnell *et al.,* 2010).

As non-habitat permeability decreases, e.g. due to physical barriers or behavioural avoidance of urbanised areas, between-patch movement eventually ceases (Tracey *et al.,* 2014). Thus, habitat fragmentation has the potential to isolate groups – or even single individuals – from the rest of the population. Similar social isolation may be observed due to declining population sizes, which result in sparser distributions of individuals, thus decreasing the overlap between territories and making social interactions less likely. Spatial isolation of groups due to habitat fragmentation is likely to increase within-group transmission due to individuals being forced into closer proximity, while decreasing between-group transmission (Chapter 2; Laiolo and Tella, 2005; Tracey *et al.,* 2014), which may have important implications for the uptake and transmission of novel behaviours. If social groups become too sparse, leading to single individuals becoming isolated, locating suitable demonstrators can become difficult, and individuals may become more reliant on their own personal experiences (Chapter 5; Crates *et al.,* 2021). This may exacerbate species decline by limiting social interactions essential to sustain the population, such as mating (Banks *et al.,* 2007). Plus, for species that rely on social learning to gain important survival skills, social isolation threatens to limit the maintenance of adaptive behaviours.

Thus, depending on a species' reliance on social interactions with conspecifics, social isolation alone may have a profound impact on its survival, even if the fragmented habitat theoretically contains enough resources to sustain them. Recent work, for example, has revealed that population decline has resulted in a degradation of vocal culture in critically endangered regent honeyeaters (*Anthochaera phrygia*) because their sparse distributions mean that juvenile males are unable to locate male tutors to learn their songs from. As songs are used to attract females in this species, the increase of atypical songs by socially isolated males is contributing to the species' decline by reducing successful pairings (Crates *et al.,* 2021). This illustrates how a species' dependence on particular social interactions can produce Allee effects (Stephens *et al.,* 1999) that are highly sensitive to anthropogenic activities. Similar patterns of reduced acoustic connectivity and erosion of vocal culture due to habitat fragmentation have been documented in the Dupont's lark (*Chersophilus duponti*) (Laiolo and Tella, 2005, 2007; Laiolo *et al.,* 2008) and Grey Shrikethrush (*Colluricincla harmonica*) (Pavlova *et al.,* 2012). Even when individuals are not geographically isolated, alterations to habitat composition caused by human activities, such as the removal of mature trees, can drive acoustic changes in vocalisations, which may ultimately have an impact on important social interactions (Goretskaia *et al.,* 2018). Interestingly, because behavioural inheritance occurs over much shorter timescales than genetic inheritance, cultural erosion (e.g. loss of diversity in bird song) could be used as an early warning sign for detecting population disturbances (Laiolo and Tella, 2005; Laiolo, 2010), which may allow us to deploy conservation management strategies before these disturbances become too severe to combat.

Predicting how species will respond to environmental change and anthropogenic disturbances therefore requires an understanding of the importance of that species' social behaviour on its survival. A population's reliance on social interactions, plus their natural movement and dispersal patterns, for example, will likely determine how impacted they are by habitat fragmentation. Models of gene flow on Australian woodland birds have revealed that habitat fragmentation adversely affects both sedentary and mobile species – and both philopatric and dispersive individuals – in different ways. While sedentary individuals are forced into smaller and smaller habitats due to their resistance to crossing over non-habitat areas, novel barriers to movement can impede the dispersal abilities of mobile individuals (Amos *et al.,* 2014). In Chapter 2, I demonstrated how a subset of highly mobile individuals can act as important connectors of more sedentary subgroups. In addition to the adverse effects on gene flow, anthropogenic barriers to dispersal may block important information channels by disrupting the natural movement patterns of such individuals. The resilience of social networks should therefore be considered in our conservation efforts – perhaps even treated as a conservation goal. Spatially explicit, agent-based models such as that described in Chapter 2 could offer a very promising way of establishing the individual-level characteristics that make a population more vulnerable (or more robust) to habitat fragmentation, thus allowing us to identify species that are more at risk and mitigate against the effects of anthropogenic activities on these species. In the case of habitat fragmentation described above, for example, conservation planning may wish to consider differences in the dispersal abilities of different individuals and plan accordingly, e.g. by focussing efforts on (i) improving the habitat quality for philopatric individuals and (ii) identifying highly dispersive individuals and reducing their barriers to movement.

