# Does success matter? Nest failure does not affect copying in zebra finches (*Taeniopygia guttata*), contrary to the *copy-when-dissatisfied* strategy

by

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# Abstract

Social learning theorists have developed social learning strategies to predict when an individual is most likely to copy the behaviour of another individual, based on the benefits and costs social learning might convey. Much of the research investigating social learning strategies has come from experiments examining foraging decisions. One domain where there is little research investigating the role that social learning may play is that of physical cognition, which is the ability of an animal to gather and acquire information regarding either space, time or quantity of some aspect of the physical world (Shettleworth, 2009). One behaviour within the physical cognition domain that has seen a recent increase in research attention is animal construction behaviours, which includes nest-building behaviours in birds. Previous research into learning in nest-building behaviours has found that birds with no nest-building experience will use social information when choosing material to build their nest (Guillette, Scott, & Healy, 2016). Specifically, first-time nest-building zebra finches (*Taeniopygia guttata*) copy the nest-building material choice of familiar conspecifics. One thing that is unknown regarding social learning in nest building is whether having previous nest-building experience will affect social learning in a subsequent nest-building attempt. The *copy-when-dissatisfied* social learning strategy predicts that an Observer will copy a Demonstrator's behaviour if the Observer perceives the outcome of their own behaviour to be sub-optimal (Laland, 2004). Thus, I conducted an experiment asking: a) will experienced nest-building birds copy the material choice of familiar conspecifics in a second nest-building attempt, and b) will success in the previous nest (producing chicks or failing to produce chicks) differentially affect social learning. To test this, I had male-female zebra finch pairs build an initial nest that was either Successful (produced and fledged chicks) or Unsuccessful (eggs experientially removed during incubation). After completing the initial nest-building experience, I tested both the Successful and Unsuccessful pairs for their preference for two novel nest-building materials. Both the Successful and Unsuccessful pairs (the *Observers*) observed a pair of conspecifics (the *Demonstrators*) building a nest using the *Observers* non-preferred material. After having the opportunity to observe the *Demonstrators*, the *Observers* were again tested for their preference for the two novel nest-building materials they had been presented before the observation opportunity. Neither the Successful nor the Unsuccessful group copied the material used by the conspecifics. These results do not support the *copy-when-dissatisfied* strategy but may provide indirect support for an alternative social learning strategy, the *copy-when-uncertain* strategy.

# Preface

This thesis is an original work by Tristan S. Eckersley. The research project, of which this thesis is a part, follows the Animal Care (CCAC) Guidelines and Policies and received research ethics approval from the University of Alberta Research Ethics Board, the Animal Care and Use Committee for Biosciences at the University of Alberta (AUP00002923, October 23, 2018). I was responsible for the data collection, behavioural scoring, data analysis, and manuscript composition. I set up all apparatuses for the experiment with help from Connor T. Lambert and Andrés Camacho-Alpízar in building and arranging cages and help from Isaac Lank and Phillip May with setting up the recording apparatuses. The care and husbandry for all birds while in the colony room was provided by a combination of the Science Animal Support Services (SASS) team and the Animal Cognition Research Group (the laboratory with which this thesis was conducted). Care and husbandry during the *Demonstrator* training and initial nest-building experience were provided by Tristan S. Eckersley, Connor T. Lambert, Andrés Camacho-Alpízar, Gopika Balasubramanian, Briana S. Kroeker, Brittany Perkins, and Cora-Lee Kashuba. I provided all care and husbandry during the initial preference tests, pre-observation phase, observation phase, and final preference tests. Lauren M. Guillette was the supervisory author and was involved with developing the research project and manuscript revision. No part of this thesis has been previously published.

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# Table of Contents

# List of Tables

# List of Figures

*Figure 15*. **Groupwise preference for orange string for all *Observers*, the Successful group and the Unsuccessful group.** The preference for the orange string (y-axis) during the initial preference test for all *Observers*, the Successful group and the Unsuccessful group (x-axis) are shown. The horizontal black lines represent the median preference score for each group. The red dot and vertical line represent average preference +/- the standard deviation. The dashed line at 0.50 represents a preference for the Demonstrated string that is equivalent to chance (i.e., having no preference). Of the 29 *Observers* (both the Successful and Unsuccessful groups combined), 25 males preferred orange string while four preferred pink. In the Successful group, 12 males preferred orange string, while two preferred pink string. In the Unsuccessful group, 13 males preferred orange string and three preferred pink string.

*Figure 16*. **Effect of observing a *Demonstrator* building a nest on the material colour preference in the Successful group versus the Unsuccessful group.** The preference for the Demonstrated string (y-axis) for both the Successful and Unsuccessful groups (x-axis). The solid dots represent the preference for the Demonstrated string in the initial preference test. The open-faced dots represent the preference for the Demonstrated string in the final preference test. The horizontal black line represents the median preference score. The red diamond and vertical line represent average +/- the standard deviation. Each male is represented by a dot in each phase of the experiment. The dashed line at 0.50 represents chance (no preference).

*Figure 17*. **The latency to the first string touched by males from the Successful and Unsuccessful groups.** The cumulative proportion of males (y-axis) to first touch either the Demonstrated or Non-demonstrated string over time (measured in seconds) from the start of the final preference test (x-axis) for both the Successful (black line) and Unsuccessful (grey line) groups. Each tic along the x-axis represents 1000 seconds. Within 6000 seconds of the trial start, all males in both the Successful and Unsuccessful group had touched a piece of string at least once.

*Figure 22*. **The latency to deposit of all the provided string by males from the Successful and Unsuccessful groups.** The cumulative proportion of males (y-axis) to deposit 50 pieces of string over time (measured in seconds) from the start of the final preference test (x-axis) for both the Successful (black line) and Unsuccessful (grey line) groups. Each tic along the x-axis indicates 100000 seconds. Within 100000 seconds of the trial start, all males in the Successful group had deposited all 50 pieces of string, while 87% of all males in the Unsuccessful groups had deposited all 50 pieces of string.

*Figure 23*. **Effect of observing a *Demonstrator's* material choice on the colour of string first touched by males in the Successful and Unsuccessful groups.** The number of males (y-axis) who first touched the Demonstrated string compared to the number of males who first touched the Non-demonstrated string during the final preference test (x-axis) in both the Successful group (white bar) and the Unsuccessful group (black bar).

*Figure 24*. **Effect of observing a *Demonstrator's* material choice on the colour of string first picked up males in the Successful and Unsuccessful groups.** The number of males (y-axis) who first picked up the Demonstrated string compared to the number of males who first picked up the Non-demonstrated string during the final preference test (x-axis) in both the Successful group (white bar) and the Unsuccessful group (black bar).

*Figure 25*. **Effect of observing a *Demonstrator's* material choice on the colour of string first carried by males in the Successful and Unsuccessful groups.** The number of males (y-axis) who first carried the Demonstrated string compared to the number of males who first carried the Non-demonstrated string during the final preference test (x-axis) in both the Successful group (white bar) and the Unsuccessful group (black bar).

*Figure 26*. **Effect of observing a *Demonstrator's* material choice on the colour of string first deposited by males in the Successful and Unsuccessful groups.** The number of males (y-axis) who first deposited the Demonstrated string compared to the number of males who first deposited the Non-demonstrated string during the final preference test (x-axis) in both the Successful group (white bar) and the Unsuccessful group (black bar).

*Figure 27.* **The preference for the Demonstrated string predicted by the number of days taken to complete the initial nest.** The *Observers* preference for the Demonstrated string during the final preference test (y-axis) where 1 indicates all of the first 25 pieces of string deposited were the Demonstrated string and 0 indicates that none of the first 25 pieces of string deposited were the Demonstrated string, correlated with the time it took pairs to complete the initial nest in the initial nest-building experience (x-axis). Preference for the Demonstrated string is shown for males in both the Successful (grey dots) and Unsuccessful (black triangles) groups. The grey line represents the regression curve for the Successful group (McFadden's $R^2$ =0.11), the black line represents the regression curve for the Unsuccessful group (McFadden's $R^2 = 0.03$).

*Figure 28*. **The preference for the Demonstrated string predicted by initial nest size.** The *Observers* preference for the Demonstrated string during the final preference test (y-axis) where 1 indicates all of the first 25 pieces of string deposited were the Demonstrated string and 0 indicates that none of the first 25 pieces of string deposited were of Demonstrated string, correlated with the amount of coconut fibre used by males to build their initial nest in the initial nest-building experience (x-axis). Preference for the Demonstrated string is shown for males in both the Successful (grey dots) and Unsuccessful (black triangles) groups. The grey line represents the regression curve for the Successful group (McFadden's $R^2 = 0.07$), the black line represents the regression curve for the Unsuccessful group (McFadden's $R^2 = 0.01$)

*Figure 29*. **The preference for the Demonstrated string predicted by the time before the initial preference test.** The *Observers* preference for the Demonstrated string during the final preference test (y-axis) where 1 indicates all of the first 25 pieces of string deposited were the Demonstrated string and 0 indicates that none of the first 25 pieces of string deposited were of Demonstrated string, correlated with the time between the removal of a pair's initial nest and the start of the initial preference test (in days) experienced by each pair (x-axis). Preference for the Demonstrated string is shown for males in both the Successful (grey dots) and Unsuccessful (black triangles) groups. The grey line represents the regression curve for the Successful group (McFadden's $R^2 \leq 0.01$), the black line represents the regression curve for the Unsuccessful group (McFadden's $R^2 = 0.04$).

*Figure 30.* **The preference for the Demonstrated string predicted by the number of initial preference test trials.** The *Observers* preference for the Demonstrated string during the final preference test (y-axis) where 1 indicates all of the first 25 pieces of string deposited were the Demonstrated string and 0 indicates that none of the first 25 pieces of string deposited were of Demonstrated string, correlated with the number of initial preference test trials taken by each pair before the males' initial colour preference could be identified (x-axis). Preference for the Demonstrated string is shown for males in both the Successful (grey dots) and Unsuccessful (black triangles) groups. The grey line represents the regression curve for the Successful group (McFadden's $R^2 = 0.01$), the black line represents the regression curve for the Unsuccessful group (McFadden's $R^2 = 0.09$).

Figure 31. **The preference for the Demonstrated string predicted by the amount of interaction with the novel material in the initial preference test.** The *Observers* preference for the Demonstrated string during the final preference test (y-axis) where 1 indicates all of the first 25 pieces of string deposited were the Demonstrated string and 0 indicates that none of the first 25 pieces of string deposited were of Demonstrated string, correlated with the amount of time (sec) that each male spent interacting with the tied down bundles of string during the initial preference test (x-axis). Preference for the Demonstrated string is shown for males in both the Successful (grey dots) and Unsuccessful (black triangles) groups. The grey line represents the regression curve for the Successful group (McFadden's $R^2 = 0.13$), the black line represents the regression curve for the Unsuccessful group (McFadden's $R^2 = 0.17$).

Figure 32. **The preference for the Demonstrated string predicted by the duration of the pre-observation phase.** The *Observers* preference for the Demonstrated string during the final preference test (y-axis) where 1 indicates all of the first 25 pieces of string deposited were the Demonstrated string and 0 indicates that none of the first 25 pieces of string deposited were of Demonstrated string, correlated with the duration of the pre-observation phase experienced by each pair (x-axis). Preference for the Demonstrated string is shown for males in both the Successful (grey dots) and Unsuccessful (black triangles) groups. The grey line represents the regression curve for the Successful group (McFadden's $R^2 = 0.01$), the black line represents the regression curve for the Unsuccessful group (McFadden's $R^2 = 0.07$).

# Glossary of Terms

| | |
|---|---|
| Nest completion | When a female zebra finch lays an egg in the nest. |
| Incubation onset | The male and/or female is/are present in the nest at least once an hour, for every daylight hour for one whole day after a clutch has been laid. |
| *Observer* | Focal experimental pair that watch the *Demonstrators* build a nest using the Demonstrated string in the observation phase.<br>**Observer(s)* italicized to differentiate the group of birds in the experiment referred to as *Observers* from the general social learning term of Observer(s). |
| *Demonstrator* | Experienced nest builders, trained to build with orange and pink string<br>**Demonstrator(s)* italicized to differentiate the group of birds in the experiment referred to as *Demonstrators* from the general social learning term of Demonstrator(s). |
| Successful pair | An *Observer* pair pseudo-randomly assigned to raise chicks to fledging in a nest and then care for chicks until nutritional independence. |
| Unsuccessful pair | An *Observer* pair pseudo-randomly assigned to have their eggs removed seven days post-incubation onset and any subsequent eggs removed immediately thereafter. Unsuccessful pairs were yoked to Successful pairs with regards to time spent with the nest-building material |
| Non-demonstrated string | The string of the colour preferred by *Observer* males in the initial preference test. |
| Demonstrated string | The string of the colour not preferred by *Observer* males during the initial preference test. |
| Touch | When the male makes contact with the string with any part of his body other than just his tail |
| Pick up | When the male takes a piece of string in his beak and raises the string above the cage floor. |
| Carry | When the male moves with a piece of string in his beak but does not deposit the string at the nest. |
| Deposit | When the male releases string into their nest or the bird is standing on the nest and releases string. |

| | |
|---|---|
| Copying | The outcome of social learning where an Observer's acquired behaviour matches or has components that match the behaviour of the Demonstrator with a level of similarity greater than chance. |
| Time with coconut fibre | A measure of the total number of days an *Observer* pair had access to coconut fibre during the initial nest-building experience. The duration started from the day pairs were first provided coconut fibre and ended when the coconut fibre was removed. |
| Nest size | Amount of coconut fibre (grams) an *Observer* pair used to build their nest during the initial nest-building experience. |
| Time before initial preference test | Time (days) between the removal of an *Observer* pair's nest to the movement of that pair to the experimental testing room in which the pair underwent the initial preference test. |
| Initial preference test duration | The total number of initial preference test trials an *Observer* pair underwent before the male's initial colour preference could be established. |
| Total initial preference test interaction | Time (seconds) that an *Observer* male spent interacting with both the tied down orange and pink bundles of string during the initial preference test. |
| Pre-observation phase duration | Number of hours that the pre-observation phase lasted for an *Observer* pair in which the *Demonstrators* began building a nest using 100 pieces of the Demonstrated string. |
| Observation phase duration | Number of hours that the observation phase lasted for an *Observer* pair in which the *Demonstrators* began building a nest using 50 pieces of the Demonstrated string. |

# Introduction

## What is learning?

Learning is the mechanism through which an individual procures, stores, and then acts, based on information available in their environment (Shettleworth, 2009). As long as an environment has at least some stability (or predictability), then the environmental stimuli will produce repeatable consequences. Learning whether these consequences are harmful or helpful to an animal's fitness can be beneficial, as the animal can avoid the harmful stimuli, while taking advantage of the helpful stimuli (Cheng, 2016; Hoppitt & Laland, 2013; Kendal, Coolen, van Bergen, & Laland, 2005). For instance, one might learn what foods are safe to eat or not, how to avoid a predator, whether an individual is a prospective mate or rival, and if there are places to seek shelter. Learning occurs in two forms, either asocially or socially, and the latter was the focus of the present thesis. Asocial learning refers to an organism gathering information or developing a behaviour through their own efforts, through mechanisms such as Pavlovian conditioning, operant conditioning or trial-and-error (attempting to learn a solution to a problem through implementing various behaviours to see which produces the best payoff; Heyes, 1994; Hoppitt & Laland, 2013; Young, 2009). For instance, in asocial learning, a foraging red squirrel may find food by leaving its burrow to scour the environment for seeds to eat. By comparison, social learning involves an organism learning by observing another individual's behaviour or the consequences of the other individual's actions (Heyes, 1994; Hoppitt & Laland, 2013). Returning to the foraging squirrel example, in social learning, instead of scouring the environment themselves, a squirrel could watch the search efforts of another squirrel and learn where seeds might be found through this observation rather than through searching on their own. I am next going to provide a more in-depth discussion of social learning.

**Social learning.**

In this section, I discuss social learning, terminology relevant to the study of social learning, and briefly address some mechanisms through which social learning may occur. Social learning is taxonomically widespread, being recorded in bird, fish, mammal, and insect species (Galef & Laland, 2005; Heyes, 2012). Social learning allows an individual to acquire information without engaging with the environment directly, instead learning via watching another's behaviour (Heyes, 1994). Figure 1 is a diagram presenting the red squirrel example from above. In this example, one squirrel (A) is engaging in asocial learning, as this squirrel is searching various sites in the environment for seeds and learning where they can find seeds. Meanwhile, the other squirrel (B) is engaged in social learning as this squirrel is observing the foraging efforts of the other squirrel (A) rather than searching for seeds themselves. In Figure 1, the area where squirrel A might forage for seeds is represented by the circle. Within the foraging area, there are sites where a squirrel will find seeds (blue triangles) and sites where the squirrel will not find seeds (black triangles). In order to find seeds, squirrel A will need to travel to the various sites, of which only some are rewarding. Through observation, squirrel B can learn which sites will provide seeds from the outcome of the search efforts of squirrel A without having to engage in any search efforts of their own. Animals who perform a behaviour such as the foraging squirrel are referred to as a Demonstrator. In contrast, animals who observe the Demonstrator behaving, like the squirrel who was observing the foraging squirrel, are referred to as the Observer. The outcome of social learning ranges from the replication of the Demonstrators behaviour by the Observer (i.e., copying), to an Observer paying more attention to an environmental location or stimuli after the demonstration (i.e., local and stimulus enhancement; Heyes, 1994). The red squirrel example from above would be representative of local enhancement because the Observer squirrel is learning to associate locations visited by the Demonstrator with an outcome (finding seeds). Social learning has been proposed to provide an Observer with various benefits, which are advantageous for the Observer's survival, which I will address next.

### Benefits of social learning.

Social learning can provide an Observer with benefits that increase the Observer's fitness in ways that asocial learning can not. Here, I will discuss several benefits that an Observer might acquire through social learning. I will also provide an overview of the mechanism(s) through which these benefits occur and provide examples of animals incurring these benefits as a result of social learning. I will first discuss how social learning allows for a lower expenditure of both time and energy in learning a behaviour, or solution to a problem, than would result from trial-and-error learning. Next, I will discuss how social learning allows an individual to avoid environmental hazards such as predation. Then I will discuss how social learning can allow for the development of a novel behaviour by observing a Demonstrator behaving. Finally, I will discuss how social learning allows for conformity and culture to occur and the resultant benefits.

#### *Reduced energy and time costs.*

Through social learning, an individual avoids having to spend the energy and time that would be required to learn something through trial-and-error (Grüter, Leadbeater, & Ratnieks, 2010; Rendell et al., 2010; Rieucau & Giraldeau, 2011; Van Leeuwen, Cronin, Schütte, Call, & Haun, 2013). Social learning has been shown to decrease the time required to learn how to perform a novel behaviour (May & Reboreda, 2005; Schuetz, Farmer, & Krueger, 2017) and to navigate through an environment (Vila Pouca, Heinrich, Huveneers, & Brown, 2020). An example of the benefits of social learning on reducing time and effort can be seen in Thonhauser et al. (2013), where freshwater stingrays (*Potamotrygon falkneri*) provided the opportunity for social learning took less energy and time to learn a behaviour that stingrays without the opportunity for social learning. Thonhauser et al. (2013) trained one group of stingrays to retrieve a food reward from an apparatus. After training, these experienced stingrays became Demonstrators for a group of Observer stingrays. After observing the Demonstrator stingrays retrieving the food reward from the apparatus, the Observer stingrays were tested to see if the Observer stingrays learned to access the apparatus's food reward through observation. The Observer stingrays took fewer trials to learn how to access the food from the apparatus compared to the Demonstrator stingrays, who had to learn through asocial learning (Thonhauser et al., 2013). From the behaviours of the stingrays in Thonhauser et al. (2013), we see that social learning helped save these animals time and effort in a foraging context. The ability of social learning to save an individual time and effort in learning behaviours can also be seen in behavioural contexts other than foraging, as the following example will demonstrate.

Laboratory work with rats has found that, through social learning, one can save time and effort when engaging in spatial navigation of a maze (Yamada & Sakurai, 2018). Yamada and Sakurai (2018) trained two groups of Long-Evans hooded rats (*Rattus norvegicus*) to navigate a Barnes maze. The Barnes maze is a circular maze with a series of holes running the maze's perimeter, one of which the subject could escape through to a chamber below. The goal of the Barnes maze is for the animal to navigate to the same escape hole across a series of trials across which the animal’s orientation is randomly altered. The first group of rats were trained to solve the maze through asocial means, and acted as Demonstrators for the second group, who were trained to solve the maze through social learning (hereafter referred to as the Observers). After training the Demonstrators to solve the maze, Yamada, and Sakurai (2018) then trained Observer rats to solve the maze. Before the start of each Observer trial, an Observer was placed in the centre of the maze and watched a Demonstrator solve the maze. The Observer and Demonstrator would then be removed from the maze so the maze could be cleaned to eliminate odour cues such that the rat could only rely on spatial orientation to solve the maze. The Observer was then returned to the centre of the maze and oriented in the same direction as the Demonstrator had been during the observation. The Observer was then tested for their ability to complete the maze by finding the appropriate hole in the apparatus as the Demonstrators had been. Both Demonstrator and Observer rats underwent the same number of trials. The researchers compared the latency from trial start to trial completion in each session between the two groups of rats (Yamada & Sakurai, 2018). Yamada and Sakurai (2018) found that Observer rats spent less time completing the maze than the Demonstrator rats in both the first and final trials, and that Observers continued to learn or improve across subsequent trials, unlike the Demonstrators. As the Observer rats managed to get to the correct escape hole faster than the Demonstrators (who learned to do asocially), by the end of the last trial, and as Observers continued to improve across trials, we can say that social learning allowed the Observer rats to spend less time and energy solving the task. However, as the number of trials did not differ between the Demonstrators and Observers, it is unclear whether the Observers learned the behaviour faster. Both the behaviour of the stingrays and the rats indicate that social learning allows an Observer to learn a behaviour faster and can expend less energy to perform that behaviour than would otherwise need to through asocial learning. Further, these data are from studies testing the ability of animals to learn about behaviours in different contexts (foraging and spatial navigation respectively), which suggests that social learning that the finding of social learning saving an Observer time and energy is a robust finding, repeatable across domains. Further by spending less time out in the open in the environment as a result of social learning, an individual also decreases their chances of succumbing to environmental hazards, which is the focus of the next section.

***Safety from predation and environmental hazards.***

While engaging in behaviours such as foraging and spatial navigation, an animal may encounter (environmental) hazards, some of which may be fatal. Social learning can significantly reduce the risk of succumbing to environmental hazards, as an Observer can learn about environmental hazards by observing a Demonstrator's behaviours and experiences. Animals face hazards both in the form of predators, and in interacting with novel stimuli without adequate information about the stimuli’s safety (Griffin, 2004; Rieucau & Giraldeau, 2011; Webster & Laland, 2008). While the risk from encountering a predator is more apparent, the risk of novel stimuli in the environment is most evident when an animal finds novel food while foraging as the food could be lethal to consume (Galef, Dudley, & Whiskin, 2008; Kendal et al., 2005; Laland, 2004). Through social learning, an animal can gain information about whether another animal or stimuli is hazardous and how to avoid the risk these hazards pose without ever having to engage with the environment directly. In terms of research into social learning, there is, as of now, little research investigating social learning about predators (Griffin, 2004). Research investigating social learning about predators has been primarily done with fish, with sparse data also having been collected from research with birds and mammals (Conover & Perito, 1981; Keen, Cole, Sheehan, & Sheldon, 2020; Lindeyer & Reader, 2010; Manassa & McCormick, 2012; Thornton & Clutton-Brock, 2011). These data suggest that social learning can assist in both predator recognition and predator avoidance (Lindeyer & Reader, 2010; Manassa & McCormick, 2012). For instance, zebrafish (*Danio rerio*) can learn escape routes from predators faster when exposed to an experienced individual (Lindeyer & Reader, 2010). Lindeyer and Reader (2010) tested whether zebrafish (Observers) could learn to escape a simulated predation event faster when paired with trained individuals (experienced Demonstrators), compared to zebrafish paired with untrained individuals (naïve Demonstrators). They also tested whether the Observers would maintain any socially learned behaviours in the absence of Demonstrators. To do this, Lindeyer and Reader (2010) made use of an apparatus depicted in Figure 2. The apparatus was a large tank divided into two sections by an opaque barrier. At opposite ends of the opaque barrier were two differently coloured holes through which the fish could travel from one side of the apparatus to the other. All fish would start on the left side ('predation side') of the apparatus, with the goal of the experiment being for fish to escape a simulated predation event by swimming through the holes to the right side ('safe side') of the apparatus.

