To Copy, Camouflage or Do Neither? The Role of Asocial and Social Information in Affecting Nest Material Choices of Zebra Finches (*Taeniopygia guttata)*

by

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Abstract

Animals can use asocial cues from the environment or information obtained from other individuals, called social information to make decisions. Further these different sources of information can be simultaneously available. How do animals evaluate and prioritize asocial and social information sources while making decisions? Here I examined this question in the context of nest building. Nest building is a key reproductive event in the lives of many organisms which in many cases includes making decisions about nest material. Research has shown that nest material selection can come under the influence of asocial and social information. For example, zebra finches (*Taeniopygia guttata*) choose coloured nest material that reduces the conspicuousness of their nest against a background (use camouflaging material; asocial information). Zebra finches are also known to copy the material choice of nest-building conspecifics (use socially demonstrated material; social information). However, the understanding of how nest material selection operates in circumstances where both asocial and social information are available is limited. In this experiment I specifically tested how zebra finches made nest material decisions in two circumstances – one in which asocial and social information agreed with each other (Agree group) and another in which asocial and social information were in conflict with each other (Conflict group). In the Agree group, since the socially demonstrated material was also the camouflaging material, I predicted that birds would predominantly use the socially demonstrated (also camouflaging) material to build their nest. The material preference of birds in the Conflict group was expected to reveal whether the birds prioritised asocial or social information while choosing nest material. I conducted the experiment in three phases. First, zebra finch male-female pairs were given an initial preference test among three differently coloured materials and an initially preferred material of the male (primary nest builder) was established. Second, zebra finch pairs gathered social information about nest material by watching conspecifics build a nest with one of the pair's initially non-preferred colours. In the final phase, pairs got an opportunity to build their own nest against a coloured background cue (asocial information), also of an initially non-preferred colour which either agreed (Agree group) or conflicted (Conflict group) with the social information. I found that in both Agree as well as Conflict groups, observers' preference for the initially preferred material decreased in the final phase. For observers in the Agree group, contrary to the prediction there was no increase in preference for the socially demonstrated (also camouflaging) material. Observers in the Conflict group showed an increase in preference for the socially demonstrated material and no change in preference for the asocial (camouflaging) material, suggesting that social information takes precedence over asocial information when changes in material preferences occur. The majority of observers also had a preference for green coloured material that might have rendered material preferences less susceptible to change via asocial or social information. Overall, these results suggest that making decisions about nest material when more than one source of information and multiple material options are available could be more nuanced than expected.

Preface

This thesis is an original work by me, Gopika Balasubramanian. The research presented here was conducted with research ethics approval from the University of Alberta Research Ethics Board (AUP00002293) and complied with the Animal Care Guidelines and Policies stated by the Canadian Council for Animal Care (CCAC). I collected the data, performed the analysis and wrote up the work in the form of this thesis. Dr. Lauren Guillette was the supervisory author of this study, with whose inputs I developed the project and this thesis. I used the apparatus (cages) previously assembled by Tristan S. Eckersley and Andrés Camacho-Alpízar for this study. I obtained help from Isaac Lank and Phillip May for setting up the recording devices. Science Animal Support Services (SASS) provided animal care and husbandry for part of the duration that birds were housed in the colony rooms. I primarily did animal care and husbandry for the birds when birds were in the experiment, with help from Andrés Camacho-Alpízar and Connor T. Lambert. No part of this thesis has been previously published anywhere.

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Last but not least, I would like to thank all of the birds that participated in this study.

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Glossary of Terms

Asocial Material	Non-preferred material option for Conflict group that matched the colour of the background.
Carry	Male observer held the material in his beak and moved.
Conflict Treatment Group	Observer watched a demonstrator build a nest with material that did not match the colour of the background.
Agree Treatment Group	Observer watched a demonstrator build a nest with material that matched the colour of the background.
Demonstrator	Male-female pair of zebra finches with nest-building experience.
Deposit	Male observer picked up and released material held in the beak into the nest or male observer was on the nest cup/nest and released material.
Final Preference	Value obtained for each material type. Proportion of deposits of each material type made by the male observer during the final preference test.
Initial Preference	Value obtained for each material type. Proportion of time the male observer spent interacting with each material during the initial preference test (time spent interacting with particular material divided by total time spent interacting with all material).
Initial Preference Strength	Initial preference value for initially preferred material
Initially Preferred Material	Material with highest initial preference value among three provided material types.
Interaction	Any time the male observer’s beak, feet, -or body (except the tail by itself) came in contact with nest material during the initial preference test.
Non-preferred Materials	Two materials that had lower initial preference values than initially preferred material.
Observer	Male-female pair of zebra finches. Each observer watched a familiar male-female pair (demonstrator) build a nest.

Observation Phase Duration	Time taken by demonstrator to deposit 50 additional pieces of material into the nest.
Opt out material	Material type for Agree group that was neither the initially preferred material nor the socially demonstrated material.
Pick up	Male observer held the material in his beak and lifted material from surface level.
Pre-observation Phase Duration	Time taken by demonstrator to deposit 100 pieces of material into the nest.
Socially Demonstrated Material	Non-preferred material that matched colour used by demonstrator to build a nest.
Total Interaction Time	Total time the male observer spent interacting with all material types during the initial preference test.
Touch	Male observer came in contact with material either with beak or feet.

Introduction

Making decisions is part and parcel of life. Whether the implications are big or small, we are continually making decisions – weighing in different factors and finally selecting what seems to be the best choice. The animal world is no different than ours when considering the variety of circumstances that require resolutions. Thinking in terms of what might be most important to almost every animal's life – we can come up with a few decisions an animal might have to make – such as where to feed, whom to mate with or how to build a nest. How do animals make these decisions? What are the different factors influencing their decisions? These ideas form the very broad premise of this work.

Information, as we intuitively understand the term, can help us make decisions. Jablonka (2002) defines information as 'a property of a source to which a receiver reacts, such that the reaction potentially or actually changes the state of the receiver in a functional manner'. Wagner & Danchin (2010) in their paper 'Taxonomy of Biological Information' define information as 'factors that can affect phenotype in ways that may affect fitness'. As per these definitions, information can come from a variety of sources, for example – from genes in the DNA, learning through individual experience or trial-and-error, from environmental cues (e.g., climate), or as information from other individuals (Bonnie & Earley, 2007; É. Danchin, 2013; Schmidt et al., 2010; Wagner & Danchin, 2010). Based on the source, information can be broadly categorized as asocial or social information. Asocial (non-social) information includes information gathered through an individual's own experience as well as an individual's use of cues while making decisions (Wagner & Danchin, 2010). Social information on the other hand, refers to information obtained from other individuals (Bonnie & Earley, 2007). The main focus of this thesis is to understand how asocial and social information are weighted while making decisions.

Learning is defined as the process by which animals acquire, process, store, and use information (Shettleworth, 2010). A bee foraging in a patch of flowers, for example, could learn that flowers of a particular colour are more rewarding than others from its own experience of feeding from different flowers and could use this information while foraging in the future (Leadbeater & Florent, 2014). The foraging bee could also have innate or pre-existing preferences to visit flowers of certain colours (Gumbert, 2000; Maharaj et al., 2019). In both these cases, the decision of the individual foraging bee is based on its own information. But what if the foraging bee also had access to social information in the form of observing a conspecific feeding on a particular flower? How does this 'social' information affect the decisions of the foraging bee? In the next sections, I introduce social information and discuss how and when social information might be used, in the light of asocial information an animal could also possess.

Social Information

What is Social Information?

Most animals, in their environment have access to information that results from the presence or behaviour of other individuals. Such information obtained from other individuals is called social information (Bonnie & Earley, 2007; Kendal et al., 2018). Following from this, social information use is said to occur when the behaviour of a focal individual changes as a result of information derived from others (Bonnie & Earley, 2007; Hoppitt & Laland, 2013). While talking about social information use – conventionally, the individual that acts as the source of the information is called the demonstrator while the receiver of the information is called the observer (Hoppitt & Laland, 2013).

Social information includes biological signals – that explicitly evolved for the purpose of communication between individuals, such as an alarm call of a meerkat alerting its conspecifics of a predator's presence, the waggle dance of a returning forager bee indicating the location of a foraging source to its hive-mates, or ants that leave a pheromone trail (Danchin et al., 2004; Grüter & Leadbeater, 2014; Manser, 1999; Seppänen et al., 2007).

However, social information could also be 'inadvertent' such that information is available to an observer as a by-product of a demonstrator's behaviour that isn't necessarily specialized for communication (Danchin et al., 2004). Going back to the example of a foraging bee, one way in which social information use could operate, is if the foraging bee (observer) decided to visit a particular flower after having observed a conspecific (the demonstrator) on the flower (Avarguès-Weber & Chittka, 2014). Here the social information is not necessarily a biological signal for observer bees observing the demonstrator conspecific on the flower but rather is an inadvertent by product of the demonstrator bee's presence or behaviour. Similarly, a bird using the presence of nests in an area to indirectly infer habitat quality, a fly using cues left behind by conspecifics to decide where to oviposit, a young chimpanzee watching an adult and learning how to use a tool are all representative of social information use, in which evolved biological signals for communication are not involved (Durisko et al., 2014; Ringhofer & Hasegawa, 2014; Tomasello et al., 1987). Teaching in the animal world is seen as a special case of transfer of social information where the teacher is not inadvertently but rather is actively facilitating the transfer of information to the learner, incorporating feedback from the learner's behaviour (Hoppitt et al., 2008). One example of teaching in animals is the transfer of prey-handling skills from adult meerkats (*Suricata suricatta)* to young meerkats. Adult meerkats bring meerkat pups prey that is either killed or disabled, as appropriate for the age of the pup, and nudge pups to interact with prey to facilitate the development of prey-handling skills (Thornton & McAuliffe, 2006).

Types of Social Information Use

Social learning represents a form of social information use – wherein learning in an individual is facilitated by the observation of or interaction with other individuals or products of other individuals (Heyes, 1994; Laland, 2004). Social learning is also referred to as social information use that leads to a change in an individual's behaviour that persists even after the social stimuli is removed (Kendal et al., 2018; Mesoudi et al., 2016; Webster & Laland, 2017). For example, Webster & Laland (2017) investigating whether or not observer fishes use social information about location of food from demonstrator fishes, use the term social information use to indicate observers joining currently-feeding demonstrators at a feeding location and the term social learning to indicate observers continuing to choose the demonstrated feeding location when demonstrators were no longer present. Other forms of social information use that are found in the literature include studies on what are termed public information use and social eavesdropping (Bonnie & Earley, 2007). Public information use has its origins in the field of behavioural ecology and specifically deals with animals obtaining and using social information about quality of an environmental resource, such as quality of a foraging patch based on the success of other foragers at the patch (Bonnie & Earley, 2007). As an example, nine-spined sticklebacks (*Pungitius pungitius*) use public information in the form of observing feeding rates of other individuals to infer profitability of different patches of food (Coolen et al., 2005). In social eavesdropping, animals observe interactions between other individuals and obtain information about individuals involved in those interactions (Bonnie & Earley, 2007). For example, Oliveira and colleagues (1998) found that male Siamese fighting fish (*Betta splendens)* monitored the aggressive interactions or fights between conspecifics and extracted information about the relative fighting ability of the individuals involved. Subsequently when confronted with the winners and losers of such interactions, observers took longer to initiate fights with the winners as compared to the losers, showing evidence of having engaged in social eavesdropping (Oliveira et al., 1998).

Who Uses Social Information?

Regardless of the specific type, social information taken as a whole is a widespread phenomenon across both taxa and contexts (Galef & Laland, 2005; Kendal et al., 2005). Evidence of social information use is found in insects, birds, reptiles, fish, and mammals; in the contexts of foraging, mate-choice, anti-predatory behaviour and habitat selection among others (Danchin et al., 2004; Galef & Laland, 2005). Solitary species, which do not live in groups also show evidence of social information use when given the opportunity to observe a conspecific's behaviour. For example, the red-footed tortoise (*Geochelone carbonaria*), a solitary reptile has been found to be capable of social information use while learning how to solve a detour task by watching a conspecific solve the task first (Wilkinson et al., 2010). Moreover, social information use is not restricted to using information from conspecifics, and extends to using information from heterospecifics as well (Seppänen et al., 2007). For example, bumblebees (*Bombus terrestris*) are known to be capable of learning to associate rewarding flowers with the presence of heterospecific honeybees (*Apis mellifera*) just as they are capable of learning from conspecific bumblebees (Dawson & Chittka, 2012). Migrant pied flycatchers (*Ficedula hypoleuca*) and Collared flycatchers (*Ficedula albicollis*) have been shown to use social information from the presence of resident tits (*Parus species*) to inform nest-site selection. The arriving flycatchers preferred to choose nest-sites that had the same arbitrary symbol as the ones marking resident tits' nests, over other alternatives (Seppänen & Forsman, 2007).

Mechanisms of Social Learning

What are the processes by which social learning can occur? In mechanisms such as local or stimulus enhancement, the observers are attracted to a specific location or stimulus after observing a demonstrator's presence at said location or interaction with said stimulus respectively, which could then lead to observers learning something about said location or stimulus (Heyes, 1994; Hoppitt & Laland, 2013). In observational conditioning, demonstrator's unconditional response to a stimulus acts as an unconditional stimulus to an observer, eliciting the same response as the demonstrator (the stimulus then becomes the conditioned stimulus; Heyes, 1994; Hoppitt & Laland, 2013). Processes such as imitation and emulation respectively involve the observers copying the behaviours of the demonstrators in a step-by-step fashion (imitation) or performing behaviours that have the same effect or reach the same end goal as that of the demonstrator (emulation; Heyes, 1994; Hoppitt & Laland, 2013). Whether or not there is similarity in the cognitive processes underlying social and asocial learning is an ongoing debate; some researchers suggest that associative learning that operates in asocial learning can explain social learning as well (Heyes & Pearce, 2015; Leadbeater, 2015). For example, Dawson and colleagues (2013) showed that social learning in foraging bumblebees (*Bombus terrestris*) represented second-order conditioning (two-step associative process). Bees that had the experience of associating conspecific presence with food reward, learnt the association between the colour of the flower conspecifics were on and the food reward and subsequently landed more frequently on said coloured flowers as compared to alternatives. However, bees that had experience of associating conspecific presence with an aversive solution (instead of a food reward) learnt to avoid coloured flowers conspecifics were on; giving strength to the idea that associative learning mechanisms underlie social learning (Dawson et al., 2013; Heyes & Pearce, 2015; Leadbeater, 2015). Heyes (2012) in their paper 'What's social about social learning' suggests that the channel or input through which the information is obtained is what makes social learning different from asocial learning, and that 'perceptual, attentional, or motivational processes' of animals could bias them towards social information, facilitating subsequent learning. Other researchers maintain the idea that learning mechanisms of asocial and social learning in nature are likely to be different in certain aspects – citing that at least in some situations the pattern of learning arising from use of asocial and social cues are different (Avarguès-Weber & Chittka, 2014; Kendal et al., 2018). For example, Avarguès-Weber & Chittka (2014) found that the pattern of learning displayed by foraging bumblebees (*Bombus terrestris*) trained with live conspecifics as opposed to bees trained with non-social (asocial) or model immobile bee cues were different. Bees that foraged with live conspecifics in the training phase were in a later test phase able to generalize preference towards the colour of flowers that was 'socially indicated' (cued by a model bee), and visited both cue-occupied and cue-unoccupied flowers of the indicated colour, showing stimulus enhancement. However, bees that had access only to non-social cues or immobile model bees in the training phase, later in the test phase only visited specific flowers that were cue-occupied (cued by a model bee) showing local enhancement, and did not generalize preference to the cue-unoccupied but still rewarding flower colours. This example shows how prior experience with asocial or social stimuli might lead to different patterns of learning (Avarguès-Weber & Chittka, 2014).

Social Information – Benefits and Costs

That many animals use social information in a variety of contexts, must not be taken to mean that social information is used all the time, whenever available (Giraldeau et al., 2002; Grüter & Leadbeater, 2014; Kendal et al., 2018; Rieucau & Giraldeau, 2011). While the widespread nature of evidence supporting social information use does hint at the possible benefits of using social information, social information use is not without costs (Kendal et al., 2005; Rieucau & Giraldeau, 2011). In this section, I outline the possible benefits and costs associated with using social information which in turn can help one understand why animals might use social information in certain circumstances but not others, as discussed in a later section.

Benefits of Social Information. For young and naïve individuals that have just started out in the world – social information is particularly valuable (Galef & Laland, 2005). Day-old chicks (*Gallus gallus*) for example, learn to avoid pecking at an aversive stimulus upon observing a disgust response of a fellow chick towards said stimulus (Johnston et al., 1998) . Young Norway rats (*Rattus norvegicus*) glean knowledge about what foods to eat via social information, eating only foods that have been marked as eaten by older conspecifics (Galef & Clark, 1971). Similarly, seeing older meerkats (*Suricata suricatta*) consume certain foods increases the chance of younger meerkats consuming the same foods (Thornton, 2008). Such information about what foods to consume to potentially avoid negative consequences can also extend to adults, when encountering novel food types. Wild jackdaws (*Corvus monedula*) for example, were more likely to consume novel food (cheese dyed in atypical colours), after observing a conspecific consume similar novel foods (Greggor et al., 2016).

Apart from information about safety of novel foods, social information use also allows for learning of novel behaviours that could be advantageous to animals. In an example of learning a foraging technique, young black rats (*Rattus rattus*) learn how to remove scales from pinecones by observing an adult using a particular method of scale-removal (Aisner & Terkel, 1992). In another example, great white pelicans (*Pelecanus onocrotalus*) that observed a conspecific using its beak to retrieve food from an opaque box (a novel set-up) were able to retrieve food from the box while pelicans that did not observe a conspecific performing the task were unable to retrieve food from the box (Danel et al., 2020). In a clear demonstration of social learning of novel foraging skill via observational learning, Aplin and colleagues (2013) showed that naive blue tits (*Cyanistes caeruleus*) that observed conspecific demonstrators use one of two techniques - 'piercing' a foil cap or 'flipping' a lid to solve a novel foraging task, learnt to solve the foraging task using the same technique as the corresponding demonstrator they had observed. On the other hand, naïve blue tits that did not have access to a demonstrator did not acquire either type (piercing or flipping) of foraging skill (Aplin et al., 2013).

Social information can also help animals learn about predators or other potentially harmful stimuli (Griffin, 2004). In a famous example, Cook & Mineka (1989) showed that young lab-reared monkeys (*Macaca mulatta*) learnt to respond fearfully to a predator (a snake) they had not encountered before by watching videos of older conspecifics reacting fearfully to the predator. Similarly, young fairy-wrens (*Malurus cyaneus*) (hosts) learn to recognize the bronze-cuckoo (*Chalcites basalis*), a brood parasite that attacks fairy wren nests, as a harmful stimulus using social information (Feeney & Langmore, 2013). Naïve fairy-wrens initially were not responsive to cuckoos. However, having once watched experienced fellow fairy-wrens react to a model cuckoo's presence by physically mobbing the model cuckoo and making alarm calls;

previously naïve fairy wrens also showed similar mobbing behaviours towards the model cuckoo when the model cuckoo was presented later (Feeney & Langmore, 2013). As another example, in the presence of experienced zebra fish *(Danio rerio)* that were trained to escape through one of two differently coloured holes when a harmful stimulus (a moving trawl) was introduced, naïve zebra fish chose to escape through the same-coloured hole in spite of the other hole being an equally viable alternative (Lindeyer & Reader, 2010). Further, the choice of hole remained consistent even after the removal of all experienced fish that were originally trained to escape through the demonstrated hole.

A more general benefit that is usually credited to social information use is that it saves time and energy expended by animals (Kendal et al., 2005; Rieucau & Giraldeau, 2011). For example, starlings (*Sturnus vulgaris*) that observed lack of foraging success of a conspecific partner in a foraging patch, departed more quickly from the unprofitable patch as compared to control birds that did not receive such information from other individuals (Templeton & Giraldeau, 1996). Shiny cowbirds (*Molothrus bonariensis*) that observed a conspecific demonstrator display a novel foraging behaviour - pecking a key when the key was illuminated resulting in food provisioning, acquired the key-pecking response faster than control birds that did not have access to a demonstrator or birds that had access to a 'ghost' demonstrator where the key was illuminated and the food was automatically dispensed after a 10 second delay (May & Reboreda, 2005). Similarly, freshwater stingrays (*Potamotrygon falkneri*) that received conspecific demonstration of a foraging task wherein an earthworm (food reward) placed inside a cylindrical tube had to be removed, reached learning criterion in fewer trials than stingrays that did not receive any demonstration (Thonhauser et al., 2013). As an example of a non-foraging context, first time nest building zebra finches (*Taeniopygia guttata)* that had previously observed a conspecific pair of birds nesting were quicker to complete nest building than zebra finches that did not observe a pair of nesting conspecifics, showing probable latent learning (Camacho-Alpízar et al., 2021b). Seppänen & Forsman (2007) found that migrant flycatchers (collared flycatchers, *Ficedula albicollis* and pied flycatchers, *Ficedula hypoleuca,* in different study plots) that arrived late to breeding sites were more likely to use social information about nest box type from resident tits (*Parus major* and *Parus caeruleus*), by choosing to nest in nest boxes marked with the same arbitrary geometric symbol as the one marking resident tits' nests over nest boxes marked by a different alternative symbol. Interestingly, flycatchers that arrived earlier in the season did not copy the arbitrary symbol marking the resident tits' nests – and showed a similar level of preference for both nest boxes marked with resident tits' nest box symbol and the alternative symbol. Though this example doesn't directly show how social information use helps individuals save time in making decisions; one possible reason for the findings as suggested by the authors is that late arriving birds capitalize on social information because they don't have sufficient time to inspect the nest boxes themselves and hence use locally available social information (Seppänen & Forsman, 2007).

Social information is also helpful to animals under risky situations – such as when there is an imminent threat of predation. Dawson & Chittka (2014) conducted an experiment in which bumblebees (*Bombus terrestris*) were allowed to forage from two differently coloured flowers, one flower colour was associated with a simulated predator attack (foam pincers in the flower closing in and trapping the bee for a little time before release) – called the 'dangerous' flower and the other flower colour indicating a 'safe' flower. Subsequently, when bees were allowed to forage from an array of all 'dangerous' coloured flowers or all 'safe' coloured flowers along with trained conspecific demonstrators, with the demonstrators being trained to feed from specific flowers in each array – bees joined feeding conspecifics only when the foraging array contained all ‘dangerous’ flowers (Dawson & Chittka, 2014). In a similar study, minnows (*Phoxinus phoxinus*) were first given a chance to observe conspecifics feeding from one of two identical feeders in a tank (Webster & Laland, 2008). Later, the minnows’ choice of feeder was noted when allowed to choose between the demonstrated and the non-demonstrated feeder, under three levels of predation risk; In the high predation condition shelters (artificial vegetation cover) in the tank was removed and a model predator was situated adjoining the feeding area, in the indirect predation risk condition the shelter was removed but a model predator was not present and in the low predation risk condition, shelter was available and a model predator was not present. The researchers found an increasing trend of minnows using social information – measured as entering the demonstrated feeder zone first and time spent in demonstrated feeder zone with increasing level of risk from low to indirect to high predation risk condition (Webster & Laland, 2008).

Role of Social Learning in Culture. Social learning has been implicated as a process forming the basis of culture (Aplin, 2019; Whiten, 2019, 2021a). Culture can be defined as a set of traditions, in the form of shared behaviours, skills and beliefs (for humans) that are persistent in a population and socially transmitted within and across generations (Whiten, 2019, 2021b). Culture has allowed humans to flourish. What about culture in animals, given the evidence that animals do learn and obtain information socially? One of the well-known examples of animal culture is the expanse of variation in songs by songbirds; songbirds learn songs socially and populations are known to exhibit differences in song dialects that vary across geographical regions (Catchpole & Slater, 2008; Whiten, 2019). Cetacean vocalizations too are likely cultural with new song variations being socially learnt and transmitted across huge populations

(Whitehead et al., 2019). Similarly, different groups of chimpanzees have shown differences across multiple traditions such as foraging, courtship, and grooming techniques; with variation in the local environment across groups by itself being unable to explain these differences (Whiten, 2021b). A study with fruit flies *Drosophila melanogaster* in the laboratory has shown that mate preferences can be culturally transmitted (Danchin et al., 2018). Female fruit flies learn mate preferences socially – observer females that watched demonstrator females mate with males of a particular phenotype (for example, a 'green' dusted male) and reject a male of another phenotype (say a 'pink' dusted male), subsequently preferred to mate with a male of the demonstrated phenotype. Danchin and colleagues (2018) showed that this form of mate preference could be transmitted across age-class and also be maintained across a population of flies in an experimental chain. Further, the study also brought forth the likely role of conformity in facilitating the bias to copy a particular male phenotype. Observer females were exposed to mating events of multiple demonstrators simultaneously, where the number of demonstrator females mating with 'green' males and 'pink' males was varied. Some observer females viewed a majority of demonstrators mating with 'green' males, and other observer females viewed a majority of demonstrators mating with 'pink' males. Additionally, a control group of observers viewed an equal number of demonstrators mating with 'green' and 'pink' males. The researchers found that observer females developed a preference for whichever male phenotype was observed as being preferred by the majority; control observer females however did not develop a preference for males based on green or pink phenotype (Danchin et al., 2018). Multiple individuals in a group engaging in a particular form of behaviour, could suggest that the behaviour is 'locally adaptive', and hence the behaviour might be adopted by other individuals (Whiten, 2019). Such behaviours may help indicate group membership and further could be beneficial to newcomers – such as young or immigrant individuals (Aplin, 2019; Cantor & Whitehead, 2013; Van De Waal et al., 2013). In an example that demonstrates this, Van De Waal and colleagues (2013) trained a group of wild vervet monkeys (*Chlorocebus aethiops*) to avoid corn-cobs of one colour (say 'blue') by making it unpalatable, while offering a palatable alternative of a different colour (say 'pink'). A different group of monkeys were trained similarly, albeit the colours indicating palatability vs. unpalatability were reversed. The researchers found that preference for the palatable blue- or pink-coloured corncobs were respectively maintained in the two different groups. Moreover, young weaning monkeys naïve to the colour-palatability relationship also adopted the preference of the group possibly learning by observing their mothers. Immigrant males also adopted the preference of the group they were entering, in spite of originally being from a group that had the opposite colour preference (Van De Waal et al., 2013).

Costs of Social Information Use. In spite of the many benefits as outlined above, social information use is not indiscriminate (Giraldeau et al., 2002; Kendal et al., 2018; Laland, 2004). As we will shortly see, animals do not use information from others in all instances – thereby warranting a look at the costs and benefits in using social information in particular situations (Rieucau & Giraldeau, 2011).

One potential cost associated with using social information is that simply, other individuals might have the wrong information or information that risks being outdated, especially if the information is about an ephemeral resource such as a patch of food (Giraldeau et al., 2002). Perhaps the behaviour being displayed by other individuals does not reflect the most adaptive behaviour for the current scenario. In a classic example of how using social information might sometimes lead to maladaptive behaviour, Laland & Williams (1998) first trained groups of guppies (*Poecilia reticulata*) to take either a long circuitous route to a food source or a short route to a food source by using a trap to block use of the alternative route (that is for fish trained to take the long route the short route was blocked and vice versa). These trained fish were called the ‘founder’ population. Next, naïve guppies were introduced one-by-one into both long-route and short-route founder guppy groups and were monitored for their choice of route with both long and short routes now being equally accessible. Further, as the experiment progressed across days, the researchers gradually replaced founder guppies with new naïve guppies one-by-one. The goal of the researchers was to test if naïve guppies in both groups would follow the routes that respective founder guppies were trained to take and if the choices would persist even if all founder guppies were eventually removed, thus indicating a ‘tradition’. The researchers found that naive guppies in both groups took the routes established by the respective founder guppies, and that the route preference persisted to some degree even after complete replacement of the original founder population. That naïve guppies took the long route to a food source when foraging with long-route founder guppies, in spite of the availability of a viable less circuitous alternative, shows how social information can sometimes lead to maladaptive behaviour. This preference for taking the long-route continued to persist for a few days, although the proportion of guppies taking the long-route decreased in that duration (Laland & Williams, 1998). In another experiment, Avarguès-Weber and colleagues (2018) trained bumblebees (*Bombus terrestris*) to use social or non-social cues or a combination of both to discriminate low-rewarding vs. high rewarding flowers. In each case, the cue presence on a flower indicated that it was low-rewarding with the alternative flower option being highly rewarded. Bees that were trained to use non-social cues and a combination of both social and non-social cues to identify low rewarding flowers, learnt to avoid low-rewarding flowers and prefer the highly-rewarding alternative. However, bees trained with only social cues were not able to learn as well to avoid the low-rewarding flowers. Thus, bees were unable to use conspecific presence on low rewarding flowers as an avoidance cue and continued to forage on low-rewarding flowers in spite of the suboptimal gains (Avarguès-Weber et al., 2018).