We may also be able to take advantage of the natural social learning capabilities of animals to aid active conservation efforts. If we can understand, for example, which survival skills are best learnt independently and which are best learnt socially, while accounting for variation in learning preferences and abilities between individuals, and the best ways to teach these skills to individuals, we may be able to help buffer populations against anthropogenic change and boost the success rates of wildlife reintroductions. For example, reintroduction programmes of the Mississippi sandhill cranes (*Grus canadensis pulla*) – a species with prolonged periods of parental care – became substantially more successful after the incorporation of anti-predator conditioning, which involved exposing naïve individuals to live, tame predators in the presence of adult cranes that were known to use appropriate predator responses (Heatley, 2002). Similarly, captive-reared juvenile black-tailed prairie dogs (*Cynomys ludovicianus*) were more adept at recognising and responding appropriately to a variety of predators and had higher post-release survival rates – comparable to those of wild-reared juveniles – when trained in the presence of an adult female demonstrator compared to when trained alone (Shier and Owings, 2007). Anti-predator training programs such as these could be beneficial for the reintroduction of a wide variety of endangered species, from fish to birds to mammals – particularly for species with predator-induced alarm calls that conspecifics must learn to respond to appropriately (Griffin, 2004). The incorporation of social learning into hatchery rearing practices also has the potential to significantly impact post-release survival rates of fish (Brown and Laland, 2001). This includes the learning of important foraging skills – for example, pairing juvenile Atlantic salmon (*Salmo salar*) with demonstrators trained to target benthic prey items substantially increased their benthic foraging success (Brown *et al.,* 2003). We may even be able to tap into animals' natural abilities to learn from each other to train populations to avoid anthropogenic dangers such as roads (Proppe *et al.,* 2017) and windfarms (May, 2015).

Most conservation efforts of this type involve training animals individually, however if we can harness the natural social learning processes of a population, we should be able to improve the efficiency and lower the costs of such training programs by introducing a desired behaviour into the population and then allowing it to diffuse naturally. If we have enough understanding of the population in question, including inter-individual variations in behaviours, preferences, learning abilities and social relationships – all of which have been demonstrated throughout this thesis to have important influences on information transmission dynamics – we may even be able to identify candidate individuals (i.e. those who are likely to transmit novel behaviours efficiently to the larger social group) to focus our training efforts on. Identification of a suitable candidate would depend on the characteristics of the population in question. If many individuals share a bias towards learning from dominant individuals, for example, then prioritising the training of dominant individuals may be the best way to introduce a desired behaviour into the population. On the other hand, it may also be possible to arbitrarily choose a candidate for teaching and artificially boost its influence over others – if individuals tend to learn from more successful demonstrators, for example, then artificially increasing the success rates of individuals performing the desired behaviour may be sufficient for others to begin copying. In many species, social learning is frequency-dependent (e.g. Coolen *et al*., 2005; Pike and Laland, 2010; Aplin *et al*., 2015; Danchin *et al*., 2018) and so a large proportion of the social group may need to be trained before the information starts to be transmitted naturally. In other cases, efforts may be best placed identifying and training specific 'keystone' individuals who, for whatever reason – be it a tendency to learn a task rapidly or attend to a task more often, a high level of connectivity to others, some characteristic that makes them receive high levels of attention, a willingness to actively display novel information to others, or some combination of these factors – have a disproportionately large influence over the behaviours of their conspecifics, as discussed above.

Once a candidate is chosen, an understanding of its individual preferences and learning skills could then help inform the best way to train it. Is it best to allow it to learn the novel skill asocially, for example? If it tends to learn from others rather than by itself, is it possible for a human demonstrator to teach the skill, or must this information come from a member of its own species? If the latter is true, a second candidate may need to be identified (perhaps an individual who lacks the desired level of influence over its social group but is more capable of independent learning and therefore easier to teach) who can then be partnered with the original candidate to allow it to learn the task from a conspecific. In some cases, rather than teaching a candidate individual a novel behaviour, it may be enough to simply introduce a novel task – something that represents the conservation issue in question – to the population and allow each individual to learn naturally and at their own pace. Of course, all this is easier said than done. Actually implementing such a scheme would require an in-depth knowledge not just of the species, but of the population and the individual personalities of its members – and while it may be possible to successfully emulate natural experiences through training programs (Shier and Owings, 2007), it will always be difficult to predict exactly how animal populations will respond. However, if anyone is best placed to have this knowledge, it will be the people already placed in the front line, working hard to preserve these populations, both in captivity and in the wild, and save these species from decline.