Demonstrators in the experienced Demonstrator group were first placed into the predation side of the apparatus and left to acclimate. After acclimation, the experienced Demonstrators were exposed to a simulated predation event, where a net would be moved towards the opaque barrier from the far side of the predation side of the tank where all Demonstrators were currently residing, simulating a predator 'chasing' the fish. The net would be moved back from the opaque barrier to the side of the tank. The movement of the net to and from the opaque barrier would be repeated four times. The goal of the training was for Demonstrators to escape the predation event by travelling through a hole in the opaque barrier from the predation side of the tank to the safe side. Of the experienced Demonstrators, half were trained to go through one coloured hole, while the rest were trained to go through the opposite-coloured hole. The naïve Demonstrators underwent the same acclimation period, but the holes from the predation side to the safe side were blocked, and there was no predation simulation.

After the Demonstrators were provided with the experiences described above, the Observers then underwent the same predation simulation that the experienced Demonstrators had. During this experience, Observers were paired with either naïve Demonstrators or experienced Demonstrators. After experiencing the predation simulation event with either the naïve Demonstrators or the experienced Demonstrators, the Demonstrators were then removed. The Observers then underwent a test trial where they underwent the same predation simulation event as before, only now without the Demonstrators. Lindeyer and Reader (2010) measured both the latency from trial start to the Observers escaping to the safe side of the apparatus as well as which route the Observers chose (which coloured hole they escaped through). If Observers who had been paired with the experienced Demonstrators escaped to the safe side faster than Observers paired with the naïve Demonstrators, that would suggest that socially learning from individuals with relevant experience is increasing the Observers likelihood of predator avoidance. Further, if Observers paired with trained Demonstrators copied the specific route used by the Demonstrators, that would provide more robust support for the claim that copying is occurring as both routes lead to safety, yet the Observers are maintaining the behaviours performed by the Demonstrators. We see just these outcomes in the results, as Observers paired with the trained Demonstrators do escape faster than Observers paired with the naïve Demonstrators and continue using the same route learned from the Demonstrators even when the Demonstrators are removed.

Social learning also allows an individual to learn whether an environmental stimulus is hazardous to their health or not while avoiding any negative consequences, particularly when that stimulus is a novel food. If an individual comes across a novel food but is unaware if consuming the food would be lethal, learning asocially through consuming the food could be fatal. However, if an individual observes a conspecific eating the novel food, the Observer gains insight into the food's risk. Investigations of socially learned food aversions have been done in various species, including hooded rats and house sparrows (*passer domestics*; Fryday & Greig-Smith, 2016; Strupp & Levitsky, 1984). Behavioural evidence from these studies suggests that observing another individual becoming ill after eating a food source can lead to a food aversion in the Observer even when no sick-inducing agent is present (Fryday & Greig-Smith, 2016; Strupp & Levitsky, 1984).

Alternatively, if an Observer sees another individual eat a novel food without becoming ill, the Observer will prefer that same food when tested for a preference. Such behaviour is found in various mammals, including Norway rats (*Rattus norvegicus*), spiny mice (*Acomys cahirinus*), Belding's ground squirrels (*Spermophilus beldingi*), hooded rats, and Mongolian gerbils (*Meriones unguiculatus*; Galef Jr. & Whiskin Elaine, 2003; Galef Jr. & Wigmore, 1983; McFadyen-Ketchum & Porter, 1989; Peacock & Jenkins, 1988; Strupp & Levitsky, 1984; Valsecchi, Choleris, Moles, Guo, & Mainardi, 1996). These preferences have been found to develop based on olfactory cues alone and may even be maintained for long periods of time (Galef Jr. & Whiskin Elaine, 2003; Galef Jr. & Wigmore, 1983). Galef and Whiskin (2003) had two groups of Norway rats, one which acted as Demonstrators the other acted as Observers. The Demonstrators were provided with a diet that contained either cinnamon or cocoa for two days. After being on these diets, Demonstrators were presented to different Observers, providing olfactory cues related to the different foods they had consumed. After exposure to the Demonstrators, the Observers were then tested for their preference between two novel foods. One of the novel foods matched the olfactory cues provided by the Demonstrator, while the other food did not. Observers were tested for their preference between these two foods either immediately after being provided with the olfactory cues, one week after being provided with the olfactory cues, or one month after being provided with the olfactory cues. The researchers then measured the amount of each food consumed by the Observers. If the Observers were attending to these olfactory cues, we would expect the Observers to eat a greater proportion of the amount of food whose odour matched the odour cues provided by the Demonstrators. If, however, the Observers ate an equal proportion of both foods, then there be no indication of social information use in the Observers behaviours. The Observer rats were found to prefer the food indicated by the olfactory cues across all of the time delays (immediately after being provided the olfactory cues, a week after being provided the olfactory cues and a month after being provided the olfactory cues). The rats choosing the novel food based on the cues provided by the conspecific indicates that becoming aware that a food is not hazardous through the experience of another is a reliable cue about the safety of a food source, which then prompts the Observers copying of the food indicated by the odour cues provided by the conspecific. In these food preference studies, an Observer gains insight into a food's safety or risk without incurring any harm to themselves.

### ***Novel behaviour.***

Another benefit of social learning is that an Observer can learn a novel behaviour through watching a Demonstrator. A novel behaviour is often learned from a Demonstrator when the Observer is naïve, meaning the Observer lacks experience in a given context and does not know how to behave appropriately (Kappeler, 1987; Kis, Huber, & Wilkinson, 2015). However, an experienced Observer may also copy the behaviour of a Demonstrator if the payoff of the Demonstrator’s behaviour appears to be better in some way. For example, chimpanzees (*Pan troglodytes*) will copy the foraging techniques of a conspecific when the conspecific’s behaviour is more efficient than the foraging behaviour the chimpanzee is currently implementing

(Yamamoto, Humle, & Tanaka, 2013). Yamamoto and colleagues (2013) discovered the finding mentioned above by having chimpanzees engage in a tool-use task requiring the chimpanzees to access juice from a closed-off apparatus using a straw tool. The focal subjects initially displayed a 'dipping' technique where they dipped the tool into the apparatus and licked off the juice. The focal chimpanzees then observed Demonstrator chimpanzees using a 'straw sucking technique'. The straw sucking technique involved the chimpanzees putting the tool into the apparatus and then sucking the juice out, which was more efficient as a chimpanzee could get more juice while exerting less effort. After the demonstration, the Observers adopted the straw sucking technique, abandoned the less efficient dipping technique. The opportunity to learn novel behaviours, as in the example provided, is enhanced when one lives in a group. Living with a larger number of individuals increases the number of social interactions an individual may encounter, thereby increasing the number of potential Demonstrators. Living in a group not only increases the number of potential Demonstrators for a given behaviour, but also provides Demonstrators of a larger repertoire of behaviours, as the other individuals in a group may have differing experiences resulting in the development of different behaviours. As an individual demonstrates the behaviours they have learned that are novel to their group, we see the basis of conformity and culture as the demonstrated behaviour diffuses through the group.

### ***Conformity and culture.***

The final benefits of social learning I will discuss are benefits gained from conforming to the traditions and culture of a group. Culture is defined as the adoption of the same behavioural variation by a group of individuals living together in the same environment (Hoppitt & Laland, 2013). Culture had long been considered a trait exclusive to humans (Laland & Hoppitt, 2003; Shettleworth, 2009). However, both observational and experimental data suggest cetaceans, insects, non-human primates, and birds (Allen, 2019; Aplin, 2019; Whiten et al., 1999) show evidence of culture. For instance, great tits (*Parus major*) in the UK developed the behaviour of pecking open milk jug lids to get access to the cream inside (Aplin, Sheldon, & Morand-Ferron, 2013). There were mixed views on how the milk jug opening behaviour spread through the great tit population in the UK, and whether or not the diffusion of this behaviour constituted cultural transmission. To better understand the diffusion of the milk-jug pecking behaviour, Aplin and colleagues (2013) conducted an experiment with great tits. In their experiment, Aplin and colleagues (2013) had three groups of Demonstrator great tits. Two groups of Demonstrators were trained in behaviours to open an apparatus and retrieve food, and one group of Demonstrators was used as a control. The apparatus was a series of containers that had either foil caps or cardboard lids. One group of Demonstrators was trained to pierce foil caps to access the food, while the other group of Demonstrators was trained to flip cardboard lids. The control Demonstrators were never exposed to the apparatus, meaning they never learned a method to open the apparatus. After Demonstrator training, a group of naïve Observers were exposed to Demonstrators from one of the three Demonstrator groups. The researchers recorded the acquisition of either the piercing or flipping behaviours by Observers. If Observers were exposed to the control Demonstrators and showed evidence of the piercing or flipping behaviours, these data would suggest evidence of asocial learning as Observers learned an appropriate behaviour without a Demonstrator modelling a behaviour, meaning there was no behaviour to socially learn. Whereas if Observers exposed to the control Demonstrator did not learn a behaviour to open the apparatus, but Observers exposed to trained Demonstrators did, these data would suggest social learning is occurring as only when a trained Demonstrator is present do Observers learn how to solve the task. Aplin and colleagues (2013) found that Observers exposed to a trained Demonstrator acquired a solution to the apparatus to a far greater extent than those exposed to a control Demonstrator. Further, the solution acquired by Observers watching a trained Demonstrator matched the behaviour performed by the Demonstrator to a degree greater than chance. These findings suggest that cultural variations in a behaviour can be learned observationally from an experienced Demonstrator (Aplin et al., 2013). Through culturally transmitted behaviours, individuals gain ready access to information regarding widespread, and potentially adaptive behaviours, as other individuals of the same species are implementing the same behaviour in the same circumstance all over the environment.

Cultural behaviours can also help identify whether an individual is kin or from another group. Being able to recognize group members/kin through cultural traditions helps one to avoid inbreeding and can aid in the decision of whether the benefits from helping another individual outweigh the costs (often when the other individual indirectly continues your genetic line; Hamilton, 1964; Waldman, 1988). An example of a cultural tradition that provides insight as to whether an individual is from the same group or not comes in signals such as bird songs and calls (Slater, 1989), which vary across geographical regions. For instance, Nowicki (1983) found evidence of variation in the call in black-capped chickadees (*Poecilia atricapillus*) and argued this might be evidence of cultural variation. Nowicki (1983) conducted tests with chickadees to determine whether flocks of chickadees living in different territories behaved differently in response to a ‘chick-a-dee’ call of a foreign versus a resident individual. To do this, Nowicki (1983) presented playbacks to different flocks of chickadees of either resident or foreign individual’s calls at a feeder he set up in their territory. Nowicki then measured the number of response calls produced by the flock and the number of individuals who foraged at the feeder before and after playbacks. Nowicki (1983) found that in response to foreign calls, the flocks demonstrated an increased call response compared to baseline or a resident call playback. Further, in response to the resident calls, there was no change in the rate of foraging from the feeder. In contrast, foraging during the playback of the foreign calls decreased significantly. Through modifying their behaviour in response to an unfamiliar individual, the chickadees avoid risking conflict with an unfamiliar individual or conspicuous predators (Nowicki, 1983).

### Costs of social learning.

Thus far, I have presented evidence to support the idea that social learning can be beneficial to an individual in several ways. There is, however, mixed evidence of animal learning socially rather than learning asocially when the opportunity is present to do both, with animals sometimes engaging in the former and other times the latter (Giraldeau, Valone, & Templeton, 2002; Rendell et al., 2010; Rieucau & Giraldeau, 2011). The inconsistent nature of animals choosing to learn socially rather than asocially seems to vary across species and contexts. One possible reason which may influence an animal's decision to opt against social learning is that social learning is not without costs. While the costs of social learning may be fewer in number relative to the benefits of social learning discussed, the magnitude of these costs can be more severe. The costs of social learning I will discuss are the consequences of copying 'bad' information and the consequences of having too many social learners in a group.

#### *Bad information.*

As previously discussed, social learning is advantageous as an Observer takes advantage of a Demonstrator's efforts to acquire information. However, an Observer can only acquire the previously discussed benefits from social learning if the information acquired from a Demonstrator is actually 'good', which in reality may not be the case due to various factors (Giraldeau et al., 2002; Rieucau & Giraldeau, 2011). The information an Observer may obtain from a Demonstrator may be ‘bad’ due to environmental variability, resulting in the Observer acquiring social information that is no longer up to date with the current environment. For instance, if a deer (the Observer) is searching for food patches to eat at in the environment, it might appear beneficial to look for a conspecific (the Demonstrator) to follow rather than search for food patches. However, it might be that the Demonstrator is travelling to a food patch that has either been entirely or nearly depleted since the Demonstrator was last there. In these cases, through social learning, the Observer will have either expended energy fruitlessly copying the Demonstrator in the case of the former or risk competition over scarce resources in the latter case, which could result in an injury. However, both of these things could perhaps be avoided if the Observer had searched on their own. The consequences of ‘bad’ information may range from extra expended energy to more significant risks such as death (Franz & Matthews, 2010; Kendal et al., 2005; Lachlan, Crooks, & Laland, 1998).

The consequences of observing bad information can be seen in work done with guppies (*Poecilia reticulata*), which found evidence of socially learning a behaviour that resulted in excess energy expenditure and the development of a maladaptive tradition (Laland & Williams, 1998). In the example mentioned above, two groups of guppies were trained to take different routes through a maze to a food reward. One group was trained on an energy-expensive route (long route), the other an energy-saving route being one-third the length of the energy-expensive route (short route), however at all times, fish had access to both routes. After these groups were trained, members of each group were gradually replaced with naïve conspecifics who again had access to both routes through the maze. However, despite having access to both options, fish in both conditions continued to maintain the behaviour learned from the initially trained fish, even after none of the initially trained fish remained. Through maintaining an energy-expensive route, the long-route guppies incurred a cost that could have been avoided through asocial learning. Furthermore, the long-route guppies' behaviour demonstrates that while social learning may be ‘easier’ than asocial learning, social learning does not always lead to an optimal behaviour.

### ***Frequency-dependent costs of social learning.***

The other cost of social learning I will discuss involves the decreasing payoff that social learning provides an individual as the number of social learners in a group increase. To better understand how the decrease in payoff occurs, social learning needs to be viewed as ‘informational parasitism’ (Giraldeau et al., 2002). In other words, an Observer acts much like a parasite exploiting a host’s body, except in social learning, the Observer is taking advantage of a Demonstrators behaviour and produced information (Giraldeau et al., 2002; Laland, 2004; Rieucau & Giraldeau, 2011). To exemplify the informational parasitism aspect of social learning, consider again the example of the foraging squirrels introduced at the beginning of the introduction.  One squirrel was actively searching for food (the asocial learner - the Demonstrator, also the producer in this scenario). The other was observing the search efforts of others to find food (the social learner – the Observer, also the scrounger in this scenario). The Observer squirrel acts similar to a parasite attempting to increase its chances of survival by scrounging the seeds found by others. By taking advantage of the producers’/Demonstrators’ efforts, the scrounger reaps the benefit (the food) without incurring any cost (energy spent searching). The benefits of scrounging are best then when there are few scroungers/Observers relative to the number of producers/Demonstrators. If the scales are tipped too far in the other direction (there are too many individuals scrounging/socially learning relative to the number of producers/asocial learners), the rewards a scrounger/social learning get are diminished. Or more precisely, when there are too many individuals trying to learn socially and thereby scrounge from the spoils a producer gets through asocial learning, the scroungers/Observers incur a cost compared to the reward that could have been gained producing for themselves. Thus, theory predicts that for social learning to be favoured or exist in a population, the population must distribute themselves such that, for a given behaviour, there are a small number of Observers learning socially relative to the numbers of Demonstrators who learn asocially (Rieucau & Giraldeau, 2011). As of now, there is scarce data to support the prediction that a group of individuals will distribute themselves to consist of fewer social learners than asocial learners, unlike the cost of copying 'bad' information, which is one of many reasons social learning is becoming a big focus for cognitive research (Rieucau & Giraldeau, 2011).

### Experimental methods testing social learning.

In this section, I discuss how one might go about testing social learning experimentally. As previously outlined, social learning often involves an Observer learning from the behaviour of a Demonstrator. Experimental tests of social learning take advantage of the Observer-Demonstrator relation by asking various kinds of questions regarding both (1) what factors drive an Observer to copy and (2) the diffusion of behaviours through a population. Depending on the researcher's question, the researcher may train a Demonstrator to engage in a specific behaviour and have the Observer watch the Demonstrator perform that behaviour. Or researchers may record how behaviours develop and are learned without Demonstrator training. In many social learning examples, the Demonstrators behaviour is not intended to convey information to the Observer. Rather, the Demonstrator performs a behaviour that happens to occur in the Observer's presence. While the Observer, like an informational parasite, is taking advantage of the Demonstrator in order to acquire information. After watching the Demonstrator perform a behaviour, the Observer is then tested to see whether having had that opportunity to observe affects the Observers behaviour somehow. If the Observer engages in the same behaviour that the Demonstrator did, we call this copying (Heyes, 1994). There are various experimental designs based on this Observer-Demonstrator paradigm in which social learning might be tested, but I am going to focus on the 'traditional design' as that is what I made use of in the current study[1].

The traditional design involves the use of one Demonstrator performing a behaviour for one Observer and then a test of whether the demonstration may have influenced the Observers behaviour (Hoppitt & Laland, 2013). The traditional method of testing social learning has been heavily favoured because it allows for both a controlled test of social learning while also allowing for the opportunity to test the mechanism through which social learning may occur (Hoppitt & Laland, 2013). In addition, the traditional design allows for the opportunity to ask questions regarding differences between groups of Observers, such as differences between Demonstrator's (i.e., watching a male or female Demonstrator). Alternatively, the researcher might ask questions regarding what situational factors might affect social learning, depending on the researcher's hypothesis. For instance, there might be situations when an animal is more likely to copy a Demonstrators behaviour (i.e., there is a lot of risk involved in acquiring asocial information), and others where an animal would not copy (i.e., if the Observer had previously obtained reliable asocial information). In doing so, the researchers may evaluate not only the social learning mechanism but also whether contextual factors drive social learning.

### Social learning strategies.

In this section, I will introduce social learning strategies, including what social learning strategies are, why they arise, and the two broad categories of social learning strategies

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[1] See the Table in Appendix 1 for information on the other experimental deigns for testing social learning.

introduced in Laland (2004), from which I formed the theoretical bases of my thesis. As previously discussed, social learning may provide an animal with benefits that can assist in their survival, but there are also potential costs. As such, research over the past 30-40 years has been conducted attempting to examine when an animal is most likely to engage in social learning. The theory resulting from the work investigating what factors lead to social learning is what we refer to as social learning strategies. Social learning strategies predict what factors will most likely drive an animal to engage in social learning, with the measurable outcome being copying (Hoppitt & Laland, 2013; Kendal et al., 2005; Laland, 2004; Rendell et al., 2010). Social learning strategies are categorized into two different groups: strategies predicting social learning occurring due to Demonstrator characteristics (Who strategies), and social learning based on the context in which the behaviour occurs (When strategies; Laland, 2004). In the present thesis, I tested two different When strategies. However, in order to so, I also had to ensure that there were no differences in Demonstrator characteristics (or Who strategies) which might act as confounds affecting social learning.

### ***Who strategies.***

In this section, I will provide a more in-depth discussion of Who strategies, reviewing what these strategies entail. While I did not test Who strategies in my thesis, I controlled for Who strategies known to affect social learning in the domain of interest to this project, which I will also discuss here. Who social learning strategies predict the occurrence of social learning based on the characteristics of the Demonstrator (Hoppitt & Laland, 2013; Laland, 2004). Who strategies focus on either the relation between the Demonstrator and Observer, the outcome of the Demonstrators behaviour's behaviour, or the prevalence of the Demonstrators behaviour. Of the various who strategies proposed by Laland (2004), I am going to discuss two Who strategies (the "*copy-friends*" and "*copy-kin*" strategies), combining them into a broader category, the "*copy-familiar-individuals*" strategy. I combined the two strategies as both posit social learning is more likely to occur when an Observer is friends or kin with the Demonstrator, both of which imply a degree of familiarity or strong social relation (Laland, 2004).

We find examples of socially learning from familiar individuals across an array of species (Agee, Jones, & Monfils, 2019; Figueroa, Solà-Oriol, Manteca, & Pérez, 2013; Kavaliers, Colwell, & Choleris, 2005; Swaney, Kendal, Capon, Brown, & Laland, 2001). The high prevalence of Observers readily copying familiar individuals is because familiar individuals have more opportunities for demonstration (Laland 2004). Specifically, kin often share the same environment during development, both through sibling and parental lines. While "friends" are usually members of the same group living in the same environment. The reason these familiar individuals have more opportunities to both observe and demonstrate for each other is that being in the same group allows for more contact with each other relative to individuals from a different group. Benskin and colleagues (2002) tested the *copy-familiar individuals* in zebra finches (*Taeniopygia guttata)*. In their study, Benskin and colleagues (2002) conducted three experiments where two zebra finch Demonstrators differing in some characteristic were simultaneously presented to an Observer zebra finch, feeding from either a black or white feeder (Benskin, Mann, Lachlan, & Slater, 2002). Each Demonstrator had access to both coloured feeders but could only feed from a feeder of one colour. After watching the two Demonstrators feeding, the Observer was then tested for their preference between a black and a white feeder to see if the Observer developed a feeder colour preference based on observing the Demonstrators' choice. Preference was indicated by the proportion of seeds eaten from each feeder over 30 minutes, with the feeder that the Observer ate a greater proportion of seeds from indicating their preference. I am only going to focus on the results from the third experiment, in which male Observer zebra finches watched either a familiar or unfamiliar Demonstrator eating from the feeders before being tested for their preference. The findings from this study saw Observer zebra finches preferentially eating from the feeder matching the colour used by the familiar Demonstrator. This finding provides evidence of the *copy-familiar-individuals* strategy as despite there being no apparent benefit or cost to choosing either feeder, Observers opted to choose from the same feeders as the familiar Demonstrator.

### ***When strategies.***

When social learning strategies focus on the contextual factors that affect the occurrence of social learning, unlike Who strategies that focus on features of the Demonstrator (Laland, 2004). As my thesis involved testing two specifics When strategies, I am going to focus my discussion exclusively on these two strategies. The two strategies I will focus on are the '*copy-when-uncertain*' strategy and the '*copy-when-dissatisfied*' strategy. The former, the *copy-when-uncertain*, posits that an Observer will more readily copy the behaviour or information of a Demonstrator when the Observer either lacks relevant information or the Observer's information is not reliable or up-to-date (Laland, 2004).

An example of the *copy-when-uncertain* strategy would be if a naïve rat were put into a maze from which the rat could obtain a food reward for completing the maze with a trained conspecific. If the naïve rat copied the route used by the trained conspecific to escape the maze rather than attempt to solve the maze on their own, the naïve rat would be said to be employing the *copy-when-uncertain* strategy. Here, the naïve rat is acting as an Observer who has not experienced this maze and is thus uncertain about how to complete the maze. Whereas the trained conspecific would have more experience with the maze due to the training and thus would be certain about solving the maze. The key here is that the Observer is attempting to decrease their uncertainty about navigating the maze by copying the Demonstrator, rather than attempting to figure out how to navigate the maze through trial-and-error.