Smolla and colleagues (2015) have proposed that competition between social learners converging on the same resources might also be a cost associated with social learning. Aljadeff and colleagues (2020) conducted an experiment wherein groups of sparrows (*Passer domesticus*; four in a group) were trained to feed from foraging grids. Sparrows in one group were trained as shape specialists on a foraging grid marked with shape cues, where symbol “X” instead of symbol “O” indicated food reward. Sparrows in another group were trained as colour specialists on a foraging grid marked with colour cues, where purple colour indicated food reward instead of green. The trained sparrows’ group (demonstrators that were shape or colour specialists respectively) were then each joined by two naïve conspecifics on mixed foraging grids, in which both shape and colour cues could be used to find food, under the same contingencies (“X” and purple cues indicated food reward while “O” and green cues did not). Demonstrators continued to exploit cues they were trained on previously (either shape or colour) to find food on the mixed foraging grids. The naïve individuals in the group with the demonstrators, however, used the rewarding cue that was not socially demonstrated to find food; that is naïve individuals in the group with shape specialists used colour cues to find food while naïve individuals in the group with colour specialists used shape cues to find food. These results indicate that while foraging in a group where resources are limited, animals might not conform to socially demonstrated behaviours if alternatives are available; showing that the value of socially demonstrated behaviour decreases in a negative-frequency dependent manner (Aljadeff et al., 2020).

Social Learning Strategies. Taking into account the different costs and benefits associated with social information use – the consensus is that animals do not use social information indiscriminately (Laland, 2004). Laland (2004) proposed social learning strategies as a framework to explain situations under which animals might copy other individuals, that is match their behaviour to the socially demonstrated behaviour. A variety of strategies corresponding to different determinants of social learning (or more precisely copying) have been proposed (Kendal et al., 2018; Laland, 2004). Such as 'when' and 'who' strategies for example. 'When' strategies are primarily concerned with situational factors affecting copying – such as *copy-when-naïve* strategy wherein animals that do not have the experience of performing a behaviour might copy the socially demonstrated behaviour (Kendal et al., 2018; Laland, 2004). For example, guppies (*Poecilia reticulata*) without experience of feeding from either one of two available feeders, when given social information in the form of conspecific demonstrators feeding at one of the feeders, subsequently visited the demonstrated feeder (Kendal et al., 2004). Similarly, *copy-when-dissatisfied* is also a state-based strategy which suggests that animals might copy if their current behaviour was unrewarding (Kendal et al., 2018). Jones and colleagues (2013) conducted a study in which frog-eating bats (*Trachops cirrhosis*) learnt to associate a training cue (ringtone) with food under different degrees of reliability – the training cue either predicted rewards unreliably (50% of the time) or reliably (100% of the time). Bats that were trained with reliable or unreliable cues were then presented with an opportunity to forage with a conspecific demonstrator that used a novel cue (different ringtone) to retrieve food or an opportunity to forage just in the presence of a novel cue without a conspecific demonstrator. The researchers found that bats which had the experience of training cues being associated with unreliable rewards and hence a 'dissatisfying' experience in terms of rewards, were more likely to approach the novel cue demonstrated by conspecifics than bats which had a satisfying previous experience of reliable rewards or bats that did not have access to a conspecific demonstrator - thus lending support to the *copy-if-dissatisfied* strategy (Jones et al., 2013).

The identity of demonstrators could also direct social learning (Kendal et al., 2018; Laland, 2004). The *copy-familiar-individuals* strategy suggests that animals might copy familiar over unfamiliar individuals; as an example of this strategy, Guillette and colleagues (2016) found that naïve zebra finches (*Taeniopygia guttata*) that had not built a nest before copied the nest material choice of familiar over unfamiliar conspecifics. Biases towards familiar individuals could be favorable since familiar individuals are more likely to occur in the same environment and provide more demonstrations, and might even arise from previous positive experiences of using information from familiar individuals (Laland, 2004; Munch et al., 2018). These ideas revolve around the question how social learning strategies evolve, which is still largely unknown except for a few studies making inroads. In one such study, Farine and colleagues (2015) showed how factors such as developmental stress might impact the type of social learning strategies animals use later in life. The researchers found that zebra finches that were subject to early life stress as juveniles (in whom a high level of stress hormone was induced) were more likely to socially learn a novel foraging skill from unrelated adults than parents. Control juveniles on the other hand, preferred to socially learn from their parents and not from unrelated adults. This experiment thus demonstrates one way in which social learning biases could develop in individuals (Farine et al., 2015).

Social Information and Asocial Information

Given that both social and asocial sources of information can potentially affect the choice behaviour of animals and can be available at the same time, it is imperative to consider how these sources interact to give rise to the animal's resultant behaviour. In nature, asocial and social sources of information can be available to an animal such that both convey the 'same' or 'different' choice behaviours as appropriate. To avoid the confusion that stems from not knowing what information is being inferred from social demonstration – here the terms 'same' or 'different' simply refer to whether or not the choice of behaviour influenced by asocial information alone is expected to match ('same') or not match ('different') the socially demonstrated behaviour. First, I consider examples of how having sources of asocial and social information in agreement affects decisions animals make. Second, I consider situations where asocial and social sources of information could be in conflict. Conflicts could stem from having prior experience, preferences, or access to cues that inform behaviour in a way that does not match the socially demonstrated behaviour. Such conflict studies can give us insights about the scope of social information use – the circumstances under which an animal might turn towards social information and why using social information might be adaptive in particular circumstances.

Social and Asocial Sources of Information in Agreement. Black garden ants (*Lasius niger*) are capable of using their own route memory to find their way to a food source (Czaczkes et al., 2011). These ants also lay pheromone trails (social information). Czaczkes and colleagues (2011) asked how having these two sources of information helps guide the ants to a location of a food source. The researchers carried out an experiment with a 2x2 design, the factors being whether ants had own memory (asocial information - yes/no) and whether the ants had access to a pheromone trail (social information - present/absent). On observing the walking speeds as well as sinuosity of paths taken by ants in each condition, the researchers found that ants that had both own route memory as well as a pheromone trail walked the faster and in straighter paths than ants with only one source of information or no source of information, showing how having multiple sources giving consistent information leads to a synergistic effect on behaviour (Czaczkes et al., 2011). Similarly, bumblebees (*Bombus terrestris*) were subject to a foraging task which required discriminating rewarding vs. unrewarding flowers using use asocial alone (flower cue to identify rewarding flower) or both asocial and social cues (flower cue and model bee presence to identify rewarding flower). The study found that bees which received consistent asocial and social information about rewarding flowers made fewer errors in the foraging task than individuals which received only asocial information (Baracchi et al., 2018). Social information use can also be modulated by innate biases towards the socially demonstrated options (Jones et al., 2015). Jones and colleagues (2015) showed that bumblebees (*Bombus terrestris dalmatinus*) that had a dissatisfying experience of feeding on low quality flowers of a particular colour continued to feed on low-quality flowers if no social information about an alternative flower colour was provided. When given access to social information in the form of a conspecific model marking the alternative-coloured flowers, bees that had a dissatisfying experience used social information – but only if there was an innate preference for the flower colour being socially demonstrated (Jones et al., 2015). An example of a case where asocial and social information being in agreement leads to the consistent information not being chosen, is a part of the study on foraging guppies by Trompf & Brown (2014). Female guppies (*Poecilia reticulata*) first acquired asocial information about two foraging patches as being either a rich foraging patch or a poor foraging patch through individual experience. After observing conspecific demonstrators feeding from the rich patch (the ‘rich patch’ that is socially demonstrated is consistent with the ‘rich patch’ indicated by individual experience), bold female guppies as opposed to shy guppies opted for the alternate foraging patch even though it was of poor quality. The authors suggest that bolder guppies in this scenario might have combined their asocial and social information to infer that the rich patch was likely to be depleted while shy fish might have prioritized safety (Trompf & Brown, 2014). Moving on from the foraging context, Thorogood & Davies (2016) found that reed warblers (*Acrocephalus scirpaceus*) that had individually observed presence of a common cuckoo (*Cuculus canorus;* a brood parasite) at their nest and also obtained social information from conspecifics about presence of cuckoo at a neighbour's nest via playbacks of mobbing calls - had higher egg rejection rates than reed warblers that received no information or received only one type of information. Combining asocial and social information in this manner, might be giving the reed warblers a better estimate of the risk posed by the brood parasite, in terms of how likely their nests were to be parasitized (Thorogood & Davies, 2016).

Social and Asocial Sources of Information in Conflict. As briefly introduced in the section on social learning strategies, different factors can modulate whether or not social information is used – including availability of asocial information, state of the observers, and identity of demonstrators (Kendal et al., 2018). In this thesis I focus on how animals weigh asocial and social sources of information while making decisions. A variety of studies, across different species and contexts have observed the resultant behaviour of an animal under conflicting sources of information to suggest which one of the sources is being prioritized in that particular situation. Such studies can give us insights into costs and benefits associated with each source of information.

Betts and colleagues (2008) studied how the black-throated blue warbler (*Dendroica caerulescens*), a migrant songbird, made settlement decisions. Specifically, did the birds primarily use vegetation cues (asocial information) or presence of other breeders as inferred from post-breeding songs (social information) to decide where to settle? The researchers experimentally manipulated presence of other breeders by placing song playbacks across the habitats with vegetation types for which the songbirds had low, medium or high preference. By monitoring the settlement decisions of these birds, it was found that when given social information, birds even settled in habitats with vegetation types that were otherwise unpreferred and would typically not be chosen. Social information here in the form of post-breeding songs might be preferred by birds as an indicator of the outcome - reproductive success (Betts et al., 2008). Similarly, egg laying decisions in the insect cactus bug (*Narnia femorata*) is known to be influenced by the quality of the resource available – more eggs are laid on a high-quality resource (cactus with fruit), as compared to a low-quality resource (cactus without fruit; Miller et al., 2013). However, Miller and colleagues (2013) found that when given social information in the form of presence of conspecific or heterospecific juveniles on both high as well as low quality resources; the was no association between the number of eggs laid and the resource quality, cactus bugs laid eggs in the low- or high-quality resource in a similar manner. In an example showing the role of social and asocial information's influence in the context of anti-predatory behaviour, minnows (*Pimephales promelas*) first acquired asocial information about a novel odour cue as being 'safe', by repeated exposure to the novel odour cue without any negative consequences ('safe' cue; Crane & Ferrari, 2015). Later, minnows were presented with conflicting social information in two ways – a) via conspecifics showing an anti-predatory response in the presence of the 'safe' cue or b) via social information in the form of alarm cue from injured conspecifics in presence of the 'safe' cue. Minnows that had experienced conflicting social information via conspecifics' anti-predatory behaviour to the 'safe' cue, displayed anti-predatory responses during subsequent presentation of the previously learnt 'safe' cue; showing that conflicting social information in this case was able to override previous individually learnt associations. However, the type of social information also mattered - minnows that received social information as alarm cues of injured conspecifics along with the ‘safe’ cue did not show evidence of anti-predatory responses to the ‘safe’ cue when presented later; showing how the acquired asocial information inhibited social information use to some degree. In contrast, minnows that did not receive an opportunity to learn individually about the safety of the novel cue, learnt to respond to the novel cue from both conspecific behaviour as well as alarm cues in a similar fashion (Crane & Ferrari, 2015). In an example showing conflict in mate-choice decisions, female fruit flies (*Drosophila melanogaster*) were allowed to individually evaluate males in two different conditions as potential mates – a good condition male, reared in nutritionally rich medium and a poor condition male reared in nutritionally poorer medium (pre-test; Mery et al., 2009). The time spent by females in the zones containing the good condition or the poor condition males revealed that males in good condition were perceived to be more attractive. Later, the females either observed a conspecific demonstrator (model female) in the zone with the good condition male, in the zone with the poor condition male or observed no conspecific demonstrator at all (control). Finally, the females were allowed to re-evaluate the same males they had previously evaluated alone. The results showed that females did not display a change in attractiveness towards good condition males after good condition males were socially demonstrated, or in the control condition with no social demonstration. Social demonstration of poor condition males however, lead to a marked increase in attractiveness towards the poor condition males from the pre-test phase (Mery et al., 2009).

In other situations, researchers have found that animals preferentially rely on asocial rather than social information. Goats that had asocial information about location of a food source a on a particular side of a corridor (right or left) when given social information in the form of a feeding conspecific at an alternate side, did not prefer to go to the demonstrated side and continued to prefer the previously rewarding location according to individual experience (Baciadonna et al., 2013). Similarly, black garden ants (*Lasius niger*) that had route memory (asocial information) of food location (in one arm of a T maze), when given conflicting social information or in the form of a pheromone trail leading to the alternative arm of the T maze, exhibited a preference for using asocial information. Most ants preferred to visit the arm for which they had the route memory (Grüter et al., 2011). Additionally, while strength of the pheromone trail – being weak or strong did not affect the results, ants exhibited a greater preference to visit the arm indicated by route memory as they made more trips (more individual experience; Grüter et al., 2011). In another study with the same species of ants studying similar asocial and social information in conflict, the researchers found that when ants were given information about a potential better-quality food (as compared to what their individual experience was), in the form of a small droplet or via contact with other returning foragers whilst in the corridor of a Y maze, then more ants preferred to use social information over asocial information – potentially for the incentive to exploit a better food source (Czaczkes et al., 2019). A similar question as to whether social information would be exploited in anticipation of a better food source was asked with chimpanzees (*Pan troglodytes*) as subjects (van Leeuwen & Call, 2017). Chimpanzees were first trained to exchange a particular token type with a human experimenter to obtain a reward (carrot). Once trained, chimpanzees then observed a conspecific demonstrator use a different token type other than the one the subject chimpanzee was trained on to either obtain a better food (banana; test condition) or the same food (carrot; control condition). The researchers predicted that subject chimpanzees might use a *copy-if-better* strategy and switch to using the socially demonstrated token in the test condition but not the control condition. While a few chimpanzees did choose to use the socially demonstrated token in the test condition showing the use of the *copy-if-better* strategy; the majority of chimpanzees in both test and control conditions continued to use the token they had been trained on, which had reliably predicted some reward (van Leeuwen & Call, 2017). In an example of a study looking at a different context other than foraging – Cronin (2013) looked at the role played by asocial and social information in nest relocation choices of ants (*Myrmecina nipponica*). Ants were first given an opportunity to evaluate different nests that varied in parameters such as nest height, volume, dryness, and light available, and a baseline preference for the different nests was established. Later, ant colonies were given a choice between a preferred nest vs. a non-preferred nest, with varying levels of preference differences – moist or dry nest (high preference for moist over dry), dark or light nest (weak preference for dark over light), and small entrance vs. large entrance (weak preference for small entrance). Further, the choice tests occurred in the presence or absence of a pheromone trail (social information). When present, a pheromone trail (social information) always led up to the non-preferred nest in each combination. The researchers found that presence of social information influenced nest choices of relocating ants only in the cases where the difference between preferred vs. non-preferred nests was weak. That is, presence of social information marking a non-preferred nest led to more ants choosing that nest as compared to the case where social information was absent. However, this change was seen only in the case where the non-preferred nest was only weakly and not strongly non-preferred (Cronin, 2013).

Other studies have investigated the roles of different factors in tipping the balance in favour of asocial or social information. For example, reliability of each source of information. Foraging bumblebees (*Bombus impatiens*) that had experience with different levels of reliability (low, medium, high) in the use of asocial information (flower colour) as well as social information (presence of conspecific demonstrator) in predicting rewarding flowers, generally used the more reliable information when both sources of information were in conflict (Dunlap et al., 2016). However, in conditions where social information was at least moderately reliable, bees preferred to use social information instead of highly reliable asocial information or equally reliable asocial information (Dunlap et al., 2016). Costs associated with using either information in a particular situation can also affect the trade-off. Guppies (*Poecilia reticulata*) in a foraging task used asocial over social information in a conflict scenario that is guppies preferred to feed from foraging patches that were previously experienced over choosing to feed with demonstrator conspecifics. However, when using asocial information came with a cost – that of breaking visual contact with conspecifics, guppies favoured social information instead (Kendal et al., 2004). Other characteristics such as number of demonstrators is also known to affect social information use. Nutmeg mannikins (*Lonchura punctulata*) that had the experience of using the appearance of a green dot in a foraging apparatus as a reliable predictor of feeder location (asocial information), were given conflicting social information in the form of conspecifics feeding at an alternate feeder. Additionally, the number of social demonstrators (feeding conspecifics) was varied from one demonstrator to six demonstrators. The results showed that having increasing number of demonstrators feed from the alternate feeder switched the mannikin's feeder preference – the mannikins no longer preferred to feed from the feeder predicted by the green dot and instead fed from the socially demonstrated alternate feeder (Rieucau & Giraldeau, 2009).

Overall, the fraction of studies outlined here shows the wide variety of ways in which animals weigh asocial and social information, depending on the context and ecology. This variety makes it imperative to extend studies of information use across different behaviours and contexts to specifically understand why in a particular circumstance, animals might use one source of information over the other. One of the contexts in which the role of information use is being increasingly studied in is nest-building, which I introduce in the next section.

Nest building

Nests are structures built by animals, the primary function of which in most cases is to provide shelter and raise young (Hansell, 2000; Mainwaring et al., 2014). While many animals build nests including invertebrates such as wasps, fish like the three-spined sticklebacks, and mammals like squirrels - birds are almost synonymous with nests (Hansell, 2000; Healy et al., 2008). Thanks to the sheer number of birds that build nests and the variation that exists in the type of nests birds build – from scrapes on the ground, to modified cavities in trees or intricately woven structures (Breen et al., 2016; Hansell, 2000). No matter the kind, nests built for the purpose of raising young are important for the fitness of the parents, making nest building a crucial behaviour to study (Mainwaring et al., 2014).

A long-held belief was that nest building in birds was a wholly innate behaviour (Breen et al., 2016). However, now we know that this is not the case - many birds have been shown to be flexible with respect to nest building, and are able to use information to help make nest building decisions (Breen et al., 2016; Guillette & Healy, 2015). Broadly, the two kinds of decisions a nest building bird might have to make include where to build the nest and what material to use for the nest. Nest-site selection is an important activity involving considerations about resource availability in the habitat and safety from predation (Breen et al., 2016). For example, Siberian jays (*Perisoreus infaustus*) exposed to playback calls of corvid predators in the vicinity of their nests, shifted their nests to almost twice the distance in the subsequent year as compared to distances by which nests were shifted in previous years. Further, birds exposed to simulated predators also preferred to nest in more dense vegetation during the subsequent breeding attempt. Control birds on the other hand that were not exposed to playback calls of predators showed no atypical changes in nest-site selection (Eggers et al., 2006). For birds that do not build nests, such as secondary cavity nesters that use cavities lined with nest material left behind by primary cavity nesters, nest site selection can be based on how soft the nest material lining the available cavity is (Morinay et al., 2021).

Level of reproductive success experienced by birds can also impact nest-site selection in the subsequent years. Data analysing the relationship between nest failure or success with nest site fidelity in northern flickers (*Colaptes auratus*) over a seven year period found that birds that experienced an unsuccessful breeding attempt were more likely to move to a different nest-site for the next breeding attempt (Fisher & Wiebe, 2006). Information about local habitat quality can also be gleaned from the success of conspecifics. Kittiwakes (*Rissa tridactyla*) that suffered a failed breeding attempt in a locality where conspecific breeders were successful, were more likely to return to the same breeding site as compared to kittiwakes that were unsuccessful breeders in a locality where other conspecifics were also unsuccessful breeders (Boulinier et al., 2008). Such use of social information about nest site quality can also be obtained from heterospecifics nesting in the area (Forsman & Seppänen, 2011).

Selecting nest material is also an important activity performed by nest building birds. Nest materials can serve a wide variety of functions, and determine the structural integrity of the nests and its quality as a shelter (Breen et al., 2016; Mainwaring et al., 2014). Birds can choose materials on the basis of a wide variety of features such as comfort or insulation provided (Hilton et al., 2004), rigidity of material (Bailey et al., 2014), role in reducing conspicuousness (Bailey et al., 2015; Hansell, 2000), and role in keeping out ectoparasites (Suárez-Rodríguez & Garcia, 2017). For example, Biddle and colleagues (2018) measured the nest composition of four species across thrushes and finches and found that the material incorporated in different parts of the nest varied according to strength and rigidity. Materials incorporated in the outer parts of the nest were stronger, and stiffer than materials selected for the cup lining (Biddle et al., 2018). In a way to reduce conspicuousness of their nests, birds such as blue-grey gnatcatchers (*Polioptila caerulea*), and long tailed tits (*Aegithalos caudatus*) incorporate lichen flakes as nest material – presence of lichens in a continuous mosaic-like fashion achieves background matching against the tree trunk structure (Hansell, 2000). Paradise flycatchers (*Terpsiphone*) and Cocos flycatchers (*Nesotriccus ridgwayi*) also incorporate materials like lichen to reduce conspicuousness by altering the perceived boundaries of the nest structure (Hansell, 2000). Similarly, Japanese quails (*Coturnix japonica*) too choose to lay eggs in substrates that reduce conspicuousness of the eggs (Lovell et al., 2013). Nest material can also function to ward off ectoparasites. House finches (*Carpodacus mexicanus*) are known to respond to increasing ectoparasite load in their nests by increasing the amount of cigarette butt fibers incorporated as nest material (Suárez-Rodríguez & Garcia, 2017).

Studies investigating the role of information use in nest material selection have found that both asocial factors such as individual experiences with material (learning to prefer stiff over flexible string for example), and individual breeding success associated with nest material can modify subsequent nest material selection (Bailey et al., 2014; Muth & Healy, 2011). Additionally, studies have also investigated the role played by social factors - early social environment (Breen et al., 2020), watching conspecifics build with particular material (Guillette et al., 2016), and observing artefact nests of other individuals are all known to influence subsequent nest material selection (Camacho-Alpízar et al., 2021b). Much of the work investigating these topics have been done with zebra finches in the laboratory, and are expanded upon in the section below.

Model system

The zebra finch (*Taeniopygia guttata*) is a small, colonial passerine native to the arid deserts of Australia (Zann, 1996). Nevertheless, these birds also find home in laboratories around the world as an immensely popular model system for asking a range of questions - spanning across communication, neurobiology and cognition among other fields (Griffith & Buchanan, 2016; Healy et al., 2010). This popularity is in part credited to the amenability of these birds to the laboratory (Griffith & Buchanan, 2016). Apart from being easy to obtain and maintain, of particular relevance to this thesis is the utility of zebra finches in studying nest-building behaviour in captivity. Zebra finches readily build nests in the lab with a range of provided material, have short reproductive cycles where the young typically fledge within five weeks, and also reach sexual maturity within 90 days of fledging (Griffith & Buchanan, 2016; Zann, 1996).

Wild zebra finches are opportunistic breeders, breeding throughout the year whenever conducive conditions such as rainfall arise (Zann, 1996). Males and females mate monogamously, typically forming life-long pair bonds and nest within colonies where the number of breeding pairs has been observed to range from 4 to 136 (McCowan et al., 2015; Zann, 1996). The zebra finch male is the primary nest-builder and is responsible for collecting and depositing nest material – which in the wild has been observed to be twigs or stems from the ground varying in length and flexibility, along with soft material such as plant wool and feathers for lining the nest inside (Zann, 1996). Though more often found in thorny shrubs or small trees, zebra finch nests are also found in human settlements, at the base of raptor nests, and even in rabbit holes or bleached cattle skulls (Zann, 1996). The final breeding nest typically takes a spherical domed shape, although variation in dimensions has been noted both within and across different colonies (Zann, 1996).

Zebra finches are able to identify and distinguish different materials on the basis of properties such as length, flexibility, and colour - demonstrating an understanding of physical properties that are likely used while evaluating different materials for building a nest (Lambert et al., 2021; Breen et al., 2016). For example, Muth & Healy (2014) showed that when given a choice between long and short string as nest materials and a nest box with a small entrance hole (small enough for only the short material to fit), zebra finches chose short material over long material while initiating nest building in the small-holed nest box. Similarly, zebra finches when given nest materials of different colours (different coloured pieces of paper), preferred to build with material that matched the colour of their environment - that is, camouflaged their nests (Bailey et al., 2015). Both these examples show that zebra finches do pay attention to material properties and select 'appropriate' material depending on the environment in which they are building their nest. Further, individual experience with and/or pre-existing preference for certain materials can also play a role while making nest material related decisions (Camacho-Alpízar et al., 2021b; Muth & Healy, 2011; Sargent, 1965). In one of the earliest experiments investigating nest material selection in zebra finches, Sargent (1965) found that nest building experience with a certain coloured nest material influenced the birds' choice of nest material for subsequent nests. For example, birds in Sargent (1965) experiment seemed to have a pre-existing preference for brown over other coloured materials (green and red) before they had any nest building experience. However, once birds had built a nest recently with green material, they subsequently showed a preference for green material. Interestingly though, such an experience-mediated change in preference did not extend to red coloured material; birds continued to show a dislike for red material and did not prefer to use it over green or brown material in spite of having built a nest recently with red material (Sargent, 1965). Zebra finches are also capable of learning about nest material rigidity with experience – once males had built a partial nest out of flexible string (first experience), when given both flexible and stiff string during a second nest building opportunity, males preferred the stiff string which was the better material in the sense that fewer pieces of that material were required to build a nest (Bailey et al., 2014). However, males that had built a partial nest out of stiff string during their first experience were indifferent to either string type during the second nest building opportunity (Bailey et al., 2014). In addition to just an experience of having built a nest, level of success experienced during a breeding attempt with particular coloured material is also known to affect nest material choice in subsequent breeding attempts (Muth & Healy, 2011). Similar to Sargent (1965) however, the extent to which this experience of success or failure affected subsequent choice was also dependent on the pre-existing preference for each material. Males that built their first nest with a non-preferred colour material, increased preference for the non-preferred colour in a subsequent breeding attempt if the first attempt had been successful (Muth & Healy, 2011). However, males that built their first nest with a preferred colour continued to choose the preferred colour irrespective of the outcome of the first breeding attempt (Muth & Healy, 2011). Extending beyond nest material colour, associations between breeding success are also made to nest material type in general - whether or not zebra finches had a successful breeding experience using a particular material (coconut fiber) for their first breeding attempt, has been found to affect how much of familiar (coconut fiber) or novel material (white jute string) is used during a second breeding attempt (Camacho-Alpízar et al., 2021a). Birds that had a successful experience building with coconut fiber incorporated similar amounts of the familiar coconut fiber and novel white string while building their second nest, however, birds that had experienced nest failure during their first breeding attempt building with coconut fiber incorporated more of the novel white string as compared the familiar coconut fiber during their second breeding attempt (Camacho-Alpízar et al., 2021a).

As a group-living species, zebra finches also have access to the behaviours of other individuals from whom potentially useful information could be gleaned. Perhaps the most well studied context in which such transfer of social information occurs, especially considering the strong familial associations in the zebra finch, is the learning of song by young juvenile males from their fathers (Slater et al., 1988). Zebra finches also show transfer of social information regarding the presence or quality of a foraging source or a novel foraging skill – the extent to which such social information is used has been found to be dependent on different factors like sex, familiarity, pairing status, and ontogeny of individuals involved (Benskin et al., 2002; Farine et al., 2015; Templeton et al., 2017). Zebra finches in the wild are known to visit or prospect the nests of breeding conspecifics (Brandl et al., 2018; Mariette & Griffith, 2012). Brandl and colleagues (2019) showed that wild zebra finches were attracted to nests of breeding conspecifics via playbacks of begging calls made by chicks in the conspecific nests. Further, the researchers found that there was more visitation to conspecific nests which had playbacks of begging calls by larger broods (seven chicks) as compared to ones with playbacks of smaller broods (three chicks) or white noise (controls; Brandl et al., 2019). While these findings show that wild zebra finches might be collecting social information about nesting from other breeders by prospecting nests, why zebra finches engage in such nest prospecting or what information they gather is unclear. Further, other field studies have revealed that wild zebra finches do not use conspecific reproductive success to make decisions regarding where to build a nest (Brandl et al., 2018).

Multiple experiments in the laboratory with zebra finches in captivity have shown the use of social information in nest material selection and handling. Guillette and colleagues (2016) showed that zebra finches that had not built a nest before (and hence were naïve to nest building) copied the material colour choice of familiar demonstrators after observing the demonstrators build a nest with a particular-coloured material (*copy-when-uncertain* strategy since the observers were naïve). Additionally, as is observed with many cases of social information use being 'directed' towards a certain class of demonstrators, naïve observers only copied from familiar individuals and not unfamiliar individuals; thereby lending support to both *copy-when-uncertain* and *copy-familiar-individuals* social learning strategies (Guillette et al., 2016).