Finally, the most effective conservation efforts gain the support of the local human communities, and successfully engaging these communities in conservation requires an understanding of local opinions, social influences and cultural traditions. Recognising which species are best chosen as flagship species for conservation efforts in different regions and determining the best methods for gaining public support may, for example, depend on the attitudes and underlying culture of local residents. For example, attitudes towards eighteen animal species in Valparai, India varied depending on audience characteristics, including stakeholder group (i.e. whether they were locals, tourists or conservation practitioners), gender, religion and education (Kanagavel *et al.,* 2014). Negative attitudes were often associated with human-wildlife conflict and female opinions were strongly influenced by how threatening the species was perceived as – e.g. women showed an increased dislike for king cobras (*Ophiophagus hannah*) and lion-tailed macaques (*Macaca silenus*) compared to men, but were more willing to support the conservation of bird species. In some societies, the level of support for animal conservation is directly related to how aesthetically pleasing the species in question is (Liordos *et al.,* 2017). In such cases, conservation projects might be aided by raising awareness for the importance of species that are generally perceived as less attractive for ecosystem functioning – e.g. educated women in Greece were more likely to support conservation efforts for species that they perceived as fearsome (Liordos *et al.,* 2017). In other societies, placing an emphasis on 'cultural keystone species' (species of plants and animals that directly underpin local cultures) may be the best way to engage local people in conservation efforts (Garibaldi and Turner, 2004). In addition, recognising the local public's preferences for conservation management policies may help to gain their support and even encourage them to get actively involved. An online assessment of public conservation preferences in the USA, for example, revealed that, when presented with five case studies in which one species was pitted against another, the majority of participants favoured habitat protection as the best solution (over lethal control or no action) in almost all cases and the level or support for lethal control methods was extremely low (Lute and Attari, 2017). Listening to public opinion in such cases may avoid conflict over how species should be conserved and encourage active involvement.

6.5.2. Human-animal interactions and conflict

Understanding how animals learn from each other – and how humans learn from each other – has important implications for understanding and regulating human-animal interactions and conflict. From the animal perspective, if we can identify how individuals learn conflict behaviours, we may be able to discourage the transmission of such behaviours through animal populations or even encourage human avoidance behaviours. Grizzly bear offspring, for example, appear to learn conflict behaviours from their mothers (Morehouse *et al.*, 2016). Thus, discouraging conflict behaviours in female bears has the potential to reduce conflict in subsequent generations. Similarly, from the human perspective, understanding how and why prejudices towards certain species arise, and how these prejudices are transmitted through local populations, may aid outreach programs and mitigation strategies that allow us to better coexist with nature. For example, in India, where compensation schemes are in place to help resolve issues of human-wildlife conflict within human settlements located in or around protected areas, a lack of participation in these schemes was found to be a critical problem for the resolution of conflict (Ogra and Badola, 2008). The likelihood of participation was influenced by individual factors such as wealth and gender, but was also impeded by ineffective communication, delays in receiving compensation and a lack of trust in the officials overseeing the scheme. In particular, illiteracy, policy biases and lack of connections to powerful advocates often discouraged poor and female-headed households to apply for compensation (Ogra and Badola, 2008) – despite women generally bearing the brunt of the conflict (Ogra, 2008). Understanding the best way to communicate necessary information about conflict resolution schemes to the affected communities, including encouraging members of the community to communicate this information amongst themselves and selecting more trusted advocates, could go a long way to improving participation rates. This would require knowledge of who the most influential and/or highly connected individuals are in the community.