Naivety is just one example of uncertainty. Another example of uncertainty would be if an Observer's information has become less reliable due to changes in the environment. Smolla and colleagues (2016), for example, found that foraging bumblebees (*Bumbus terrestris*) implement the *copy-when-uncertain* strategy when foraging after the certainty of a food reward becomes more variable (Smolla, Alem, Chittka, & Shultz, 2016). In their experiment, Smolla and colleagues (2016) trained bees to forage for sucrose water from artificial flowers in a laboratory setting. In the first phase of the experiment, half of the bees were trained to use social cues, while the other half were trained to use non-social cues. For the bees trained to use social cues, the social cues were wax bee models placed on one-third of the artificial flowers from which the bees could forage. Of the flowers where the wax bee models were present, only half of the flowers (one-sixth of the total number of flowers) contained sucrose water. For the bees trained using the non-social cues, the non-social cues were coloured pieces of foam placed on one-third of the artificial flowers from which the bees could forage. Only half of the flowers where the pieces of foam were placed contained sucrose (one-sixth of the total number of flowers). After successfully learning to forage using social cues or non-social cues, the bees were then trained to forage using the same cues with an additional manipulation, this time to the variability of the reward. Half of the bees trained to use social cues were put into a low-variance reward condition (equal sucrose level across all flowers). The other half were put into a high-variance reward (one-sixth of the flowers contained all of the sucrose). The same was done for the bees trained to use non-social cues, half of these bees were put into a low-variance reward condition (equal sucrose level across all flowers), the other half were put into a high-variance reward (one-sixth of the flowers contained all of the sucrose). Finally, in the test phase, all bees were tested using the same coloured-flower setup. One-third of the flowers provided social cues, and another third providing non-social cues; however, no flower actually provided a reward. The researchers recorded the bees first choice of flower to forage at during the test phase. The results indicated that bees trained in high-variance reward condition were more likely to rely on social cues compared to those trained in the low-variance reward condition. The increased reliance on social cues is indicative of the *copy-when-uncertain strategy* as the high-variance of the reward decreased the quality of information the bees had access to, making the bees more uncertain.

The second When strategy I am going to discuss is the *copy-when-dissatisfied*. The *copy-when-dissatisfied* strategy, unlike the *copy-when uncertain* strategy, predicts that an Observer will copy a Demonstrator's behaviour if the Observer perceives the outcome of their own behaviour or experience to be sub-optimal (Laland, 2004). Further, the *copy-when dissatisfied* strategy is unique in that copying is predicted to occur based solely on the Observer’s evaluation of the outcome of their own behaviour and does not require the Observer to know anything about the outcome of a Demonstrator’s behaviour, unlike other When strategies (Laland, 2004). We see an example of the *copy-when-dissatisfied* strategy in Galef et al. (2008), which investigated social learning about food preferences in Norway rats. Galef and colleagues (2008) conducted three experiments investigating how readily rats copied the simulated food preference of conspecifics when made dissatisfied or uncertain regarding their own diet or environment. Each experiment had Observer rats assigned to either a treatment group (a group who underwent a manipulation) or a control group. In all the experiments, after undergoing their assigned treatment, the Observers were then made to interact with another group of conspecifics. These conspecifics acted as Demonstrators who provided social information in the form of olfactory cues about a food source the Demonstrator had eaten but was novel to the Observers. Demonstrators were only provided with one diet food prior to being exposed to the Observers, which was equally distributed between the two novel food sources. After the Demonstrators were provided with the food, Observers were then allowed to interact with the Demonstrators. After interaction with the Demonstrators and acquiring the social information of the olfactory cue, Observers were then tested for their choice of two novel food sources: one matching the olfactory cue provided by the Demonstrator (cued food) and one the Observers had received no information about (non-cued food). The novel foods used differed across the three experiments, such that each set of novel foods were novel in each experiment.

The first experiment was designed to test how Observer dissatisfaction with the current diet affected copying. The treatment group was placed on an energetically dilute diet, considered unpalatable as a non-nutritive substance was added to it (and thus was deemed to be dissatisfying). In comparison, the control group was fed a palatable diet. After being on these diets for one week, the Observers underwent the procedure described above, being exposed to a Demonstrator providing olfactory cues about one of two novel food sources and then being tested for their preferences between the cued food and the non-cued food. The researchers measured the amount of both the cued food and the non-cued food eaten by Observers. Observers in the treatment group ate a greater proportion of the cued food than the non-cued food compared to the Observers in the control group.

The second experiment tested whether Observer dissatisfaction with the environment rather than their diet would influence copying. Here, the treatment group was scheduled to have more hours of light than the control. The treatment group was also deprived of bedding materials and experienced an increased room temperature (constituting a dissatisfying environment). Whereas the control group was maintained on a regular number of light hours, continued to have access to bedding materials, and their room temperature was maintained. As in experiment one, the Observers were either exposed to the treatment or control conditions for one week. Observers then underwent the same procedure as previously described, being exposed to a Demonstrator who provided olfactory cues about the cued food. Then the Observers were tested for their preference for the cued food and non-cued food. Again, Observers in the treatment group ate a greater proportion of the cued food rather than non-cued food compared to Observers in the control group.

Experiment three tested how Observer uncertainty regarding novel food flavours in their diet affected copying. The rats in the treatment group were exposed to a diet with two novel flavours (novel flavour A and novel flavour B). Immediately after eating the food, the rats were injected with a solution that made them sick. The control group was exposed to either novel flavour A or novel flavour B, after which they were injected with a solution that made them sick. Galef and colleagues (2008) reasoned that Observers in the control group were made certain about which flavour caused them to be sick as they were only exposed to one flavour before injection. Whereas Galef and colleagues (2008) reasoned that Observers in the treatment group were made uncertain as there were equal amounts of both flavours A and B in their diet, either of which could have caused them to be sick. The intent being to make the treatment group wary about whether any future flavours might also cause the same illness reaction as the previous diet had done. After these treatments, the Observers underwent the same procedure as before, being exposed to a Demonstrator who provided olfactory regarding the cued food rather than the non-cued food, neither of which had flavour A or flavour B. Observers were then tested for their preference between the cued food and the non-cued. Observers in the treatment ate a greater proportion of the cued food rather than the non-cued food compared to Observers in the control group, similar to the previous two experiments.

As Observers in the treatment group copied the food choice indicated by the olfactory cues provided by the Demonstrator in both experiments one and two, these data provide support for the *copy-when-dissatisfied* strategy. These data support the aforementioned strategy as according to the *copy-when-dissatisfied* strategy, Observers will copy when their satisfaction with the payoff from their behaviour is sub-optimal. While the diet provided and environment in which the treatment group is housed are not behaviours themselves, the rats would have engaged in eating the energy dilute diet in experiment one and would have engaged in behaviours such as sleeping and eating in the dissatisfying environment in experiment two. Compared to the control groups, whose experiences could be said to be satisfying, the treatment group had greater reasons to be dissatisfied in their experiences experiments one and two encouraging social learning, which the results support.

Whereas in experiment three, as the Observers in the treatment group ate a greater proportion of the cued food, this provides support for the *copy-when-uncertain* strategy. The copying by the treatment group in experiment three supports the *copy-when-uncertain* strategy as this strategy postulates that an Observer will socially learn from a Demonstrator when the Observer either lacks information about an environmental stimulus or the nature of that stimuli is unclear. As previously discussed, the intent of Galef and colleagues (2008) was to make the treatment group uncertain about whether novel flavours will cause the rats to be sick after their ingestion. To do so, the rats in the treatment group were provided with two novel flavours in their diet simultaneously during the manipulation component of experiment three, unlike the control group, who were only provided with one flavour and then made to be sick. In experiment three then, the copying by the treatment group could be indicative of the rats circumventing any uncertainty they might have about whether novel flavours will make them sick by mirroring the Demonstrators, who show no signs of being sick after eating one of the two food sources.

So far, I have discussed social learning, the benefits, and costs of socially learning, and the theoretical strategies with which we attempt to predict the occurrence of social learning, with the last two strategies discussed being the focus of this thesis. In the next section, I will introduce the model behaviour in which I investigated these strategies.

### Physical cognition.

Much of what is currently known about social learning comes from research in the context of foraging, with a lesser extent of this research investigating mate choice, patterns of movement and predator avoidance, and to a lesser extent, tool use (Galef & Laland, 2005; Heyes, 1994, 2012; Hoppitt & Laland, 2013). While we have gained a good understanding of social learning from the research in these domains, there are behaviours in other domains in which animals socially learn that have received less focus. One domain in which we know far less about how social learning plays a role is physical cognition. Physical cognition is the ability of an animal to gather and acquire information regarding either space, time or quantity of some aspect of the physical world (Shettleworth, 2009). Given the scope of the definition of physical cognition, cognitive abilities such as spatial cognition, timing, numeracy, tool use and construction behaviours all fit within this field (Shettleworth, 2009). Given the breadth of these abilities, I am only going to discuss those most relevant to the current study: tool use and construction behaviours.

Tool use is the process whereby an animal manipulates an object from their environment (via an appendage or beak) to perform some task (Van Lawick-Goodall, 1971). In comparative cognition, tool use is a behaviour that has seen a heavy research focus, as being able to wield a tool is seen as a very ‘human-like’ behaviour. Thus, animals who possess the ability to use tools have been seen as more intelligent (Hansell & Ruxton, 2008). Examples of tool use include the use of hook tools in New Caledonian crows (*Corvus moneduloides*; Hunt, 1996), and chimpanzees using tools for fishing ants/termites (Whiten, Horner, & De Waal, 2005; Yamamoto et al., 2013). There is evidence that both the ability to use tools and to manufacture tools can be learned both asocially (Jelbert, Hosking, Taylor, & Gray, 2018) and socially (Auersperg et al., 2014). However, given the limited spread of tool use taxonomically, my work attempts to better understand the role of social learning in a physical cognition ability that is far more common than tool use and involves very similar mechanics.

Like tool use, animal construction behaviours involve an animal manipulating an object in their environment for some purpose. Not much distinguishes animal construction behaviours from tool use, asides from the fact that the tool needs to be carried or held during the behaviour in tool use. In contrast, animal constructions do not need to be held during animal construction behaviours to be classified as such (Hansell & Ruxton, 2008). Despite the mechanical similarities between tool use and animal construction behaviours, there are far fewer studies investigating animal construction behaviours (Guillette & Healy, 2015; Hansell & Ruxton, 2008). Given the lack of examples of tool use in the wild compared to the number of examples of animal construction behaviours, the focus on tool use to better understand physical cognition seems paradoxical (Guillette & Healy, 2015). Not only that, but animal construction behaviours are found in a broader number of taxa (Guillette & Healy, 2015; Hansell & Ruxton, 2008), meaning the interpretations of any findings from investigating the cognitive abilities involved in animal construction behaviour may provide more generalizable results. My thesis helps bridge the gap in our understanding of social learning in the domain of animal construction behaviours, using nest-building in birds as a model behaviour.

### Nest building.

In this section, I will introduce the behaviour of nest building and discuss some of the experimental efforts to date investigating what birds can learn about nest building, both socially and asocially. A nest is important for several functions, including protection from the elements and a place to care for ones' young (Healy, Walsh, & Hansell, 2008). While nest building has been reported in fish, mammals, reptiles, and insects (Barber, Nairn, & Huntingford, F., 2001; Downing, 1992; Lin, Chen, Kuang, Wang, & Tsien, 2007; Lovich et al., 2014), I am going to focus my discussion of nest building to nest building in birds given how heavily associated birds and nest building are (Healy et al., 2008). Until recently, nest building had long been thought a 'genetically predisposed' behaviour (Breen, Guillette, & Healy, 2016; Sargent, 1965). However, research done in the field and laboratory has produced evidence that various aspects of nest building are learned.

#### *Learning in nest building.*

There are two features of a nest for which we have evidence of learning in birds, the first being the nest-site selection, and the second being the choice of nest-building material. Birds learn both asocially and socially regarding both the site of the nest and the material with which to build the nest. Deciding where to build one's nest is an important decision, influenced by a number of factors include nest shape, the prevalence of predators in the environment or other environmental hazards, and whether the previous nest successfully filled its primary functions

(Dow & Fredgat, 1983; Eggers, Griesser, Nystrand, & Ekman, 2006; Healy et al., 2008; Herlugson, 1981; Injaian, Poon, & Patricelli, 2018). For example, if a bird built their nest and began breeding in it, but later found that every time the bird returned from foraging, their eggs had been predated, the bird may learn from this experience and move their nest to a different location where it is harder for predators to access their nest. Both wild mountain bluebirds (*Siaglia currucoides*; Herlugson, 1981) and goldeneyes (*Bucephala clangula*; Dow & Fredgat, 2016) alter their nest-site selection behaviours based the previous breeding attempts. Both female mountain bluebirds and goldeneyes whose nest fail to produce chicks are more likely to change nesting site. While goldeneyes whose previous nest successfully produced chicks are more likely to have more offspring and start breeding earlier in the subsequent season (Dow & Fredgat, 1983; Herlugson, 1981). These findings indicate that these birds have implemented asocial learning as after undergoing a failed breeding attempt, the females altered their nest-building behaviour.

Evidence of social learning in nest-site selection can be seen in the behaviours of pied flycatchers (*Ficedula hypoleuca*), a migratory bird species (Forsman & Seppänen, 2011; Seppänen & Forsman, 2007; see Figure 3). Being migratory means these birds have a limited window for breeding, thus getting up-to-date information about where best to build a nest is essential. Research with pied flycatchers suggests that these birds will prospect the nest of resident great tits and blue tits (*Cyanistes caeruleus*) to acquire information. Prospecting is when a bird enters the nest of another bird to learn about and evaluate the nest. Pied flycatchers have been shown to choose nest boxes with the same symbol as that of nest boxes used by resident tits (Seppänen & Forsman, 2007). Seppänen and Forsman (2007) painted symbols (either a triangle or circle) on nest boxes currently in use by resident tits (see Figure 3). The researchers painted the alternative symbol on a nest box near the one in use by the resident tit. At nest boxes in a region further away from the one where the resident tit resided, the researchers painted both the symbol matching the one on the resident tits nest and the opposite symbol on two other nest boxes. Seppänen and Forsman (2007) found that rather than nest in the box near the resident tits, the pied flycatchers chose to nest in the nest boxes further away from the resident tit but had the matching symbol. This finding indicates that the prospecting pied flycatchers decided to copy this artificial feature of the resident tits nests rather than nest near the resident tits, as all opposite symbolled nests were empty perhaps indicating nest abandonment to the pied flycatchers (Seppänen & Forsman, 2007). Flycatchers have also been shown to chose a nesting site based on the success of resident tits choosing to nest near individuals whose nests had more eggs (à la *copy-successful-individuals*; Forsman & Seppänen, 2011).

Birds also learn about nest material selection. When we talk about learning regarding nest material selection, we are most often talking about birds learning to prefer one material type over another. Certain bird species seem to present intraspecific variation in material preference preferences, the cause of which is unclear (Camacho-Alpízar, Eckersley, Lambert, Balasubramanian, & Guillette, 2021). However, in addition to having initial preferences, birds also appear to learn to favour one material over another based on various factors learned both socially and asocially (Breen et al., 2016). For instance, zebra finches will learn to prefer nest-building materials based on physical properties such as rigidity (Bailey, Morgan, Bertin, Meddle, & Healy, 2014) or colour (Guillette et al., 2016; Muth & Healy, 2011). Further, just as some bird species learn to associate a nest site with the success of their previous breeding attempt, zebra finches learn to associate the colour of nest-building material used in their previous breeding attempt with the success of their previous breeding attempt, later preferring that colour of the material in the future (Muth & Healy, 2011). Naïve zebra finches can also implement the *copy-familiar-individuals* with respect to choosing nest-building material, with naïve zebra finches copying the material colour preference of a familiar conspecific (Guillette et al., 2016). As evidenced by the examples provided, much of recent experimental research investigating social learning in nest-building material choice has been done with zebra finches, including the current study. In the next section, I will discuss the zebra finch and provide detail on the last two examples of learning about nest-building material choice, as both studies directly pertain to the current study.

### Model system.

For my thesis project, I investigated social learning in the context of nest building using zebra finches (see Figure 4). Zebra finches are a small nomadic passerine bird, part of the Estridline family native to Australia's arid regions (Zann, 1996). Zebra finch males are known to produce a song, which is a series of sequential notes produced to attract a female (Kroodsma & Byers, 1991) which the males socially learn to copy a male tutor's song (Zann, 1996). Zebra finches are a useful model species for studying nest building in the laboratory because zebra finches build nests and reproduce readily in a laboratory setting (Boogert, Lachlan, Spencer, Templeton, & Farine, 2018). In zebra finches, the male is the primary nest builder of the species, consistently bringing material to the nest site and then manipulating the nest material into a dome-shaped nest (Zann, 1996). Zebra finch males only begin nest building when pair-bonded with a female. Thus, researchers will pair male and female zebra finches when investigating nest building but solely focus on the male’s behaviour.

Zebra finches are also a useful species for nest-building research as zebra finches show a readiness to engage in social learning both in the laboratory and in the field. Fieldwork investigating nest-site selection in zebra finches has found that travelling zebra finches copy the nest-site selection of resident zebra finches who have only recently begun breeding rather than those whose chicks had started or were partway through incubation and fledging (Brandl, Griffith, & Schuett, 2019). Brandl and colleagues (2019) set up nest boxes at a field site in the wild where zebra finches could nest. During each trial, three different nest boxes at various locations at the field site were initially occupied by a resident breeder pair who either: had set up their nest but currently had no eggs, had eggs and had recently begun incubation, or had fully-fledged chicks. In the area where each resident breeder pair was nesting, there was an adjacent empty experimental nest box, for which arriving zebra finch pairs could nest. Brandl and colleagues (2019) measured whether any of the nest boxes were being used for nest building and egg-laying by arriving zebra finch pairs. If arriving zebra finches randomly allocated their nest box choice, that would indicate that the breeding stages of resident zebra finches do not affect nest-site selection in the arriving zebra finches. However, if the arriving zebra finches allocated their choice of nest preferentially by a resident breeder pair in a particular stage of breeding, that would provide evidence of social learning, as the arriving individuals would need to prospect the nests' of the resident zebra finches to learn whether different individuals are at a different breeding stage and then copy the nest site choice of those who appear to be at the earliest stages of breeding. The arriving zebra finch overwhelmingly chose to nest by the resident breeding pairs in the earliest stages of breeding (those who had either just laid or not yet laid nests).

Besides the above fieldwork, a growing body of research shows that zebra finches learn about nest-building materials in the laboratory. These studies have found that zebra finches will build nests in the laboratory using a variety of materials which include coloured paper, coconut fibre (see figure 5) and coloured string (see figure 6; Bailey et al., 2014; Breen, 2018; Breen, Bonneaud, Healy, & Guillette, 2019; Muth & Healy, 2011). Two of these studies that are of particular relevance to the current project include Muth and Healy (2011), where zebra finch pairs learned to associate the pair's breeding success with the colour of the material used in the nest. Further, Guillette et al. (2016) found that zebra finch Observers naïve to nest building copied a familiar conspecifics material choice after observing the familiar individual building a nest with nest-building material of the Observers non-preferred colour. In the former study, Muth and Healy (2011), male-female zebra finch pairs were tested for the male’s initial preference between two differently coloured bundles of coconut fibre. Each pair was randomly assigned to either build a nest using the males' non-preferred colour or the males' preferred colour. Each pair was subsequently assigned to either be Successful, where the pair built a nest and then were allowed to raise chicks to nutritional independence. Or to be Unsuccessful, where pairs built a nest and had their eggs removed partway through incubation. Pairs were then tested for their preference between the two differently coloured bundles of coconut fibre again. Pairs that had successfully fledged chicks and had built with their non-preferred material changed their preference to the colour used during their successful breeding attempt. This study shows that whether or not the pair was successful in a previous breeding attempt can influence their material preference in the future, and that preference is not static. The other study mentioned, involved testing whether naïve nest-building zebra finch males copied the material choice of a familiar individual (Guillette et al., 2016). Similar to Muth and Healy (2011), Guillette and colleagues (2016) tested naïve nest-building zebra finch pairs for their preference between two differently coloured bundles of material (string). The naïve pairs then observed either a familiar or unfamiliar pair of conspecific Demonstrators building a nest using the male’s non-preferred colour. Pairs that observed a familiar pair copied the Demonstrator's material choice, whereas pairs that observed an unfamiliar pair did not. This example of copying is one of the first examples of social learning about nest-building material. It also indicated that in nest building, zebra finches appear to implement the *copy-familiar-individuals* strategy.

**Current Study.**

In the current study, I investigated two questions regarding social learning in the nest-building behaviours of birds. First, I asked would birds who have previously built a nest copy the nest material colour preference of conspecifics when deciding which of two novel materials to build their second nest. Second, I asked if social learning were to occur, would the degree of copying differ between birds whose previous nest produced chicks versus those whose nest did not? To answer these questions, I had naïve zebra finch pairs build an initial nest using coconut fibre. Pairs assigned to the Successful group went on to have nests and raised chicks, while pairs assigned to the Unsuccessful group built a nest but did not have chicks. Following their initial nest-building experience, I tested all *Observers* (both the Successful and Unsuccessful group) for their preference between two novel nest-building materials, orange and pink string. After ascertaining their preference, all *Observers* (both Successful and Unsuccessful groups) observed a pair of conspecifics (*Demonstrators*) building a nest using the string of the *Observers* non-preferred colour (the Demonstrated string; see glossary). To control for the *copy-familiar-individuals* Who strategy discussed earlier, all *Demonstrators* were familiar to the *Observers* prior to the start of the current project. I then tested the *Observers* preference for pink and orange string again to see whether having the opportunity to observe the *Demonstrators* would affect the *Observers* material colour preference. If *Observers* (both the Successful and Unsuccessful groups combined) copied the Demonstrated string in the final preference test, that would suggest that zebra finches conform their nest material choice to match others, which is indicative of culture. Whereas if the *Observers* do not copy the Demonstrated string in the final preference test, that would support the *copy-when-uncertain* strategy as these *Observers* have experienced nest building and know how to build a nest, unlike naïve individuals (Guillette et al., 2016). If *Observers* in the Unsuccessful group more readily copy the Demonstrated string compared to the Successful group, that would support the *copy-when-dissatisfied* strategy as the Unsuccessful group would be employing social learning as their previous nest failed to produce chicks which would constitute a dissatisfying experience. However, if copying does not differ between the Successful and Unsuccessful group, that would suggest that zebra finches failing to produce chicks in their initial nest does not constitute a dissatisfying experience that is strong enough to warrant copying.

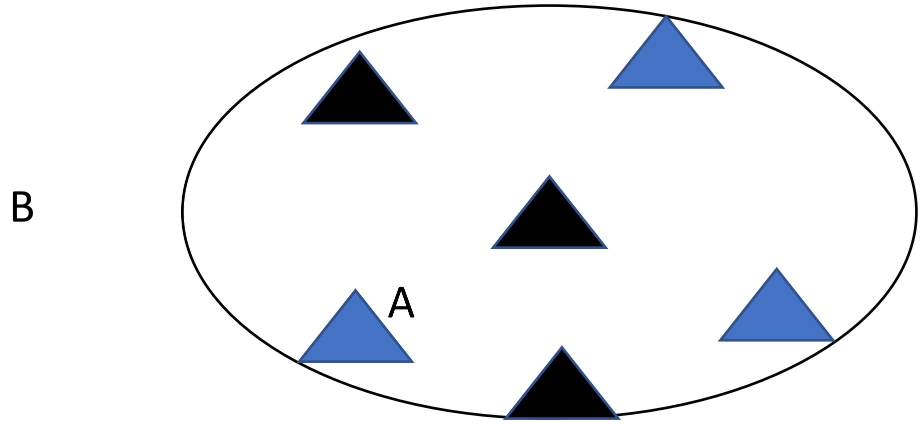

*Figure 1.* **Diagram of hypothetical social learning versus asocial learning in foraging behaviours by red squirrels.** A is a red squirrel foraging for seeds by travelling to various sites within a foraging area (represented by the circle), who will learn where to find seeds through asocial learning. B is a red squirrel observing the search efforts of A, who will learn the location of seeds via social learning. The blue triangles represent locations where seeds can be found, while the black triangles represent locations where seeds cannot be found.