Apart from obtaining social information from nest building conspecifics, naïve zebra finches have also shown the capacity to extract information from nests that are artefacts (products of behaviour) by increasing preference for the material colour of the artefact nests (Camacho-Alpízar et al., 2021b). In terms of other social factors, Breen and colleagues (2020) found that while material encountered in the natal nest did not influence nest material choice of birds constructing their first nest, the social and physical environment encountered as a juvenile did influence first time nest construction. Zebra finch males that as juveniles had access to both a particular coloured material and an unrelated adult preferred to use the same-coloured material while constructing their first nest (Breen et al., 2020). Overall, evidence is suggestive of the role played by the social environment in informing nest-building decisions of zebra finches, especially ones that have had no previous nest building experience.

Even though a variety of social and asocial factors have been known to influence nest-building decisions in the zebra finch as outlined in this section, studies have yet not considered how birds make decisions when multiple factors are present together. For example, how do birds decide which material to use when both social as well as asocial factors are present, each of which separately has been shown to influence nest material selection? – In this thesis, I attempt to answer this question.

Current Study

From previous studies by Bailey and colleagues (2015) and Guillette and colleagues (2016), we know that zebra finches are capable of using asocial as well as social information while making decisions about nest material. Bailey and colleagues (2015) showed that zebra finches, when given a chance to match nest material colour against a background colour, preferred to build a camouflaged nest. Guillette and colleagues (2016) showed that naïve zebra finches that had not built a nest before copied the nest material choice of familiar demonstrators, as identified by nest material colour. In the current study, I wanted to see how having access to both asocial and social information that could be used to make decisions regarding nest material, impacted nest material choice in first time nest building zebra finches.

For reasons that are not clear, zebra finches show preferences for nest material colour, and even associate material colour with breeding success (Camacho-Alpízar et al., 2021b; Muth & Healy, 2011; Sargent, 1965). Perhaps, variations in colour of material are likely indicative of structural properties such as strength and rigidity and hence might make colour a relevant factor to pay attention to while selecting material. Additionally, as Bailey and colleagues (2015) showed, colour of material chosen might serve a more direct function of reducing conspicuousness. Such a function might be relevant in the wild, given the high frequency of predator attacks zebra finches are subject to by predators that depend on vision for locating prey (Bailey et al., 2015; Zann, 1996).

Observing a conspecific build a complete nest with a particular-coloured material might function as information about the utility of that material in contributing to the structure of a nest, and hence might be preferentially used by first time nest builders who lack such information (Guillette et al., 2016). In other case, conforming material-choice of own nest to nests built by other individuals in the vicinity might be advantageous for some reason – such as indicating an individual's nest as belonging to a particular colony or reducing risk for a single nest, drawing parallels with studies showing how preferences about food colour in vervet monkeys or mate phenotype in fruit flies spread in a group (Danchin et al., 2018; Van De Waal et al., 2013).

Both these sources of information – asocial and social, are likely to be available to a zebra finch that's initiating nest building. Further the sources could present themselves in one of two ways – that is, the asocial and social sources could be in agreement such that the material that matches background colour (asocial) is also the one being socially demonstrated. Alternatively, the sources could be in conflict, such that the material that matches the background (asocial) is different from the material being socially demonstrated. In the conflict case, the resultant behaviour of the birds can tell us how the birds' preference to copy material choice from others (social information) is traded off with the preference to reduce conspicuousness of one's nest (asocial information). In this experiment I investigated both situations - where asocial and social information were in agreement and where asocial and social information were in conflict.

There were two treatment groups, each to reflect situations where information sources were in agreement (Agree group) or in conflict respectively (Conflict group), and the experiment was conducted in three phases. The first phase was identical for both the groups. In the first phase, I paired male and female zebra finches as the subject pairs (hereafter, observers) and gave each observer pair an initial preference test between three different coloured materials (pastel green, yellow and pink; all three of which were previously used in (Bailey et al., 2015). The materials were tied to one end of the cage and therefore could be interacted with but not be carried away or deposited. Further, the background of the cage was white coloured at this stage. Following the establishment of an initially preferred material (other two materials were considered non-preferred), observers moved on to the next phase which was the observation phase. In the observation phase, observers in the Agree group observed a familiar demonstrator build a nest with one of the observer's initially non-preferred colours against a same-coloured background. Observers in the Conflict group observed a familiar demonstrator build a nest with one of the observer's initially non-preferred colours against a background that did not match the socially demonstrated material, but was still non-preferred by the observer. In the final phase, observers in both groups were given an opportunity to build their first nest with all three coloured materials, against a non-preferred coloured background. For observers in the Agree group, the socially demonstrated material (social information) matched the background (asocial information), while for observers in the Conflict group, the socially demonstrated material (social information) did not match the background (asocial information). Presenting both the socially demonstrated colour as well as the background colour as non-preferred colours allows one to attribute any subsequent change in the observer's preference for material colour after the initial preference test to the effect of demonstration and/or background matching.

Going from the initial to the final phase, we predicted observers in both groups to lose preference for the initially preferred material because of the influence of asocial and/or social sources of information. Further for the Agree group, we predicted observers to use the material which corresponded to both asocial as well as social information, since both are equivalent and expected to produce the same effect in this situation. For observers in the Conflict group, we did not have a prediction as to whether social information or asocial information would be prioritized. If observers in the Conflict group prioritized using social information over asocial information that would imply that the benefits associated with matching conspecific nests outweigh the benefits obtained by camouflaging the nest, and make a stronger case for social information use in nest-building birds. On the other hand, if asocial information is prioritized over social information that would lend support to the idea that social information is likely beneficial and used only when there is no other source of information available.

Methods

Subjects

I used 76 (38 males and 38 females) wild-type zebra finches *(Taeniopygia guttata)* as subjects in this experiment. All of the birds were bred in the laboratory at the University of Alberta between September 2019 and March 2020 in brown coloured coconut fiber nests (see Appendix I Part A and Appendix I Part B for detailed breeding procedure) and were naïve to nest building prior to the experiment. All birds were sexually mature (>90 days post-hatch) at the time of the experiment and the average age of the subjects was 312 days for males (range 230-386 days) and 322 days for females (range 227-441 days).

Housing

Birds were housed in two same-sex colony cages (184 cm length × 66 cm width × 165 cm height) except during the experiment. The colony cages were in rooms with full spectrum ceiling fluorescent lights (Standard, 32W, T8 Daylight) programmed to run on 14:10 light dark cycle. Floodlights (HDX 250W Portable Work Light) that switched on 30 minutes prior to lights-off and stayed on until 15 minutes after were also present in the rooms to serve as a lights-off cue for the birds. Further, the colony cage rooms were maintained under temperature and humidity levels ranging between 20-23ºC and 45-60 % respectively. The birds in the colony cages had *ad libitum* access to food (Hagen Finch Staple VME Seed Mix), demineralized water, combination of grit (Hartz Grit' n' Gravel) and oyster shells (Canadian Lab Diet), water baths, and cuttlebones (Canadian Lab Diet). Vitamin water (Hagen Canada) and greens (spinach) were provided to the birds three times a week, and spray millet (Hagen Canada) was provided once a week. Other items the colony cages were equipped with include multiple tree branches, wooden dowels, and ropes.

Apparatus

For the purpose of the experiment, I used one housing room and two experimental rooms which were all set to run on the same 14:10 light cycle as the colony rooms. The housing room was used to hold the subject birds after they had been separated from the colony cages and paired as male-female subject pairs (hereafter, observers). The observers remained in the housing room until partaking in the experiment (in one of the experimental rooms). After the experiment, the observers were returned to the housing room as potential demonstrators. Subsequently, the observers, some after having acted as demonstrators, were moved back to the colony room.

Housing Room

The housing room contained stacked King's cages (each 100 cm length × 50 cm breadth × 50 cm height; King Cages International LLC) separated by opaque plastic sheets (Figure 1). Two feeder cups with food (Hagen Finch Staple VME Seed Mix) and two water cups were supplied per cage. The water cups were replaced with water tubes (Hagen Canada) for three days a week when the birds were given Vitamin water (Hagen Canada). Each cage also had a total of six perches, two along a long side (100 cm), and two per short (50 cm) side of the cage. The cage tray bottoms were lined completely with brown Kraft paper (U-line Kraft paper) and supplied with cuttlebones (Canadian Lab Diet), and a mix of grit (Hartz Grit' n' Gravel) and oyster shells (Canadian Lab Diet). The housing room also had a floodlight (HDX 250W Portable Work Light) identical to the one in the colony rooms, serving as a lights-off cue for the birds. The temperature in the housing room ranged between 19-24ºC while the humidity levels varied between 35-60%.

Experimental Rooms

Both the experimental rooms had a similar arrangement. Two King's cages (each 100 cm length × 50 cm width × 50 cm height; King Cages International LLC), same as the cages in the housing room, were present in each experimental room, to serve as the observer and the demonstrator cage, respectively (Figure 2). Each cage had two long sides (100 cm), front and back, with the back (100 cm) side having openings to access the cage inside. The observer and demonstrator cages were oriented to face each other along the respective front (100 cm) sides, and were separated by 10 cm. An opaque plastic sheet was used to act as a visual barrier between the two cages. Three holes were made at the top of the sheet into which wooden dowels were inserted, and the sheet was then hung in between the two cages. Opaque plastic sheets were also used to completely cover the top of each cage.

Located along the bottom of the back (100 cm) side at the two extreme ends were feeder cups containing food (Hagen Finch Staple VME Seed Mix). One water bottle was supplied per short side (50 cm) of each cage. Each cage had removable trays on the bottom, which were completely lined with brown Kraft paper (U-line Kraft paper), and supplied with cuttlebones (Canadian Lab Diet) and a mix of grit (Hartz Grit' n' Gravel) and oyster shells (Canadian Lab Diet). There was a total of six plastic perches per cage, with two perches on each short (50 cm) side and two perches on the back (100 cm) side. Three in cage mini-BNC cameras (OSY CAMS) were also present in each cage to capture the inside of the cage completely. One camera was located at the top center of each short (50 cm) side and one camera was located along the top center of the front (100 cm) side. BNC cables were used to connect the three cameras per cage to a DVR (Jodan) which stored continuous video recordings in one-hour chunks. These videos could be viewed and downloaded remotely for later use. The two DVRs in each room were also connected to a monitor, which was used to check for proper orientation of the in-cage cameras before every phase of the experiment. Each experimental room also had a floodlight (HDX 250W Portable Work Light) to serve as a lights-off cue for the birds. Further, temperature and humidity in the experimental rooms were maintained at similar levels as the housing room, ranging between 19-24ºC and 35-60% respectively.

Coloured Cage Backgrounds. For the purpose of setting backgrounds for the cages in each room, two cardboard pieces were cut out such that the entirety of the cage back (100cm) sides would be covered. One side of the cardboard was covered completely using white paper (Staples 30% recycled Pastel Coloured Copy Paper) while the other side was left uncovered. To create coloured backgrounds, each of pastel versions of green-, pink- and yellow-coloured papers (Staples 30% recycled Pastel Coloured Copy Paper) were glued together to make a single-coloured sheet the size of the cardboard. There were two such sheets of each colour per experimental room, so as to serve as the coloured background for demonstrator and observer cage respectively. Holes were punched at the top corners of the coloured sheets as well as the cardboard so that the required coloured sheet could be tied onto the uncovered side of the cardboard. Binder clips were used to tightly affix the coloured sheet to the cardboard at the two bottom ends. White jute twine (Jute Craft Twine, James Leaver CO) was used to tie the cardboard, along with the coloured sheet, to the top of the cage at both ends such that the entire back side of the cage was covered. Luminosity of the cages when the coloured background was on was 308 lux (median of three measurements), as measured by a luminosity meter (Dr. Meter Digital Lux Meter). For comparison, the luminosity measure without the background on was 324 lux.

Coloured Nest Cups. Wooden nest cups (12 cm length x 12 cm width x 12.5 cm height) covered with coloured paper (pastel versions of green, pink, or yellow; Staples 30% recycled Pastel Coloured Copy Paper) were also used in the experiment at different stages (Figure 3). A nest cup, whenever used, was always hung in between the two perches along the middle of the back (100 cm) side of the King's cage. Further, whenever a coloured nest cup was provided, the same-coloured cage background was also kept on.

Material Preparation for Initial Preference Test. Fifteen paper strips of the same colour (pastel versions of green, pink and yellow Staples 30% recycled Pastel Coloured Copy Paper), each measuring 15 cm x 0.7 cm were glued together on one end such that the other end fanned out to 3.5 cm in width (Figure 4). The top end was then tied to a white string (Jute Craft Twine, James Leaver CO) and glued over by the same-coloured paper to secure the attachment. This attachment was done to ensure that the birds could only interact with the material at this stage, and not carry the material away to deposit it into a nest. Each coloured material was then stuck to the front side of an extra cage pan by its top end using white duct tape at equidistant positions (separated by 18 cm), and in one of two possible orientations depending on the experimental room (Figure 6).

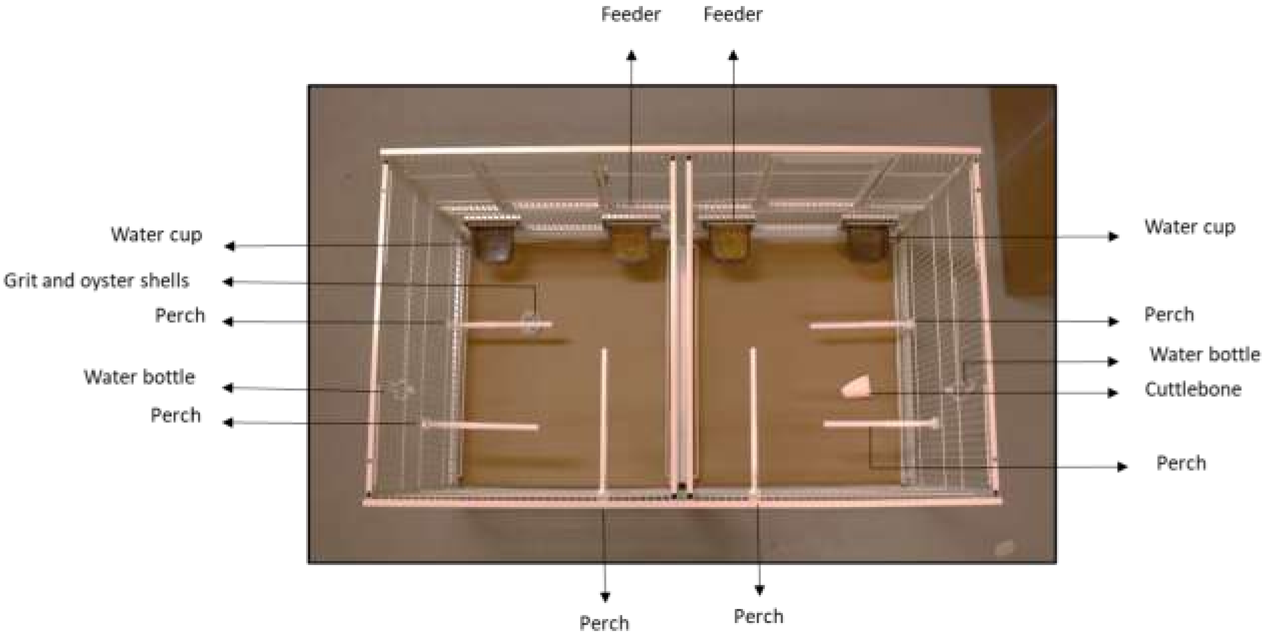
Material Preparation for Pre-observation Building and Observation Phases. To prepare inaccessible coloured materials that would be placed in the demonstrator cage during the pre-observation building and observation phases, paper strips of each colour (each measuring 15 cm x 0.7 cm) were glued over to create a block that resembled a bunch of 100 paper strips – thereby making these coloured materials inaccessible in terms of being carried away or deposited (Figure 5).

Animal Husbandry

Daily animal husbandry in both housing and experimental rooms included topping up food, cleaning water cups or tubes, providing demineralized water or vitamin water as appropriate (thrice a week), and topping up grit 'n' gravel as required. Birds in the housing room also received greens (spinach) thrice a week and spray millet once a week. Birds in the experimental rooms however did not receive these weekly supplements. Please see Appendix II for detailed procedure of animal husbandry.

Figure 1

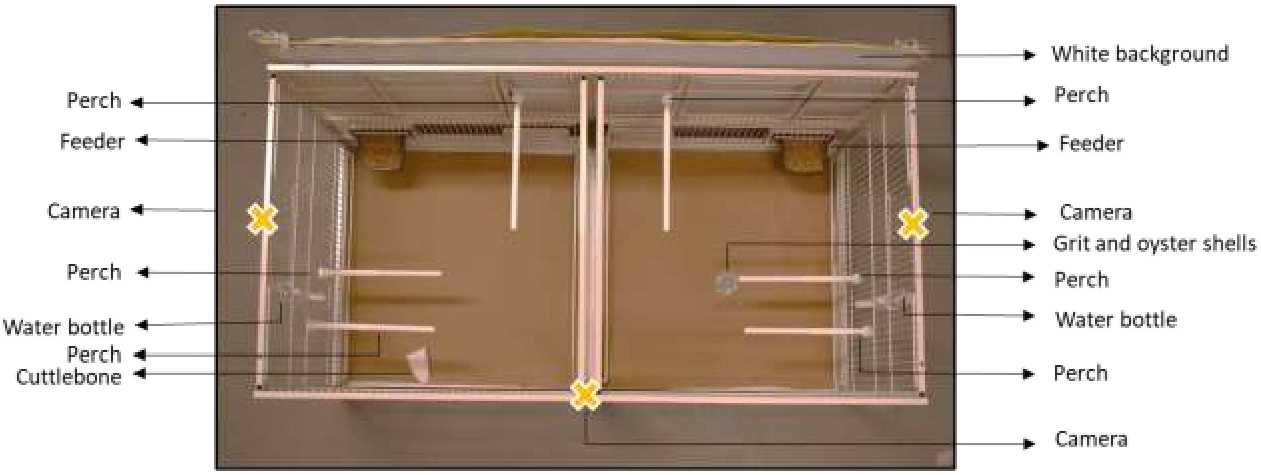
Housing Cage



Note. Top-down view of a housing cage. The dimensions of the cage were 100 cm length x 50 cm width x 50 cm height.

Figure 2

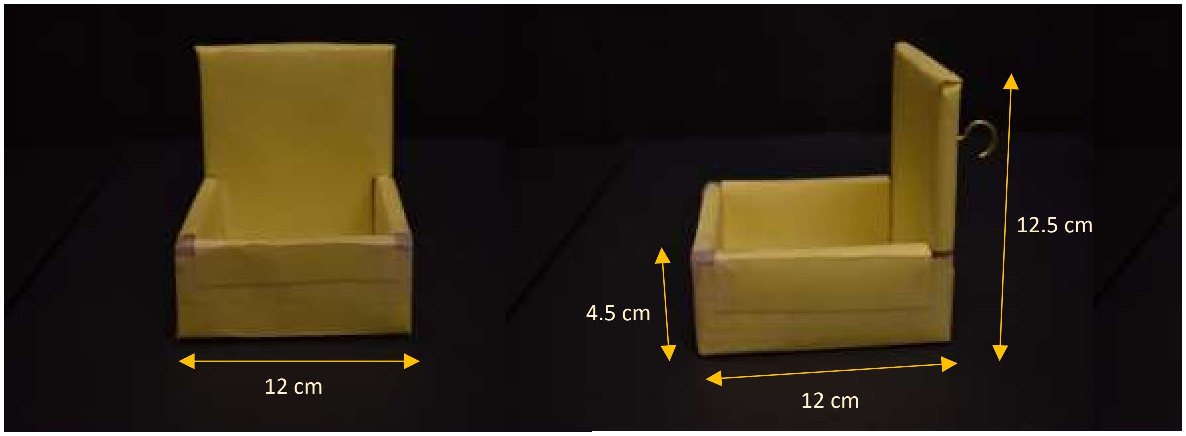
Experimental Room Cages – Observer and Demonstrator Cages



Note. Top-down view of the observer cage and demonstrator cage before the initial preference test phase (one picture is shown here since the set up was identical for both observer and demonstrator cages; dimensions of each cage were 100 cm length x 50 cm width x 50 cm height). The observer cage had the same layout for the pre-observation and observation phases.

Figure 3

Coloured Nest Cup



Note. This figure has the front (left) and side view (right) of a wooden nest cup covered with coloured paper (yellow coloured; 12 cm length x 12 cm width x 12.5 cm height).

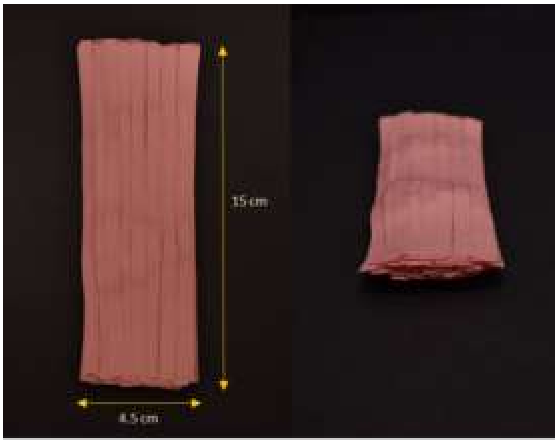
Figure 4

Initial Preference Test Material

Note. This figure is a top-down view of an initial preference test material (yellow coloured; 15 cm length x 3.5 cm width).

Figure 5

Inaccessible Coloured Material



Note. This figure has the top (left) and side view (right) of an inaccessible material (block of glued pink paper strips; 15 cm length x 4.5 cm width).

Procedure

First, I arranged all available male and female subjects from the oldest to youngest into blocks of seven to ten individuals each, where individuals of the first block went through the experiment first followed by individuals in the next block and so on. This part was necessary to ensure that all birds had attained maturity (approximately 90 days from hatch date) and spent comparable time with other individuals in the colony cage before partaking in the experiment. I then used Research Randomizer (randomizer.org) to create random male and female observer pairs within each block. In case a created pair (say pair 8) included a male and a female that were siblings, I randomly chose a pair from the rest of the pairs (say pair 4) and swapped the females between the two. Following such pairing of all observers, I again used Research Randomizer (randomizer.org) to randomly assign pairs to each of the two treatment groups.

Demonstrators

Pairs used as demonstrators in this experiment, except the very first demonstrator pair, all went through the complete experiment as observers first and then acted as demonstrators for subsequent observers. To give the first demonstrator pair (randomly paired male and female) nest-building experience before demonstration, I provided the pair a wooden nest cup covered with coloured paper, same coloured background, and 60 coloured paper strips. Once the material was deposited in the nest cup, the demonstrator was considered experienced and ready for demonstration. Each demonstrator pair was used up to a maximum of two demonstrations. A total 23 demonstrator pairs were used over the course of the entire experiment.

After being paired for a minimum of four days, each observer pair underwent an initial preference test to establish a preferred colour material amongst three different material options (pastel versions of green, yellow and pink paper strips; Staples 30% recycled Pastel Coloured

Copy Paper). Once the preferred colour material of the male of the observer pair (male is the nest builder in this species) was identified (say preferred colour material is pink), the other two colours were considered the observer's non-preferred colours (non-preferred colours are yellow and green). In the next phase of the experiment, I gave the observers an opportunity to view a demonstrator pair build a nest with one of the observer's non-preferred colour materials which became the socially demonstrated material (say non-preferred colour yellow is chosen as the socially demonstrated material). In the final phase I presented the observers a non-preferred colour background to build their nest against. If the observers belonged to the Agree treatment group, then the non-preferred colour background matched the socially demonstrated colour (non-preferred colour background is yellow). On the other hand, if the observers belonged to the Conflict treatment group, then the non-preferred colour background did not match the socially demonstrated colour (non-preferred colour background is green). After the observation phase if observers in the Agree treatment group showed a preference for the initially non-preferred socially demonstrated colour material which also matched the background, that would imply an effect of demonstration and/or background matching on changing material preference. Similarly, if observers in the Conflict treatment group showed a preference for the initially non-preferred socially demonstrated colour material that would imply an effect of demonstration on changing material preference. Instead, if the observers in the Conflict treatment group showed a preference for the initially non-preferred colour material which matched the background, that would imply an effect of background matching on changing material preference.

Phase 1: Initial Preference Test

An observer pair was moved into an experimental room the afternoon prior to testing (before 16:00 hours). Following daily care, the white background of the observer cage was left on and the birds were left undisturbed until the initial preference test the following day (Figure 6). The initial preference test began in the second hour post light onset in the morning and continued for four hours. At the start of the test, I attached the three different coloured materials to the extra cage trays. All six possible combinations in which the three coloured materials could be ordered were randomized across the observers. I then switched out the regular cage trays present in the observer cage out for the extra cage trays with attached materials. Finally, I adjusted the orientation of the in-cage cameras so that all the three coloured materials were in view. After the set-up, I left the experimental room and noted the time. Four hours later, I switched out the extra cage pan with attached material for the regular cage pan and thus ended the initial preference test. All four hours of video captured by the central in-cage camera was then immediately downloaded and scored.

Scoring and Determining Initial Preference. To determine the initial preference for material from the videos, I used BORIS version 7.9.8 (Friard & Gamba, 2016), an event-logging software that allows to track coded behavioural events in terms of frequency and duration. I specifically tracked the interactions of the male of the observer pair with the attached material. An interaction was defined as any instance where the observer male came in contact with the attached material through his beak, foot or body. The observer male’s tail alone coming in contact with material was not considered interaction. The time the observer male spent interacting with material of each colour was then obtained for the four-hour session. The minimum amount of total interaction required with one or more of the attached materials to establish a preference was 30 seconds. If an observer male spent less than 30s interacting with material in a day’s session, the initial preference test was repeated daily up to a maximum of five days until a cumulative minimum of 30s interaction was achieved (18 observers took more than one day of initial preference test). Subsequently, the coloured material with the highest proportion of interaction was considered the observer's preferred colour material while the other two materials (second preferred colour and least preferred colour) were considered non-preferred.

Phase 2: Pre-observation Demonstrator Building

This phase of demonstrator building began as soon as the preferred colour material of the observer was established (videos were scored on the same day each initial preference test took place). As the first step, one of the observer's two non-preferred colours was chosen to be the socially demonstrated colour. For half of the observers, allotted randomly, the socially demonstrated colour was the second preferred colour, while it was the least preferred colour for the other half (in case of a tie between the interaction proportion for the two materials, one of them was chosen randomly as the socially demonstrated colour - this happened in 6 cases). After the (to be) socially demonstrated colour was identified, I transported an available demonstrator pair (hereafter demonstrator) into the demonstrator cage. Next, I provided the demonstrator all three coloured materials. However, only the (to be) socially demonstrated material was freely accessible, in that 100 loose paper strips (each measuring 15 cm x 0.7 cm) of that colour were provided. The other two coloured materials were blocks of glued paper strips, hence inaccessible. The three coloured materials were either stuck (in case of the inaccessible paper strip blocks) or placed (in case of the loose collection of 100 paper strips) along the front (100 cm) side of the demonstrator cage at equidistant positions. Further, these positions mirrored the location of the attached colour materials of the observer's initial preference test.

Immediately following material provision, the demonstrators were provided a coloured nest cup with background for their cage. The nest cup and background colour was determined according to the treatment group of the observer, in the following manner. If the observer belonged to the Agree treatment group, the non-preferred colour chosen as socially demonstrated material also acted as the colour of the demonstrator nest cup and background (Figure 7). On the other hand, if the observer belonged to the Conflict treatment group, then the corresponding demonstrator nest cup and background colour was the observer's other non-preferred colour, distinct from the non-preferred colour chosen to be the socially demonstrated colour (Figure 8). Essentially, the preferred colour of the observer in either treatment group was never the socially demonstrated colour or the background colour of the demonstrators. After the demonstrators were provided with material, followed by the nest cup and background, I checked the orientation of the in-cage cameras of the demonstrator cage and made sure that the entire cage was properly captured on the video. The visual barrier between the observer and demonstrator cage was left as is in this phase so the observer was not able to see the demonstrators. I continued to monitor the progress of the demonstrator building twice per day in person and remotely other times. Once there was no more material of the socially demonstrated colour left on the cage tray for the demonstrators to deposit in the nest cup, the pre-observation building phase ended. The pre-observation phase was carried out to ensure that the demonstrators were engaged in nest building prior to the observation phase. The pre-observation phase lasted for a maximum of four days.