6.5.3. Epidemiology

The underlying interaction network of a population determines not only the transmission of information, but also the transmission of pathogens. Therefore, research on social transmission pathways, including the use of network-based analyses and knowledge of the factors that promote or inhibit interactions between individuals, can be also applied to epidemiological research. As many pathogens are transmitted through direct contact between individuals, spatially explicit models are a particularly important asset for predicting the spread of disease in different scenarios. For example, social network and spatial analyses by Emch *et al.* (2012) demonstrated that cholera and shigellosis transmission patterns in Bangladesh were always clustered in space and, to a lesser degree, followed kinship-based social networks. Similarly, in Chapter 2, I demonstrated that variation in space use, where clusters of individuals are connected to each other via a minority of long-distance travellers, has the potential to rapidly speed up disease transmission. Such movement patterns are akin to the connection of distant human populations by bouts of high mobility, such as air travel, which have resulted in a growing number of epidemics by allowing pathogens to move beyond their natural geographic boundaries (Findlater and Bogoch, 2018). Due to the human-aided ability of pathogens to move rapidly into novel regions, it is crucial that we focus our research efforts on the early detection of potentially dangerous pathogens while transmission is still limited to localised areas in order to effectively mitigate against the global spread of dangerous diseases. In the face of a potential pandemic, imposing air travel restrictions, particularly in countries that act as transportation hubs, may be the most effective way to contain disease transmission to more manageable localised regions where public health measures can then be focussed – as demonstrated in network analyses of Covid-19 transmission (Chu *et al.,* 2020; Lai *et al.,* 2020; Tiwari *et al.,* 2021). From a conservation perspective, environmental changes that result in unnatural clustering of animal populations could increase the population's vulnerability to the spread of disease. For example, Bonnell *et al.* (2010) demonstrated that habitat alterations resulting in a heterogeneous landscape in which few resource-rich sites are scattered may increase the spread of parasites through populations of the already endangered red colobus monkey (*Procolobus rufomitratus*) by increasing contact rates at the resource-rich sites.

6.5.4. Understanding and preserving plant-plant communication

Communication and social transmission of information are important not only for animal species, but for plants as well. Inter-plant communication is possible both through the production of volatile organic compounds (VOCs) (Bouwmeester *et al.,* 2019; Ninkovic *et al.,* 2021) and via networks of symbiotic mycorrhizal fungi under the soil that allow the transfer of nutrients and chemical signalling between the roots of individual trees (Gorzelak *at al.,* 2015; Simard, 2018; Baluška and Mancuso, 2020). In response to signals from neighbours, plants can show adaptive responses in their own behaviour, such as increased defences against herbivores in response to warnings from attacked neighbours (Engelberth *et al.,* 2004; Markovic *et al.,* 2021) or changes in growth and allocation of biomass when neighbouring plants detect abiotic fluctuations (Kegge *et al.,* 2015). Plants are also capable of learning from past experiences (Karban, 2008; Gagliano *et al.,* 2016). Therefore, just like animals, plants can be viewed as belonging to social communities and, while very different communication mechanisms are involved, research into plant-plant communication and learning – which is currently in its infancy – can potentially be informed by research on social transmission in animals.

Based on the findings of this thesis alone, a number of striking parallels can be identified in the patterns of social transmission between animal and plant populations. In tree populations, for example, individual trees (and/or mycorrhizae) are connected in a non-random, scale-free topology, resulting in strongly connected clusters of individuals with weaker connections between those clusters (Simard, 2018). Despite the sedentary nature of trees, this pattern of connectivity is remarkably similar to the structuring of social networks resulting from the varied spatial movements of individuals described in Chapter 2 and could suggest selection for efficient information transfer. Rapid growth of mycorrhizae in response to environmental cues such as novel resources can connect distant plants together (Agerer, 2006; Simard, 2018) much like the long-distance travellers in the simulated population described in Chapter 2. Minorities of highly connected individual plants can also act as ‘hubs’ of information (Simard, 2018) – just as the zebra finch aggressors discussed in Chapter 3.

In common with animal populations, anthropogenic activities can adversely affect plant communities by interfering with their pathways of communication. Air pollutants, for example, significantly reduce the distance at which plants can communicate via airborne VOCs (Blande *et al.,* 2010). Logging activities, even if very few individuals are harvested, may have a disproportionate impact on tree communities if highly connected keystone individuals are removed. Spatial isolation caused by habitat fragmentation will likely have adverse effects on plants that would normally gain adaptive benefits from communicating with their conspecifics. Fragmented habitats containing patches of plant life – or even single, isolated individuals – that are too distant from one another to be connected by mycorrhizal networks may become especially vulnerable to environmental changes that they can no longer communicate to one another. As plants form the basis of many ecosystems, their responses to anthropogenic activities and environmental changes will have a knock-on effect on the organisms that depend on them – including us. In addition, the physical and chemical activities of plants can significantly manipulate both their biotic and abiotic environment, making them significant players in the fight against climate change (Baluška and Mancuso, 2020). Considering plants as intelligent organisms capable of communication and the development of complex societies is therefore essential if we are going to successfully predict future climate patterns and mitigate against anthropogenic effects on the environment.