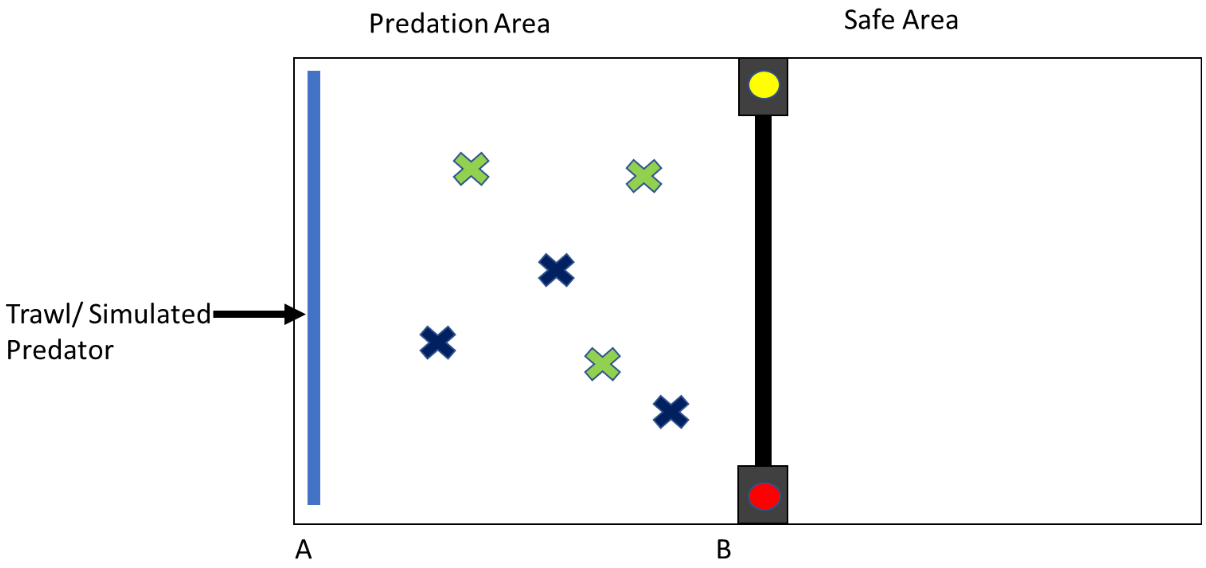

*Figure 2*. **Schematic view of the apparatus used in Lindeyer and Reader (2010)**. The tank used in Lindeyer and Reader (2010) was split in half by an opaque barrier (depicted by the black line in the centre). At opposite ends of the opaque barrier were two holes through which zebrafish could travel from the predation side to the safe side. The predation side is where all fish began their trials. The simulated predator (the net) is represented by the blue bar. The net was moved across the predation side during trials from A to B and then back to A four times to simulate a predator chasing the fish across the area. Fish could escape the predator by travelling through either the yellow or red holes in the opaque barrier. The purple X's represent Demonstrators while the green X's represent the naïve fish.

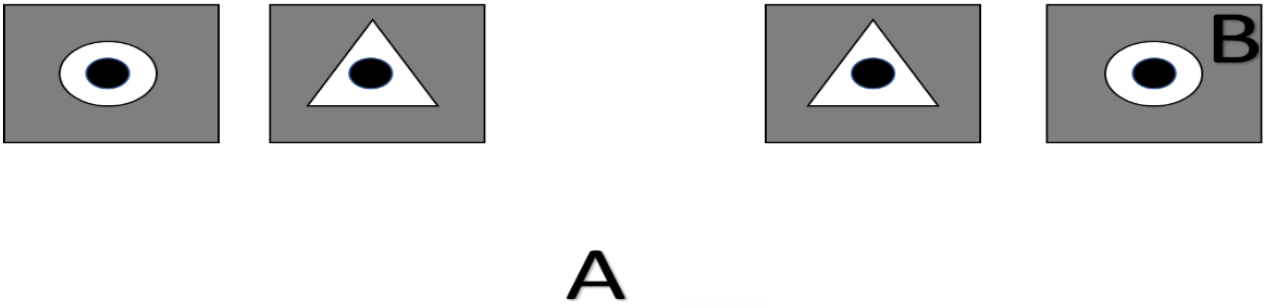

*Figure 3.* **Schematic view of experimental design implemented in Seppänen and Forsman (2007).** The grey boxes represent nest boxes, and the back holes in the centre of the boxes represent the entrances. The white shapes (triangles and circles) represent symbols placed on the nest boxes by the researchers. The B represents a nesting resident tit, while the A represents a migratory pied flycatcher arriving at the field site to breed.

*Figure 4*. **Picture of a pair of zebra finches**. Pictured on a perch are a female (left) and a male zebra finch (right). – Animal Cognition Research Group (ACRG, 2020).

*Figure 5.* **Picture of a zebra finch nest constructed out of coconut fibre.** A photo of a front-facing zebra finch nest built out of coconut fibre sitting in a nest box. – Animal Cognition Research Group (ACRG, 2019).

*Figure 6.* **Photos of nests built by zebra finches using string.** Photos of two different front-facing zebra finch nests built out of orange (top) and pink (bottom) string. Each nest was built by a different pair of zebra finches. – Animal Cognition Research Group (ACRG, 2019).

## Methods

### Subjects & housing.

In this experiment, I used 80 wild-type zebra finches (40 males, 40 females), obtained from a breeder (Eastern Bird Supplies, Quebec, Canada) as juveniles (< 90 days old) that arrived September 2018, and fully matured (90+ days old) in our laboratory colony room prior to the start of the experiment. Maturity in zebra finches can be assessed through the colouration of the beak (shift in colour from black to orange), whether the male is producing a song and presenting stripes along his upper chest and speckling patterns on his feathers, as well as through the production of eggs by females (Zann, 1996). When not in the experiment, birds were housed in single-sex colony cages (165 × 66 × 184 cm) and kept on a 14:10 light-dark cycle via overhead fluorescent full-spectrum lights (Standard, 32W, T8 Daylight), with a room temperature ranging from 19-24°C and humidity between 30-50%. Each colony cage contained perches of various materials and diameter, including wooden dowels, cotton rope, and tree branches. Each cage was provided with *ad libitum* access to demineralized water, food (Hagen Finch Staple VME Seed Mix), cuttlebones (Canadian Lab Diet), grit (Hartz Grit' n' Gravel), and Pacific Pear oyster shells (Canadian Lab Diet). Each colony cage received vitamin mixed water (Hagen Canada) and greens (e.g., parsley, spinach) three times a week and spray millet once a week (Hagen Canada). Birds were moved to a separate room for subsequent experiments before being returned to the colony cages after participation in this experiment.

### Apparatus.

During the experiment, I used six experimental rooms: two for the initial nest-building experience, one for the *Demonstrator* training, and three for the testing phases. All experimental rooms were kept at the same temperature, humidity and light-dark cycle as the colony room and each cage within each room received the same food, water, and supplements as in the colony room on the same schedule. Breeding pairs additionally received soft egg food mix (CeDe Tropical Finch Eggfood) one-two times per day until the fledglings were removed from the cage. For more information on the care provided during the experiment, please see appendix 2.

For the initial nest-building experience, pairs were housed in breeding cages. Each breeding cage (50 × 50 × 100 cm; King Cages International LLC) housed one breeding pair. Each cage had a removable tray bottom, which I lined with brown paper (U-line Kraft paper) and fitted a piece of PVC corner moulding to the front of the tray using zip ties to prevent birds from escaping the cage. Further, each breeding cage had three mini-BNC cameras (OSY CAMS) positioned in the centre of three sides of the cage as follows: two cameras (camera one and two, Figure 7) were positioned at the top of each of the 50 cm side of the cage, facing opposite directions. The third camera (camera 3, Figure 7) was positioned at the top of the front 100 cm side of the cage, facing the back 100 cm side of the cage where the nest cup would be placed. These three cameras were wired via BNC cables to a DVR (Jodan) accessible via the internet, which recorded continuous video parsed into one-hour blocks and stored on DVRs with a four Terabyte hard drive. The videos were then remotely downloaded so that nest-building behaviours could be scored at a later date. This camera set-up also allowed me to monitor the health and progress of the birds remotely. Each breeding cage also contained two food and two water cups, two perches on each of the 50 cm sides, as well as two perches along the back 100 cm side, outside of where the nest cup would be positioned (Figure 7). Opaque plastic barriers separated the breeding cages such that each zebra finch pair had vocal, but not visual contact with other pairs. Similar cages were set up in a separate experimental room, for the purpose of

*Demonstrator* training, that were nearly identical to the breeding cages, other than these *Demonstrator* training cages did not have cameras or the DVR set up.

In the remaining three experimental rooms, two cages (50 × 50 × 100 cm; King Cages International LLC) were set up 10 cm apart and oriented such that their front 100 cm sides faced out from each other (Figure 8). Like the breeding cages, these test cages, had two food cups, two water cups and three mini-BNC cameras connected to a DVR. These test cages also contained six perches like the breeding cages, however, the two perches that were positioned along the back 100 cm side of the breeding cages were positioned such that they mirrored the location from the breeding cages, now being located along the front 100 cm side, while the remaining four perches were oriented in the same positions as in the breeding cages. Further, two of the cameras (camera one and two, Figure 8) were positioned along the 50 cm sides in the same positions described for the breeding cages, while the third camera (camera 3, Figure 8) was set up at the top of the back 100 cm side in the centre. The test cages were separated by a removable opaque barrier comprised of corrugated plastic, which, when in place, prevented the *Observers* (see below) from seeing the *Demonstrators* (see below).

### Procedure.

The *Demonstrators* used in this experiment underwent training prior to observation. The purpose of the *Demonstrator* training was so that the *Demonstrators* would gain experience building nests prior to being used in the test phases as a potential source of social information. On day one of the experiment, six randomly assigned male-female pairs selected at random (randomized via https://www.randomizer.org/) from the colony room were moved to the *Demonstrator* training cages. These pairs (henceforth referred to as *Demonstrators*) were given three days to form a pair bond as indicated by behaviours including perching together and allopreening (Zann, 1996). Using these bonding criteria, if a pair failed to show signs of a pair bond, they were removed from the experiment and returned to the colony room. All pairs successfully bonded according to these criteria. After successfully establishing a bond, pairs were given a nest cup (12.5 × 12 × 12 cm, see Figure 9) made of spruce wooden sides with a plastic mesh bottom. A nest cup was placed in the centre of the rear 100 cm side of the cage hung at the top of the cage (Figure 7). *Demonstrators* were randomly assigned to build their first nest with 400 pieces of 15 cm long pink or orange string (Jute Craft Twine, James Leaver CO.). After completion of a species-typical dome-shaped nest (Zann, 1996) with one colour of string, the nest was removed and then *Demonstrators* were provided with 400 pieces of the other coloured string and allowed to build a second nest. If nests were not domed, or the string sat loosely in/off the nest, that structure was removed, and pairs were given an additional 400 pieces of string of the same colour with which to build a new nest. *Demonstrator* training was considered complete once the pair had contributed two nests, one of each colour. After each nest was complete, it was removed, photographed, and used in another experiment. *Demonstrators* remained in their *Demonstrator* training cage until such time that they were needed for demonstration purposes.

At the same time as the *Demonstrators* were undergoing training, the Successful and Unsuccessful groups (hereafter referred to as *Observers*) underwent an initial nest-building experience. In this phase of the experiment, *Observers* were given the chance to build their first nest, the success of which I experimentally manipulated. On day one, a randomly paired male and female zebra finch (randomized via https://www.randomizer.org/) were placed into a breeding cage and were allowed four days to form a pair bond (see criteria above for pair-bond formation). On day five, each pair was provided with a nest cup placed in the same location in their breeding cage as was described for the *Demonstrators* training cage. In addition, the *Observers* were given 20g of coconut fibre (Aves Canada), cut into equal 15cm lengths and distributed into two bundles of either side of the middle of the cage. Each pair was monitored daily and provided with an additional 20g of coconut fibre as their current pile was depleted until the pair completed their nest (see the glossary of terms for definition of nest completion). Each breeding pair was given egg mix daily throughout the nest-building and chick-rearing period. After a nest was complete, any additional coconut fibre not used in the nest was removed and weighed to the nearest tenth of a gram. If a pair failed to lay an egg in their nest within 14 days of initially being given the coconut fibre, the pair was removed from the experiment and returned to the colony room. Pairs that completed their nest were pseudo-randomly assigned to one of two treatment conditions: Successful or Unsuccessful. For the pseudo-randomization, I randomized pairs such that the first pair to complete their nest was assigned to the Successful treatment group, and the subsequent pair to finish was assigned to the Unsuccessful treatment group and so on. Each Unsuccessful pair was yoked to a Successful pair with regards to the time spent with the coconut fibre with which they used to build their nest, meaning the days between being given the initial nest-building material (coconut fibre) and having their nest removed was the same between each yoked Successful and Unsuccessful pair. Each pair was monitored daily for the start of incubation, defined as the presence of a male or female being present in the nest every hour for an entire day. Pairs in the Successful group were allowed to incubate and rear chicks without intervention. Their nest was removed five days after the last chick fledged (~23 days post-hatch). Successful pairs continued to care for their chicks until the chicks reached nutritional independence (~35 days post-hatch), after which the chicks were separated from their parents but remained in their natal group until they could be sexed visually (at ~40-45 days post-hatch), after which they were moved to the colony room. The parents could then be moved to the *Observer* test cage the day after their chicks were removed. (2) Pairs in the Unsuccessful group had their eggs removed seven days post-incubation onset. The Unsuccessful pairs' nest remained in their cage for the same duration as the Successful pair they were yoked to had access to their nest, thus controlling for the amount of time with which pairs in each condition had to interact with the nest material. Any subsequent eggs laid by the Unsuccessful pairs were removed daily and frozen.

### ***Phase 1: Initial preference test.***

At the end of the *Observers'* initial nest-building experience, each Successful and Unsuccessful pair were moved from their breeding cage to a test cage in a different experimental room. The initial preference test began one-hour post light onset the morning after the *Observer* pair had been moved into the experimental room. This phase allowed me to determine the male's preference for either pink or orange string so that in the following phase so I could have a *Demonstrator* build a nest using the *Observer* male's non-preferred colour. Further, by establishing the male's initial colour preference, I could assess if social learning occurred because I established a baseline preference for this colour which then allowed me to compare whether *Observer* males changed their preference after observing the *Demonstrators*. During this phase, each *Observer* pair was provided with two 25-piece bundles of 15cm long coloured string, one bundle of pink string and one bundle of orange string. The bundles were tied down to the front 100 cm side of the cage 40 cm apart (Figure 10), and their placement was randomized between the two possible locations across *Observer* pairs. By securing the string to the cage, the *Observer* male could interact with the string but not carry the string away or build a nest. The male was allowed to interact with the string for four hours, after which the bundles of string were removed from the cage. To determine a male's initial colour preference, videos were downloaded from the DVR associated with the cameras in the *Observer's* test cage. I then scored the time the male spent interacting with the string – when the male makes contact with the string with any part of his body other than just his tail – to the nearest tenth of a second using BORIS version 7.1.3 (Friard & Gamba, 2016). BORIS is an event tracking software, which allows a researcher to record the frequency and duration of behaviours of interest in video recordings of experimental trials. This testing was repeated daily as needed until the male interacted with one or both bundles of string for a minimum of 30 seconds, the minimum criteria I could use to determine string preference. A male's preference was considered to be for the bundle of string he spent a greater proportion of time interacting with. During the initial preference test, *Observers* were prevented from viewing the adjacent *Demonstrator* test cage via an opaque barrier between the two cages.

#### ***Phase 2: Pre-observation demonstrator building.***

This phase commenced immediately after the termination of the initial preference test. With the opaque barrier still in place, the adjacent *Demonstrator* test cage was set up such that it contained a nest cup hung at the top of the centre of the front 100 cm side of the cage and 100 pieces of the string the *Observer* did not prefer (hereafter referred to as the Demonstrated string) located along the 50 cm side of the cage that mirrored the side with which the *Observers* had been able to interact with it in the previous phase, which was sham tied to the cage. I also provided the *Demonstrators* with 50 pieces of the *Observer* preferred string (hereafter referred to as the Non-demonstrated string) tied to the other 50 cm side of the cage (Figure 11). By providing both strings, I allowed the *Demonstrators* to interact with the Non-demonstrated string, however, as this string was tied down, the *Demonstrators* could only build a nest with the

Demonstrated string. After setting the cage up as described, a randomly selected *Demonstrator* pair was moved into the *Demonstrator* test cage. This phase lasted until all 100 pieces of Demonstrated string had been deposited in the nest. The purpose of the phase was to ensure that *Demonstrators* had engaged in building prior to the observation phase so that *Observers* could see that *Demonstrators* had made use of the Demonstrated string.

***Phase 3: Observation.***

Immediately after the *Demonstrators* has deposited all 100 pieces of provided Demonstrated string, the *Demonstrators* were provided with an additional 50 pieces of the Demonstrated string in the same location as the previous 100 pieces of string had been, while the 50 pieces of Non-demonstrated string remained tied to the cage. The opaque barrier was removed, which allowed the *Observers* to watch the *Demonstrators* building their nest (Figure 12). This phase was completed when the male from the *Demonstrator* pair deposited the additional 50 pieces of Demonstrated string into their nest.

***Phase 4 Final preference test.***

This phase began immediately after the observation phase was complete. The opaque barrier was returned between the test cages so that the *Observers* could no longer see the nest that the *Demonstrators* had built. The *Demonstrators* were then removed from the experimental room, and the *Observers* were provided with two 25 piece bundles of 15 cm length string, one pink, the other orange, mirroring the locations each bundle was located in the *Demonstrator* test cage the pre-observation and observation phases. In addition, the *Observers* were provided with a nest cup positioned at the top of the centre of the front 100 cm side of the cage and were left undisturbed for the remainder of the day (Figure 13). This phase continued until all string was deposited in the nest. *Observers'* progress was monitored twice a day. After the *Observers* completed this phase, pairs were moved to a new colony room not used in any phase of the current experimentation to breed, after which the pairs were returned to the original colony room. To score this phase of the experiment, videos were downloaded from the DVR for all cameras from the *Observer's* test cage.

**Scoring.**

Videos from the final preference test were randomly assigned a placeholder name by one of my lab mates, so that I could blindly score the videos with respect to the *Observers* treatment group. All videos were scored with BORIS. I scored the order with which each male deposited the two differently coloured strings into his nest. I calculated the proportion of the first 25 deposits of string that matched the Demonstrated string colour. A score of zero indicated that all of the string deposited were the Non-demonstrated string, and a score of one indicated that all string deposited were the Demonstrated string. Additionally, I scored the latency from trial start to the first string: (1) touched, (2) picked up, (3) carried, and (4) deposited (see glossary) of both the Demonstrated and Non-demonstrated string to test whether being Unsuccessful in the previous nest-building attempt might affect any other nest-building behaviours other than copying the *Demonstrators* material choice. I scored the latency to deposit the first 25 and the latency to deposit all 50 pieces of string. I assessed whether the colour of the first string touched, picked up, carried, or deposited matched the Demonstrated string or not.

**Statistical Analyses.**

All analyses were conducted in R version 4.0.2 (R Core Team, 2018). A total of 34 *Observer* pairs were run in this experiment. One pair was removed from the experiment during the initial nest-building experience because they did not build a nest within fourteen days. Two Successful pairs were removed from the experiment prior to the initial preference test. One because the female died, the second because their eggs did not hatch. Two pairs were removed after they completed the final preference test. One Unsuccessful pair because a technical error caused the final preference test video to be erased, and one Successful pair because the female deposited the majority of the string into the nest. The final sample size was n = 14 Successful pairs and n = 15 Unsuccessful pairs.

*Initial nest-building experience.* Of the data collected during the initial nest-building experience, I asked four questions, all of which I answered by conducting Two-sample T-tests using the 't.test' function from the 'stats' package in R, as these data were continuous and found to be normal via Shapiro Wilks tests via the 'shapiro.test' function also from the 'stat's package in R. I asked: (1) did the time (measured in days) spent with the initial nest-building material (coconut fibre) differ between the Successful and Unsuccessful groups, (2) whether the time (measured in days) to initial nest completion differed between the Successful and Unsuccessful groups (3) whether nest size (measured in grams of coconut fibre used) differed between the Successful and Unsuccessful groups and (4) whether the time before the initial preference test (in days) differed between the Successful and Unsuccessful groups to make sure none of these experiences acted as confounds. One pair from the Unsuccessful group was removed from the time spent with initial nest-building material analysis, as the Successful pair they were yoked to (who were removed from the study) failed to hatch eggs within 63 days, resulting in this Unsuccessful pair being an outlier, leaving a final sample size for this particular analysis n =14 Successful and n = 14 Unsuccessful.

*Initial preference test.* Of the data collected during the initial preference test, I first asked two questions regarding the *Observers'* (both the Successful and Unsuccessful groups combined) initial colour preference. I asked whether the *Observers*: (1) showed a colour preference and (2) had a pre-existing colour preference for either colour. To determine whether *Observers* had a colour preference, I compared the *Observers* preference for the Demonstrated string to chance (0.5) using a Wilcoxon signed-rank test via the ‘wilcox.test’ function from the ‘stats’ package in R. To determine whether the *Observers* had a pre-existing group colour preference for either colour, I conducted a Wilcoxon signed-rank test comparing the *Observers* preference for orange string to chance (0.5). Preference for the orange string was measured as the proportion of the total time a male spent interacting with the tied down bundle of orange string. A score of one indicated the males only interacted with the orange string. A score of zero indicated no interaction with the orange string, and a score of 0.5 indicates equal interaction time with both the orange and pink string. Non-parametric tests were chosen as both the preference for the Demonstrated string and the preference for orange string are discrete data measured as proportions.

In addition to examining the data from the initial preference tests for all *Observers*, I evaluated the data separately for the Successful and Unsuccessful groups. I asked whether the Successful group: (1) showed a colour preference, and (2) had a pre-existing preference for either colour. I answered both questions in a similar manner as was used for all *Observers*, conducting a Wilcoxon signed-rank test comparing the Successful group’s preference for the Demonstrated string to chance (0.5), and a Wilcoxon signed-rank test comparing the Successful group’s preference for orange string to chance (0.5), respectively. I did the same for the Unsuccessful group.

I asked whether the Successful and Unsuccessful groups’ preference for the Demonstrated string differed from each other in the initial preference test. I addressed this by conducting a Mann-Whitney U test comparing the preference for the Demonstrated string between the Successful and Unsuccessful groups using the ‘wilcox.test’ function from the ‘stats’ package in R. I asked whether the pre-existing preference for either colour differed between the Successful and Unsuccessful groups. I evaluated whether there were any differences in group pre-existing preferences by conducting a Mann-Whitney U test comparing the preference for orange string between the Successful and Unsuccessful groups.

I conducted a third Mann-Whitney U test to address the question of whether the duration of the initial preference test differed between the Successful and Unsuccessful groups, comparing the number of initial preference test trials between the two groups. Non-parametric tests were also chosen for the number of initial preference test trials, as the number of trials was also discrete data. I addressed the question of whether the time (seconds) the male spent interacting with the tied down bundles of string differed between the Successful and Unsuccessful groups by conducting a Two-sample T-test comparing the log-transformed duration of the male interaction with the tied down bundles of string between the two groups. The data was log-transformed as a Shapiro Wilks test found these data to be non-normally distributed for either the Successful or Unsuccessful group. Of the data collected during the initial preference test, I also asked whether the latency to the first interaction with the tied down bundles of string by the male differed between the Successful and Unsuccessful groups. I addressed this by creating a survival model using the ‘coxph’ function from the ‘survival’ package in R and then conducted a log-rank test comparing the difference in survival rate between the two groups using the ‘survdiff’ function, which is also found in the ‘survival’ package.