Phase 3: Observation

Observers were given a chance to watch demonstrators continue to build a nest during the observation phase. At the start of the observation phase, I provided 50 more loose paper strips (each measuring 15 cm x 0.7 cm) of the socially demonstrated colour at the same position in which the 100 loose paper strips were previously provided (Figure 9 and Figure 10). The rest of the demonstrator cage set-up including the inaccessible materials and the nest cup was left undisturbed. Finally, the plastic sheet acting as a visual barrier between the observer and demonstrator cages was removed, marking the beginning of the observation phase. The observation phase ended when the additionally provided socially demonstrated colour material was exhausted by the demonstrators as deposits in the nest cup or a maximum of four days.

Phase 4: Final Preference Test

I replaced the plastic sheet between the observer and demonstrator cage to act as a visual barrier and moved the demonstrators from the demonstrator cage into the housing room. I then provided daily care to the observers and set up the final preference test as follows. First, I provided a coloured nest cup and background for the observers which was identical to the demonstrator's-coloured nest cup and background. Next, I adjusted the orientation of the in-cage cameras of the observer's cage so as to capture the nest cup as well as the rest of the cage. Immediately after, I placed 20 strips (15 cm x 0.7 cm) of each of the three coloured materials (green, pink and yellow Staples 30% recycled Pastel Coloured Copy Paper) at equidistant positions along the front (100 cm) side of the observer's cage. These positions mirrored the positions in which the demonstrators had been provided each of the three coloured materials in the demonstrator cage during the pre-building demonstration and observation phases (Figure 11). Finally, I left the observers undisturbed for the rest of the day. I monitored the observer's progress in the final preference test twice per day in person and remotely at other times. The final preference test ended when the observers deposited all material into their nest or a maximum of six days. Videos corresponding to the entire duration of the final preference test were downloaded from each of the three cameras in the observer's cage.

After the Final Preference Test

Once the final preference test ended, observers were returned to the housing room. Further, observers that had built a nest in the nest cup during the final preference test went on to act as demonstrators for future observers on a need-be basis.

Scoring and Determining Final Preference. The videos downloaded from each of the three cameras in the observer's cage during the final preference test were merged into one video file displaying all three filming angles using the software Wondershare Filmora Video Editor 9. Once merged, videos corresponding to each observer pair were randomly re-assigned names by an individual who wasn't involved in scoring, so that scoring could be blind with respect to the treatment. To score the (renamed) videos, I used BORIS version 7.9.8 (Friard & Gamba, 2016). I specifically measured the following behaviours of the male observer from the videos: a) Order of first 20 deposits of material into the nest in terms of the material colour (see glossary for definition of deposit) b) Order of rest of the deposits into a nest until a maximum of 60 deposits c) Colour of material that was first touched, first picked up, and first carried. After the blinding was removed, final preference of the observer for each of the three material types (that corresponded to three colours) was determined as the proportion of deposits of each material in the first 20 deposits made by the observer. In addition, I also scored the rest of the deposits made by the observer (until 60 deposits) to extract measures such as latency to complete depositing 60 pieces of material. For observers in the Agree group the three material types were initially preferred material, socially demonstrated material, and the opt out material while for observers in the Conflict group the three material types were initially preferred material, socially demonstrated material and asocial material.

Sample Size

A total of 37 pairs began the experiment and went through the initial preference test, however some pairs were excluded at different stages of the experiment due to the following reasons. Two pairs did not show minimum interaction (at least 30 seconds) with material in the initial preference test phase and did not take part in rest of the experiment. Four pairs went through the complete experiment but were excluded since the corresponding demonstrators did not finish depositing all material within the maximum duration (four days) of the observation phase. One pair was excluded since the observer tore attached material and carried the material around in the initial preference phase, thereby possibly making the particular observer's initial experience with material different from other observers in the experiment. Finally, one pair was excluded after the scoring of the final preference test since the observer did not make a minimum of 20 deposits before the maximum duration (six days) of the final preference test. Thus, a total of 29 observer pairs were included in the experiment and analyses (n=14 Agree group; n = 15 Conflict group).

Statistical Analyses

I used R 3.6.1 (R Core Team, 2019) to perform all statistical analyses. I asked questions pertaining to different phases of the experiment as outlined below.

Initial Preference Test

Initial Preference. Using the initial preference values obtained as the proportion of time spent interacting with each of the three materials, I first asked if observers overall showed a preference towards any of the three materials – assigned namely as the initially preferred material, socially demonstrated material or the third material (third material was the opt out material in case of observers in the Agree group while third material was the asocial material in case of observers in the Conflict group). I used a Friedman's test, a non-parametric equivalent of a repeated measures ANOVA; 'friedman.test' function from 'stats' package in R, to compare the initial preference values across the three assigned material types across all observers. Further, to assess amongst which material types the differences in initial preference were located (if any), I used Wilcoxon signed-rank tests as the post-hoc with Bonferroni correction to account for multiple comparisons ('pairwise.wilcox.test' function from 'stats' package in R). Additionally, I compared the initial preference values for each of the three material types against chance level (.333) using Wilcoxon signed-rank tests ('wilcox.test' function from 'stats' package in R). Non-parametric tests were chosen for all these analyses since proportional data (initial preference values) were not normal.

Colour Preference. I asked if observers overall had a preference towards a particular-coloured material. To test this, I carried out a Friedman's test comparing the initial preference values for green, yellow and pink coloured material for all observers. Following the Friedman's test, to know which colours differed in preference (if any), I used Wilcoxon signed-rank tests with Bonferroni correction as the post hoc test. Finally, I compared initial preference values for each colour to chance level (.333) using Wilcoxon signed-rank tests.

Duration. I calculated the duration of initial preference test as discrete data in terms of the number of 4-hour initial preference test sessions taken by observers to establish a preference (minimum of 30 seconds of total interaction with material). I compared the duration of initial preference test between observers in the Agree and Conflict groups using a Mann-Whitney U test. Further, I used a Welch's two sample t test to compare total interaction time (i.e., total time observers interacted with all material (in seconds) during the initial preference test) across observers in the Agree and Conflict groups after log-transforming the total interaction time data to achieve normality. I performed these comparisons to rule out any pre-treatment differences in material exposure between observers in two groups that could potentially affect interpretation of subsequent results.

Pre-observation Demonstrator Building and Observation

Duration. Similar to the previous section, to rule out any differences at the group level with regards to pre-observation phase duration, I compared the pre-observation phase duration (in daylight hours) between observers in Agree and Conflict groups using Mann-Whitney U test. I used non-parametric Mann-Whitney U tests since pre-observation phase duration data was not normal and log-transformation of data also did not result in normality. I also compared the observation phase duration (in daylight hours) between observers in Agree and Conflict group using a Welch's two sample t test after log-transforming the observation phase duration data to achieve normality.

Final Preference Test

Final Preference. For the measure of final preference, I calculated the proportion of deposits of each colour (which corresponded to a material type for each observer) in the first 20 deposits that the observer made, since the maximum available number of pieces of one material type was 20. I first asked what materials (if any) the observers in each group showed a preference towards during the final phase. To find out, I compared the final preference values across the three material types in each group (initially preferred, socially demonstrated and opt out material for observers in Agree group; initially preferred, socially demonstrated and asocial material for observers in Conflict group) using a Friedman's test. As a follow-up to see which material types differed in final preference values, I used Wilcoxon signed-rank tests as the post hoc, with Bonferroni correction applied to account for multiple comparisons. Subsequently, I compared the final preference values of each material type in each group to chance level (.333) using Wilcoxon signed-rank tests. Non-parametric tests were chosen for these analyses as the proportional data (final preference values) were discrete.

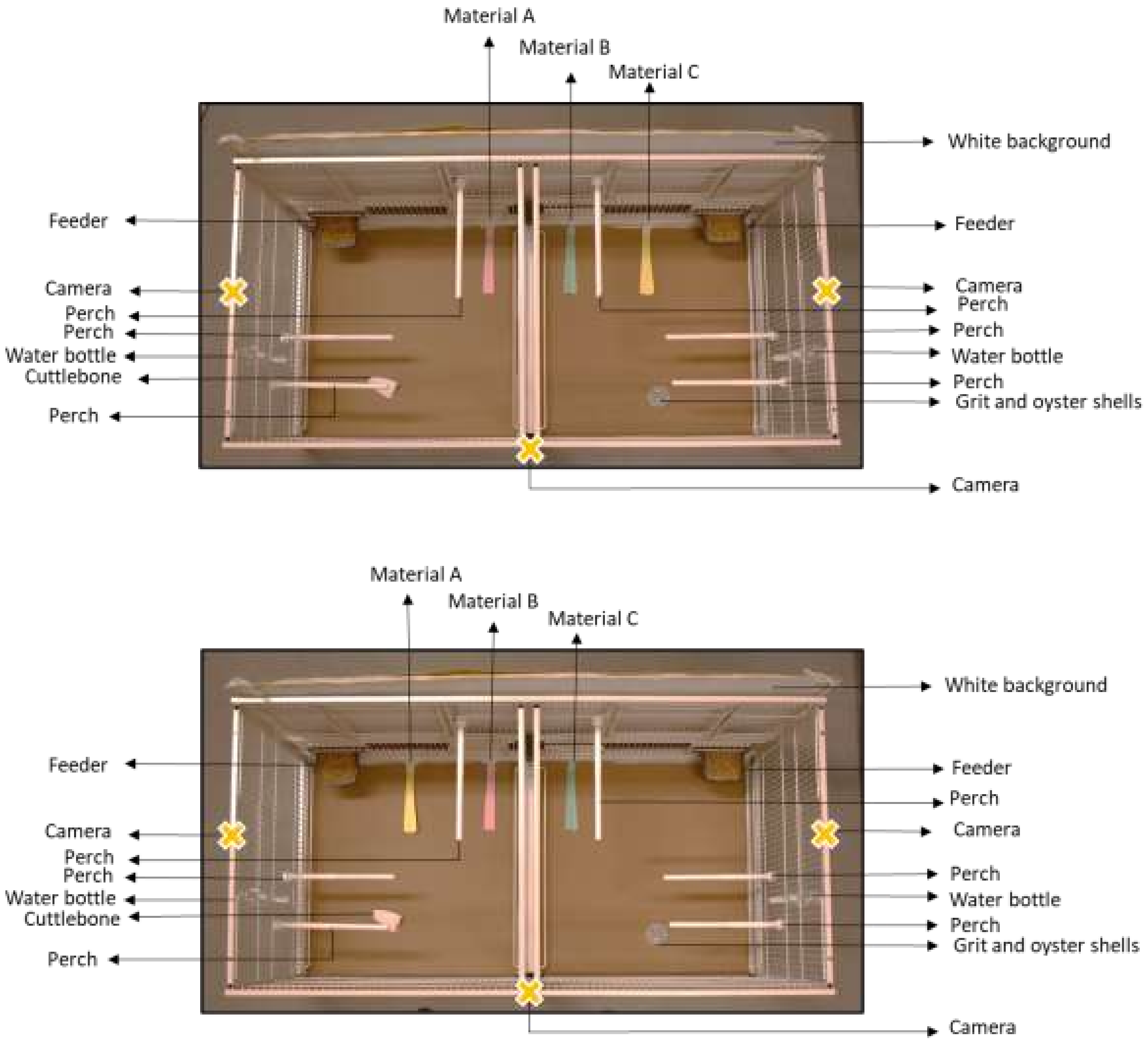
Using initial and final preference values corresponding to a material type, I asked if observers' material preferences changed between the initial and final preference test phases. For observers in each group, I performed paired Wilcoxon signed-rank tests comparing initial and corresponding final preference values for each of the material types (initially preferred, socially demonstrated and opt out material for observers in Agree group; initially preferred, socially demonstrated and asocial material for observers in Conflict group)

First Interactions. In this section, I reported the observers' first interactions with material – namely identity of material type first touched, first picked up, first carried and first deposited in the final preference test. This data could be used to glean whether or not observers acquired social or asocial information and used it, to inform their initial material choices.

Latency measures. Here I wanted to see whether having access to agreeing or conflicting sources of information about nest material had any effect on different aspects of nest building speed. Between observers in the Agree and Conflict groups, I compared the latency to first interact with material (touch, pick up, carry and deposit), latency to twenty deposits and latency to sixty deposits. I created survival curves using the 'survival' package in R and compared the survival curves of the two groups with a log rank test, using the 'survdiff' function in the 'survival' package. Note that for all latency measures, time represented is during daylight.

Figure 6

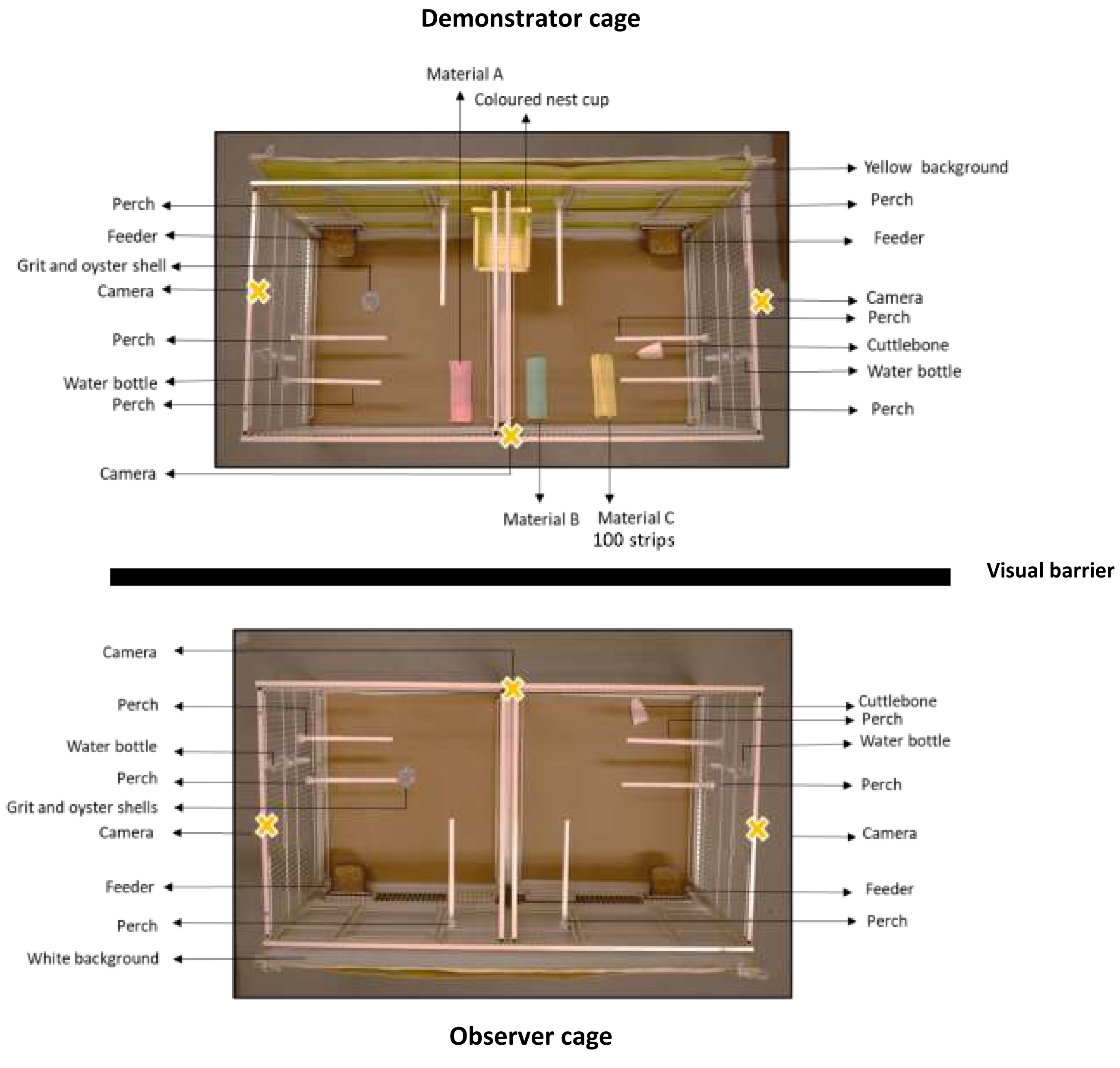
Initial Preference Test



Note. Top-down view of observer cage during initial preference test phase. The materials were oriented either in the way shown in the cage on top or in the way shown in the cage on bottom. The distance between material A and B, and between material B and C was 18 cm in both cases. The dimensions of the observer cage were 100 cm length x 50 cm width x 50 cm height.

Figure 7

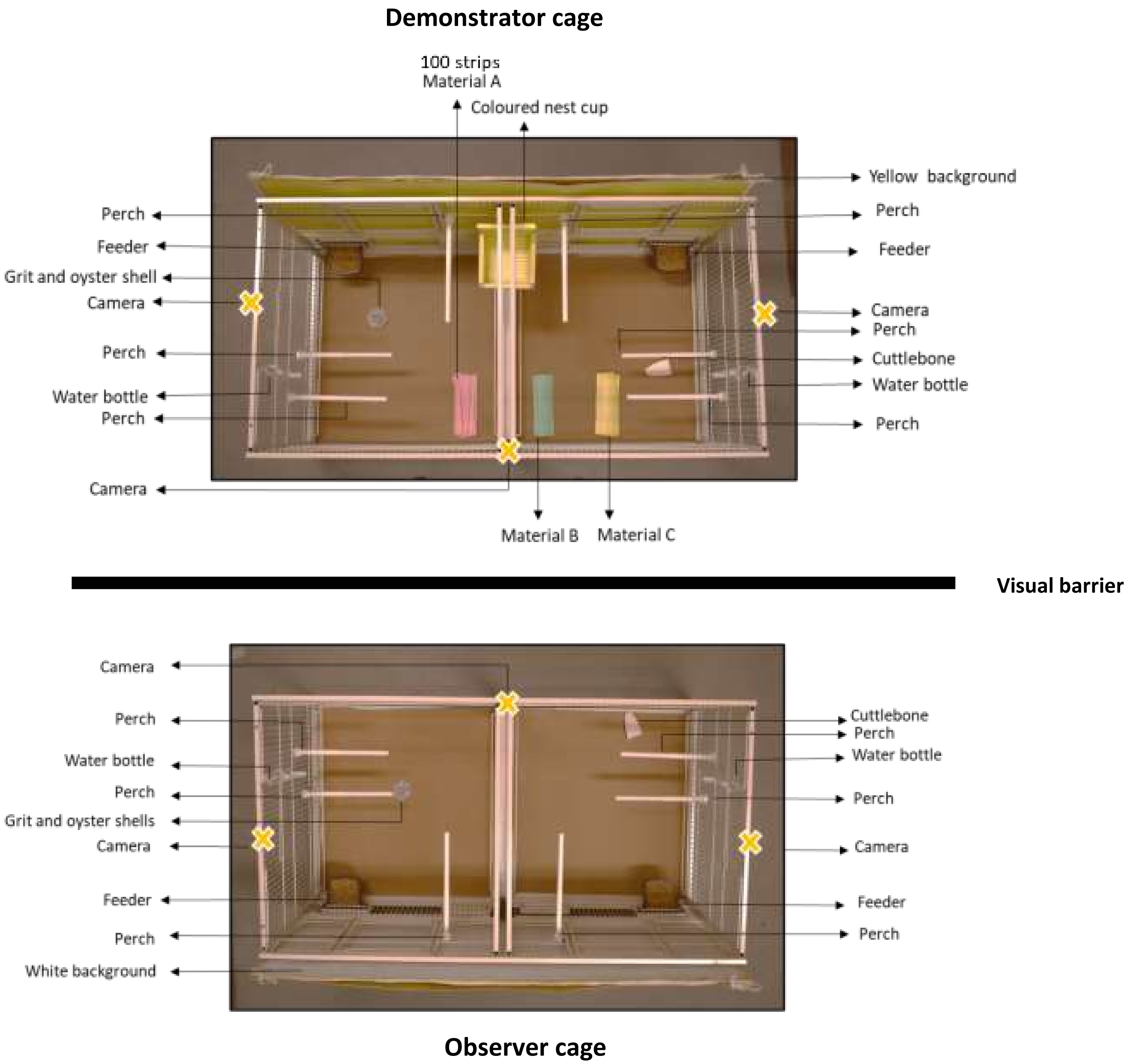
Pre-Observation Building Phase – Agree Treatment Group



Note. Top-down view of demonstrator cage (top) and observer cage (bottom; each 100 cm length x 50 cm width x 50 cm height) during the pre-observation building phase for Agree treatment group. One of the observer's initially non-preferred colour materials (here material C, yellow) was loosely available and the only accessible material in the demonstrator cage. The other materials (material A - pink and material B - green) were inaccessible materials (block of glued paper strips). The (to be) socially demonstrated material (yellow) matched the colour of the demonstrator background and nest cup (yellow) for observers in the Agree treatment group. The distance between material A and B, and between material B and C was 18 cm. Locations of all three coloured materials mirrored the locations of the same-coloured materials during the initial preference test in the observer’s cage.

Figure 8

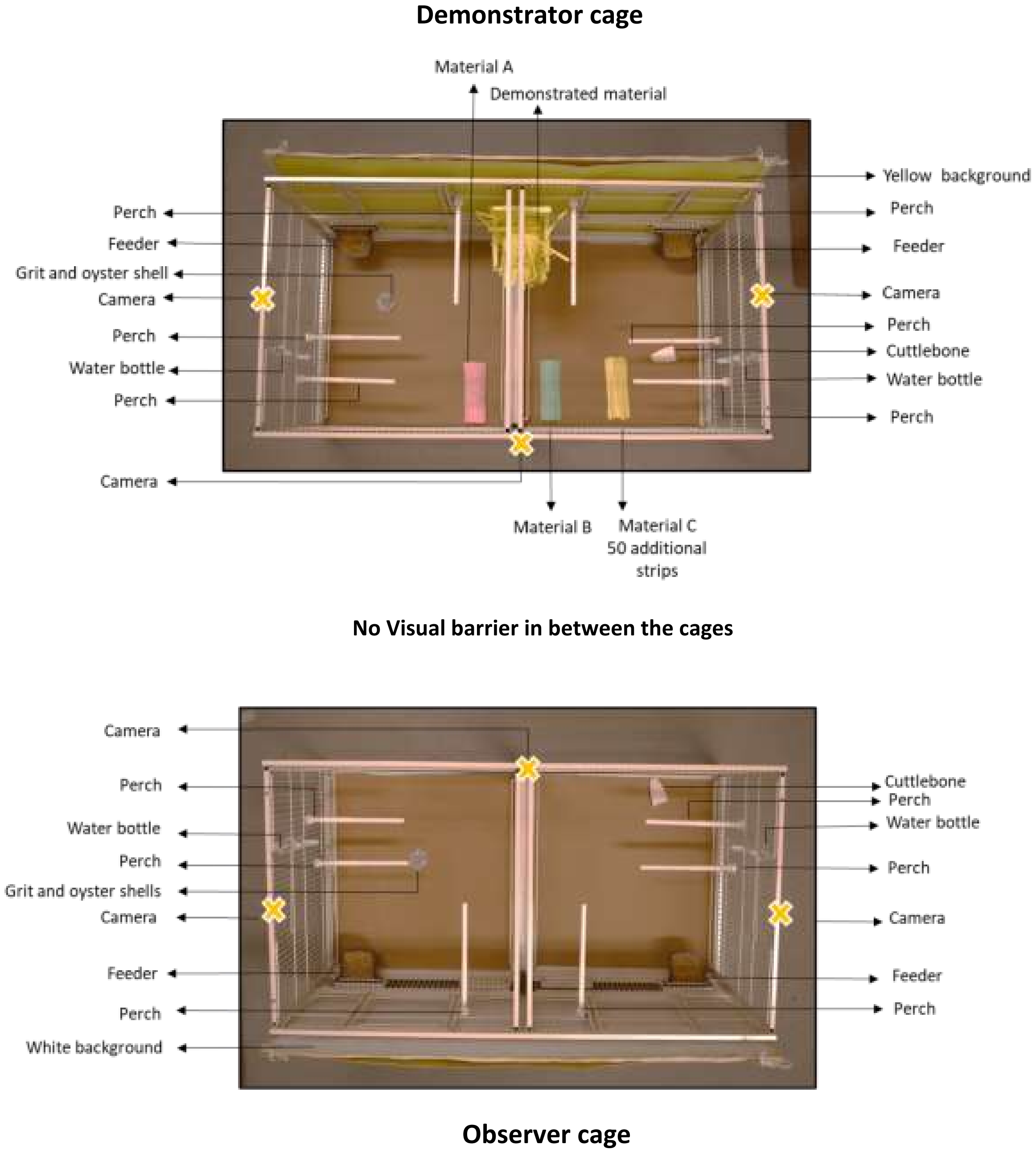
Pre-observation Building – Conflict Treatment Group



Note. Top-down view of demonstrator cage (top) and observer cage (bottom; each 100 cm length x 50 cm width x 50 cm height) during the pre-observation building phase for Conflict treatment group. One of the observer's initially non-preferred colour materials (here material A, pink) was the loosely available and only accessible material in the demonstrator cage. The observer's preferred material (here material B, green) and another non-preferred material (here material C, yellow) were inaccessible materials (block of glued paper strips). The demonstrator background and nest cup colour was a different non-preferred colour (yellow) than the (to be) socially demonstrated material colour (pink). The distance between material A and B, and between material B and C was 18 cm. Locations of all three coloured materials mirrored the locations of the same-coloured materials during the initial preference test in the observer's cage.

Figure 9

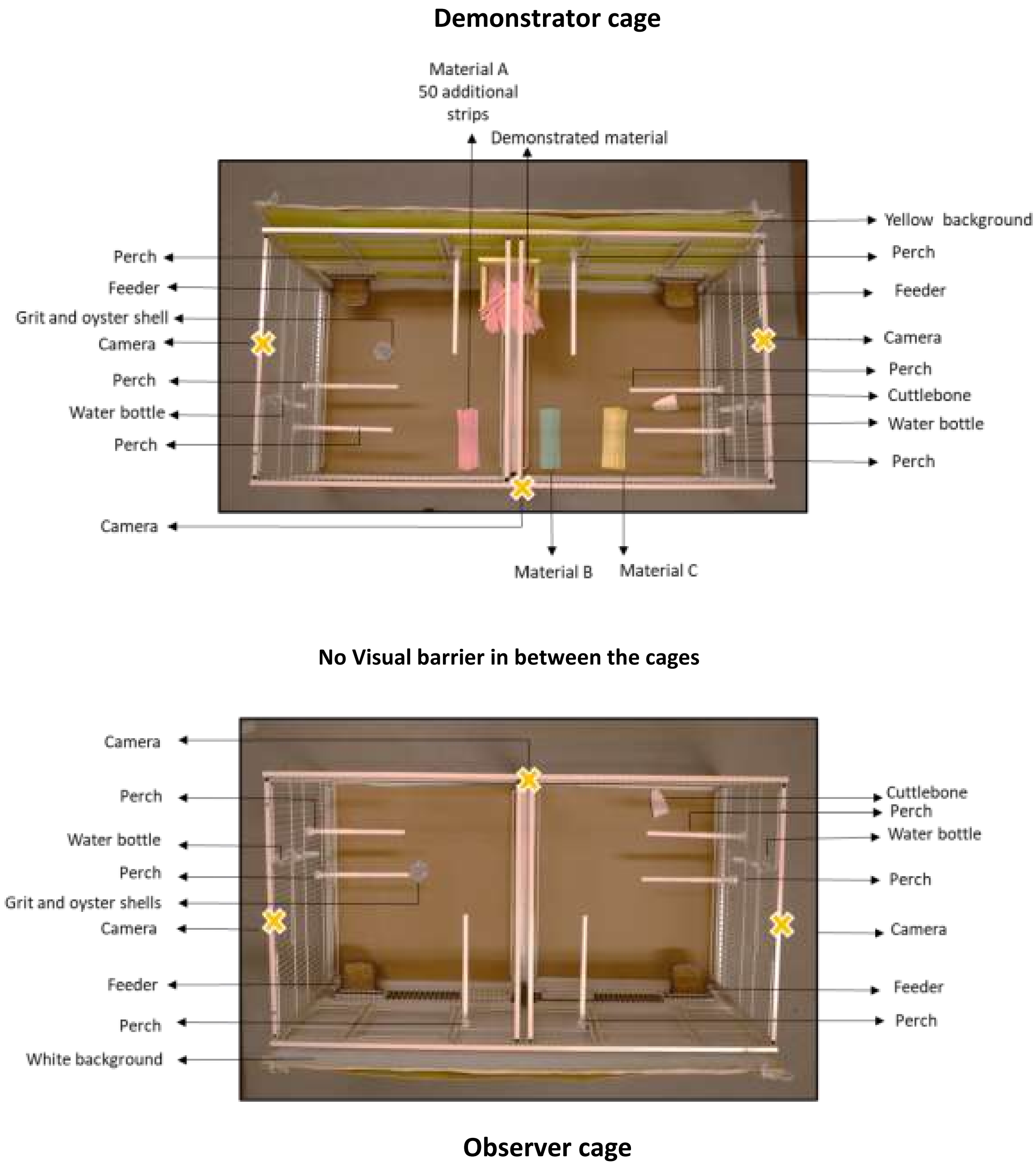
Observation Phase – Agree Treatment Group



Note. Top-down view of demonstrator cage (top) and observer cage (bottom; each 100 cm length x 50 cm width x 50 cm height) during the observation phase. Fifty additional strips of the socially demonstrated colour (yellow) were provided in the demonstrator cage and the visual barrier between the observer cage and demonstrator cage was removed.