6.5.5. Education

One of the key findings of this thesis is that individuals vary in how they learn. Traditionally, education in schools consists of a single teacher mentoring a class of students, however, we have known for some time that students differ in their cognitive styles, which means they respond differently to different types of task, different modes of presentation, different teaching styles, and so on (Riding, 1997; Riding, 2013). For example, some students respond better to verbal presentations while others respond better to pictorial presentations (Riding, 1997), and some respond better to traditional teaching styles while others respond better to computer-aided teaching (Riding and Grimley, 1999; Atkinson, 2004). Individual characteristics such as gender (Riding and Grimley, 1999; Arnup *et al.,* 2013) and ethnic background (Shade, 1982) can also influence how a student learns best. This has important implications for the development of effective teaching strategies – if individual differences in learning styles are not taken into account, students who do not respond well to the chosen method of teaching will have their performance adversely affected. Differences in student performance may be incorrectly identified as differences in cognitive ability, which is likely to demotivate students who are simply not being taught in a manner that they respond to effectively. The best teaching strategies should therefore allow individual students to choose a learning style that suits them best (Riding, 2013).

In addition to individual differences in independent learning styles, education management should consider social influences on student learning. As demonstrated in Chapter 5, some individuals put more effort into independent learning, while others rely more heavily on others for information – thus, some students may learn better left to their own devices while others may learn better in a group. Individuals also vary in who they preferentially learn from and can alter these preferences in a context-dependent manner – thus, students may respond differently depending the individual characteristics of teachers (e.g. age, gender, race, personality traits) and these preferences may vary depending on the subject being taught (Chudgar and Sankar, 2008). Where possible, having a varied pool of teachers of different ages, genders and backgrounds, and assigning these teachers to the students who are likely to learn from them the most efficiently, may help to improve student achievement. For example, Chudgar and Sankar (2008) suggested that more female teachers in Indian classrooms would enhance the learning of languages, but not mathematics. In many cases, however, student-teacher relationships, including the attitudes of teachers towards students with different characteristics, may be more important than the individual characteristics of teachers (Sansone, 2017). Thus, teachers who maintain positive learning environments and motivational relationships with students from all walks of life have the most potential to act as keystone information transmitters within the school environment.

Similarly, it is important to consider that teachers, too, learn from one another and the way in which they communicate information can have an influence on the overall functioning of the school. Educational environments are composed of subgroups of teachers and non-teaching staff connected together within a school-wide network. Certain individuals play key roles in communicating information between departments and the social isolation of teachers can significantly reduce their motivation for institutional tasks within the school (Bakkenes *et al.*, 1999). The behavioural characteristics of teachers and their actions within the school environment can determine how influential they are amongst both their students and their colleagues. Naidoo (2014) discusses extensively how teachers with certain characteristics act as 'keystone species' who play a significant role within the school environment. These characteristics include having a confident, committed, proactive attitude towards their work, a passion for their subject, a tendency to use innovative approaches to their teaching and a willingness to volunteer for extra tasks outside their required work. This was irrespective of titles or hierarchical order. These keystone teachers also showed a passion for assisting their colleagues and were found to promote collaborative efforts and actively share their knowledge with others – thus making them directly comparable to the keystone information transmitters discussed in this thesis. Passionate, innovative teachers are therefore highly likely to be central to the social networks of school environments, both due to development and maintenance of positive connections with other teachers and their active transmission of knowledge to both teachers and students.

It is also important to consider that students learn not just from their teachers but from each other. Peer learning can be extremely effective and its importance has been increasingly emphasised for higher education over the years (Boud and Lee, 2005). However, peer learning tends to be used only informally by students, particularly due to the complexities of integrating it into formal learning practices (Boud and Cohen, 2014). Peer learning can also be impeded by assessment practices that put too much emphasis on individual achievement and so cause collaborative work to be viewed as cheating (Boud *et al.,* 1999). It is therefore important that we understand when and how to promote peer learning, while avoiding disruptions to other students. As a hypothetical example, two friends sit together in class and learn more effectively together than when they are apart. However, part of this learning experience involves behaviours (e.g. joking, loud talking) that may become disruptive to the rest of the class. In this scenario, a teacher may instinctively wish to separate the friends to avoid disruption and, in some cases this may be the most effective course of action, but it may also risk lowering the performance of the students who have been separated. A better approach may be to allow the friends to remain sitting together, but to encourage them to help each other quietly and respect the feelings of their classmates.