*Pre-observation phase.* Of the data collected during the pre-observation phase, I asked whether the duration of the pre-observation phase differed between the Successful and

Unsuccessful groups to ensure that the length of this phase was not a confound. To determine whether any differences were present, I conducted a Two-sample T-Test comparing the duration (measured in hours) of the pre-observation phase between the Successful and Unsuccessful groups. I conducted a Two-sample T-test because the duration of the pre-observation phase was a continuous and normal variable as determined via a Shapiro-Wilks test.

*Observation phase.* Of the data collected during the observation phase, I asked whether the duration of the observation phase differed between the Successful and Unsuccessful groups to ensure that the length of this phase was not a confound. To determine whether any differences were present, I conducted a Two-sample T-Test comparing the duration (measured in hours) of the observation phase between the Successful and Unsuccessful groups. I conducted a Two-sample T-test because the duration of the observation phase was a continuous and normal variable as determined via a Shapiro-Wilks test.

*Final preference test.* Of the data collected during the final preference test, I first asked whether *Observers* (both the Successful and Unsuccessful groups combined) preferred the Demonstrated string, which I analyzed by conducting a Wilcoxon signed-rank test comparing the preference for the Demonstrated string to chance (0.5). I also asked the question of whether the *Observers* preference for the Demonstrated string changed between the initial and final preference tests. To address this question, I conducted a Paired-Wilcoxon signed-rank test using the ‘wilcox.test’ function from the ‘stats’ package in R. Non-parametric tests were chosen as the preference for the Demonstrated string are discrete data. As with the data from the initial preference test, I asked questions about the Successful or Unsuccessful group’s preference in the final preference test separately. I asked whether the preference for the Demonstrated string differed from chance (0.5) for either the Successful or Unsuccessful groups, performing separate

Wilcoxon signed-rank test for each group. I asked if the preference for the Demonstrated string changed between the initial and final preference tests separately for either the Successful or Unsuccessful group by performing two Paired-Wilcoxon signed-rank tests.

I asked whether the preference for the Demonstrated string differed between the Successful and Unsuccessful groups in the final preference test. I evaluated whether there was a difference in preference for the Demonstrated string between the Successful and Unsuccessful groups by conducting a Mann-Whitney U test. Non-parametric tests were chosen as the preference for the Demonstrated string is discrete data.

In addition to addressing questions regarding the preference for the Demonstrated string in the final preference test, I addressed questions about whether being Successful or Unsuccessful affected how quickly males began building their second nest. I conducted separate log-rank tests to ask whether the Successful and Unsuccessful groups differed in the latency to first: (1) touch, (2) pick up, (3) carry, (4) deposit, (5) deposit half of, and (6) deposit all of the string provided during the final preference test. All latencies were measured in seconds of daylight hours because some trials lasted overnight, and zebra finches do not engage in nest-building behaviour in the dark. Data from one pair in the Unsuccessful group was not available for the latency to the first touch, pick up, and carry string due to video loss, leaving a final sample of n=14 for both the Successful and Unsuccessful group for the first touch, pick up and carry string. The sample sizes for the latency to the first deposit, the deposit of the first 25 pieces, and the deposit of all 50 pieces of string were n =14 for the Successful group and n = 15 for the Unsuccessful group.

Of the data collected during the final preference test, I asked whether, in addition to copying the choice of string of the *Demonstrator* during the final preference test, do *Observers* copy the nest material selection (touching, picking up, carrying) and building behaviours (depositing string). I asked whether the number of pairs in the Successful and Unsuccessful group who first: (1) touched, (2) picked up, (3) carried and (4) deposited the Demonstrated string during the final preference test differed. To address these questions, I ran four separate Fisher's exact tests, one comparing each of the variables previously identified, using 'fisher.test' function from the 'MASS' package in R. Fisher's exact tests were chosen over a Chi-Squared test, as the sample sizes were small enough to affect the accuracy of a Chi-Squared test.

*Copying in the final preference test as a result of among-individual variations in experience*. In this section, I will discuss the questions and analyses I conducted, testing how variation within the variables measured across the experimental phases might influence copying. I first asked whether variation in the experience of *Observers* during the initial nest-building experience predicted the *Observers* preference for the Demonstrated string in the final preference test. To address this question, I constructed a quasibinomial logistic regression model using the 'stats' package in R to evaluate whether the time (measured in days) the *Observers* spent with the coconut fibre, the amount (measured in grams) of coconut fibre used to build the initial nest and the time (measured in days) before the initial preference test predicted the *Observers* preference for the Demonstrated string in the final preference test. Preference for the Demonstrated string was the same measure used to calculate copying in the final preference test. Namely, preference here was the proportion of the first 25 deposits of string into the nest that matched the Demonstrated string colour.

I next asked whether variations in the *Observers* experience during the initial preference test predicted the *Observers* preference for the Demonstrated string in the final preference test. To answer this question, I constructed a quasibinomial logistic regression model to evaluate whether the duration (measured by the number of trials) of the initial preference test, the time (measured in seconds) the male spent interacting with the tied down bundles of string and the interaction of these two variables predicted the *Observers* preference for the Demonstrated string in the final preference test. I asked whether the variation in the *Observers* experience during the pre-observation and observation phases predicted the *Observers* preference for the Demonstrated string in the final preference test. I addressed this question by constructing a quasibinomial logistic regression model testing whether copying by *Observers* in the final preference test predicted the *Observers* preference for the Demonstrated string in the final preference test.

I asked whether the strength of an *Observers* initial colour preference predicted whether they would copy the Demonstrated string. To address this, I constructed a binary logistic regression model to evaluate whether copying by *Observers* was predicted by the strength of the *Observers* initial colour preference. The strength of the initial colour preference was indicated by the proportion of time the male spent interacting with the string of their preferred colour during the initial preference test, where zero indicated the male only interacted with the Demonstrated string, and one indicated the male only interacted with the Non-demonstrated string. I classified whether each male had copied the Demonstrated string in the final preference test using the criteria established by Breen et al. (2019), who used Monte Carlo simulations to show that depositing seventeen or more out of the first 25 pieces of a specific material was indicative of a preference that was significantly greater than chance. I tested the significance of each logistic regression via Type II likelihood-ratio Chi-square test from the ‘stats’ package. I chose to run the separate logistic models described above using subsets of the predictor variables rather than one model containing all predictors identified, because having that many terms in one model would result in overfitting (where there are too many predictors relative to the number of observations).

To correct for multiple comparisons across the logistic regression models, I ran Holm-Bonferroni correction on the p-values to control for type I error.

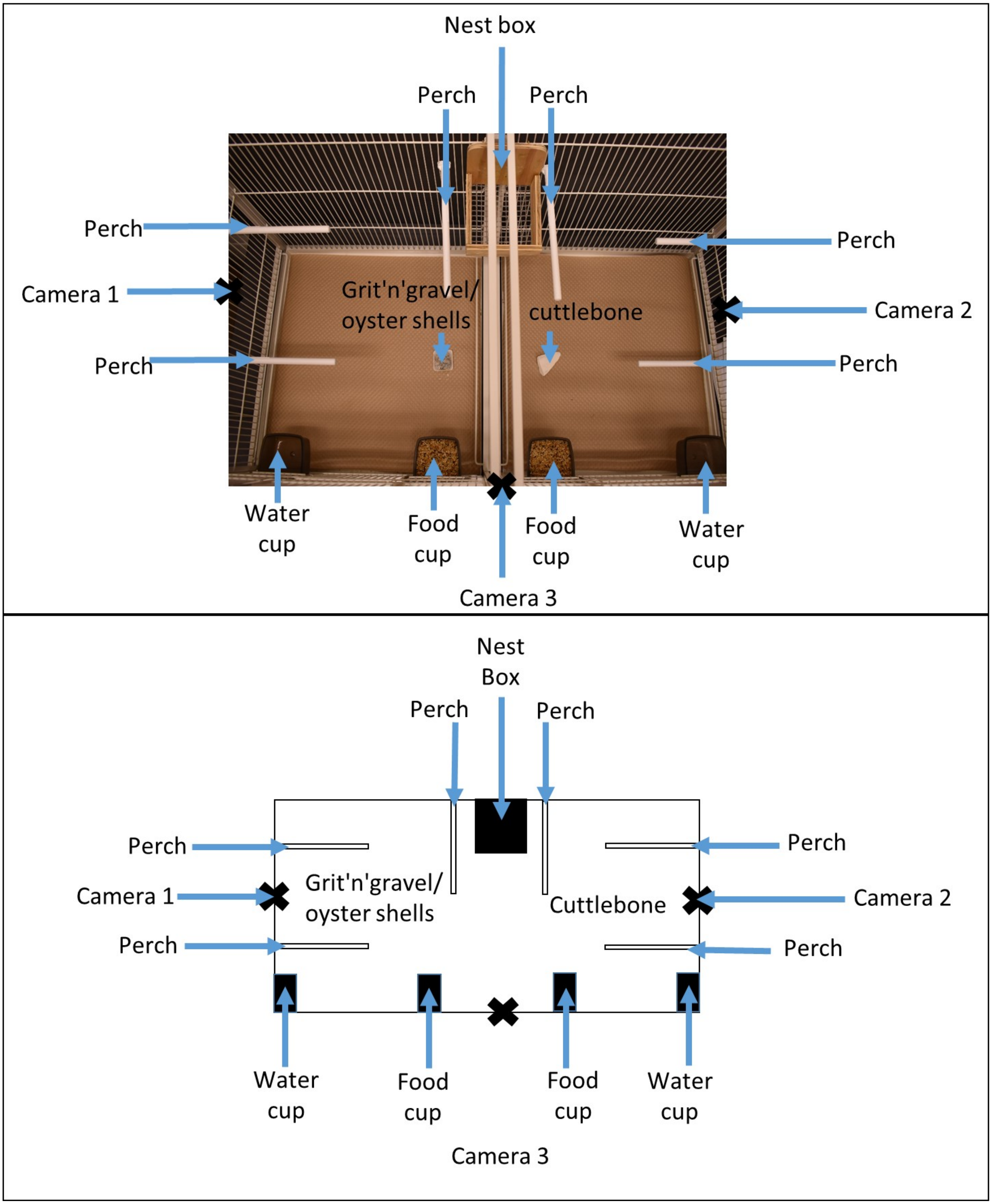

*Figure 7*. **Breeding cage.** A top-down picture (top) and schematic (bottom) of the layout of a breeding cage.

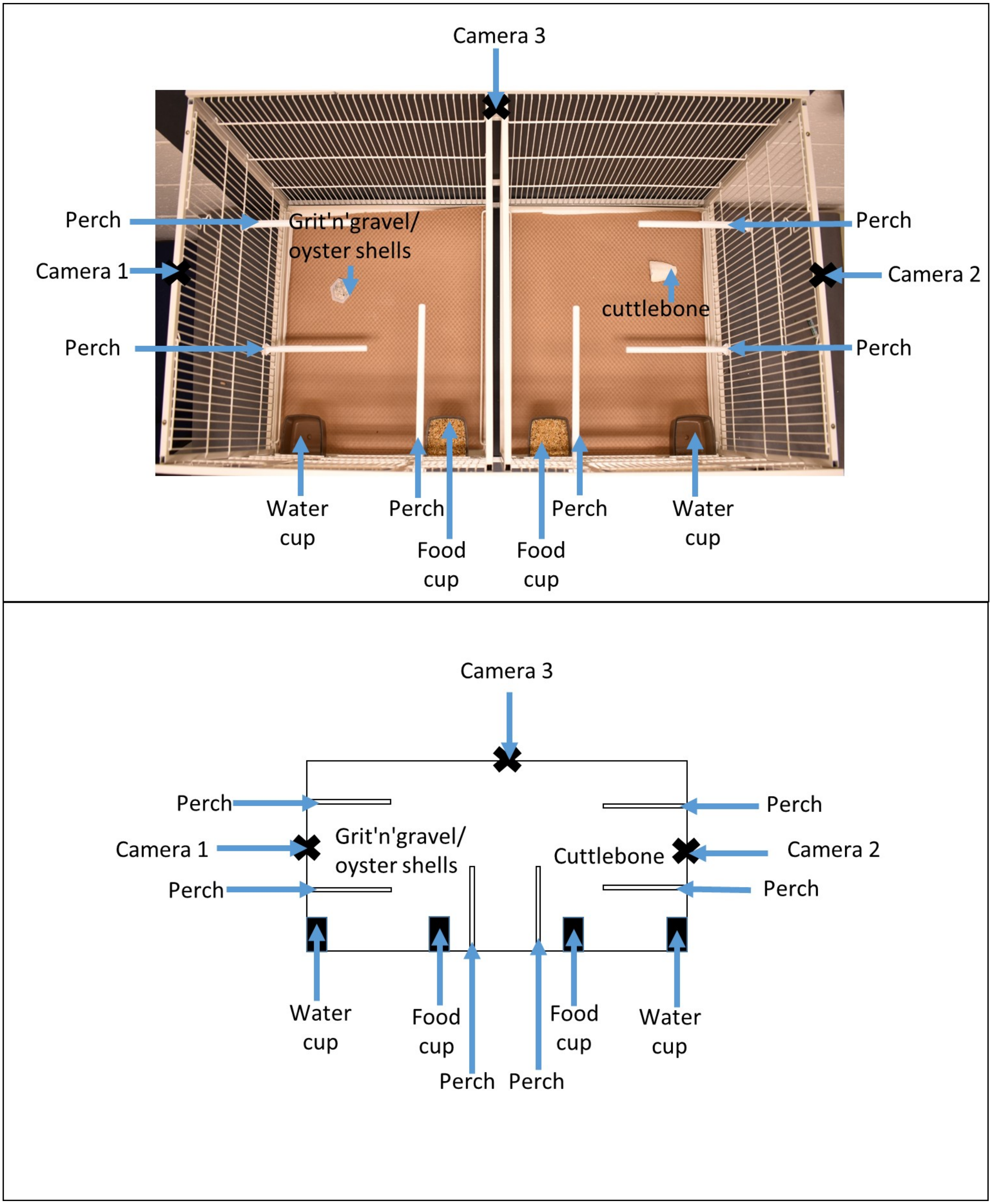

*Figure 8.* **Test cage.** A top-down picture (top) and schematic (bottom) of the layout of a test cage.

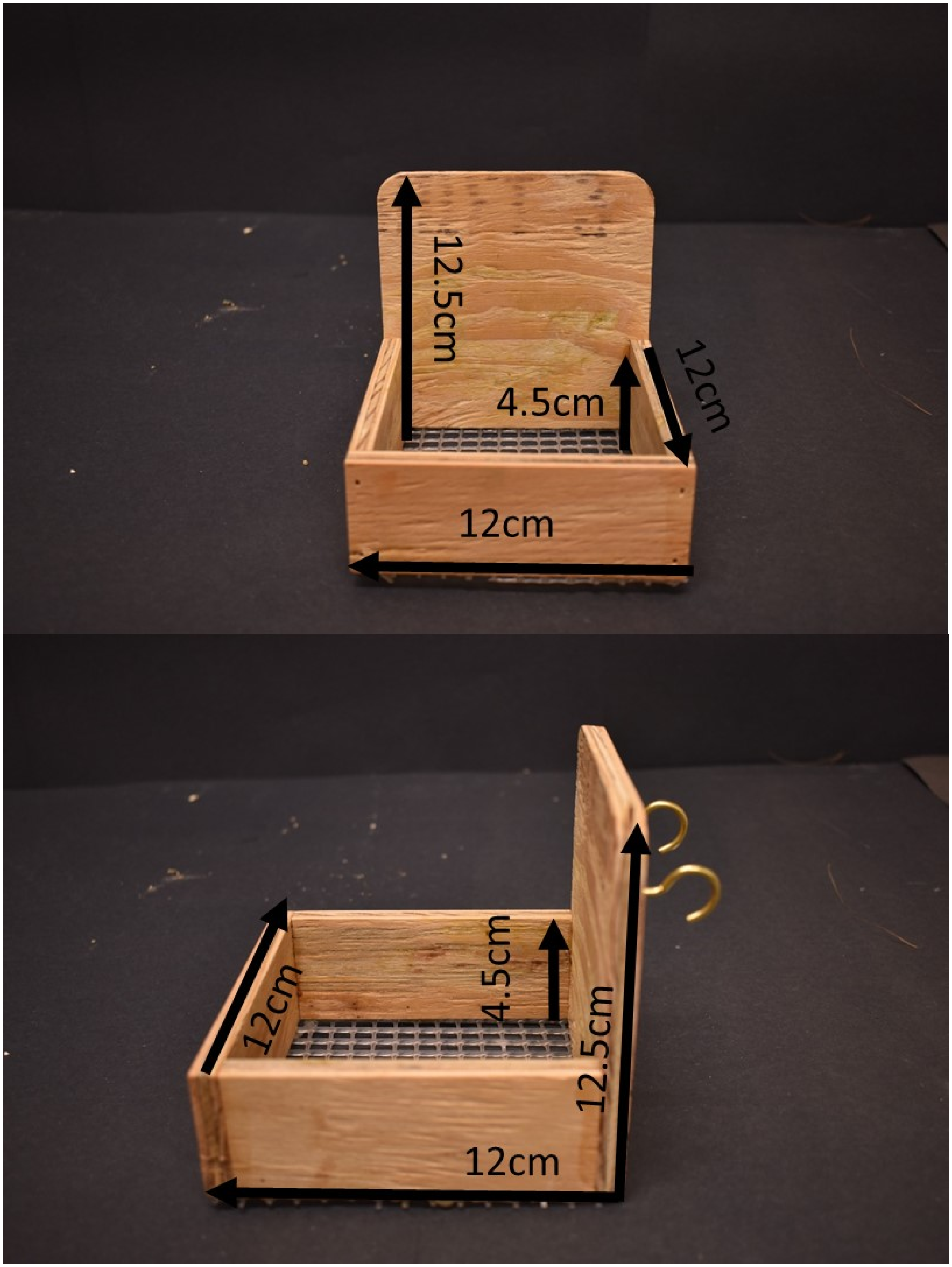

*Figure 9*. **Nest cup.** A front (top) and side (bottom) facing view of a nest cup with dimensions.

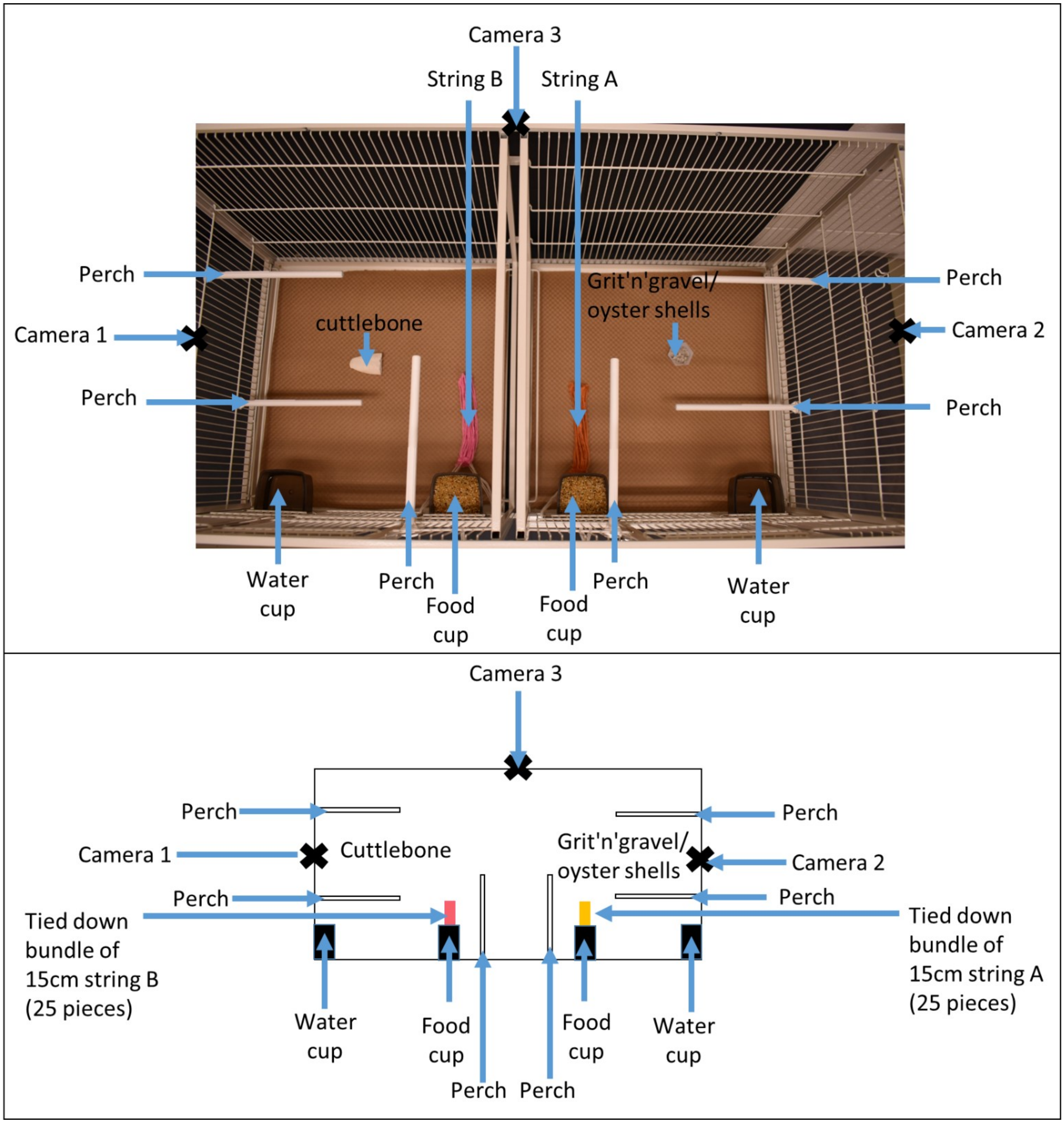

*Figure 10.* **Initial preference test set up.** A top-down picture (top) and schematic (bottom) of the layout of the initial preference test.