Figure 10

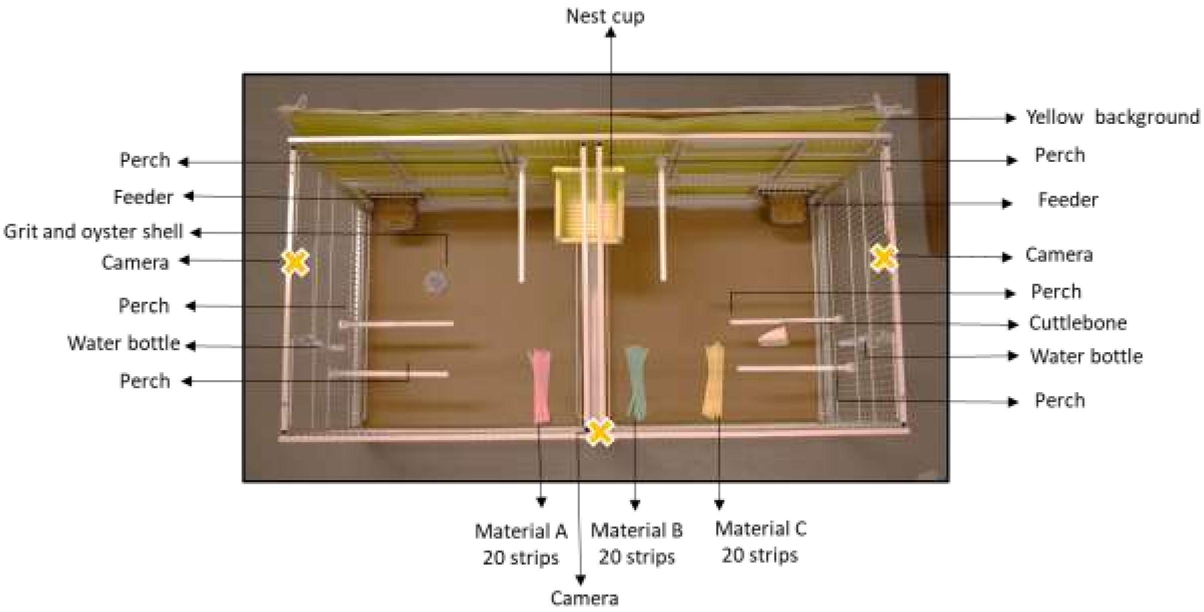
Observation Phase – Conflict Treatment Group



Note. Top-down view of demonstrator cage (top) and observer cage (bottom; each 100 cm length x 50 cm width x 50 cm height) during the observation phase. Fifty additional strips of the socially demonstrated colour (pink) were provided in the demonstrator cage and the visual barrier between the observer and demonstrator cage was removed.

Figure 11

Final Preference Test



Note. Top-down view of observer cage (100 cm length x 50 cm width x 50 cm height) during the final preference test. Twenty strips of each coloured material were provided in the observer cage, at positions mirroring the location of each coloured material in the corresponding demonstrator cage. The observers were also provided with a coloured nest cup and background the same colour as the corresponding demonstrators observed during the observation phase.

Results

Initial Preference Test

Initial Preference. The initial preference for the different material types for all observers can be seen in Figure 12. Friedman test comparing initial preference values across material types was significant ($\chi^2 = 45.46$, df = 2, $p < .001$), meaning that observers possibly showed difference in preference between the three given materials. The follow-up pairwise comparisons using Wilcoxon signed-rank tests revealed that the observers preferred the initially preferred material (n = 29, $\bar{x} = .89$, Median = .96, Lower = .83, Upper = .95, 95% CI) over the socially demonstrated material (n = 29, $\bar{x} = .06$, Median = 0, Lower = .02, Upper = .11, 95% CI; $p_{adj} < .001$) as well as the third material (material assigned as opt out for observers in Agree group and material assigned as asocial material for observers in Conflict group are combined as 'third material'; n = 29, $\bar{x} = .05$, Median = .01, Lower = .02, Upper = .08, 95% CI; $p_{adj} < .001$). The initial preference values did not differ between socially demonstrated material and third material ($p_{adj} = 1$). While comparing initial preference for each material type to chance level, observers showed a preference for the material assigned as the initially preferred material (Wilcoxon signed-rank test; V = 435, $p < .001$) but did not prefer the material assigned as the socially demonstrated (Wilcoxon signed-rank test; V = 6, $p < .001$) or third material (Wilcoxon signed-rank test; V = 0, $p < .001$). Figure 13 shows the initial preference data split across observers in the Agree and Conflict group.

Colour Preference. Friedman tests comparing initial preference across three colours for all observers (Figure 14; see Figure 15 for individual preferences) was significant ($\chi^2 = 36.70$, df = 2, p < .001). Pairwise Wilcoxon signed-rank tests conducted as a follow-up showed that observers preferred green material (n = 29, $\bar{x} = .78$, Median = .95, Lower = .65, Upper = .90, 95% CI) over yellow (n = 29, $\bar{x} = .19$, Median = .05, Lower = .08, Upper = .31, 95% CI; $p_{adj} = .002$) and pink material (n = 29, $\bar{x}$ = .03, Median = 0, Lower = -.01, Upper = .07, 95% CI; p_{adj} < .001). Observers preferred yellow over pink material (p_{adj} = .002). When comparing preference against chance level, observers preferred green material (Wilcoxon signed-rank test; V = 415.5, *p* < .001), while not preferring either yellow (Wilcoxon signed-rank test; V = 113, *p* = .024) or pink material (Wilcoxon signed-rank test; V = 2, *p* < .001).

Duration. The duration of initial preference test (discrete data in terms of number of 4-hour sessions) did not differ between observers in Agree (n = 14, $\bar{x}$ = 1.71, Median = 2.00, Lower = 1.36, Upper = 2.07, 95% CI) and Conflict groups (n = 15, $\bar{x}$ = 1.73, Median = 2.00, Lower = 1.29, Upper = 2.18, 95% CI; Mann-Whitney U test; W = 109, *p* = .86). The log-transformed total interaction time (seconds) with material did not differ between observers in Agree (n = 14, $\bar{x}$ = 1253.81, Median = 955.53, Lower = 581.57, Upper = 1926.05, 95% CI) and Conflict groups (n = 15, $\bar{x}$ = 635.73, Median = 297.44, Lower = 102.84, Upper = 1168.61, 95% CI; Welch's two sample t test; t = 1.63, df = 26.43, *p* =.11).

Pre-observation Demonstrator Building and Observation

Duration. The pre-observation phase duration (in daylight hours) did not differ between observers in the Agree (n = 14, $\bar{x}$ = 15.24, Median = 9.07, Lower = 7.52, Upper = 22.96, 95% CI) and Conflict groups (n = 15, $\bar{x}$ = 17.29, Median = 8.67, Lower = 10.01, Upper = 24.58, 95% CI; Mann-Whitney U test; W = 91, *p* = .56). The log-transformed observation phase duration (in daylight hours) with material also did not differ between observers in Agree (n = 14, $\bar{x}$ = 16.25, Median = 13.95, Lower = 11.21, Upper = 21.30, 95% CI) and Conflict groups (n = 15, $\bar{x}$ = 24.74, Median = 17.07, Lower = 15.48, Upper = 34.01, 95% CI; Welch's two sample t test; t = -1.31, df = 26.25, *p* =.2).

Final Preference Test

Final Preference. For observers in the Agree group (Figure 16) the Friedman's test comparing final preference values across material types was significant (χ^2 = 6.71, df = 2, p = .035). None of the pairwise comparisons as tested using Wilcoxon signed-rank tests were significant – final preference for initially preferred material (n = 14, $\bar{x}$ = .57, Median = .58, Lower = .37, Upper = .77, 95% CI) did not differ from that for socially demonstrated material (n = 14, $\bar{x}$ = .19, Median = 0, Lower = .01, Upper = .36, 95% CI; p_{adj} = .15) or opt out material (n = 14, $\bar{x}$ = .24, Median = .03, Lower = .04, Upper = .44, 95% CI; p_{adj} = .29). Final preference for socially demonstrated material and opt out material also did not differ from each other (p_{adj} = 1). When comparing final preference of observers in the Agree group against chance level (.333) none of the final preferences were different from chance; initially preferred material (Wilcoxon signed-rank test; V = 83, *p* = .06), socially demonstrated material (Wilcoxon signed-rank test; V = 28, *p* = .12), or opt out material (Wilcoxon signed-rank test; V = 34, *p* = .25) did not differ from chance level. Further, observers in the Agree group (Figure 20) showed a significant decrease in preference between the initial and the final preference tests for initially preferred material (Wilcoxon signed-rank test; V = 95, *p* = .008) while there was no change in preference for socially demonstrated material (Wilcoxon signed-rank test; V = 18, *p* = .20) or opt out material (Wilcoxon signed-rank test; V = 19, *p* = .13).

For observers in the Conflict group (Figure 17; see Figure 18, visual aid for a comparison alongside the Agree group), Friedman's test comparing final preference values across material types was significant (χ^2 = 6.70, df = 2, p = .035). The pairwise Wilcoxon signed-rank test comparisons in this case showed that final preference for initially preferred material (n = 15, $\bar{x}$ = .61, Median = .65, Lower = .41, Upper = .81, 95% CI) was greater than final preference for asocial material (n = 15, $\bar{x}$ = .15, Median = 0, Lower = .03, Upper = .26, 95% CI; p_{adj} =.034). Final preference for socially demonstrated material (n = 15, $\bar{x}$ = .24, Median = .10, Lower = .08, Upper = .41, 95% CI) did not differ from final preference for either initially preferred material (p_{adj} = .11) or asocial material (p_{adj} = 1). While comparing final preference against chance level (.333), observers in the Conflict group showed a preference for the initially preferred material (Wilcoxon signed-rank test; V = 101, p = .021). The final preference for socially demonstrated material was at chance level (Wilcoxon signed-rank test; V = 39, p = .24), and asocial material was not preferred (Wilcoxon signed-rank test; V = 15, p = .01). Observers in the Conflict group (Figure 21) showed a significant decrease in preference for initially preferred material (Wilcoxon signed-rank test; V = 85, p = .006) as well as a significant increase in preference for socially demonstrated material (Wilcoxon signed-rank test; V = 12, p = .02). Further, observers in the Conflict group showed no change in preference for asocial material (Wilcoxon signed-rank test; V = 12, p = .13).

Initial and final preference data for each individual observer across both groups is presented in Figure 19.

First Interactions. Figure 22 represents the first interactions of observers in each group. Out of the observers in the Agree group (left panel), 6/14 first touched, 9/14 first picked up, 7/14 first carried and 7/14 first deposited the initially preferred material. A majority of observers in the Conflict group (right panel), first interacted with their initially preferred material – with 10/15 observers having first touched, 12/15 having first picked up, 12/15 having first carried and 11/15 having first deposited the initially preferred material.

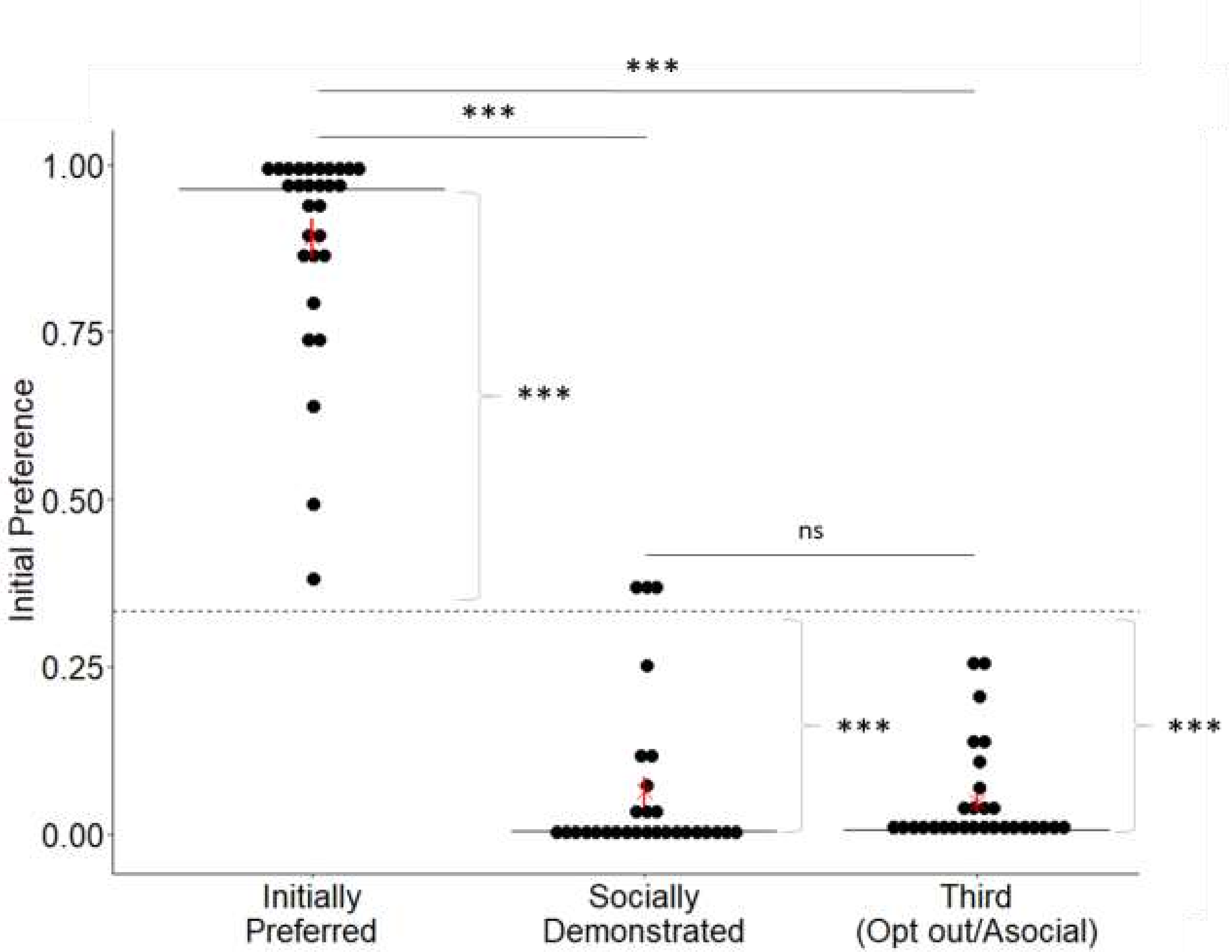
Latency measures. The latency to first touch material in the final preference test (Figure 25) did not differ between observers in Agree (n = 14, Median = 2.77, Lower = 1.13, Upper = 559.4, 95% CI) and Conflict group (n = 15, Median = 1.57, Lower = 1.28, Upper = 43.5, 95% CI; log rank test, $\chi^2 = 0.3$, $p = .6$). The latency to first pick up (Agree - n = 14, Median = 7.29, Lower = 1.35, Upper = 632, 95% CI; Conflict - n = 15, Median = 4.39, Lower = 1.35, Upper = 201, 95% CI; log rank test, $\chi^2 = 0.2$, $p = .7$) or carry material (Agree - n = 14, Median = 33.2, Lower = 2.60, Upper = 632, 95% CI; Conflict - n = 15, Median = 146.6, Lower = 1.76, Upper = 537, 95% CI; log rank test, $\chi^2 = 0.2$, $p = .6$) also did not differ between the two groups (Figure 26 and Figure 27 respectively). Similarly, the latency to first deposit material (Figure 28) did not differ between observers in Agree (n = 14, Median = 331, Lower = 257, Upper = 1641, 95% CI) and Conflict group (n = 15, Median = 282, Lower = 113, Upper = 1875, 95% CI; log rank test, $\chi^2 = 0.1$, $p = .7$). Finally, (Figure 29) the latency to complete twenty deposits (Agree - n = 14, Median = 356, Lower = 282, Upper = 2042, 95% CI; Conflict - n = 15, Median = 370, Lower = 298, Upper = 1903, 95% CI; log rank test, $\chi^2 = 0$, $p = .9$) or (Figure 30) the latency to complete sixty deposits also did not differ between the two groups (Agree - n = 14, Median = 447, Lower = 366, Upper = 2340, 95% CI; Conflict - n = 13, Median = 546, Lower = 449, Upper = NA, 95% CI; log rank test, $\chi^2 = 0$, $p = 1$)

Initial Preference Strength and Final Preference for Material. In the current experiment, the initially non-preferred material type that observers of at least one treatment group showed an increase in preference towards in the final preference test, was the socially demonstrated material (also note that preference for socially demonstrated material was at chance level in the final preference test for observers in both groups, as compared to below chance levels in the initial preference test). A previous study found that the extent to which zebra finches showed preference for the socially demonstrated material (through an artefact nest) during the final preference test was related to the birds' initial preference strength. Specifically, birds that had higher initial preference strengths were less likely to increase preference for the socially demonstrated material in the final preference test (Camacho-Alpízar et al., 2021b). To see if similar trends were seen here, I asked whether observers with higher initial preference strengths showed lower levels of final preference for socially demonstrated material. I created a generalized linear model ('stats' package in R), with the final preference for the socially demonstrated material as the response variable and initial preference strength as the predictor. I used a quasibinomial error structure for the modelling since the data was under dispersed.

In the results (Figure 31), I found that there was a negative relationship between initial preference strength and final preference for socially demonstrated material (estimate: -4.058, std. error: 1.930, t value: -2.102, p = .045). I used F test (in 'anova' function within the 'stats' package in R) to assess contribution of initial preference strength as a predictor in the model and found initial preference strength to be a significant predictor (F = 4.59, p = 0.04). The McFadden's pseudo R^2, a measure of proportional increase in explained deviance as compared to the basic (null) model was .153 (i.e., initial preference strength explained 15.3% of variation in final preference for socially demonstrated material). Finally, the odds ratio (using the 'oddsratio' package in R; Schratz, 2020) corresponding to initial preference strength as predictor was .67 (95% CI: Lower = .44, Upper = .96, increment = 0.1), which means that the odds of preferring socially demonstrated material in the final phase decreased by 33% for a 0.1 increase in initial preference strength.

Figure 12

Initial Preference across Material Types for All Observers

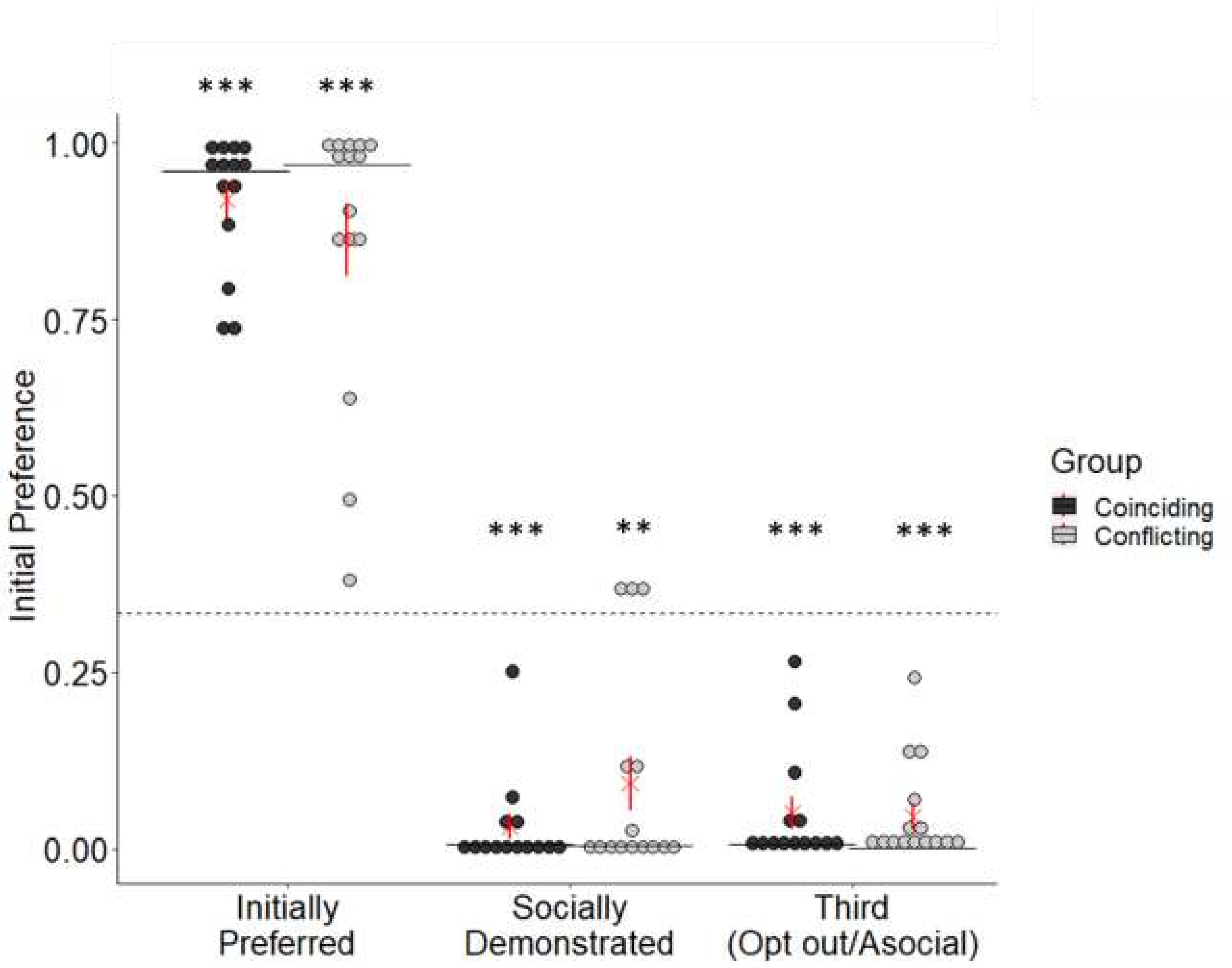


Note. Initial preference of observers (y-axis) corresponding to each of the assigned material types (x-axis) is shown. Each black dot represents the initial preference value of one male observer (n = 29) for a particular material type. Each filled black horizontal line passing through the dots represents the median. Each red cross and range represent the mean and standard error of mean respectively. The dashed horizontal line represents the chance level preference (.333). Curved brackets and associated significance markers (asterisk or 'ns') indicate the significance of the difference between corresponding material preference and chance level preference. Significance markers corresponding to preference comparisons between any two material types are indicated on top.

$^{***}p < .001$, ns – not significant.

Figure 13

Initial Preference across Material Types split by Observer Group

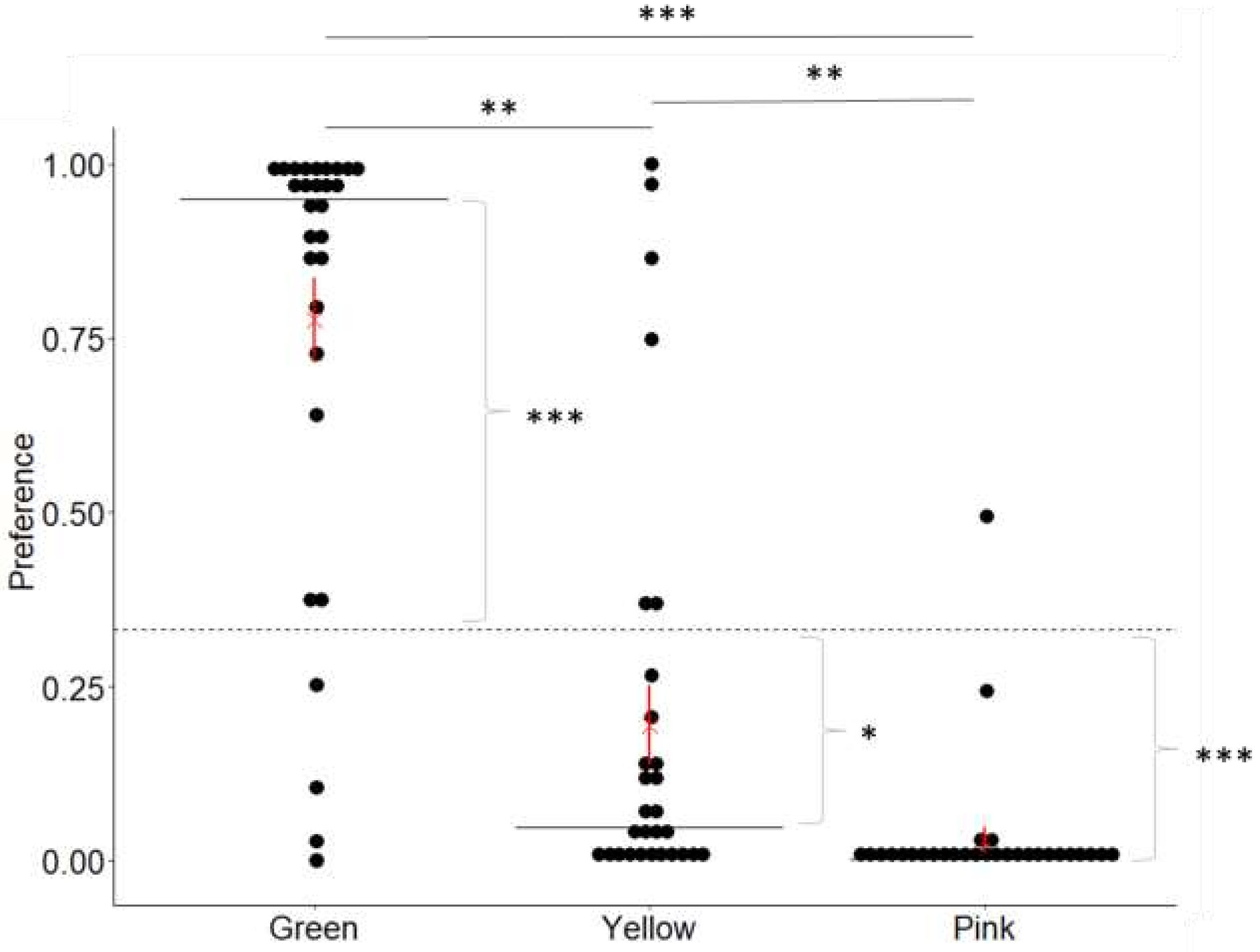


Note. Initial preference of observers split by treatment group (y-axis) is plotted against material type (x-axis). Each black dot represents the initial preference value (corresponding to a material type) for one male observer in the Agree group (n = 14) while each grey dot represents the initial preference value for one male observer in the Conflict group (n = 15). Each filled black horizontal line passing through the dots represents the median. Each red cross and range represent the mean and standard error of mean respectively. The dashed horizontal line represents the chance level preference (.333). Significance markers on top indicate the significance of the difference between corresponding material preference and chance level preference.

$^{***}p < .001$, $^{**}p < .01$.

Figure 14

Initial Preference across Material Colour for All Observers

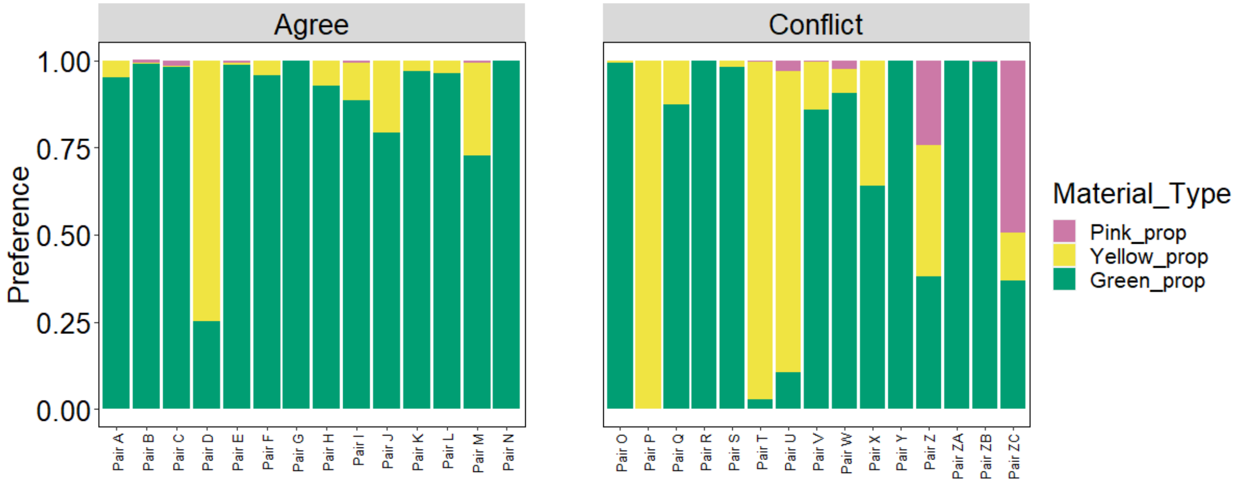


Note. Initial preference of observers (y-axis) corresponding to each of the assigned material colours (x-axis) is shown. Each black dot represents the initial preference value of one male observer (n = 29) for a particular material colour. Each filled black horizontal line passing through the dots represents the median. Each red cross and range represent the mean and standard error of mean respectively. The dashed horizontal line represents the chance level preference (.333). Curved brackets and associated significance markers (asterisk or 'ns') indicate the significance of the difference between corresponding material preference and chance level preference. Significance markers corresponding to preference comparisons between any two material types are indicated on top.