If schools are viewed as social communities, within which information flows not just from teacher to student, but throughout the entire social network (including teacher-student, teacher-teacher and student-student learning), this opens up opportunities to use network-based statistical analyses normally restricted to animal studies (e.g. Chapter 3; Allen *et al.,* 2013; Aplin *et al.,* 2015) to investigate information transmission patterns within school environments (c.f. Bakkenes *et al*., 1999). This could include identifying the most efficient social transmission pathways and factors that promote or inhibit learning from others. For example, do students display relationship-based social learning such as those demonstrated in Chapter 3 – e.g. are they more likely to learn from friends? Do the individual characteristics of students, such as their popularity or general knowledge, influence their ability to act as keystone information transmitters? Do some individuals act as vessels of information linking otherwise disconnected social groups (e.g. acting as links between different classes), akin to the long-distance travellers described in Chapter 2? Are the teachers identified as 'keystone species' by Naidoo (2014) more central to networks of teacher-teacher and teacher-student information transmission? Thus far, network-based statistical analyses have not been applied to educational environments and there is certainly a lot of potential for future research in this area.

6.6. Conclusion

Across the animal kingdom, individuals can gain beneficial information or behaviours by learning from their conspecifics in a process known as 'social learning'. The study of social learning has continued to gain interest over the past few decades, with a lot of focus on how naïve observers choose to learn. However, information exchange processes may not always lie solely in the choices of the observer. In this thesis, I have argued that the behaviours of both observer and demonstrator, plus the spatial and social factors influencing the connections between them within the larger social network, should all be taken into account to give a more comprehensive and realistic picture of information transmission processes. Through the development of novel methodologies (and the expansion of existing methodologies) designed to promote behavioural freedom and natural social learning processes, I set out to investigate how spatial, social and behavioural factors can all contribute to the patterns of social transmission at both the individual and group level. Spatially explicit, agent-based modelling revealed that behavioural variations at the individual level can have a profound effect on social network structure and information transmission processes at the population level (Chapter 2). Specifically, among-individual variation in the tendency to transmit and receive information produces an overabundance of a regulatory network motif known as the 'feed-forward loop', while variations in spatial movement increase the speed and efficiency of information transfer by linking localised clusters of individuals via a subset of long-distance travellers. A comprehensive model of social learning in a population of zebra finches, produced using a series of multi-network NBDA models, revealed the potential importance of social relationships in dictating patterns of information transmission through social groups (Chapter 3). Specifically, aggressive interactions appeared to be the main driver of information exchange about a novel foraging task, with a potential secondary social learning pathway between mates. Through the development of VERSE, a research tool used to create realistic, three-dimensional virtual social learning environments (Chapter 4), I then investigated human social learning biases within spatially and ecologically realistic scenarios (Chapter 5). Human participants showed substantial variation in their reliance on social information, but displayed an overall bias for learning independently, particularly in complex, large-scale environments. The use of social versus asocial information appeared to be weighted depending on the reliability of rewards in the environment, the additional, undemonstrated opportunities available via asocial learning and the difficulties in acquiring social information due to the movements of demonstrators over different spatial scales. When learning socially, participants displayed significant positive frequency-dependent (‘copy the majority’) and payoff-based (‘copy successful demonstrators’) biases. Thus, humans learning in complex environments appear to be strategic in their use of social information and display strong similarities to the behavioural adaptations of unrelated species. Taken together, this research has revealed how the behaviours and spatial movements of individuals, plus their social connections, can influence who learns from whom and when. Individual behavioural variations, in particular, appear to play an important role in dictating the patterns of information transmission at the population level – in some cases, resulting in the presence of highly influential ‘keystone’ information transmitters. The thesis closes with a call for acknowledging the importance of permitting unrestricted behavioural freedom and spatial realism into future work and highlights potential applications of this research in fields outside of behavioural ecology and evolution such as conservation, epidemiology, plant science and education.

6.7. References

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