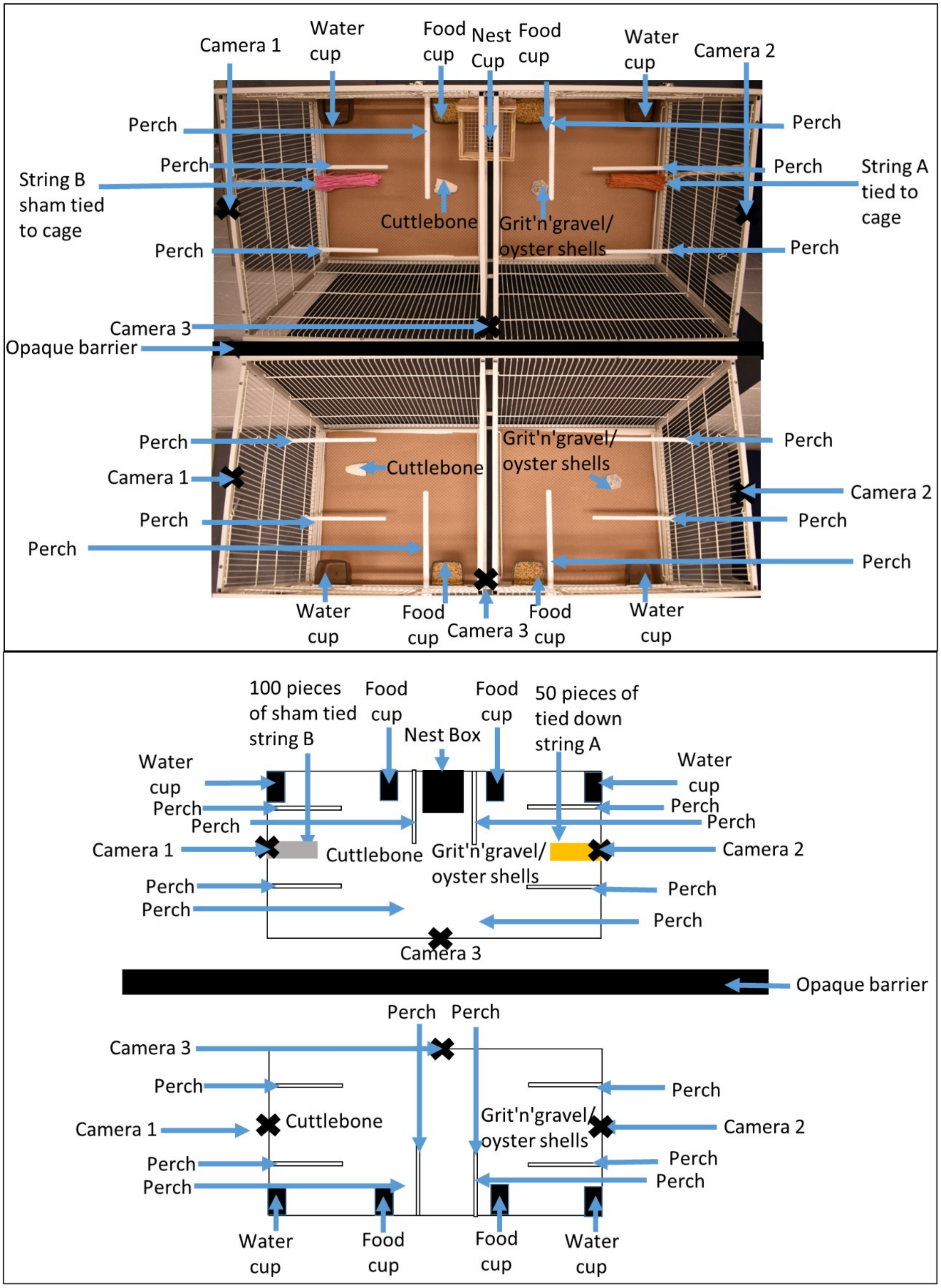

*Figure 11.* **Pre-observation phase set up.** A top-down picture (top) and schematic (bottom) of the layout of the pre-observation phase. The cage above the opaque barrier is the *Demonstrators* cage. The cage below the barrier represents the *Observers* cage.

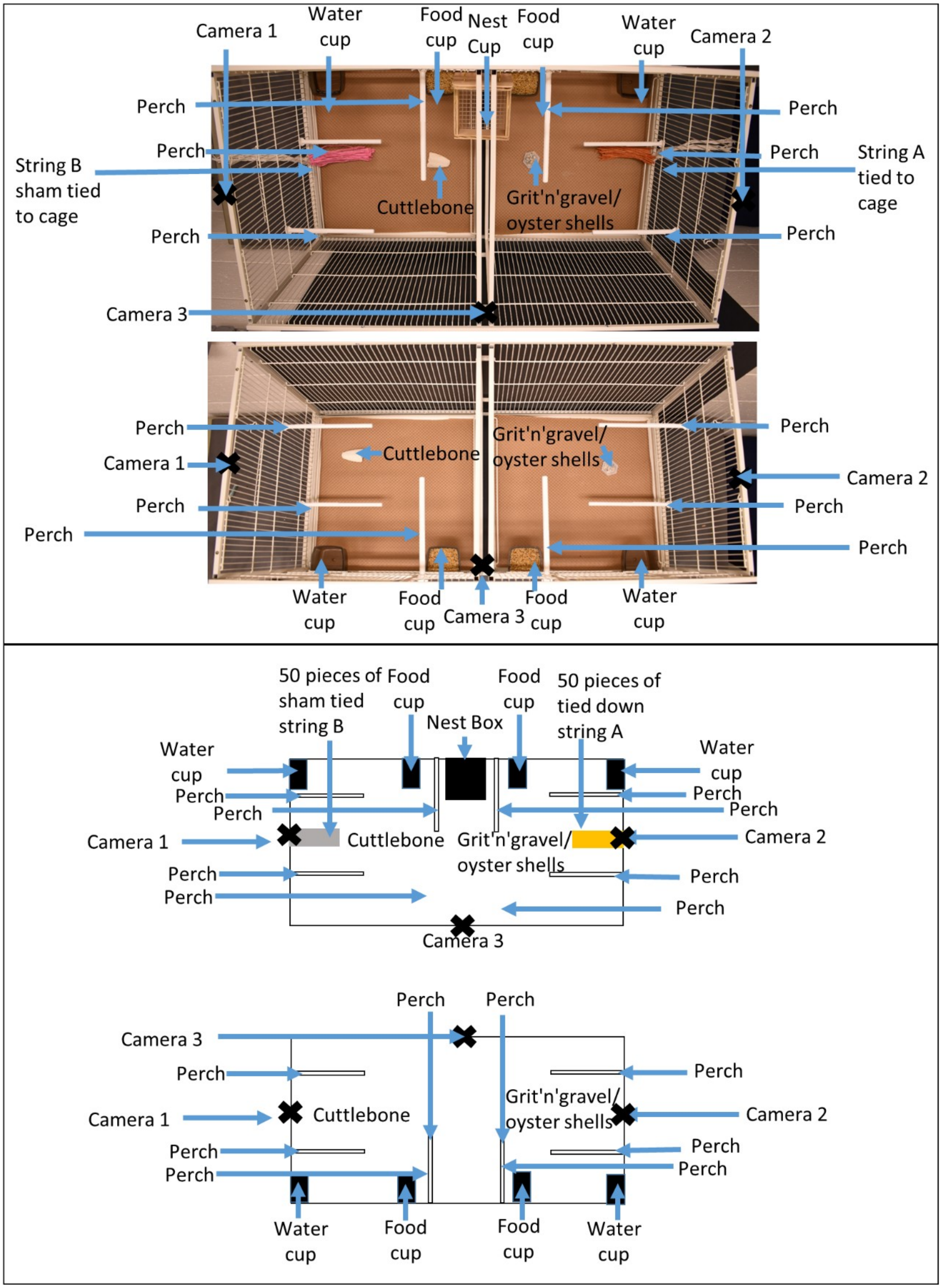

*Figure 12.* **Observation phase set up.** A top-down picture (top) and schematic (bottom) of the layout of the observation phase. The cage above the opaque barrier is the *Demonstrators* cage. The cage below the barrier represents the *Observers* cage.

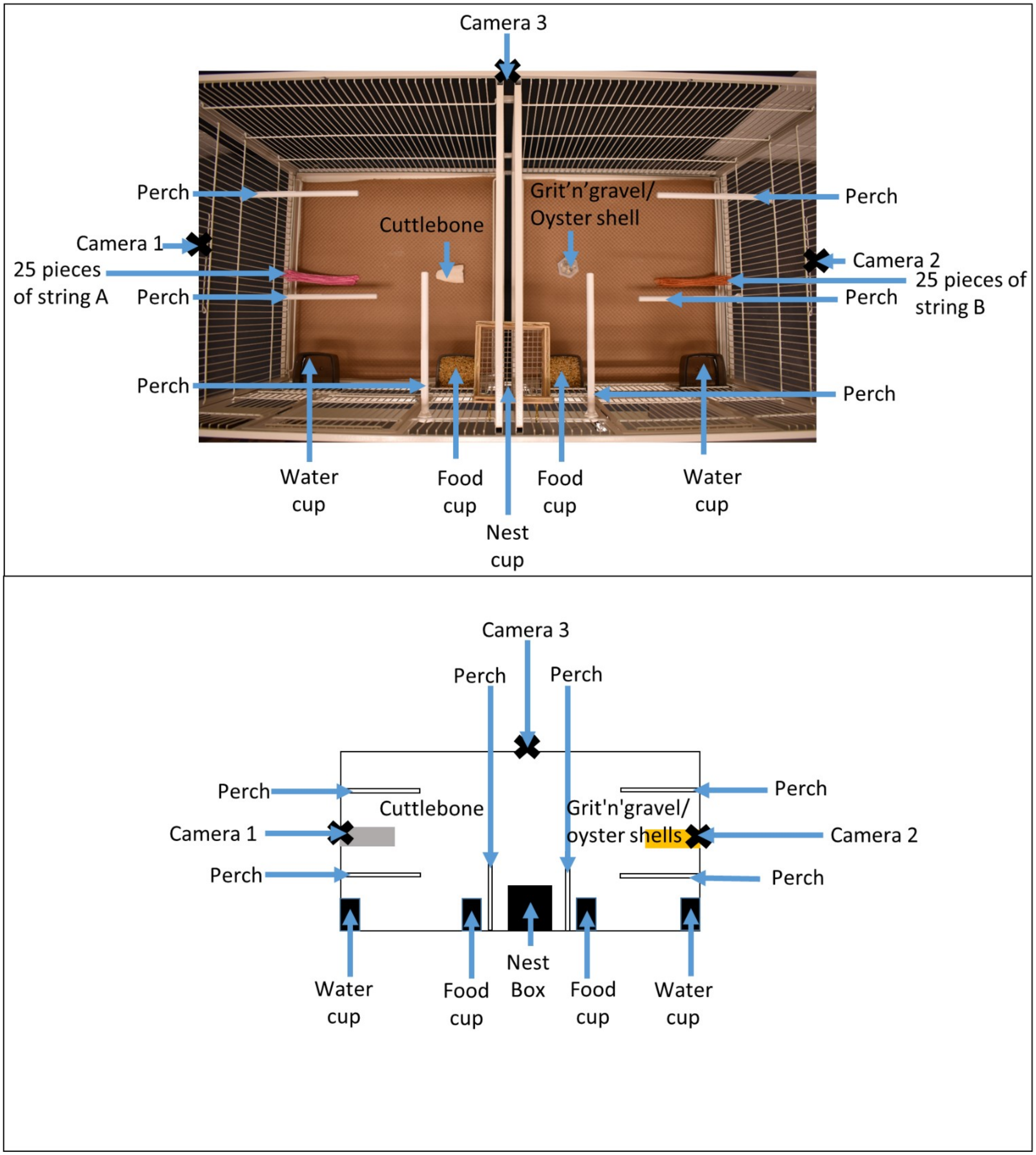

*Figure 13.* **Final preference test set up.** A top-down picture (top) and schematic (bottom) of the layout of the final preference test.

# Results

## Initial nest-building experience.

The time spent with the initial nest-building material (coconut fibre) did not differ significantly between the Successful ($n = 14$, $\bar{x} = 46.34$, Lower = 44.61, Upper = 48.25, 95% CI) and Unsuccessful groups ($n = 15$, $\bar{x} = 49.23$, Lower = 46.08, Upper = 52.44, 95% CI; Two sample T-test; $t = -1.66$, $p = 0.11$). The time to initial nest completion did not differ significantly between the Successful ($n = 14$, $\bar{x} = 6.36$, Lower = 4.71, Upper = 8.00, 95%, CI) and Unsuccessful groups ($n = 15$, $\bar{x} = 49.23$, Lower = 46.08, Upper = 52.44, 95%, CI; Two sample T-test; $t = -0.42$, $p = 0.68$). The nest size did not differ significantly between the Successful ($n = 14$, $\bar{x} = 39.71$, Lower = 32.50, Upper = 46.93, 95% CI) and Unsuccessful groups ($n = 15$, $\bar{x} = 39.61$, Lower = 31.92, Upper = 47.31, 95% CI; Two sample T-test; $t = 0.02$, $p = 0.98$). The time before the initial preference test did not differ significantly between the Successful ($n = 14$, $\bar{x} = 24.14$, Lower = 18.25, Upper = 30.04, 95% CI) and Unsuccessful groups ($n = 15$, $\bar{x} = 21.80$, Lower = 13.93, Upper = 29.67, 95% CI; Two sample T-test; $t = 0.51$, $p = 0.61$).

## Initial preference test.

The *Observers* preference for the Demonstrated string in both the initial and final preference tests can be seen in Figure 14. In the initial preference test, the *Observers* showed a colour preference that was significantly different from chance and for the Non-demonstrated string colour ($n = 29$, Median = 0.12, $\bar{x} = 0.16$, Lower = 0.10, Upper = 0.23, 95% CI; Wilcoxon-signed rank test; $V = 0$, $p \leq 0.01$). The *Observers* preference for orange string during the initial preference test can be seen in Figure 15. The *Observers* had a significant pre-existing group preference for orange string ($n = 29$, Median 0.79, $\bar{x} = 0.72$, Lower = 0.61, Upper = 0.84, 95% CI; Wilcoxon signed-rank test $V = 362$, $p \leq 0.01$).

Figure 16 shows the Successful and Unsuccessful groups preference for the Demonstrated string in both the initial and final preference tests. Both the Successful (n = 14, Median = 0.07, $\bar{x} = 0.14$, Lower = 0.05, Upper = 0.23, 95% CI; Wilcoxon-signed-rank test; V = 0, $p \leq 0.01$) and Unsuccessful groups (n = 15, Median = 0.22, $\bar{x} = 0.19$, Lower = 0.09, Upper = 0.29, 95% CI; Wilcoxon-signed-rank test; V = 0, $p \leq 0.01$) showed a colour preference that significantly differed from chance and was for the Non-demonstrated string colour. Both the Successful (n = 14, Median = 0.80, $\bar{x} = 0.73$, Lower =0.54, Upper = 0.92; Wilcoxon signed-rank test; V = 84.5, $p \leq 0.05$) and Unsuccessful groups (n = 15, Median = 0.74, $\bar{x} = 0.72$ Lower =0.56, Upper = 0.88, 95% CI; Wilcoxon signed-rank test V = 102, $p = 0.02$) initial colour preference indicated pairs in both groups had pre-existing preferences for orange string as seen in Figure 15. The Successful and Unsuccessful groups preference for both the Demonstrated string (Mann-Whitney U test; W = 91, $p = 0.55$) and the orange string (Mann-Whitney U test; U = 91, $p = 0.55$) do not significantly differ from each other. The number of initial preference test trials did not significantly differ between the Successful (n = 14, Median = 8, $\bar{x} = 10.29$, Lower = 6.58, Upper = 14.00, 95% CI) and Unsuccessful groups (n = 15, Median = 8, $\bar{x} = 8.53$, Lower = 5.65, Upper = 11.42, 95% CI; Mann-Whitney U test; U = 120, $p = 0.50$). The total log-transformed time the male spent interacting with the string during the initial preference test did not significantly differ between the Successful (n = 14, $\bar{x}_{log} = 5.92$, $Lower_{log} = 4.81$, $Upper_{log} = 7.03$, 95% CI; $\bar{x} = 1290$, Lower = 342, Upper = 2240, 95% CI) and Unsuccessful groups (n = 15, $\bar{x}_{log} = 5.60$, $Lower_{log} = 4.79$, $Upper_{log} = 6.32$, 95% CI; $\bar{x} = 19891$, Lower = 10653, Upper = 29129; Two sample T-test $t = 0.57$, $p = 0.57$). The latency to the first male interaction with the string during the initial preference test did not significantly differ between the Successful (n = 14, $\bar{x} = 19891$, Lower = 10654, Upper = 29129, 95% CI) and the Unsuccessful groups (n = 15, $\bar{x}$ = 14894, Lower = 1966, Upper = 27822, 95% CI; Log rank test model; $\chi^2 = 1.5$, n = 29, $p = 0.2$).

### Pre-observation phase.

The duration of the pre-observation phase did not significantly differ between the Successful (n = 14, $\bar{x}$ = 18.07, Lower = 12.31, Upper = 23.83, 95% CI) and Unsuccessful groups (n = 15, $\bar{x}$ = 19.13, Lower = 13.21, Upper = 25.06, 95% CI; Two-sample T-test; t = -0.28 $p$ = 0.78).

### Observation phase.

The duration of the observation phase did not significantly differ between the Successful (n = 14, $\bar{x}$ = 31.36, Lower = 23.30, Upper = 39.41, 95% CI) and Unsuccessful groups (n = 15, $\bar{x}$ = 22.8, Lower = 17.60, Upper = 28.00; Two sample T-test; t = 1.92, $p$ = 0.07).

### Final Preference test.

The *Observers* preference for the Demonstrated string in the final preference test can be seen in Figure 14. The *Observers* did not prefer the Demonstrated string (n = 29, Median 0.04, $\bar{x}$ = 0.26, Lower = 0.11, Upper = 0.40, 95% CI; Wilcoxon-signed-rank test; V = 76, $p \leq 0.01$), in fact, they significantly preferred the Non-demonstrated string. The *Observers* preference for the Demonstrated string did not change between the initial and final preference tests (Paired Wilcoxon-signed-rank test; V = 141.5, $p$ = 0.58).

The preference of the Successful and Unsuccessful group for the Demonstrated string in the final preference test can be seen in Figure 16. Neither the Successful (n = 14, Median 0.00, $\bar{x}$ = 0.29, Lower = 0.04, Upper = 0.53, 95% CI; Wilcoxon-signed-rank test; V = 19, $p$ = 0.03) nor the Unsuccessful group (n = 15, Median 0.08, $\bar{x}$ = 0.23, Lower = 0.04, Upper = 0.43, 95% CI; Wilcoxon-signed-rank test; V = 19, $p$ = 0.02) significantly preferred the Demonstrated string, in fact they significantly preferred the Non-demonstrated string. Neither the Successful (Paired Wilcoxon signed-rank test; V = 37.5, $p = 0.6$) nor the Unsuccessful group's (Paired Wilcoxon signed-rank test; V = 36, $p = 0.84$) preference for the Demonstrated string changed between the initial and final preference tests. The preference for the Demonstrated string did not significantly differ between the Successful and Unsuccessful groups (Mann-Whitney U test; W = 92, $p = 0.57$) in the final preference test.

Figures 17 through 22 show the latency to first touch, pick up, carry, deposit one piece, deposit 25 pieces, and deposit all 50 pieces of string by the males during the final preferences test between the Successful and Unsuccessful groups. There was no significant difference in the latency to first touch string between the Successful (n = 14, $\bar{x} = 825$, Lower = -77, Upper = 1727, 95% CI) and Unsuccessful groups (n = 15, $\bar{x} = 1135$, Lower = 255, Upper = 2015, 95% CI; Log rank test; $\chi^2 = 0.1$, $p = 0.8$). There was no significant difference in the latency to first pick up string between the Successful (n = 14, $\bar{x} = 1470$, Lower = -108, Upper = 3048, 95% CI) and Unsuccessful groups (n = 15, $\bar{x} = 1670$, Lower = 371, Upper = 2969, 95% CI; Log rank test; $\chi^2 = 0.1$, $p = 0.8$). There was no significant difference in the latency to first carry string between the Successful (n = 14, $\bar{x} = 1470$, Lower = 154, Upper = 3048, 95% CI) and Unsuccessful groups (n = 15, $\bar{x} = 8555$, Lower = -2630, Upper = 19741, 95% CI; Log rank test; $\chi^2 = 4$, $p = 0.05$). There was no significant difference in the latency to first deposit string between the Successful (n = 14, $\bar{x} = 5413$, Lower = 1252, Upper = 9575, 95% CI) and Unsuccessful groups (n = 15, $\bar{x} = 27322$, Lower = -11515, Upper = 66158, 95% CI; Log rank test; $\chi^2 = 1$, $p = 0.3$). There was no significant difference in the latency to deposit the first 25 pieces of string between the Successful (n = 14, $\bar{x} = 6020$, Lower = 1972, Upper = 10068, 95% CI) and Unsuccessful groups (n = 15, $\bar{x} = 30738$, Lower = -10851, Upper = 72327, 95% CI; Log rank test; $\chi^2 = 1.4$, $p = 0.2$). There was no significant difference in the latency to deposit all 50 pieces of string between the Successful (n = 14, $\bar{x}$ = 8989, Lower = 3815, Upper = 14162, 95% CI) and Unsuccessful groups (n = 15, $\bar{x}$ = 32386, Lower = -9142, Upper = 73914, 95% CI; Log rank test; $\chi^2 = 0.4$, $p = 0.5$). Figures 21 through 24 show the differences in the number of males who first touched, picked up, carried, and deposited the Demonstrated string between the Successful and Unsuccessful groups. Neither the number of males who first touched (odds-ratio = 0.50, $p = 0.68$) picked up (odds-ratio = 0.68, $p = 1$), carried (odds-ratio = 2.34, $p = 0.65$) or deposited (odds-ratio =2.12, $p = 0.65$) the Demonstrated string significantly differed between the Successful and Unsuccessful groups

### Copying in the final preference test as a result of among-individual variations in experience.

Table 1 shows the results of the logistic models testing whether variation in the experience of *Observers* predicted copying during the final preference test. The first model, testing whether variation in the experiences of *Observers* in the initial nest-building experience, found that neither the time (days) *Observers* spent with the initial nest material (coconut fibre), the amount (grams) of coconut fibre used to build the initial nest and the time (days) before the initial preference test, predicted whether *Observers* copied the Demonstrated string. The second model testing whether variation in the experience of *Observers* in the initial preference test found that neither the duration (hours) of the initial preference test, the time (seconds) the male spent interacting with the tied down bundles of string and the interaction of these two variables predicted whether *Observers* would copy the Demonstrated string. The third model testing whether variation in the duration of the pre-observation and observation phases would affect whether *Observers* found that neither predicted whether *Observers* would copy the

Demonstrated string. Finally, the last model testing found no significant effect of the *Observers* initial colour preference on whether *Observers* copied the Demonstrated string.

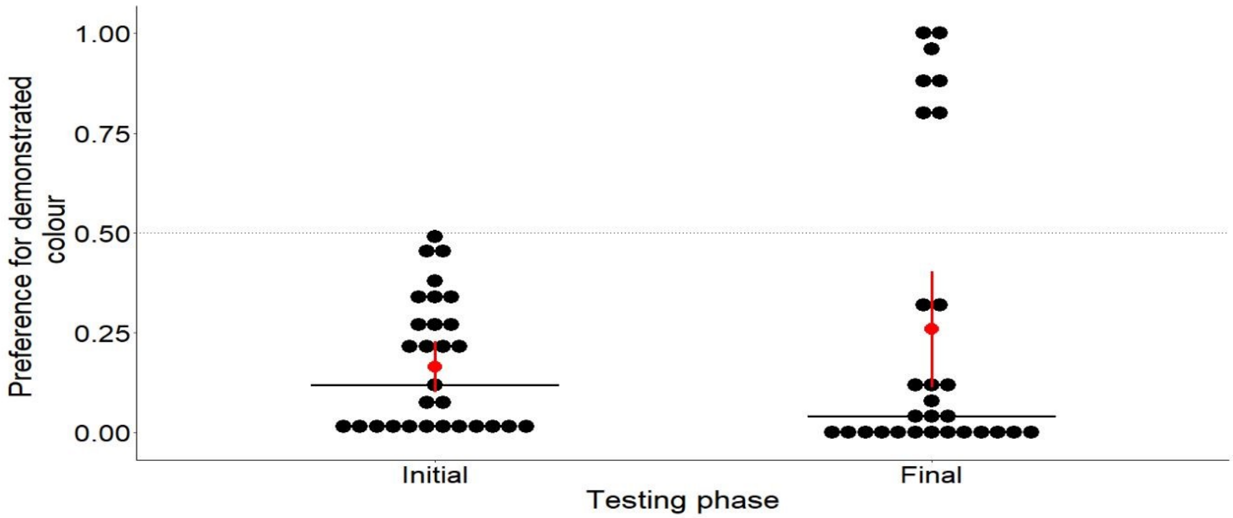

*Figure 14.* **Effect of observing a *Demonstrator* building a nest on the material colour preference of experienced nest builders.** The *Observers'* preference for the Demonstrated string (y-axis) in both the initial and final preference tests (x-axis). The horizontal black lines represent the median preference score. The red dot and vertical line represent the average +/- the standard deviation. The score for each male is represented by a black dot in each phase of the experiment. The dashed line at 0.50 represents chance (no preference).