$^{***}p < .001$, $^{**}p < .01$.

Figure 15

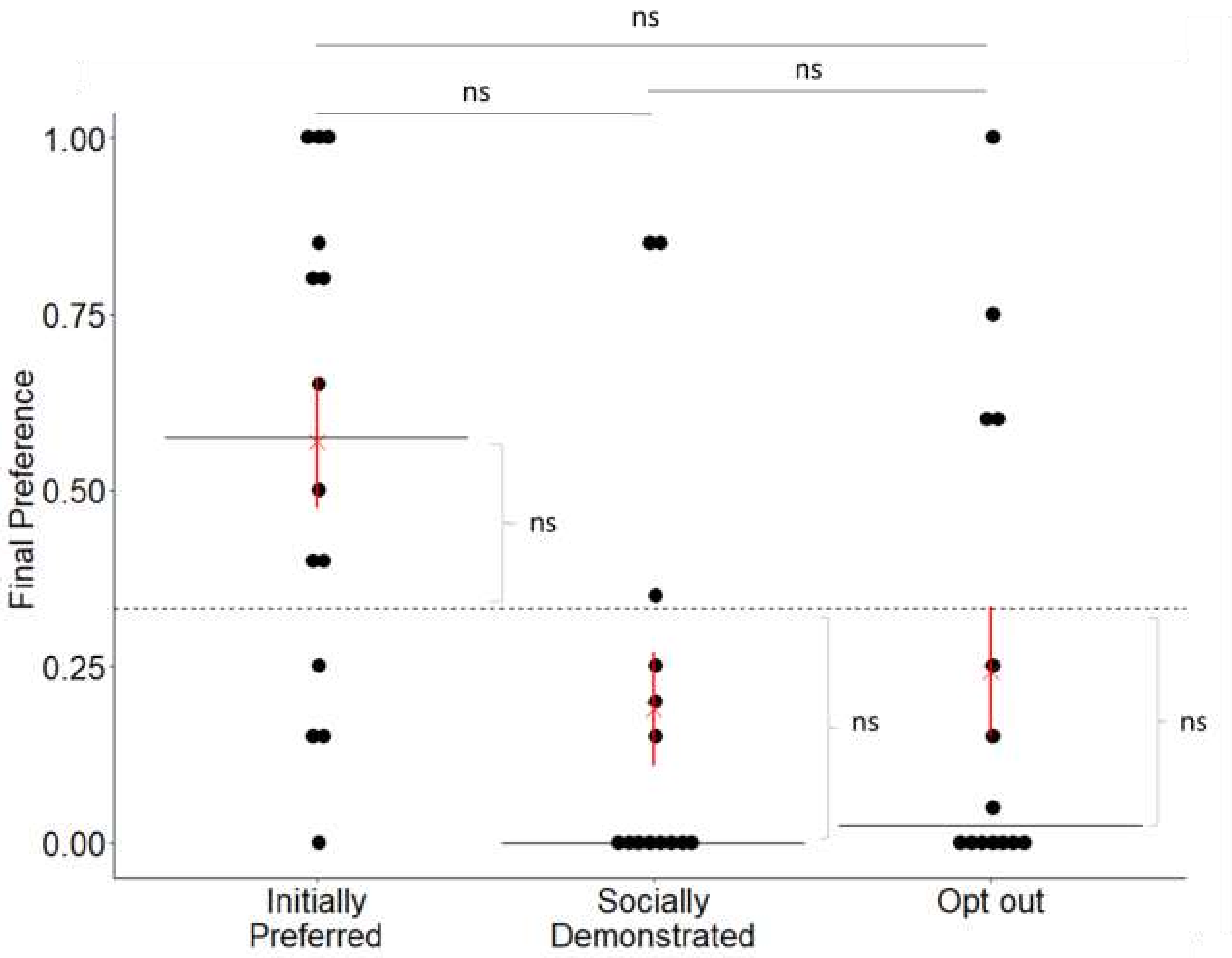
Preference across Material Colour for all Observers



Note. Preference for each material colour in the initial preference test (y-axis) is shown for individual observers (x-axis). The left panel shows the data for observers belonging to the Agree group (n = 14) while the right panel shows the data for observers belonging to the Conflict group (n = 15). The green portion of each bar (corresponding to one male observer) represents the preference for green material, the yellow portion represents the preference for yellow material while the pink portion represents the preference for pink material.

Figure 16

Final Preference across Material Types for Observers in Agree Group

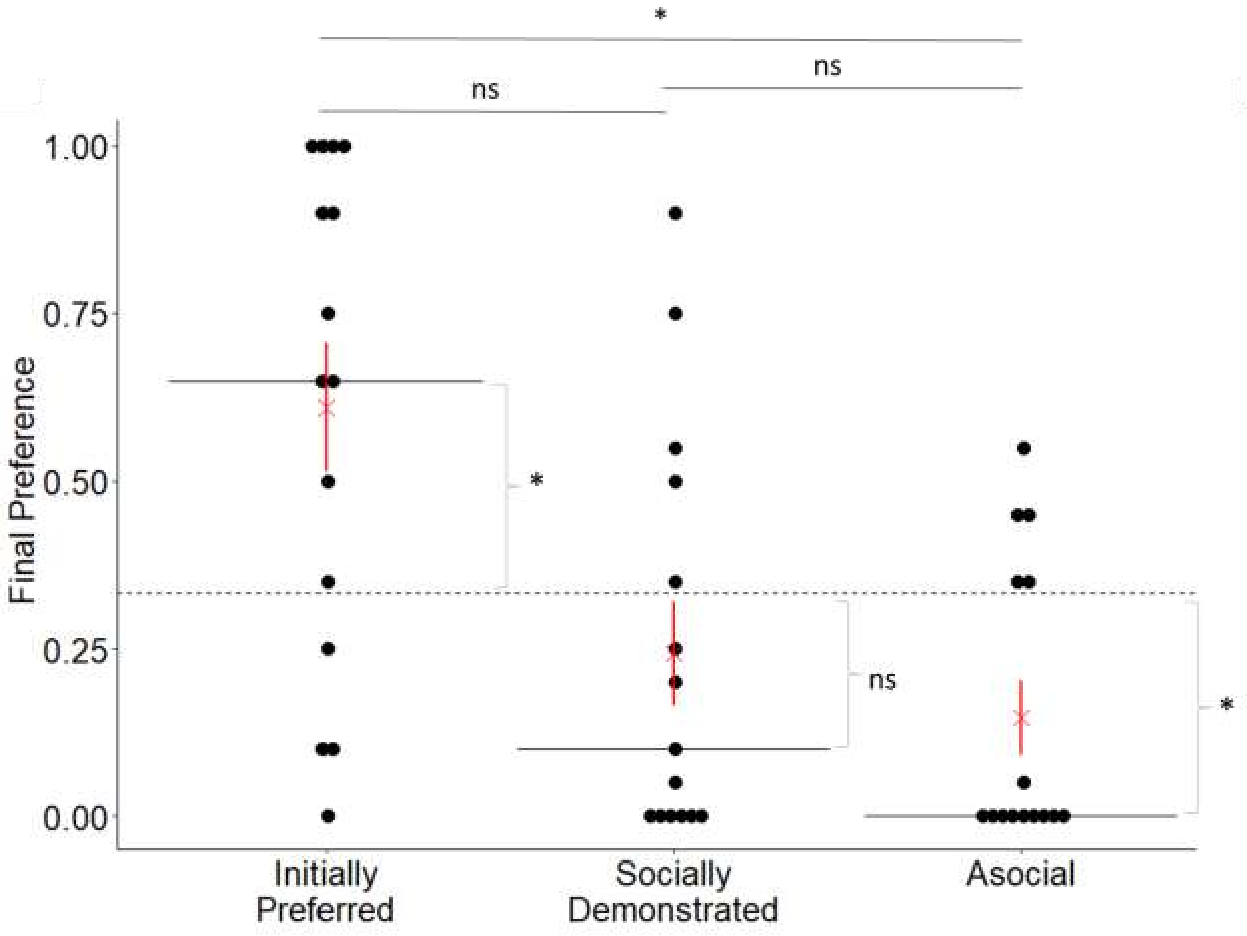


Note. Final preference of observers in Agree group (y-axis) is plotted against material types (x-axis). Each black dot represents the final preference value (corresponding to a material type) of a male observer in the Agree group (n = 14). Each filled black horizontal line passing through the dots represents the median. Each red cross and range represent the mean and standard error of mean respectively. The dashed horizontal line represents the chance level preference (.333). Curved brackets and associated significance markers (asterisk or 'ns') indicate the significance of the difference between corresponding material preference and chance level preference. Significance markers corresponding to preference comparisons between any two material types are indicated on top.

ns – not significant.

Figure 17

Final Preference across Material Types for Observers in Conflict Group

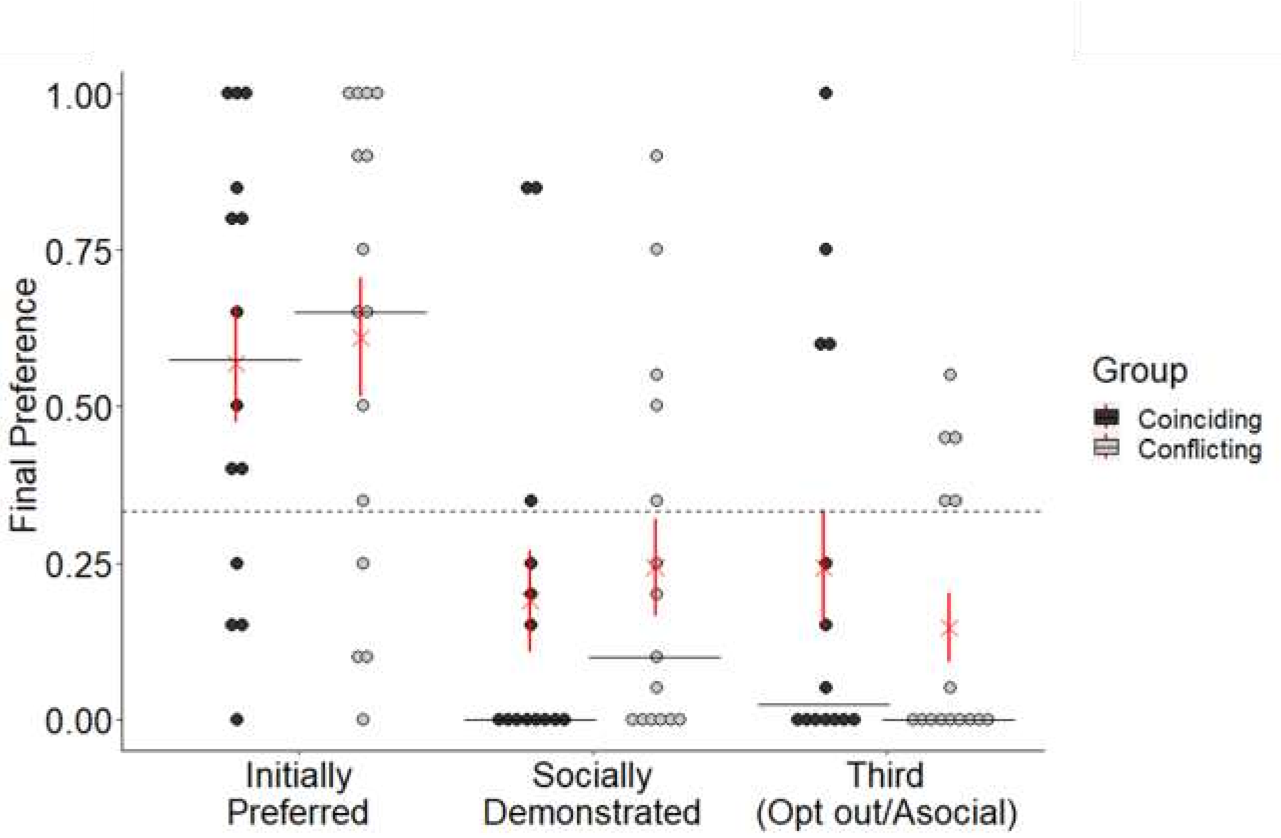


Note. Final preference of observers in Conflict group (y-axis) is plotted against material types (x-axis). Each black dot represents the final preference value (corresponding to a material type) of a male observer in the Conflict group (n = 15). Each filled black horizontal line passing through the dots represents the median. Each red cross and range represent the mean and standard error of mean respectively. The dashed horizontal line represents the chance level preference (.333). Curved brackets and associated significance markers (asterisk or ‘ns’) indicate the significance of the difference between corresponding material preference and chance level preference. Significance markers corresponding to preference comparisons between any two material types are indicated on top.

$^{*}p < .05$, ns – not significant.

Figure 18

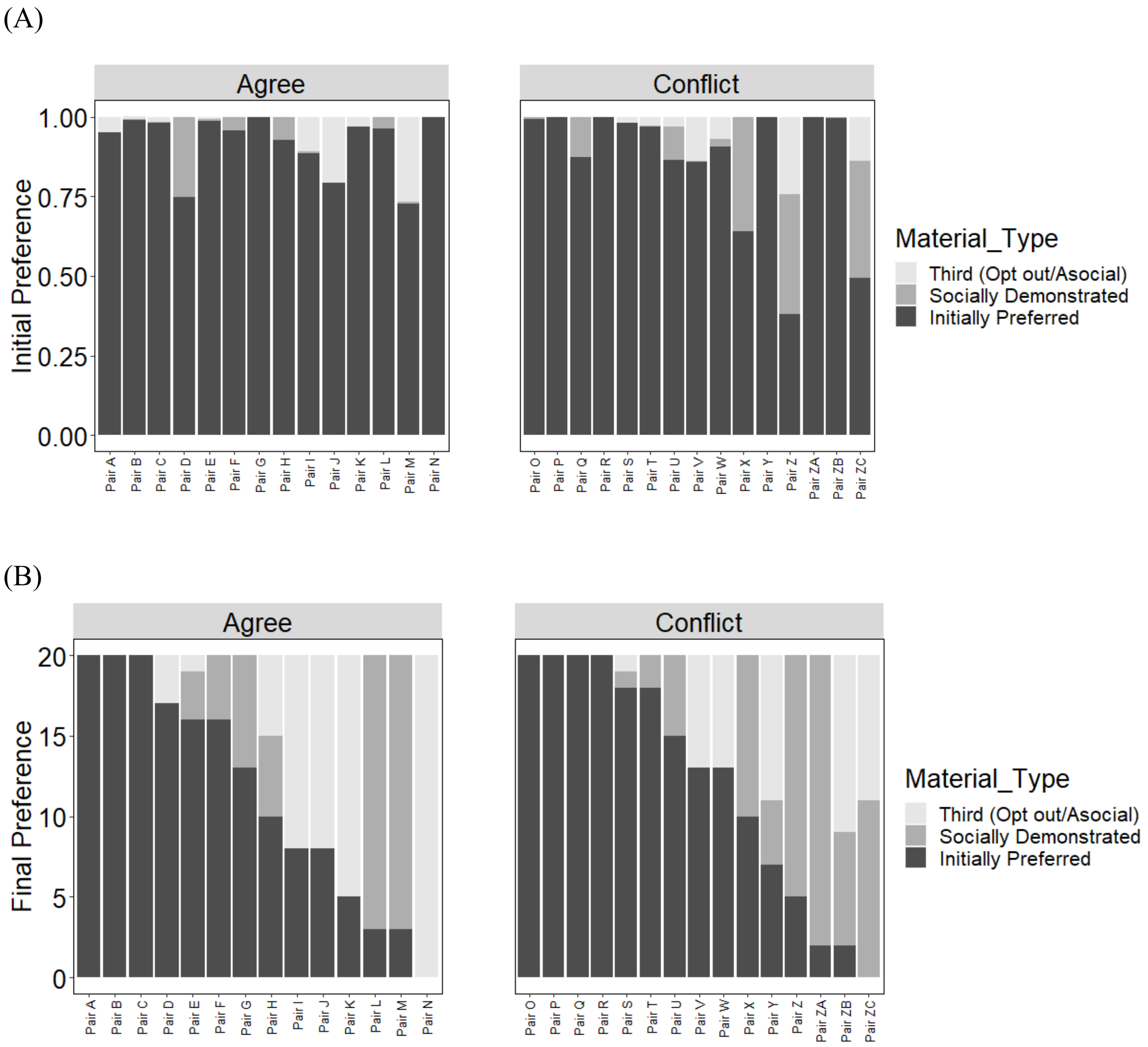
Final Preference across Material Types for All Observers



Note. Final preference of observers split by treatment group (y-axis) is plotted against material types (x-axis). Each black dot represents the final preference value (corresponding to a material type) of a male observer in the Agree group (n = 14) while each grey dot represents the final preference value of a male observer in the Conflict group (n=15). Each filled black horizontal line passing through the dots represents the median. Each red cross and range represent the mean and standard error of mean respectively. The dashed horizontal line represents the chance level preference (.333). Note that this figure is a visual aid and does not contain results of its own, see results mentioned in Figure 16 and Figure 17 for within group comparisons.

Figure 19

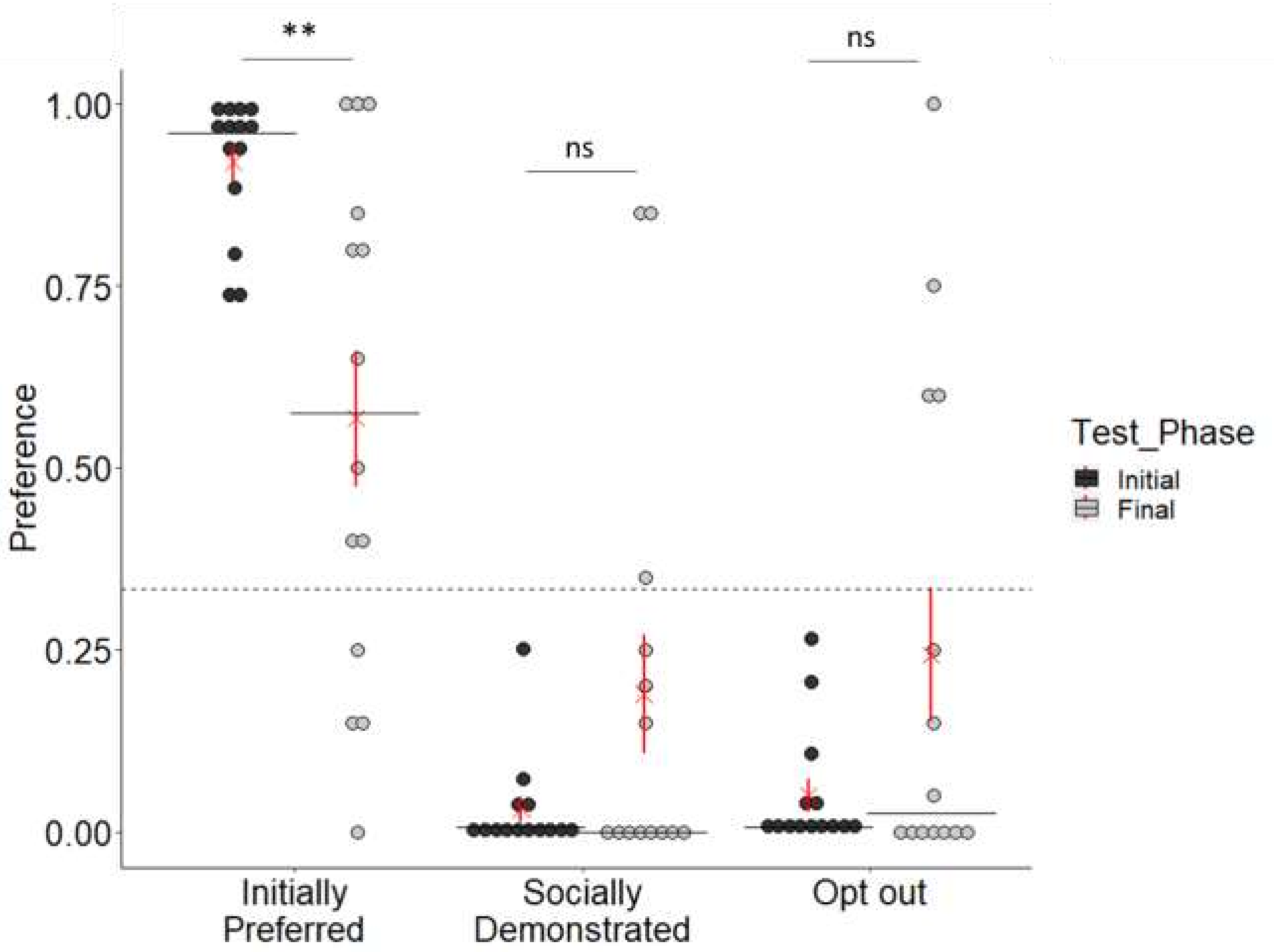
Individual Initial and Final Preference across Material Types for all Observers



Note. Top panel (A) shows each individual observer's initial preference for the three material types. Left side of top panel (A) shows the data for observers belonging to the Agree group (n = 14) while the right side of top panel (A) shows the data for observers belonging to the Conflict group (n = 15). The dark grey portion of each bar (corresponding to one male observer) represents the number of deposits of initially preferred material, the medium grey portion represents the number of deposits of socially demonstrated material while the light grey bar represents the number of deposits of third material (opt out for Agree group; asocial for Conflict group). The bottom panel (B) shows the final preference for observers in terms of number of deposits of each material type in the final preference test, made by a particular observer (x-axis). Similar to the top panel, the left side of bottom panel (B) represents observers belonging to the Agree group (n = 14) while the right side of bottom panel (B) shows the data for observers belonging to the Conflict group (n = 15).

Figure 20

Change in Preference across Material Types for Observers in Agree Group

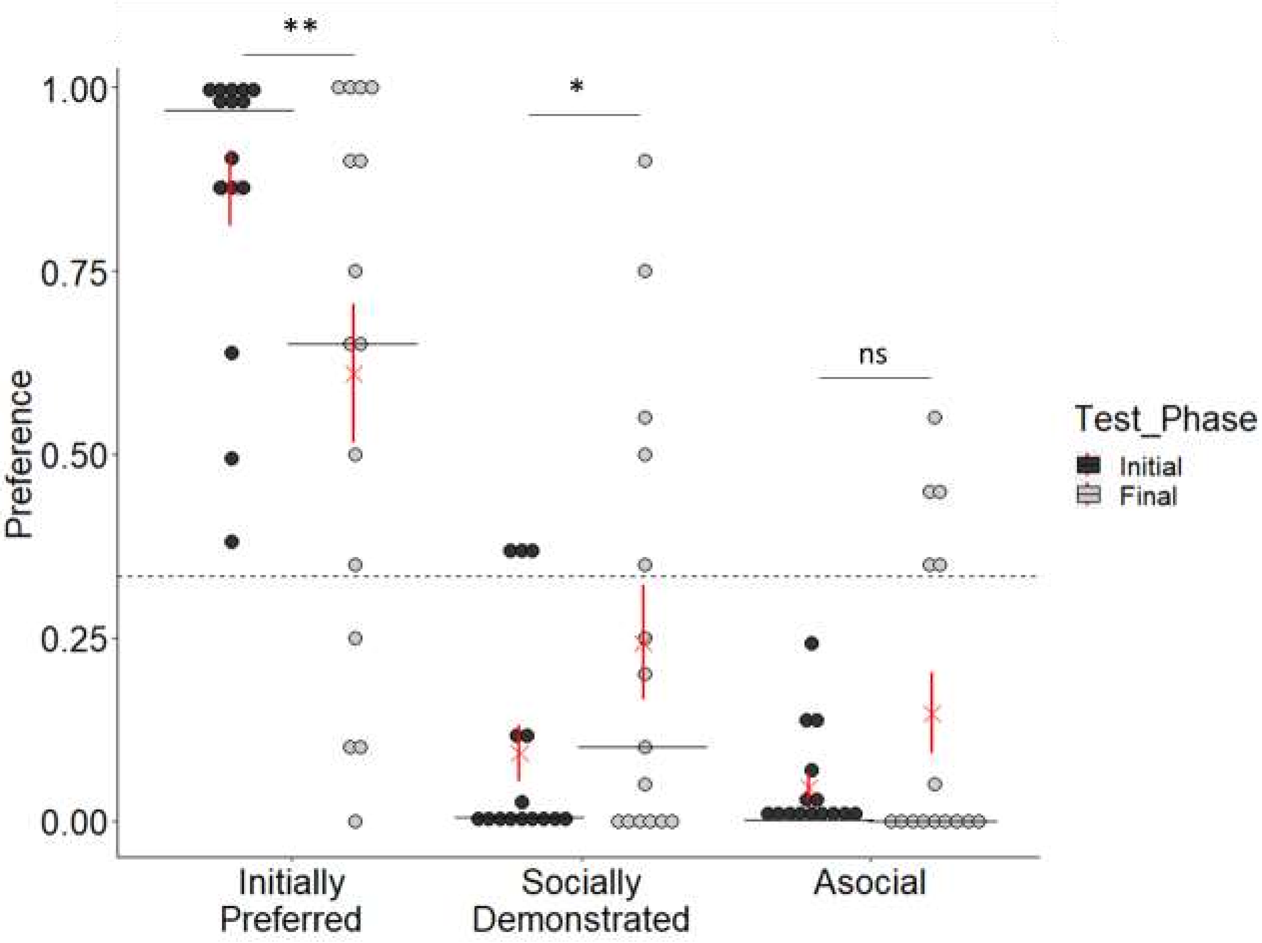


Note. Preference of observers in the Agree group during the initial and final preference test (y-axis) is plotted against material types (x-axis). Each black dot represents an observer's initial preference value corresponding to a material type while each grey dot represents an observer's final preference value (n=14). Each filled black horizontal line passing through the dots represents the median. Each red cross and range represent the mean and standard error of mean respectively. The dashed horizontal line represents the chance level preference (.333). Significance markers corresponding to preference comparisons between the initial and final preference tests are indicated on top.

$^{**}p < .01$, ns – not significant.

Figure 21

Change in Preference across Material Types for Observers in Conflict Group

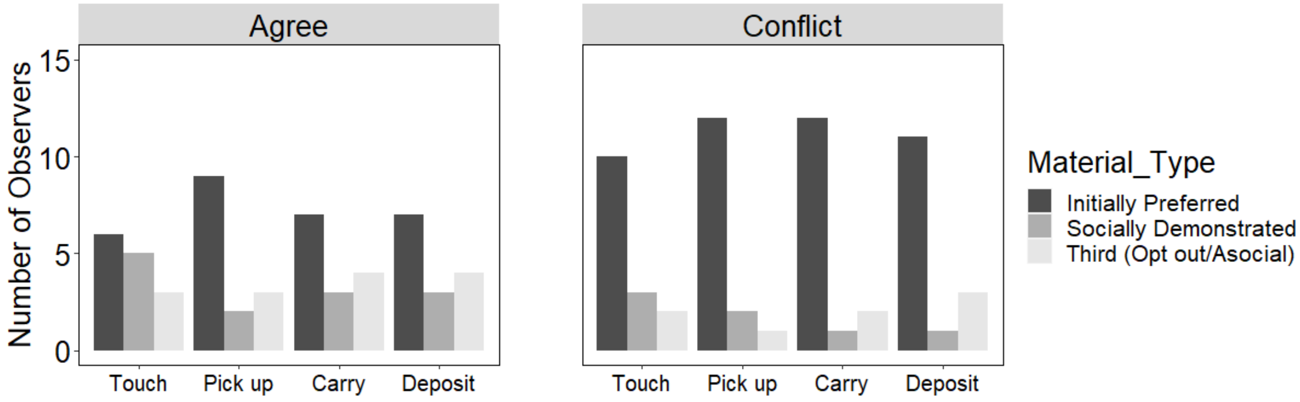


Note. Preference of observers in the Conflict group during the initial and final preference test (y-axis) is plotted against material types (x-axis). Each black dot represents an observer's initial preference value corresponding to a material type while each grey dot represents an observer's final preference value (n=15). Each filled black horizontal line passing through the dots represents the median. Each red cross and range represent the mean and standard error of mean respectively. The dashed horizontal line represents the chance level preference (.333). Significance markers corresponding to preference comparisons between the initial and final preference tests are indicated on top.