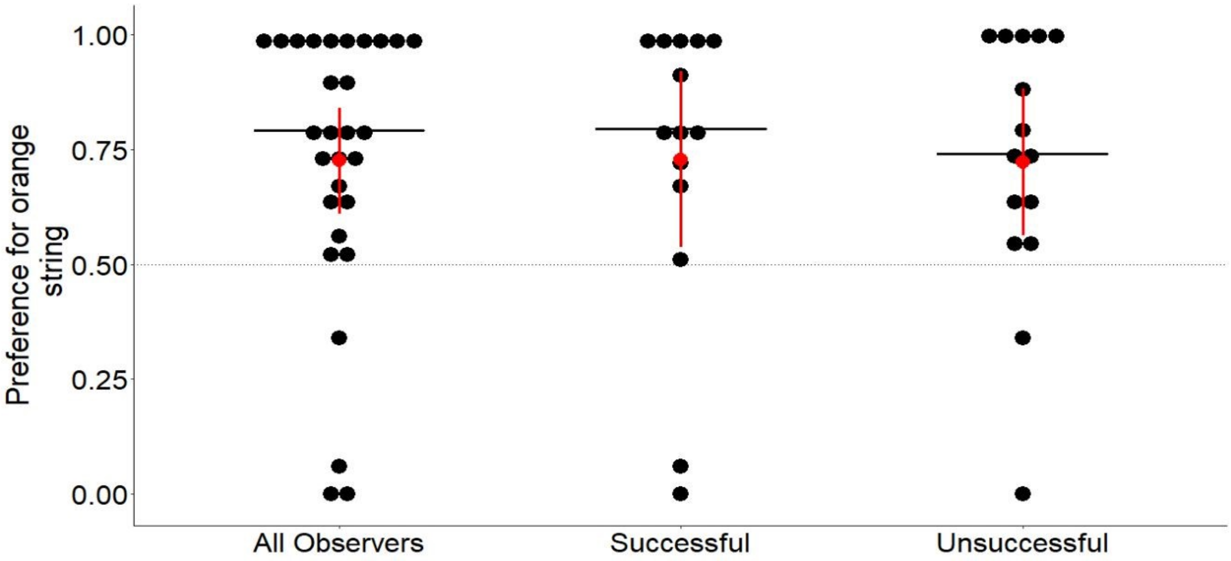

*Figure 15*. **Groupwise preference for orange string for all *Observers*, the Successful group and the Unsuccessful group.** The preference for the orange string (y-axis) during the initial preference test for all *Observers*, the Successful group and the Unsuccessful group (x-axis) are shown. The horizontal black lines represent the median preference score for each group. The red dot and vertical line represent average preference +/- the standard deviation. The dashed line at 0.50 represents a preference for the Demonstrated string that is equivalent to chance (i.e., having no preference). Of the 29 *Observers* (both the Successful and Unsuccessful groups combined), 25 males preferred orange string while four preferred pink. In the Successful group, 12 males preferred orange string, while two preferred pink string. In the Unsuccessful group, 13 males preferred orange string and three preferred pink string.

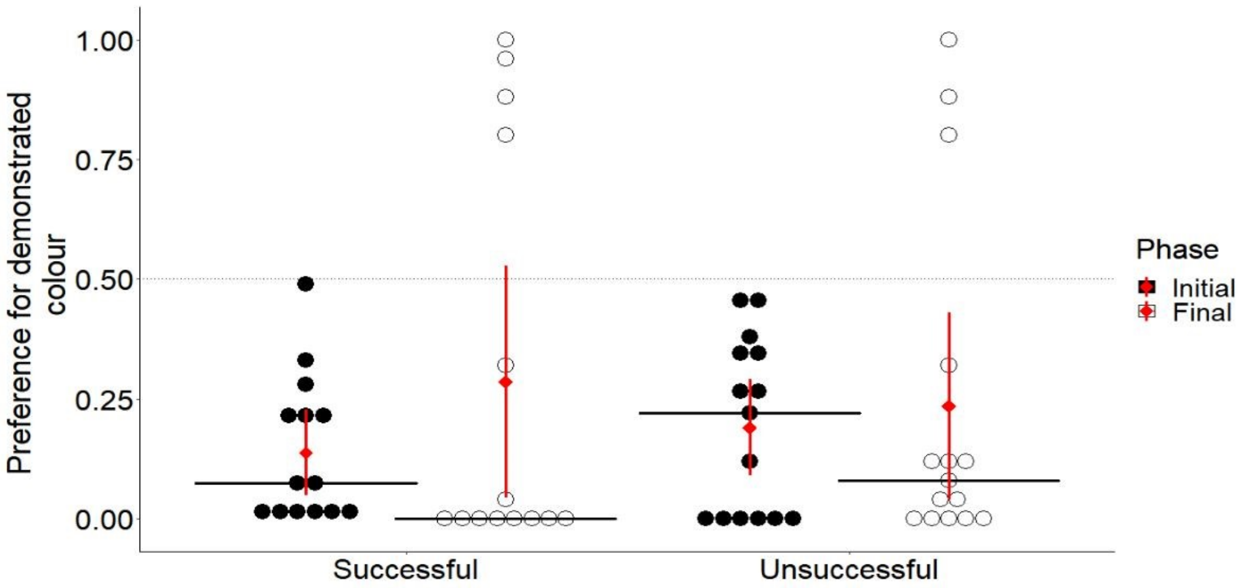

*Figure 16*. **Effect of observing a *Demonstrator* building a nest on the material colour preference in the Successful group versus the Unsuccessful group.** The preference for the Demonstrated string (y-axis) for both the Successful and Unsuccessful groups (x-axis). The solid dots represent the preference for the Demonstrated string in the initial preference test. The open-faced dots represent the preference for the Demonstrated string in the final preference test. The horizontal black line represents the median preference score. The red diamond and vertical line represent average +/- the standard deviation. Each male is represented by a dot in each phase of the experiment. The dashed line at 0.50 represents chance (no preference).

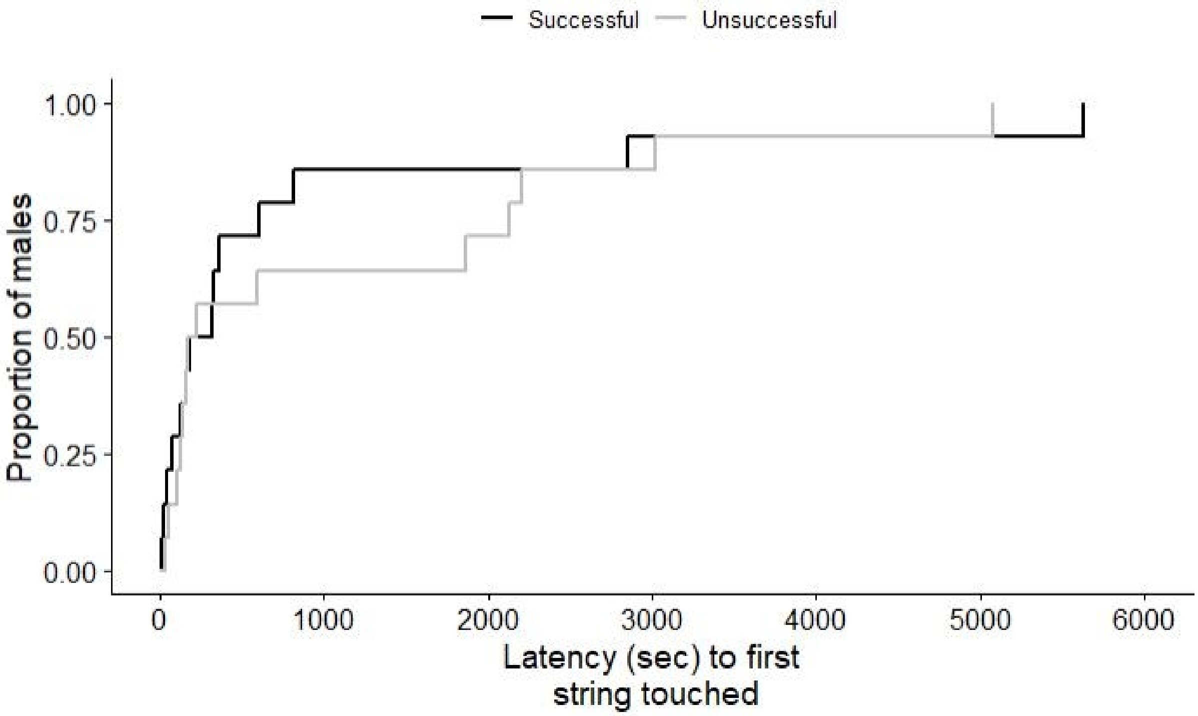

*Figure 17*. **The latency to the first string touched by males from the Successful and Unsuccessful groups.** The cumulative proportion of males (y-axis) to first touch either the Demonstrated or Non-demonstrated string over time (measured in seconds) from the start of the final preference test (x-axis) for both the Successful (black line) and Unsuccessful (grey line) groups. Each tic along the x-axis represents 1000 seconds. Within 6000 seconds of the trial start, all males in both the Successful and Unsuccessful group had touched a piece of string at least once.

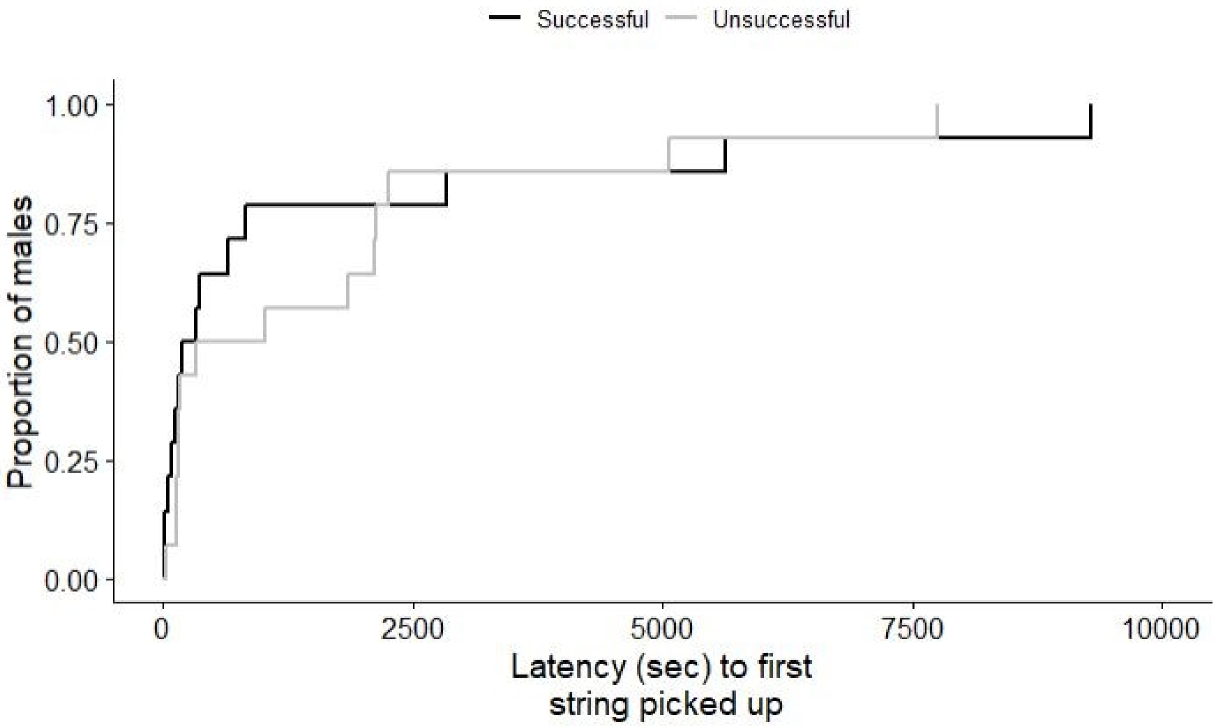

*Figure 18*. **The latency to the first string picked up by males from the Successful and Unsuccessful groups.** The cumulative proportion of males (y-axis) to first pick up either the Demonstrated or Non-demonstrated string over time (measured in seconds) from the start of the final preference test (x-axis) for both the Successful (black line) and Unsuccessful (grey line) groups. Each tic along the x-axis represents 2500 seconds. Within 10000 seconds of the trial start, all males in both the Successful and Unsuccessful group had picked up a piece of string at least once.

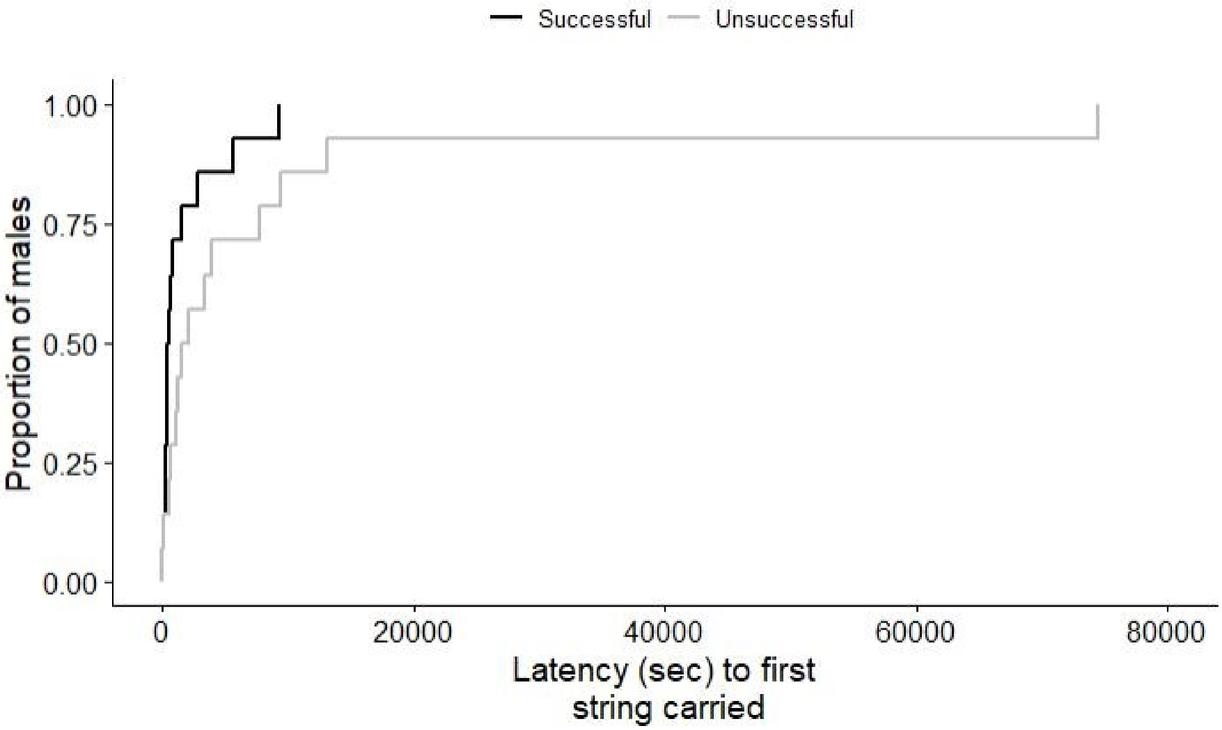

*Figure 19*. **The latency to the first string carried by males from the Successful and Unsuccessful groups.** The cumulative proportion of males (y-axis) to first carry either the Demonstrated or Non-demonstrated string over time (measured in seconds) from the start of the final preference test (x-axis) for both the Successful (black line) and Unsuccessful (grey line) groups. Each tic along the x-axis indicates 20000 seconds. Within 20000 seconds of the trial start, all males in the Successful group had carried string at least once, while 93% of all males in the Unsuccessful groups had carried string at least once.

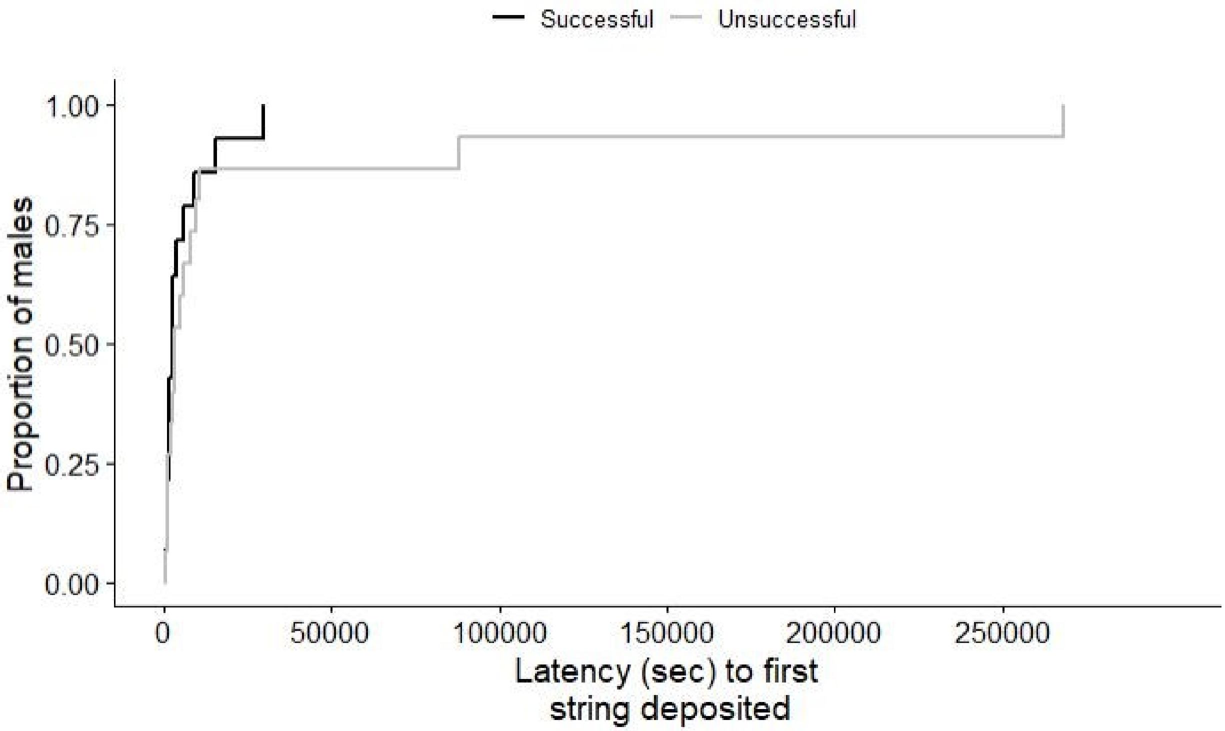

*Figure 20.* **The latency to the first deposited by males from the Successful and Unsuccessful groups.** The cumulative proportion of males (y-axis) to first deposit either the Demonstrated or Non-demonstrated string over time (measured in seconds) from the start of the final preference test (x-axis) for both the Successful (black line) and Unsuccessful (grey line) groups. Each tic along the x-axis indicates 50000 seconds. Within 50000 seconds of the trial start, all males in the Successful group had deposited at least one piece of string, while 87% of all males in the Unsuccessful groups had deposited at least one piece of string.

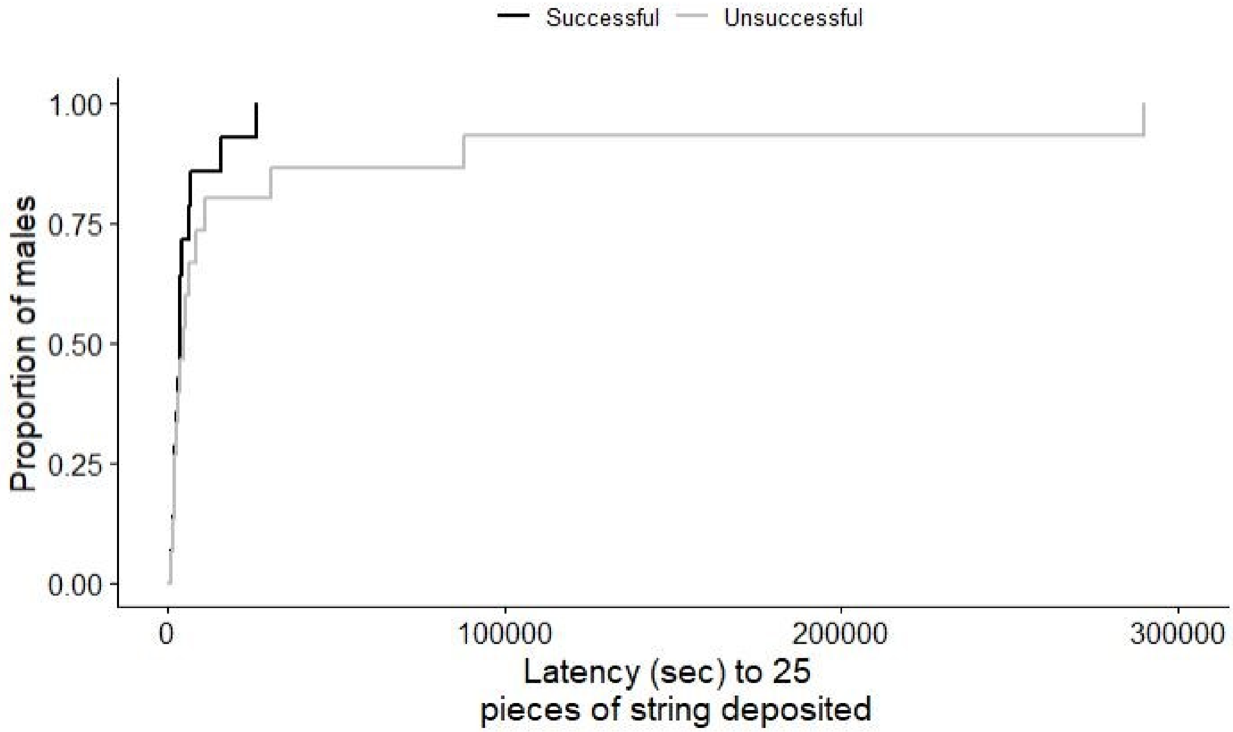

*Figure 21*. **The latency to deposit half of the provided string by males from the Successful and Unsuccessful groups.** The cumulative proportion of males (y-axis) to deposit 25 pieces of string over time (measured in seconds) from the start of the final preference test (x-axis) for both the Successful (black line) and Unsuccessful (grey line) groups. Each tic along the x-axis indicates 100000 seconds. Within 100000 seconds of the trial start, all males in the Successful group had deposited 25 pieces of string, while 93% of all males in the Unsuccessful groups had deposited 25 pieces of string.