$^{**}p < .01$, $^{*}p < .05$, ns – not significant.

Figure 22

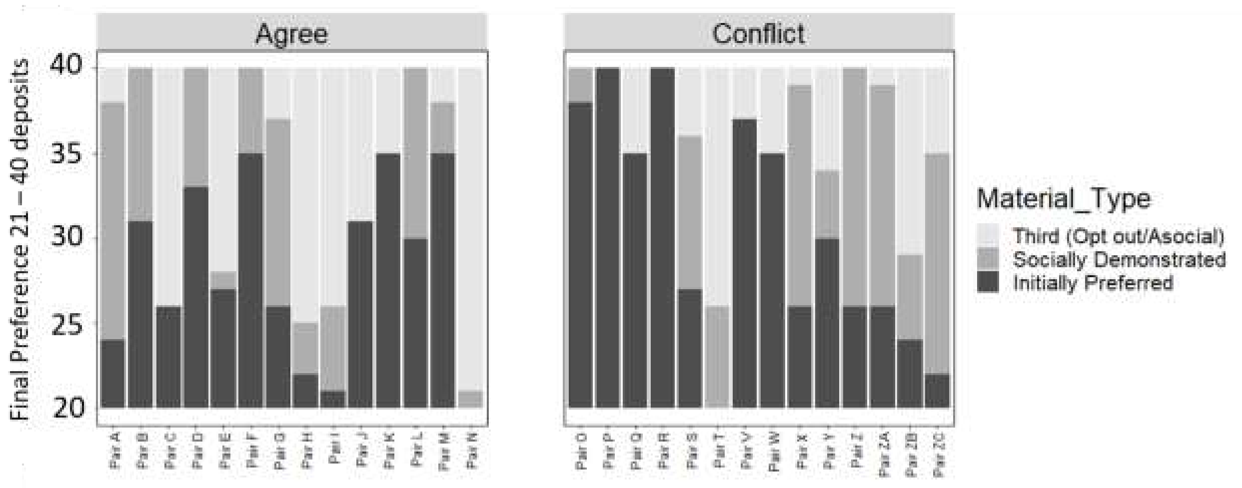
First Interactions



Note. Number of observers (y-axis) that first touched, first picked up, first carried and first deposited each material type (first interacted; x-axis) in the final preference test is shown. The left panel shows the data for observers belonging to the Agree group (n = 14) while the right panel shows the data for observers belonging to the Conflict group (n = 15). The dark grey bars represent the number of observers that first interacted with initially preferred material, the medium grey bars represent the number of observers that first interacted with socially demonstrated material while the light grey bars represent the number of observers that first interacted with third material (opt out for Agree group; asocial for Conflict group).

Figure 23

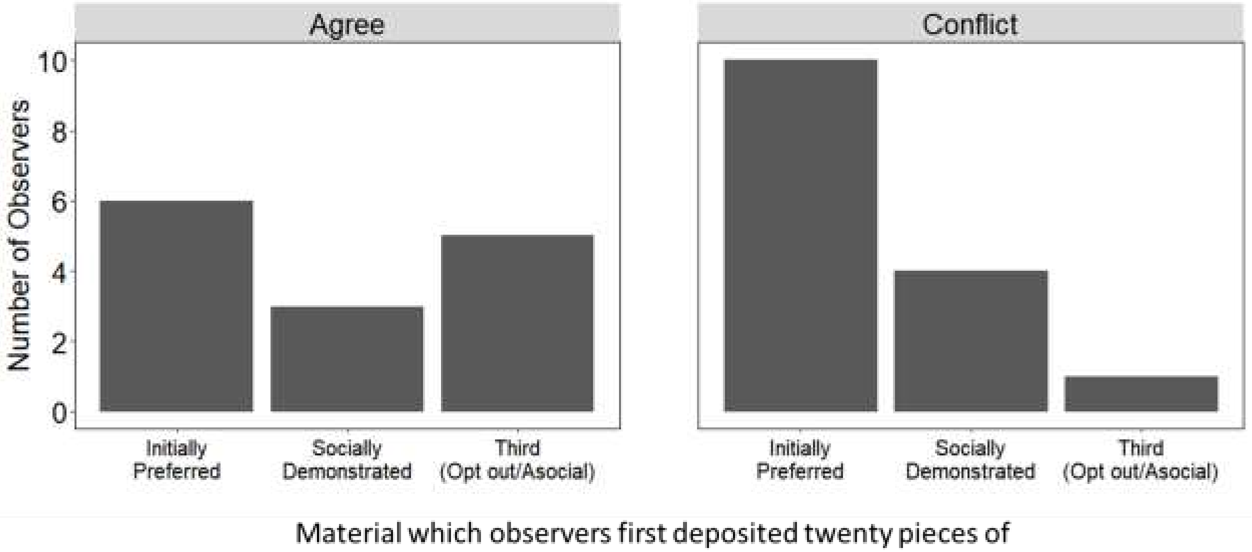
Final Preference – Twenty-first to Forty Deposits



Note. Left side of panel shows the data for observers belonging to the Agree group (n = 14) while the right side of top panel shows the data for observers belonging to the Conflict group (n = 14; since one observer did not make 40 deposits before the final preference test ended). The dark grey portion of each bar (corresponding to one male observer) represents the number of deposits of initially preferred material, the medium grey portion represents the number of deposits of socially demonstrated material while the light grey bar represents the number of deposits of third material (opt out for Agree group; asocial for Conflict group).

Figure 24

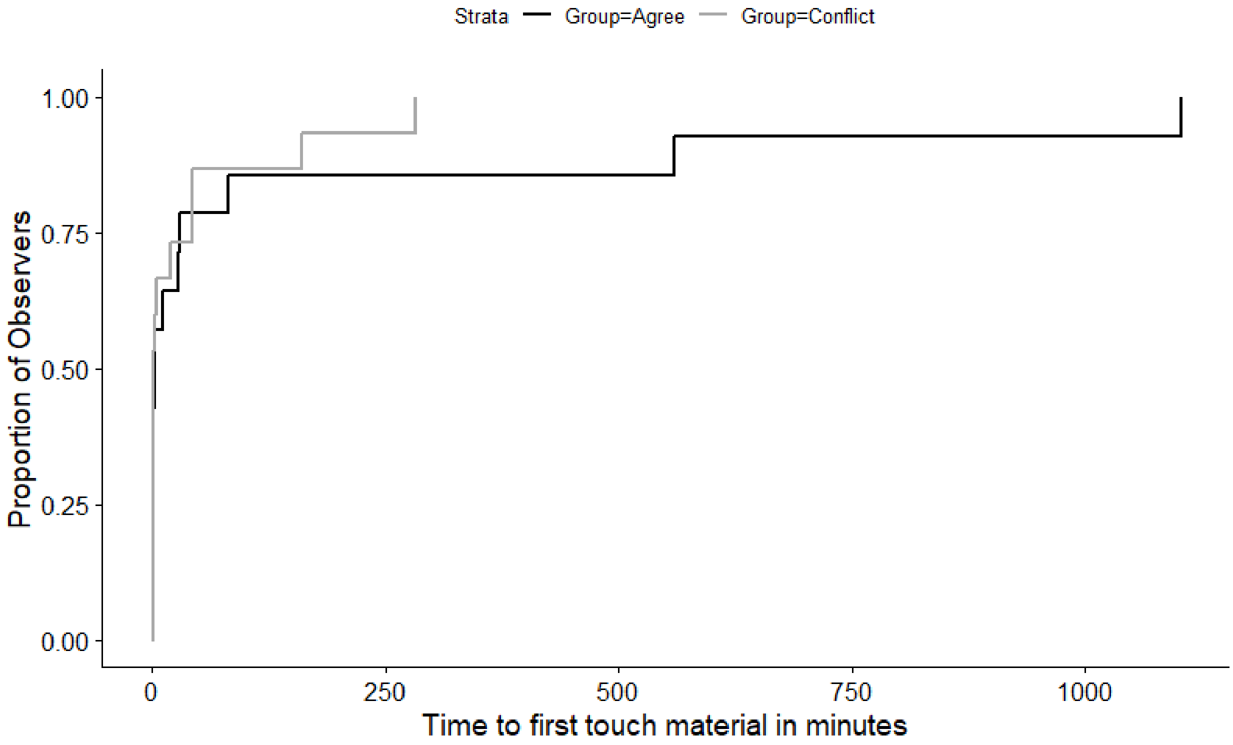
Material Type of which Observers First Completed Twenty Deposits



Note. The dark grey bars represent the number of observers (y-axis) that first completed depositing twenty pieces of either initially preferred, socially demonstrated or third material (opt out for Agree group and asocial for Conflict group; x-axis). The left panel shows the data for observers belonging to the Agree group (n = 14) while the right panel shows the data for observers belonging to the Conflict group (n = 15).

Figure 25

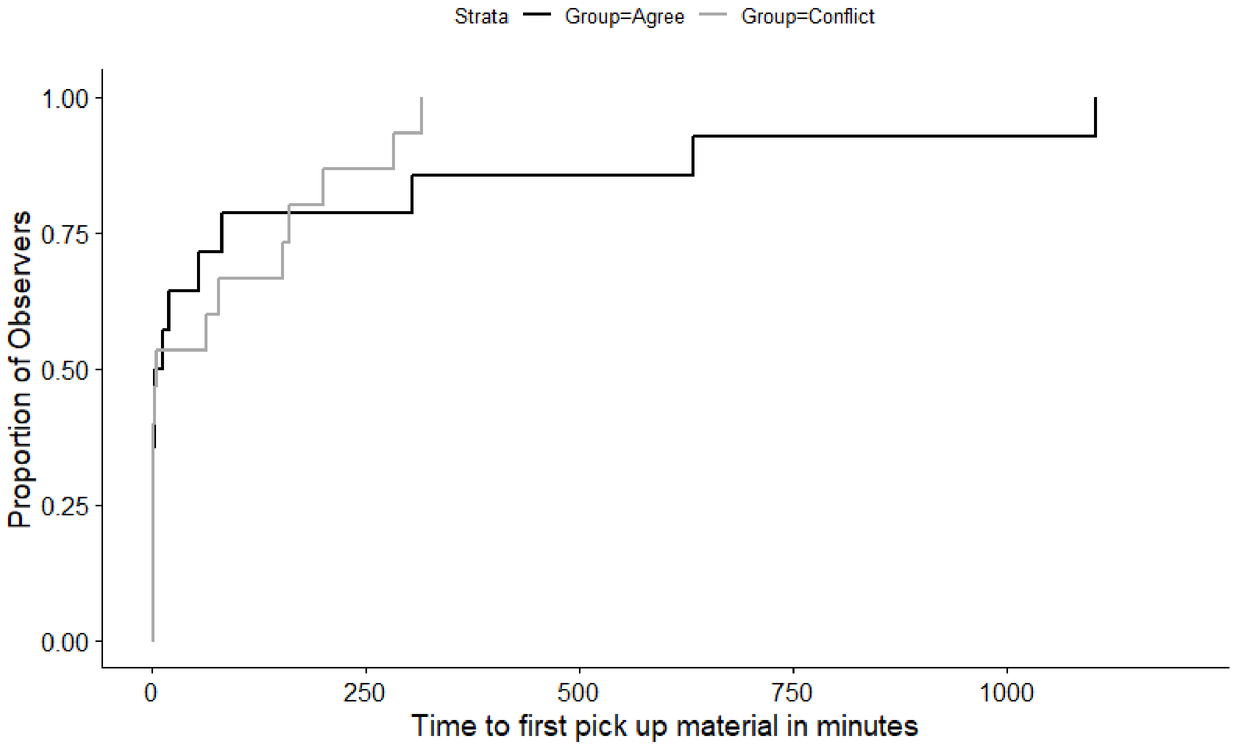
Observers' Latency to First Touch Material



Note. The survival curves corresponding to the latency of observers in Agree group (n=14; dark grey) and observers in Conflict group (n=15; light grey) to first touch any material are shown here. 50% of observers in the Agree group had first touched material by 2.77 minutes, while 50% of observers in the Conflict group had first touched material by 1.57 minutes.

Figure 26

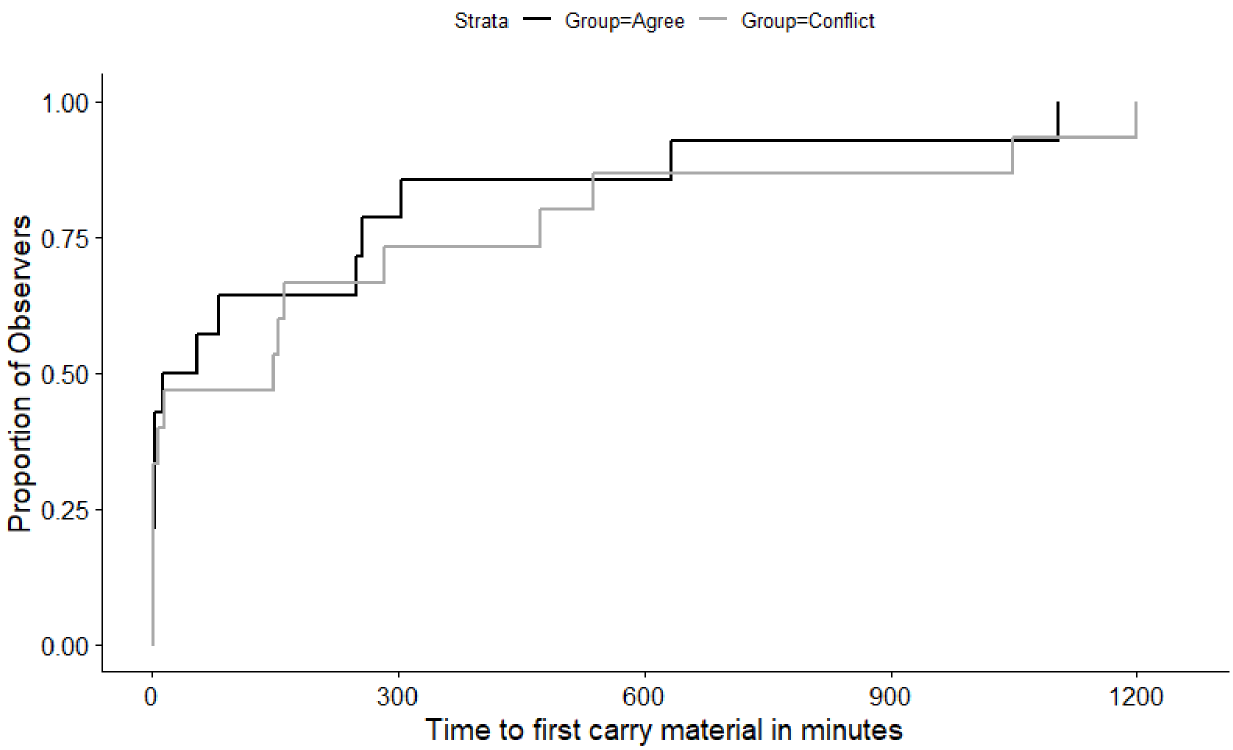
Observers' Latency to First Pick Up Material



Note. The survival curves corresponding to the latency of observers in Agree group (n=14; dark grey) and observers in Conflict group (n=15; light grey) to first pick up any material are shown here. 50% of observers in the Agree group had first picked up material by 7.29 minutes, while 50% of observers in the Conflict group had first picked up material by 4.31 minutes.

Figure 27

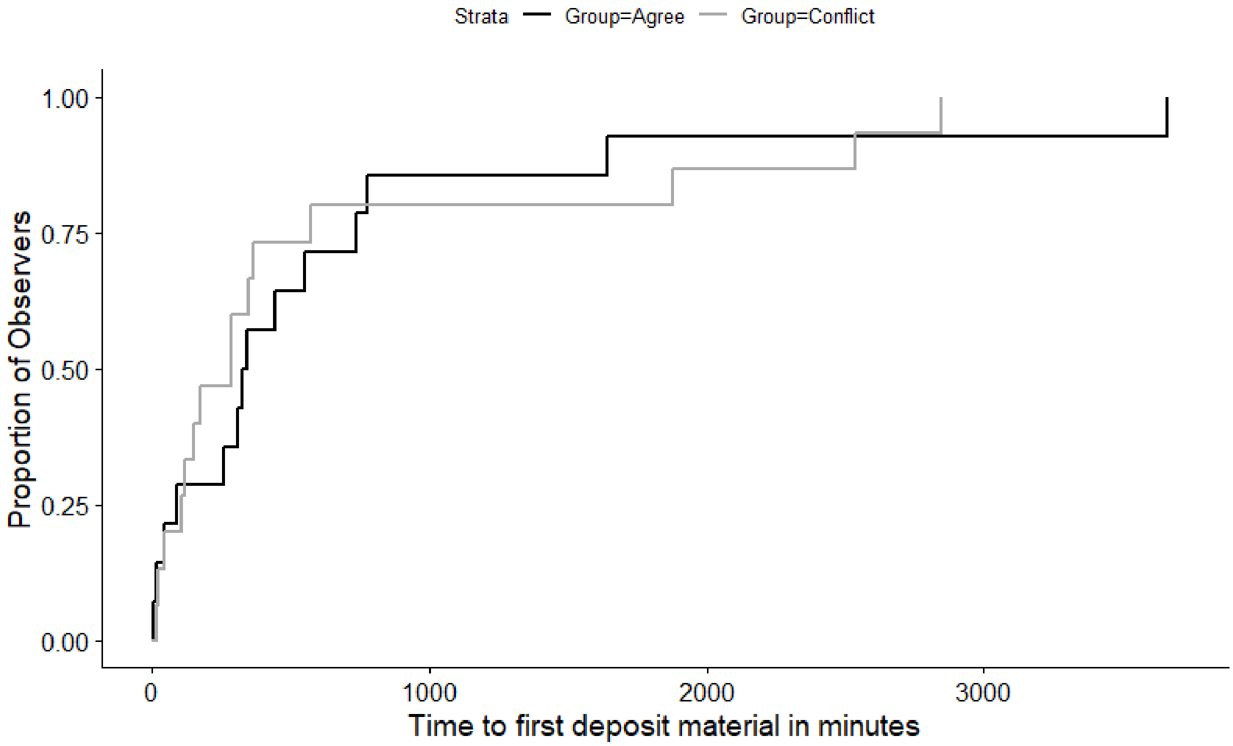
Observers' Latency to First Carry Material



Note. The survival curves corresponding to the latency of observers in Agree group (n=14; dark grey) and observers in Conflict group (n=15; light grey) to first carry any material are shown here. 50% of observers in the Agree group had first carried material by 33.2 minutes, while 50% of observers in the Conflict group had first carried material by 146.6 minutes.

Figure 28

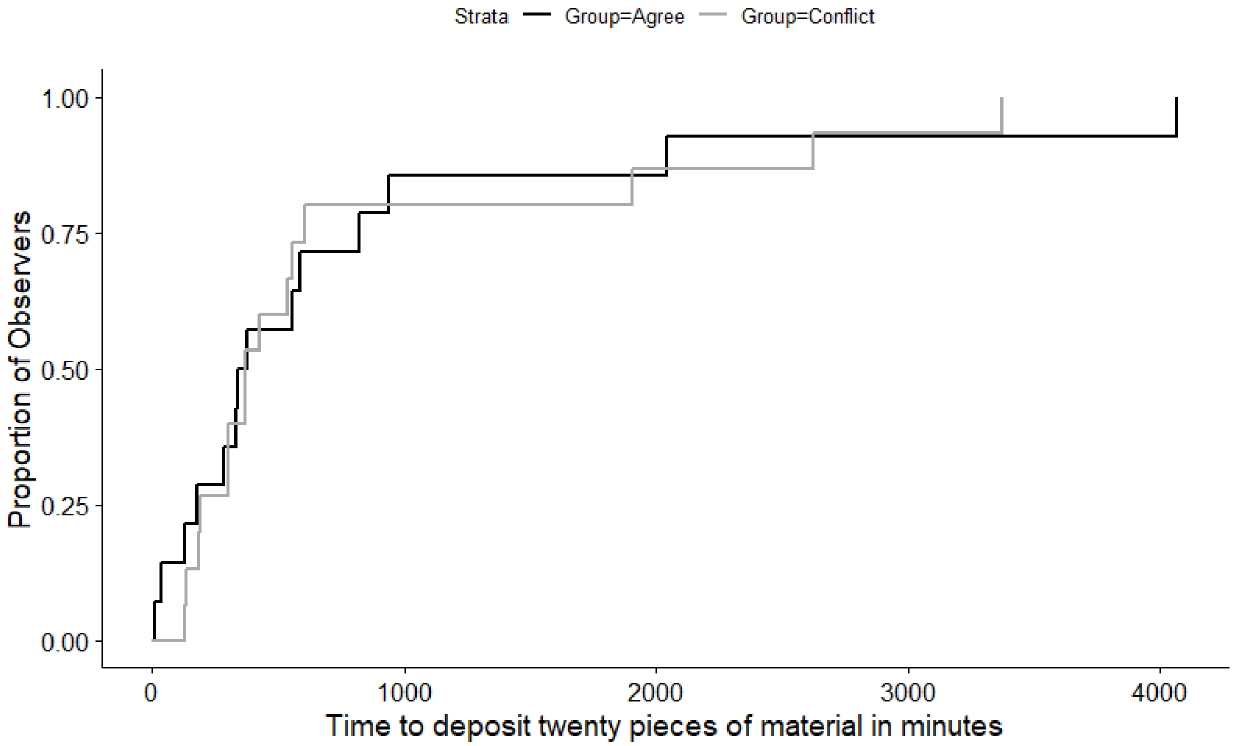
Observers' Latency to First Deposit Material



Note. The survival curves corresponding to the latency of observers in Agree group (n=14; dark grey) and observers in Conflict group (n=15; light grey) to first deposit any material are shown here. 50% of observers in the Agree group had made the first material deposit by 331 minutes, while 50% of observers in the Conflict group had made the first material deposit by 282 minutes.

Figure 29

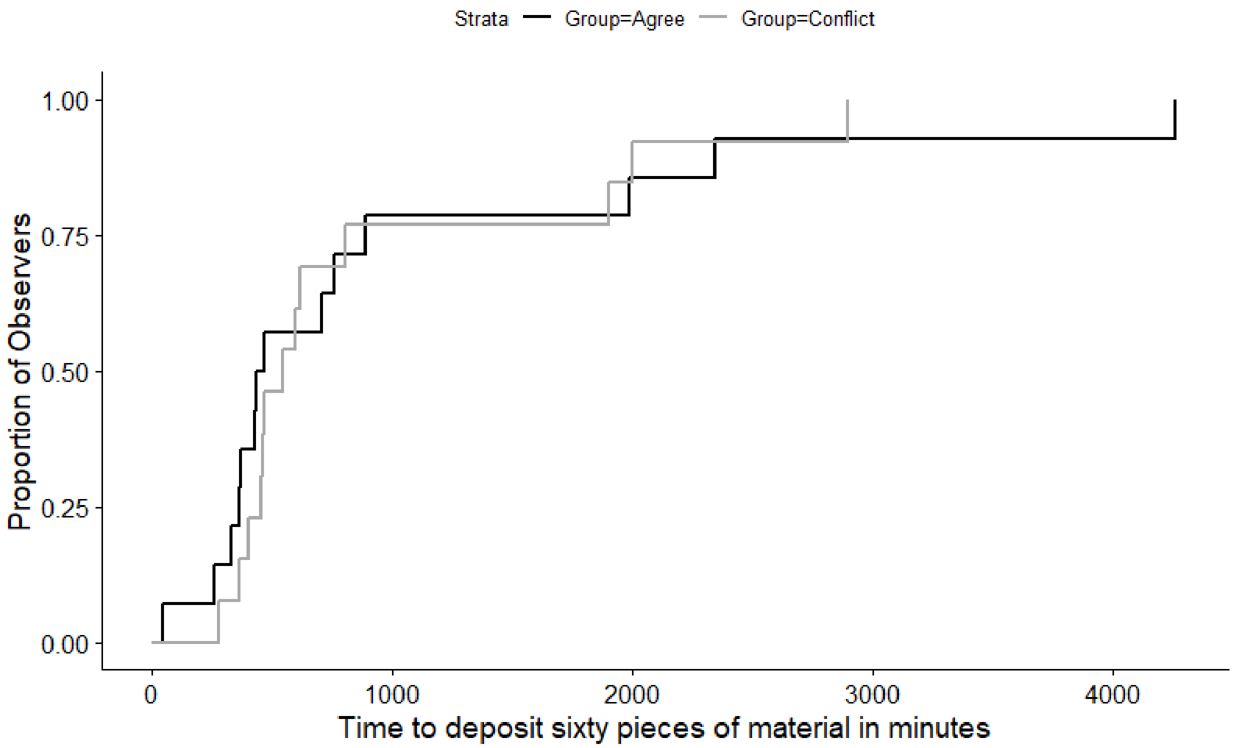
Observers' Latency to Deposit Twenty Pieces of Material



Note. The survival curves corresponding to the latency of observers in Agree group (n=14; dark grey) and observers in Conflict group (n=15; light grey) to first deposit twenty pieces of material are shown here. 50% of observers in the Agree group had deposited twenty pieces of material by 356 minutes, while 50% of observers in the Conflict group had made twenty deposits by 370 minutes.

Figure 30

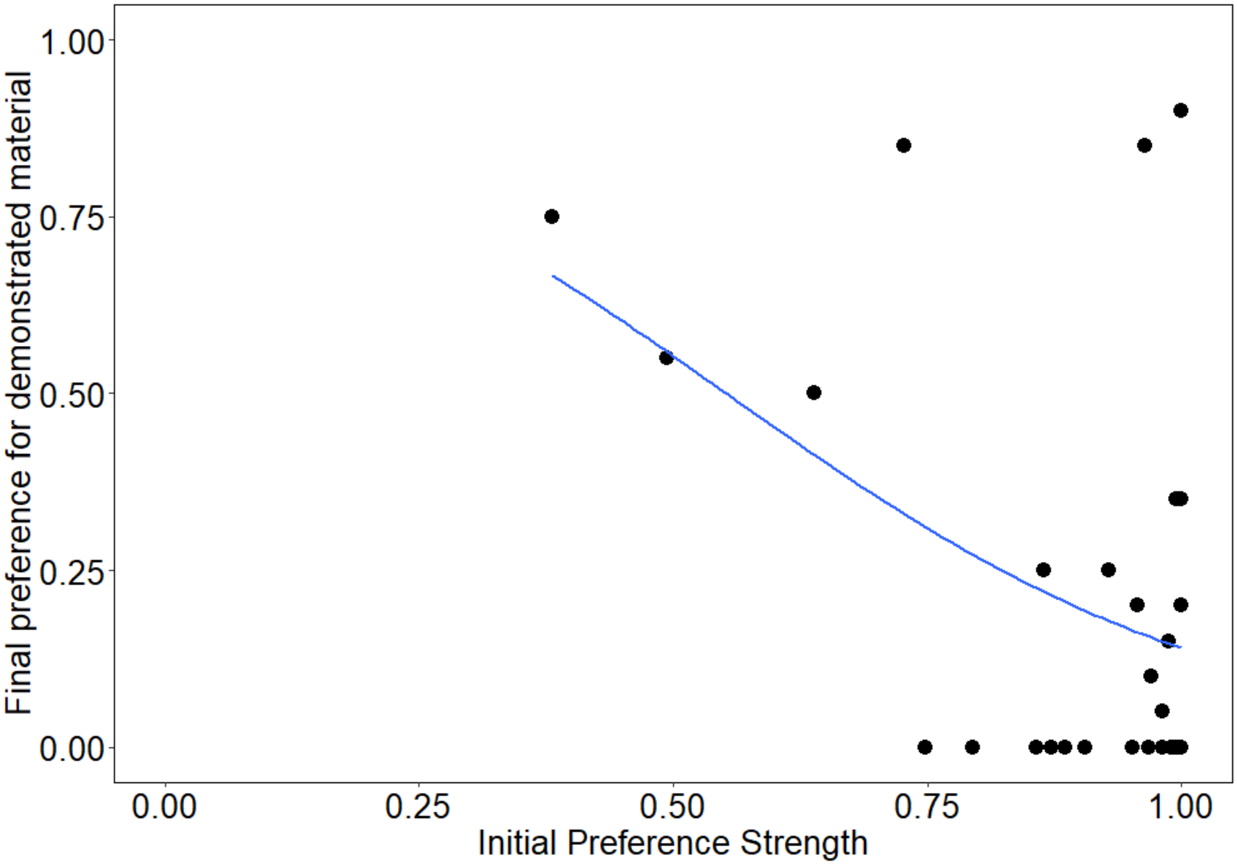
Observers' Latency to Deposit Sixty Pieces of Material



Note. The survival curves corresponding to the latency of observers in Agree group (n=14; dark grey) and observers in Conflict group (n=13; light grey) to first deposit sixty pieces of material are shown here. 50% of observers in the Agree group had made sixty material deposits by 447 minutes, while 50% of observers in the Conflict group had made sixty deposits by 546 minutes.

Figure 31

Generalised Linear Model with Final Preference for Socially Demonstrated Material predicted by Initial Preference Strength



Note. Final preference of observers for socially demonstrated material (0 to 1; low to high) (y-axis) is plotted against initial preference strength (0 to 1; low to high) (x-axis). Each black circle represents an observer (n=29), the blue curve represents the fitted regression curve (pseudo R^2 = .153).

Discussion

In this experiment, I asked how birds made nest-building decisions when they had access to both asocial and social information, which were either in agreement or in conflict with each other. I found that observer birds across both groups, after getting some information – either asocial or social, changed their initial preference for different types of nest-building material. This change can be attributed to the influence of information obtained from either asocial or social sources. This is because, previous work shows that when birds do not receive any information about material between an initial preference test and a final preference test, they maintain their preference for the initially preferred material in the final preference test (Breen et al., 2019).

For observers in the Agree group, that had access to social and asocial information that agreed with each other – I had predicted the use of socially demonstrated material which was also the suitable for camouflage in the final preference test. Contrary to the prediction, I found that observers in the Agree group did not show an increase in preference for the socially demonstrated (also camouflaging) material from the initial to the final preference test. Overall, observers in this group did not seem to prefer any material between the initially preferred, socially demonstrated (also camouflaging), or the opt out in the final preference test. In other words, material preferences were ambiguous following the treatment that is presentation of asocial and social information.

Similar to the observers in the Agree group, observers in the Conflict group showed a decrease in preference for the initially preferred material. This finding aligned with my prediction that observers in both groups would show a decrease in preference for the initially preferred material in the final preference test. In spite of the decrease, however, preference for the initially preferred material as a group was still above chance level in the final preference test.

Further, observers in the Conflict group showed an increase in preference for the socially demonstrated material from the initial to the final preference test. On the other hand, there was no change in preference for the material corresponding to asocial information (that is, the camouflaging material). This finding indicates that within the purview of material preference changes, observers prioritised social information over asocial information.

Guillette and colleagues (2016) showed that naïve observers that had not built a nest before copied the material choice of familiar conspecifics. Guillette and colleagues (2016) study lends support to *copy-when-uncertain* strategy which posits that observers copy others in the absence of relevant information (Kendal et al., 2018; Laland, 2004). Strengthening the evidence for use of this strategy by nest-building zebra finches, Eckersley (2021) found that birds that had built a nest once and hence had previous nest building experience, did not copy material choice of conspecifics while building a second nest irrespective of the level of breeding success experienced in the first nest-building attempt - showing the particular relevance of social information about nest material for naïve birds.

Observers in the current experiment were also naïve. While observers in the Conflict group of the current experiment increased their preference for the socially demonstrated material in the final preference test, observers in the Agree group did not show an increase in preference for the socially demonstrated material in spite of the material also being camouflaging. Moreover, across both groups we did not see an overarching preference for socially demonstrated material such that preference for socially demonstrated material trumped the preference for initially preferred material in the final preference test. In this light, the present findings do not make a strong case for the *copy-when-uncertain* strategy.

A crucial difference between the current experiment and the study by Guillette and colleagues (2016) is the availability of an alternative source of asocial information that the naïve birds could also use – a cue in the form of a background that matched the colour of one of the available materials. If it is the case that naïve birds ignore social information when other asocial information is available, we must have still seen observers in the Agree group predominantly use the socially demonstrated material as a byproduct of their effort to build a camouflaged nest. Further, in case of observers in the Conflict group, a preference for the asocial material must have made apparent the observers' priority to camouflage their nest against a background over copying material choices of other individuals.The evidence for neither suggests the minimal role played by asocial information in the form of a coloured background in governing material choices via camouflage in this experiment – and hence it rules out reliance on asocial information as a potential explanation for why the socially demonstrated material was not overwhelmingly preferred by observers in this experiment.

Another finding of the current study was that, among the three materials during the initial preference test, there was an overwhelming preference for one of the coloured materials over the others:green material was strongly preferred over the other options (yellow and pink) by a majority of the observers. One possible reason for the lack of a complete switch in material preferences between the initial and final preference test phases could be the limitations posed by strong pre-existing preferences for material of one colour that render material choices less susceptible to influence by asocial or social sources of information.

Studies have shown that innate or pre-existing preferences for certain cues can have a role in determining how well learning can occur in a given situation. For example, Roy and colleagues (2019) gave zebra fish an associative learning task where the fish had to learn to associate a particular colour cue (out of two colour cues) with a social reward (presence of a conspecific). The researchers found that in cases where one of the colour cues was red, associative learning was impeded in a population of zebra fishes. This was because a strong preference for red in that population resulted in fish always approaching the red cue, irrespective of whether or not red was the rewarding cue. Similar preference for red in another population of zebra fish impeded reversal learning abilities – wherein fish could learn the reversal of the contingency of the rewarding cue from green to red colour, but could not learn the reversal of the rewarding cue from red to green colour (Roy et al., 2019).

Social information can also interact with pre-existing preferences. Specifically, strong pre-existing preferences or dislikes for the presented alternatives can limit the use of social information. Jones and colleagues (2015) showed how bumblebees (*Bombus terrestris dalmatinus*) with a dissatisfying foraging experience subsequently used social information only in cases where they already had an innate preference for an alternative flower colour that was being socially demonstrated. Laland & Plotkin (1993) conducted an experiment with adult Norway rats (*Rattus norvegicus*) to see if food preferences could be transmitted socially, and found that transmission of foraging preferences was more likely if the food-type indicated by social information was the food-type for which the rats had a preference. A demonstrator rat was either given a cocoa-flavoured diet (one experimental group) or a cinnamon-flavoured diet (another experimental group) in a bowl - which after consumption, the rat marked with excretory cues. A naïve rat was subsequently given a choice to feed from the socially indicated bowl (the excretory cues) containing a particular flavoured diet or an alternative bowl containing a different flavoured diet. After the naïve rat had consumed food and its feeding choices were noted, the rat was removed and a new naïve rat was introduced to the same two bowls each containing different flavoured diets and one of them marked with excretory cues. The researchers found that social transmission of food preferences occurred in one of the experimental groups – rats preferentially chose to feed from the bowl that was socially indicated through the transmission chain only when the socially indicated diet was the cinnamon-flavoured diet but not the cocoa-flavoured diet. A control group of rats also went through similar set of experimental steps, except that there was no initial demonstration and before every new naïve rat was introduced both bowls were cleaned off cues left by previous rats. Rats in the cocoa-flavoured diet group ate more of the socially indicated cocoa-flavoured diet than rats in the control group only in the first transmission step, after which the preference to eat the cocoa-flavoured diet declined. While naïve subjects in the control group did prefer the cinnamon-flavoured diet, rats in the cinnamon-flavoured diet group who were given social information ate more of the cinnamon-flavoured diet and less of the cocoa-flavoured diet through the transmission chain as compared to rats in the control group (Laland & Plotkin, 1993). In an experiment with ants (*Myrmecina nipponica*) Cronin (2013) showed how the ants' preference for different kinds of nest characteristics affected whether or not ants used social information to choose a nest for relocation. The researcher first let ants evaluate nests that varied in physical characteristics such as light, moisture content and entrance width and obtained baseline preferences for different kinds of nests. Ants strongly preferred moist over dry nest, weakly preferred dark over light nest and weakly preferred small entrance over large entrance nest. Later, ants were given choice tests between a preferred and a non-preferred nest along with social information in the form of pheromone trail leading up to the non-preferred nest. For example, ants were given a choice between a moist nest versus a dry nest with the pheromone trail leading up to the dry nest. The researcher found that ants only used social information and followed the pheromone trail when the non-preferred nest was only weakly non-preferred. In other words, when the socially demonstrated nest was strongly non-preferred ants ignored the social information (Cronin, 2013).

Studies have shown that nest material selection in zebra finches is amenable to individual experience. However, strong preferences or dislikes for particular nest materials play a role in determining how material preference changes are mediated after experience. In contrast to the current experiment where most birds preferred green material, Sargent (1965) found that zebra finches preferred brown material over green or red material for their nest. A single building experience with non-preferred green material was enough to switch material preferences of birds from initially preferred brown material to green material. However, the same switch in preference did not occur when the building experience comprised building with red coloured material – birds after an experience building with red material continued to use the initially preferred brown material (Sargent, 1965). Similarly, Muth & Healy (2011) found that zebra finches that built a nest with an initially non-preferred colour material reversed their preference in a second nest building attempt after a successful breeding experience with the initially non-preferred colour material. However, zebra finches that built a nest with their initially preferred colour material (most birds preferred green material initially over the alternative brown material) continued to use the same material for their second nest in spite of experiencing breeding failure in the first attempt (Muth & Healy, 2011).

In adding evidence to social information use being mediated by the level of pre-existing preferences, Camacho-Alpízar and colleagues (2021b) in their experiment looking at the use of social information about nest material from artefact nests found that birds which had higher values of initial preference for a coloured material were less likely to change preference and use the alternative socially demonstrated material. In the current study also, we see that birds that had higher initial preference strengths were less likely to use the socially demonstrated material in the final preference test. In this light it is reasonable to expect that strong pre-existing preferences for a particular colour (which was green in a majority of the cases in the current experiment), might have restricted the extent to which changes in material preference could take effect.

The exact reasons for pre-existing nest material colour preferences are not clear. Previous research has shown that colour of material encountered in the natal nest likely does not have a bearing on future material colour preferences (Muth & Healy, 2012). Another way for material colour preferences to arise could be through prior positive associations with colour in a different context (Muth et al., 2013; Muth & Healy, 2011). For example, experience of receiving spinach as food outside the experiment might have biased birds in the current experiment towards the green colour (Muth & Healy, 2011). However, Muth and colleagues (2013) showed that colour preferences do not necessarily generalise across different contexts such as foraging and nest material selection. The researchers found that when given an option between three kinds of coloured foods – blue, yellow or red, zebra finches did not show a preference for a particular-coloured food. However, majority of the same zebra finches showed a strong preference for blue nest material over yellow or red nest material. Thus, colour preferences shown for nest material might be specific to the nest-building context (Muth et al., 2013).

Colour preference for nest material also seems to differ across groups of zebra finches tested in different experiments. In Sargent (1965) experiment, zebra finches preferred brown burlap strands as material over green or red burlap strands. On the other hand, Muth & Healy (2011) found that most of their birds preferred green over brown coconut fiber as material. Similarly, in the current experiment, most observers had a preference for green over yellow or pink paper material. Camacho-Alpízar and colleagues (2021b) found that a majority of birds in their experiment preferred orange over pink jute string. On the other hand, Guillette and colleagues (2016) who also used orange and pink jute string as materials did not find a majority preference for either orange or pink jute string in their zebra finches. Along with the understanding of why such nest material preferences arise, the understanding of whether and why group differences in nest material preferences exist is also limited. One way to investigate this would be to test different groups of zebra finches (sourced from different populations) for material preference across a range of coloured material options belonging to a consistent material type (for example, string or coconut fiber or paper). Further, controlling the colours zebra finches are exposed to before material interaction can uncover if apparent differences across groups are due to developmental or experiential differences.

One of the aims of Bailey and colleagues (2015) experiment was to understand if apparent preferences for nest material colour in zebra finches stemmed from the birds' effort to choose material colour that reduced the conspicuousness of their nests. In the experiment, the researchers presented two different coloured material options at a time chosen from five different coloured materials - pale blue, pale yellow, pale pink, cream and mint green colours, along with a coloured background matching the colour of one of the two materials. The researchers found that in a majority of cases corresponding to different combinations of coloured material presented, birds built with the coloured material that matched the background colour - suggesting that birds might be actively choosing material that camouflages the nest over any pre-existing colour preferences they might possess (Bailey et al., 2015). In the current experiment, using similarly coloured materials as in Bailey and colleagues (2015) experiment, we explicitly tested all observers' preferences for coloured material first in the absence and later in the presence of a matching background and did not find evidence for observers displaying a tendency to build with camouflaging material when provided with a coloured background. While observing a conspecific build a nest could in part have interfered with the observer's material choices in the current experiment – why we see such differences in the tendency to build camouflaged nests between Bailey and colleagues (2015) experiment and the current experiment is not entirely clear. In Bailey and colleagues (2015) experiment, for the number of birds that received green and an alternative colour material against the alternative colour environment (five pairs), green material did not seem to hinder the birds' tendency to camouflage nest. However, in the current experiment we observed a preference for green coloured material in majority of our birds (twenty four out of twenty-nine pairs). Perhaps, zebra finches have a bias towards material colours such as green or brown that resemble materials available in the natural setting. Zebra finches build with dead twigs and grass stems, mostly but not exclusively in shrubs or trees (Zann, 1996). In other case, birds might also have a bias towards green material due to some other function – such as addition of green plant materials to nests to ward off parasites, as seen in some passerines (Dubiec et al., 2013). It could therefore be the case that nest-building zebra finches place a greater emphasis on information obtained about nest material while distinguishing between more novel nest material colours – such as orange and pink string presented in Guillette and colleagues experiment (Guillette et al., 2016).

So far, I have discussed how an overarching preference for the socially demonstrated material in either the Agree or the Conflict group or a preference for the asocial material in the Conflict group did not emerge, such that the preference for the initially preferred material was completely trumped. I did this by offering an explanation of how strong pre-existing preferences might make material preferences less flexible. However, this is not to say there was no effect of the treatment whatsoever. We do see changes in material preferences of observers between the initial and final preference test phases. Here I break down how the preferences for materials changed in each group.

In the Agree group I predicted that observers would predominantly use the socially demonstrated material (also camouflaging) over the initially preferred material or the opt out material. This was because I expected that having 'agreeing' sources of information (socially demonstrated material was also the camouflaging material) would at least maintain if not magnify the advantages associated with using the agreeing information. However, the results of the final preference test were in contradiction to the prediction I made. What I did find was that the preference for the initially preferred material dropped in the final preference test. This drop in preference however did not reflect uniquely as an increase in preference for the socially demonstrated (also camouflaging material) material – rather material preferences in general became more ambiguous in the final preference test. A part of this lack of preference for socially demonstrated (also camouflaging) material emerging, could be attributed to rigid pre-existing preferences (all but one observer in this group preferred green material initially) as discussed earlier. However, this is not the whole story.

A closer look at how the Agree group observers' material preferences in the final preference tests changed reveals that while some observers incorporated more of the socially demonstrated material (also camouflaging) during the final preference test, there were also observers which predominantly included more of the opt out material. During the final preference test, six out of the fourteen observer pairs in this group incorporated more of an initially non-preferred material as compared to the initially preferred material. Out of the six pairs – four of them incorporated more of the opt out material than the initially preferred material while two of them incorporated more of the socially demonstrated (also camouflaging) material than the initially preferred material. This is an interesting finding given that we expected observers to primarily change preference only towards the socially demonstrated (also camouflaging) material and did not expect that observers (even some) would incorporate more of the opt out material in the final preference test. According to the set-up of the current experiment, the opt out represents an ‘irrelevant’ option which does not align with the initial preference of the observer or the material conspecifics are using, and nor does it offer any advantage in camouflaging the nest.

One possible reason why we see these results of ambiguous material preferences could be that observers through handling of different materials during nest building, learn that the different materials do not differ in structural properties such as rigidity and become ambivalent to the different materials. This explanation assumes that observers once having experience initiating building with multiple materials, give more importance to other structural properties over nest material colour. It is also possible that observers avoided using the socially demonstrated (also camouflaging) material due to perceived competition from other nest-builders for the camouflaging material, in an environment where the camouflaging material was optimal.

Whether social information (observation of a conspecific building with a different coloured material than the one observers initially preferred) influences observers by priming observers to explore all available materials instead of sticking to the initially preferred material alone would be an interesting idea to test. This is not an untenable idea – a previous experiment by Breen and colleagues (2019) has shown how social information from nest artefacts can lead to observers losing preference for the initially preferred material even though there wasn’t a marked change in preference for the socially demonstrated material. Further, we find that observers in the Agree group do not overwhelmingly show a tendency to first interact with the initially preferred material. Especially a similar number of observers first touched different material types. When looking at the second set of twenty (that is, twenty first to forty) deposits made by the observers, we find that five observers majorly deposited the opt out material while two observers majorly deposited the socially demonstrated material. Moreover, when looking at the number of observers that first make twenty deposits of a particular material type, we find a lack of trend towards first depositing all twenty pieces of a particular material type. These results therefore provide additional evidence for the ambiguous material preferences of observers in this group.

Observers in the Conflict group also showed a decrease in preference for the initially preferred material. However, the final preference for the initially preferred material was not completely lost. When considering how the preferences for the other two, initially non-preferred materials changed – we see that observers increased their preference for the socially demonstrated material from the initial to the final preference test. On the other hand, observers did not show inclination to build with the asocial camouflaging material, as evidenced by a lack of change in preference for the asocial material. This provides evidence that when social and asocial information are in conflict – observers prioritise using social information and copying nest material choice of conspecifics over using asocial information and choosing nest material that reduces conspicuousness of their nest. This is an important finding which highlights that first time nest builders might be copying other individuals not simply because there’s a lack of alternate sources of information. That observers copy others in spite of the advantages conferred by camouflage, indicates the greater emphasis placed on social information, which could be associated with its own set of advantages. What those specific advantages are – whether it is reducing single nest conspicuousness in a colony or using a ‘tested’ material from which a fellow conspecific has built a complete nest, remains to be seen. While the dominance of social over asocial information is clear from the forced choice set up of the Conflict group, interpreting these results to form a wider understanding of the scope of social information use in nest material selection becomes challenging given that we did not see a case for social information use (as use of socially demonstrated material) in the Agree group. The lack of availability of an opt out material in the Conflict group prevents us from drawing parallels with the results of the Agree group, and therefore limits the understanding of whether the effect seen in the Conflict group would still hold if a novel material option was introduced in the Conflict group. It is also possible that the value of social information is heightened in the ‘conflict’ scenario. Since observers watched demonstrators build with a material that was not suited (as camouflaging material) to the demonstrator’s environment per se – perhaps it served as an indication that some other aspect of the material in spite of its lack of suitability for camouflage was being prioritised by the demonstrator, and thereby increased the attractiveness of the socially demonstrated material to the observers. It is although interesting to note that observers in the Conflict group overwhelmingly interacted first with their initially preferred material during the final preference test, and most observers also ended up using the initially preferred material first - by first making twenty deposits of the initially preferred material. Finally, five observers in this group incorporated a major proportion of socially demonstrated material in the second set of twenty deposits as compared to two observers which majorly deposited the asocial material during the second set of twenty deposits.

Previous experiments have found that first time nest building zebra finches that have social information via observing a conspecific using a nest, complete nest building faster than zebra finches that did not have access to this social information (Camacho-Alpízar et al., 2021b). In the current experiment, to check if presenting information sources in a manner that agreed with each other (Agree group) or conflicted each other (Conflict group) affected different aspects of nest building latency, I compared the time taken by observers in both groups to first interact with material, build a partial (one-third) of a nest, and build a complete nest. There was no evidence that presenting information sources in agreement or conflict affected observers' latency to first touch, pick up or carry nest material. Further, there was no difference in latency to initiate nest building (first deposit), latency to build a 'partial' nest (deposit twenty pieces of material) or latency to 'complete' nest building (deposit sixty pieces of material) between observers in the Agree and Conflict groups.

Future directions

A follow up experiment I would be interested in, based on the results of the current study – is one in which the kind of asocial information is tweaked. Birds could be given an opportunity to gather asocial information about different materials based on properties such as rigidity. We could then see how birds weigh such asocially gathered information about material over conforming to material choices of other individuals. To carry out the experiment, zebra finches could be given different material options that differ in more than one physical property such as both colour and material rigidity (for example orange and stiff material vs. pink and flexible material). Zebra finches distinguish material based on material rigidity and learn to prefer stiffer over flexible material for building their nest – learning that one coloured string is flexible and the other coloured string is stiff could be the asocial information gathered (Bailey et al., 2014; Lambert et al., 2021). One group of observer birds could receive conflicting social information from conspecifics using the alternative-coloured material that conflicts with the material colour that corresponds to stiff material. Material preferences of this group of zebra finches that received conflicting social information could be monitored during nest building and contrasted with a group of birds that did not receive any social information.

Another observation that arises from this study is that individuals differ in social information use – while some individuals do not change preference at all between the initial and final preference tests, other individuals change preference and for example choose to use social information or explore on their own and use the opt out material. Previous studies have shown that individual differences in social information use exist. Farine and colleagues (2015) found that early-life developmental stress affected the social learning strategies of zebra finches later in life when presented with a novel foraging task. Rosa and colleagues (2012) showed the link between exploratory behaviour of female zebra finches and the individuals' propensity to use social information. More exploratory females that engaged in more sampling while searching for food were less likely to use social information in two different contexts – foraging as well as mate-choice (Rosa et al., 2012). It would be interesting to see if such individual differences in social information use also extend to the nest building context, and investigate whether factors like personality or developmental stress contribute towards an individual's tendency to use or forgo social information about nest building.

Conclusions

Naïve zebra finches (observers) when provided with social and asocial sources of information about nest material lost preference for their initially preferred material. Observers in the Agree group for whom the information sources were in agreement (socially demonstrated material was also the material suitable for camouflage), were predicted to use the corresponding agreeing information. However, contrary to the prediction observers in this group did not show an increased preference towards the socially demonstrated (also camouflaging) material and showed ambiguous material preferences. Observers in the conflict group for whom I did not have a prediction, displayed an increased preference towards using the socially demonstrated material over the camouflaging material which matched the background cue (asocial information), while still maintaining an overall preference for the initially preferred material. The reasons why we observe a change in preference for the socially demonstrated material in the Conflict group alone and not in the Agree group is not clear. I also found that a majority of observers across both groups in this experiment had a pre-existing preference for green coloured material. Strong pre-existing preferences may have limited the extent of material preference changes by social or asocial sources of information.

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Appendices

Appendix I Part A: Breeding Procedure carried out by Gopika Balasubramanian

X birds were obtained through this breeding procedure.

Equipment:

- Wooden nest box (12.5x12x12 cm)
- Nesting material (coconut fiber)

1. Prepare the material – Weigh 20g of coconut fiber (Aves Canada), cut the material into two halves across length and pull the strands apart to loosen.
2. Hang the nest box from the center back of the cage, on the strip across the length of the cage.
3. Place equal amounts of material on either side of the cage floor, avoiding placing the material directly underneath perches and feeders.
4. Replenish material as necessary - Give 20g of material if roughly less than 25% of the coconut fiber given previously is remaining.
5. Check inside the nest box every day, either visually or by gently extending a hand into the nest and feeling the bottom to see if female has laid an egg. Be careful not to exert pressure that could break the eggs.
6. Once an egg has been laid in the nest, remove the remaining non-deposited material from the cage. The nest is considered complete at this stage.
7. Weigh the coconut fiber that was removed.
8. Remove the nest box with nest 5 days after last fledgling fledges. Take pictures of the nest after removal.
9. Fledglings are separated from parents after nutritional independence is established (usually 35 days after hatching/18 days after fledging). This is done by visually observing the fledglings and checking if they are capable of feeding independently.
10. Ring all fledglings and enter them into the bird census.

Note: If a pair lays an egg on the floor, remove it. If an egg is laid in a nest that is not built in the nest box, do not remove it.

Revision History:

Created by: G Balasubramanian 10-Dec-2019

Appendix I Part B: Breeding Procedure carried out by Andres Camacho Alpizar

X birds were obtained through this breeding procedure, which was a part of a different experiment.

Equipment:

- Wooden nest box (12.5x12x12 cm)
- Nesting material (coconut fiber or string)

1. Prepare the material
    a. 200 pieces of white string (Jute Craft Twine, James Leaver CO)
    b. 22.5g of coconut fiber (Aves Canada)
2. Hang the nest box from the center back of the cage, on the strip across the length of the cage.
3. Place each kind of material on either side of the cage floor, avoiding placing the materials directly underneath perches and feeders.
4. Replenish material as necessary - Give 22.5g coconut fiber once most of coconut fiber given initially depletes. Similarly replenish with 200 pieces of white string if most of the string initially given depletes.
5. Check inside the nest box every day, either visually or by gently extending a hand into the nest and feeling the bottom to see if female has laid an egg. Be careful not to exert pressure that could break the eggs.
6. Once an egg has been laid in the nest, remove the remaining non-deposited material from the cage. The nest is considered complete at this stage.
7. Weigh the coconut fiber that was removed and count the number of strings removed.
8. Remove the nest box with nest 5 days after last fledgling fledges. Take pictures of the nest after removal.
9. Fledglings are separated from parents after nutritional independence is established (usually 35 days after hatching/18 days after fledging). This is done by visually observing the fledglings and checking if they are capable of feeding independently.
10. Ring all fledglings and enter them into the bird census.

Note: If a pair lays an egg on the floor, remove it. If an egg is laid in a nest that is not built in the nest box, do not remove it.

Revision History:

Created by: G Balasubramanian 10-Dec-2019
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Appendix II: Daily Animal Husbandry Procedure

Equipment & Locations:

419A: Cart, food, grit'n'gravel, oyster shells, cuttlebones, dirty water bucket (labelled), clean water bucket (labelled), water jug, vitamins, spray millet, broom, dustpan, squeegee, egg food, petri dishes, Kraft paper, strainer, clean food/water dishes

419R: Demineralized water line

P108: Spinach

Daily:

1. Gather supply cart from 419A
2. Enter room & check health of each bird visually (i.e., loss of feathers, blood, injury, puffy, odd behavior such as shaking)
    a. If there is a problem report to PI/Supervisor and SASS immediately
3. Complete the following before moving to next cage
    a. Top up food
    b. Top up grit'n'gravel & Oyster shells in the Petri dish if necessary (approx. 75% oyster shells, 25% grit'n'gravel)
    c. Water
        i) Mon/Wed: empty water dishes (housing rooms) or tubes (experimental rooms) into the dirty bucket, fill new tubes with vitamin water using jug and return to spot in cage
        ii) Fri: take dishes/tubes out to be cleaned and fill replacement tubes with vitamin water
        iii) Tue/Thu/Sat/Sun: top up water in dishes (housing rooms) and tubes (experimental rooms)
    d. Supplements
        i) Mon/Wed/Fri: put a few leaves of Spinach in each cage (except for cages in experimental rooms)
        ii) Thu: put one piece of Spray millet in each cage (except for cages in experimental rooms)
        iii) As necessary: replace Cuttlebone when depleted
    e. Remove any petri dishes not being in use; each cage should have mostly two petri dishes
4. Check temperature and humidity (min, max, current) – record on room checklist then reset thermometer
5. Sign checklist sheet located on wall outside of test room

Weekly:
(These tasks are to be performed Friday unless there are extenuating circumstances)

1. Clean floors with squeegee/broom/dustpan. Deposit waste into a trash can in the hallway
2. Replace Kraft paper if necessary

Notes:

1. Dirty Water: dump dirty water down a sink drain through the strainer
2. Weekly water dish cleaning and switch: In a clean bucket (labelled) bring the clean replacement dishes. Take dirty water dish and place in dirty bucket. Replace with clean dish. Wash dishes in sink in 419T using ONLY tap water, and leave them out to dry.
3. Kraft Paper replacement: – if Kraft paper needs replaced, used plastic template located in 419 A to cut paper. Roll out paper over top of template and then cut along the edge. To replace, pull out the cage trays and remove the cuttlebone and the Petri dish. Then take the old Kraft paper out, and replace with the new piece, and put the removed items back. Take the old paper out and dispose of it in the trash cans in the hall.
4. Vitamin water: using the scoop inside of the vitamin mix container, add 5 grams of vitamin mix for every 450mL in the jug
5. Virkon use: Virkon will be used to clean the room floor only when that room has been emptied of birds). Virkon is prepared by SASS in the 6th floor of the BioSci building.

Revision History:
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