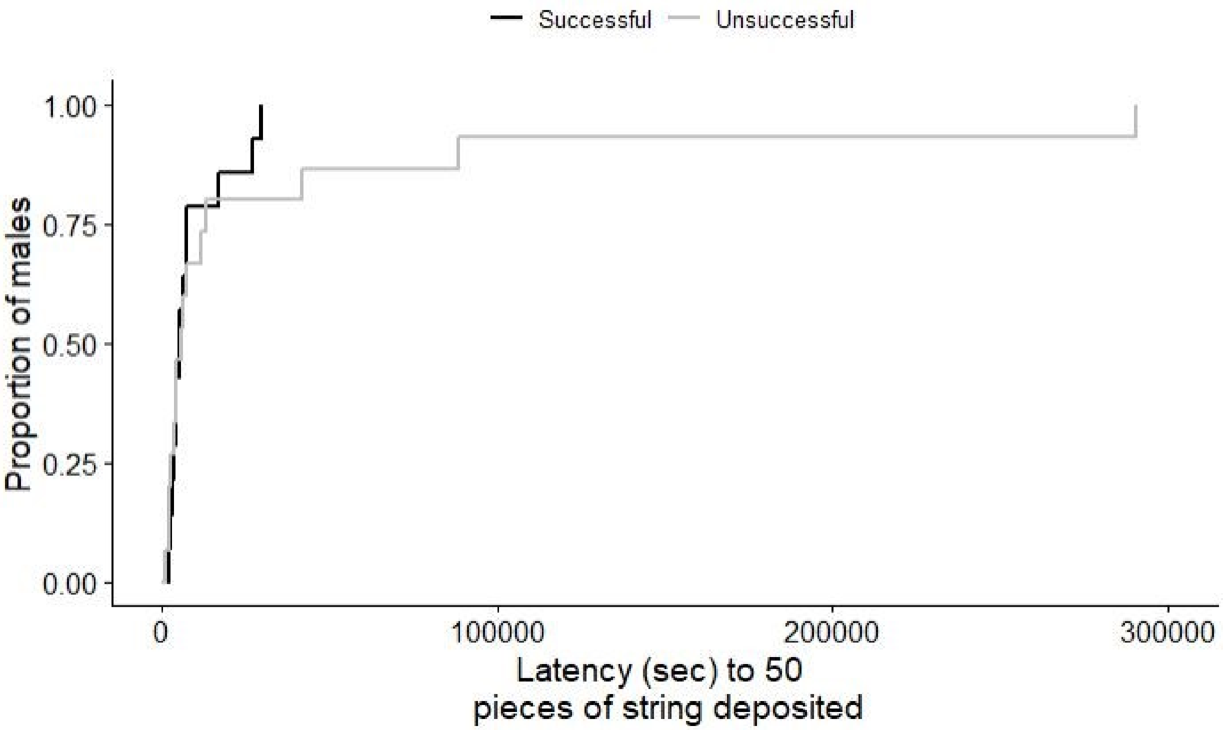

*Figure 22.* **The latency to deposit of all the provided string by males from the Successful and Unsuccessful groups.** The cumulative proportion of males (y-axis) to deposit 50 pieces of string over time (measured in seconds) from the start of the final preference test (x-axis) for both the Successful (black line) and Unsuccessful (grey line) groups. Each tic along the x-axis indicates 100000 seconds. Within 100000 seconds of the trial start, all males in the Successful group had deposited all 50 pieces of string, while 87% of all males in the Unsuccessful groups had deposited all 50 pieces of string.

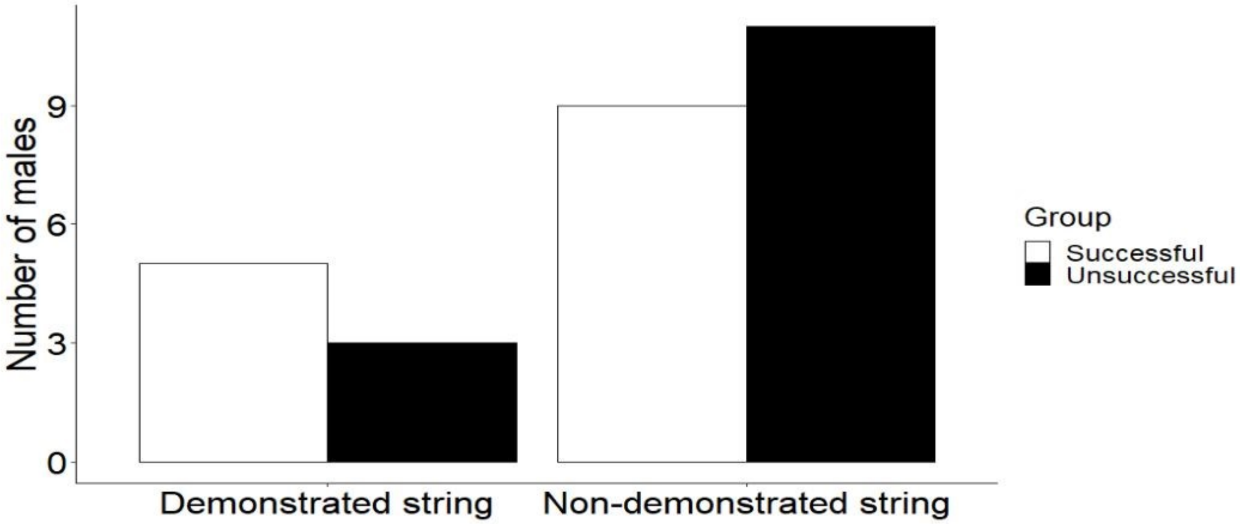

*Figure 23*. **Effect of observing a *Demonstrator's* material choice on the colour of string first touched by males in the Successful and Unsuccessful groups.** The number of males (y-axis) who first touched the Demonstrated string compared to the number of males who first touched the Non-demonstrated string during the final preference test (x-axis) in both the Successful group (white bar) and the Unsuccessful group (black bar).

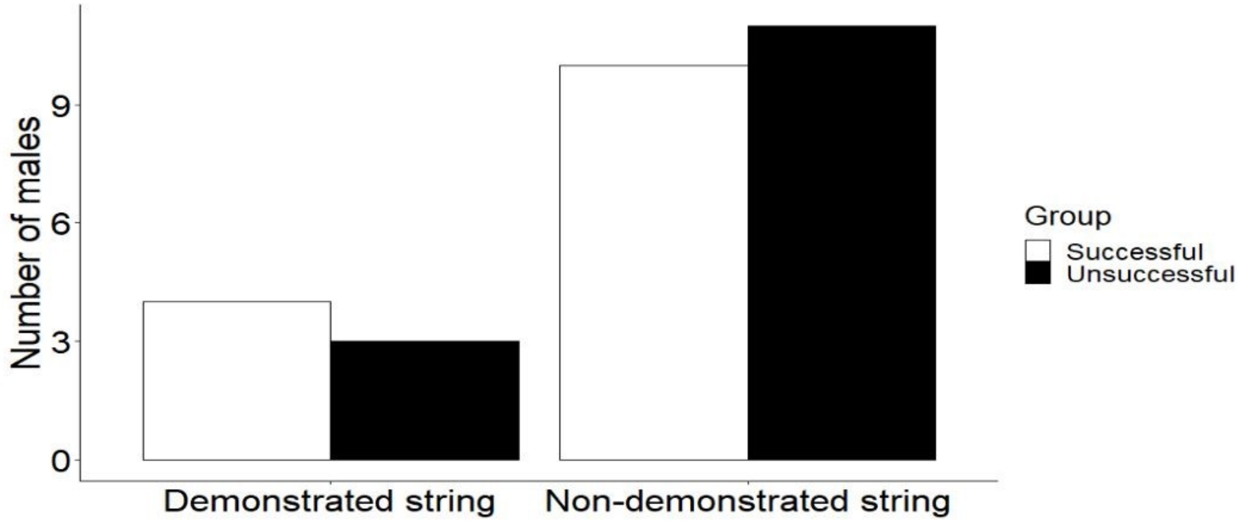

*Figure 24*. **Effect of observing a *Demonstrator's* material choice on the colour of string first picked up males in the Successful and Unsuccessful groups.** The number of males (y-axis) who first picked up the Demonstrated string compared to the number of males who first picked up the Non-demonstrated string during the final preference test (x-axis) in both the Successful group (white bar) and the Unsuccessful group (black bar).

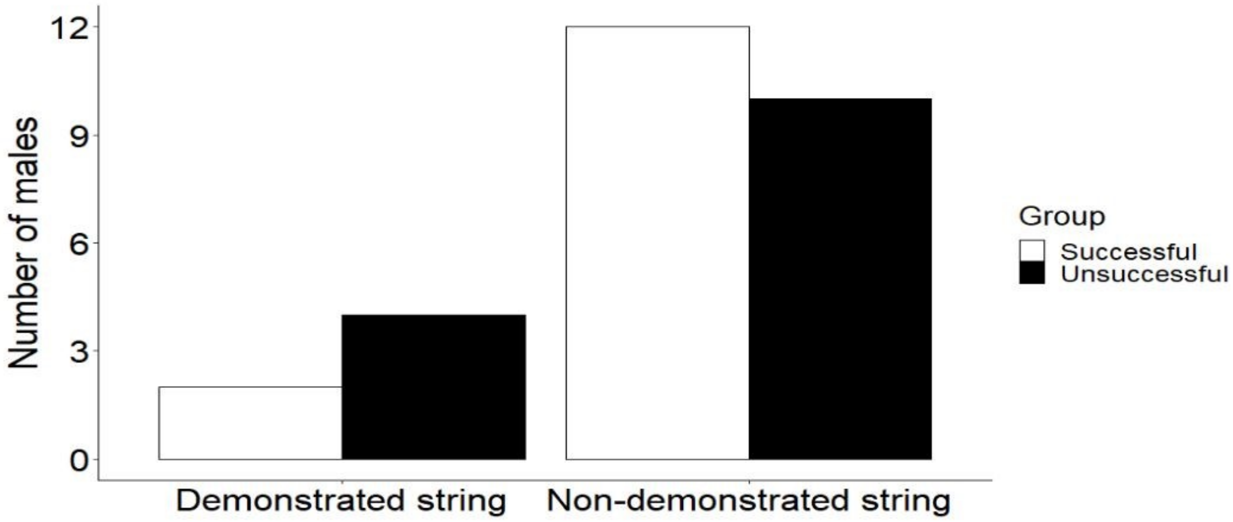

*Figure 25*. **Effect of observing a *Demonstrator's* material choice on the colour of string first carried by males in the Successful and Unsuccessful groups.** The number of males (y-axis) who first carried the Demonstrated string compared to the number of males who first carried the Non-demonstrated string during the final preference test (x-axis) in both the Successful group (white bar) and the Unsuccessful group (black bar).

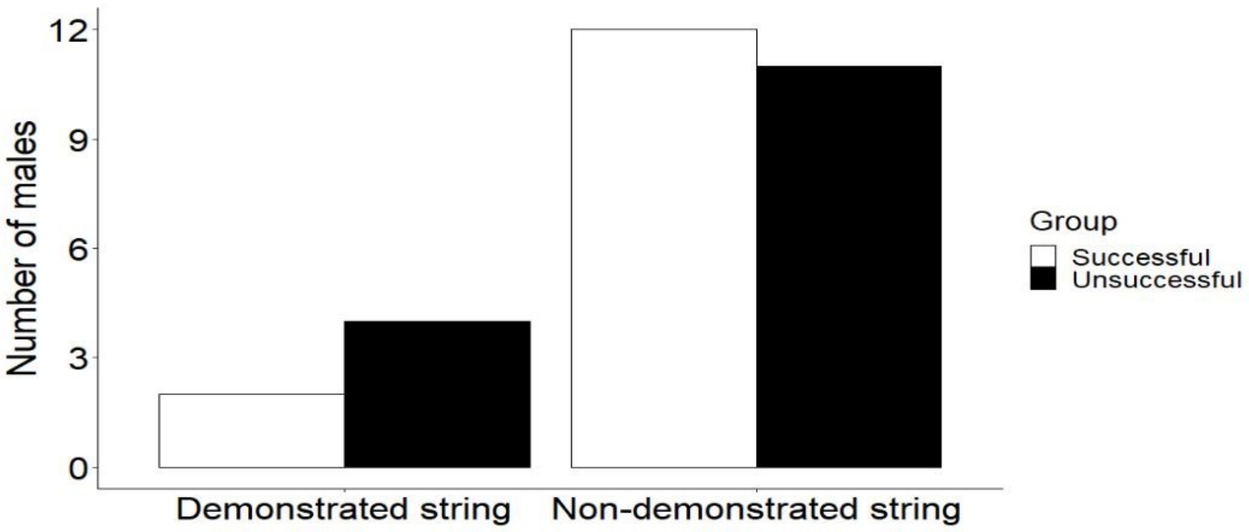

*Figure 26*. **Effect of observing a *Demonstrator's* material choice on the colour of string first deposited by males in the Successful and Unsuccessful groups.** The number of males (y-axis) who first deposited the Demonstrated string compared to the number of males who first deposited the Non-demonstrated string during the final preference test (x-axis) in both the Successful group (white bar) and the Unsuccessful group (black bar).

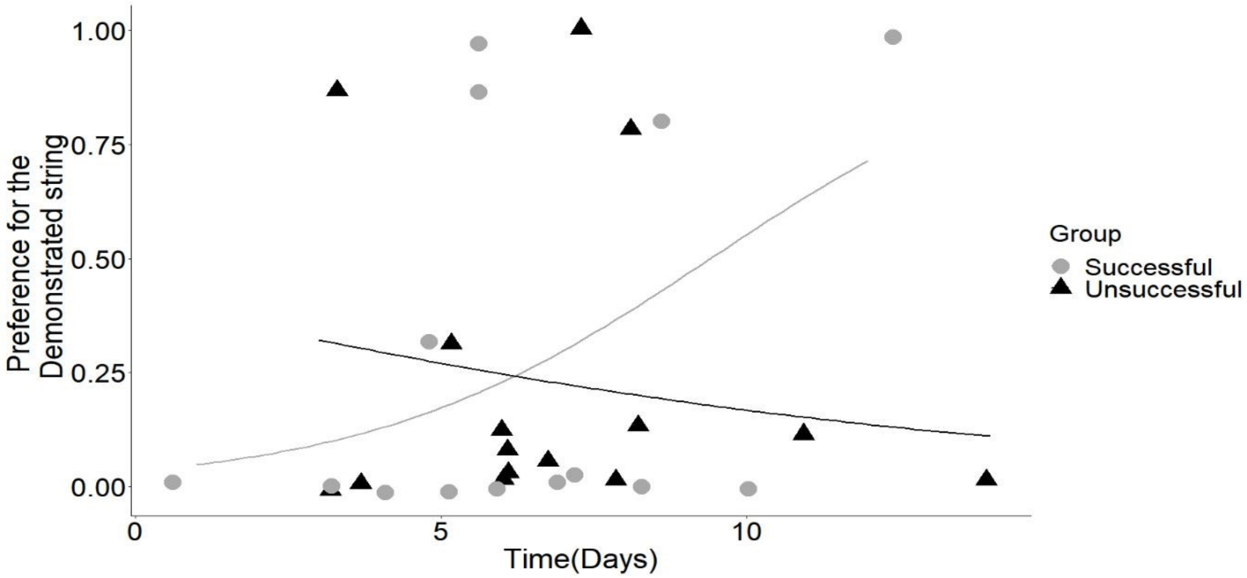

*Figure 27.* **The preference for the Demonstrated string predicted by the number of days taken to complete the initial nest.** The *Observers* preference for the Demonstrated string during the final preference test (y-axis) where 1 indicates all of the first 25 pieces of string deposited were the Demonstrated string and 0 indicates that none of the first 25 pieces of string deposited were the Demonstrated string, correlated with the time it took pairs to complete the initial nest in the initial nest-building experience (x-axis). Preference for the Demonstrated string is shown for males in both the Successful (grey dots) and Unsuccessful (black triangles) groups. The grey line represents the regression curve for the Successful group (McFadden's $R^2$ =0.11), the black line represents the regression curve for the Unsuccessful group (McFadden's $R^2$ = 0.03).

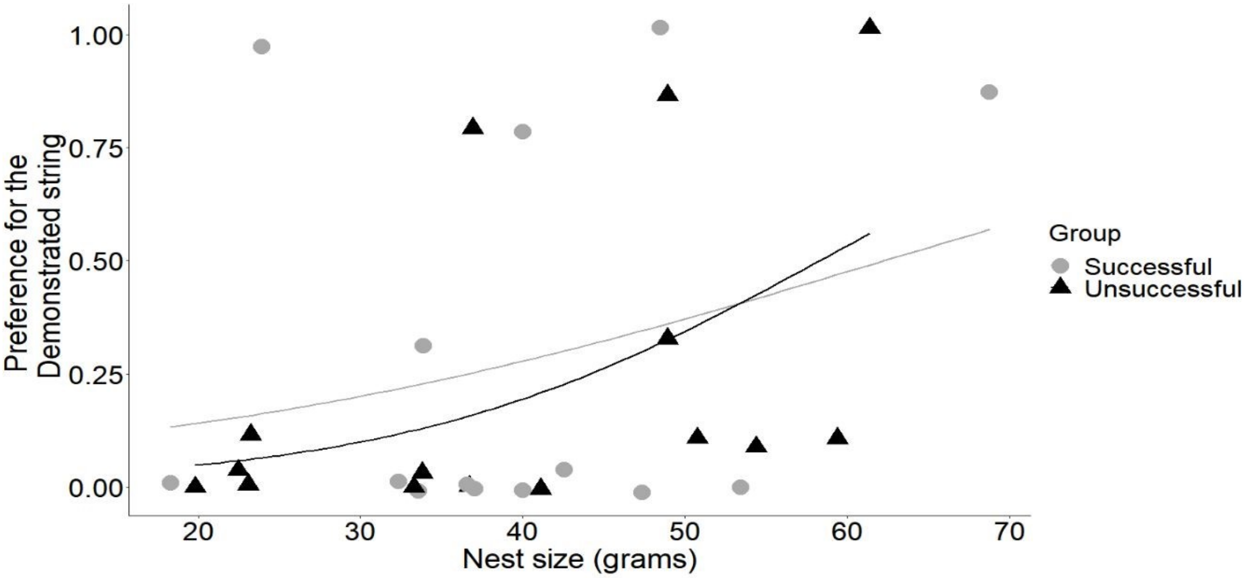

*Figure 28*. **The preference for the Demonstrated string predicted by initial nest size.** The *Observers* preference for the Demonstrated string during the final preference test (y-axis) where 1 indicates all of the first 25 pieces of string deposited were the Demonstrated string and 0 indicates that none of the first 25 pieces of string deposited were of Demonstrated string, correlated with the amount of coconut fibre used by males to build their initial nest in the initial nest-building experience (x-axis). Preference for the Demonstrated string is shown for males in both the Successful (grey dots) and Unsuccessful (black triangles) groups. The grey line represents the regression curve for the Successful group (McFadden's $R^2 = 0.07$), the black line represents the regression curve for the Unsuccessful group (McFadden's $R^2 = 0.01$)

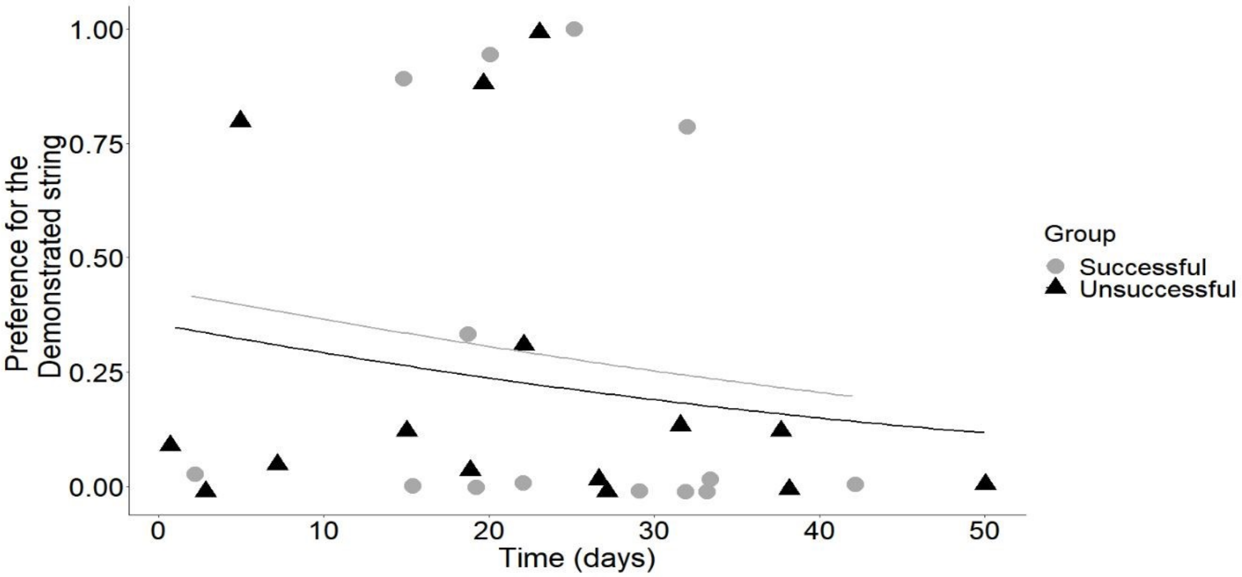

*Figure 29.* **The preference for the Demonstrated string predicted by the time before the initial preference test.** The *Observers* preference for the Demonstrated string during the final preference test (y-axis) where 1 indicates all of the first 25 pieces of string deposited were the Demonstrated string and 0 indicates that none of the first 25 pieces of string deposited were of Demonstrated string, correlated with the time between the removal of a pair's initial nest and the start of the initial preference test (in days) experienced by each pair (x-axis). Preference for the Demonstrated string is shown for males in both the Successful (grey dots) and Unsuccessful (black triangles) groups. The grey line represents the regression curve for the Successful group (McFadden's $R^2 \leq 0.01$), the black line represents the regression curve for the Unsuccessful group (McFadden's $R^2 = 0.04$).

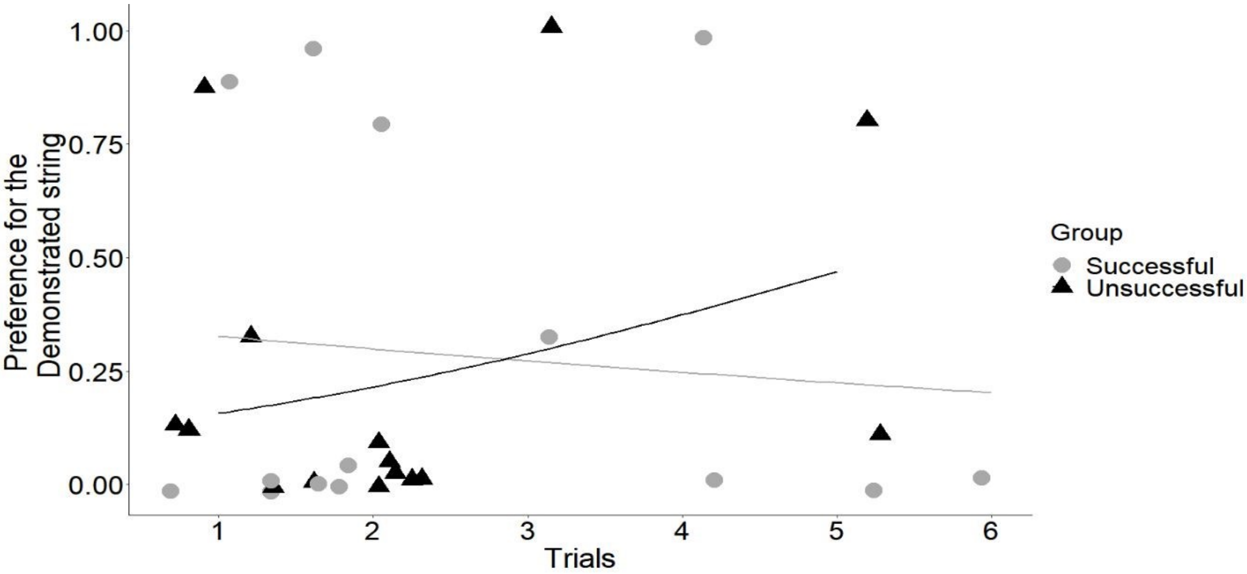

*Figure 30*. **The preference for the Demonstrated string predicted by the number of initial preference test trials.** The *Observers* preference for the Demonstrated string during the final preference test (y-axis) where 1 indicates all of the first 25 pieces of string deposited were the Demonstrated string and 0 indicates that none of the first 25 pieces of string deposited were of Demonstrated string, correlated with the number of initial preference test trials taken by each pair before the males' initial colour preference could be identified (x-axis). Preference for the Demonstrated string is shown for males in both the Successful (grey dots) and Unsuccessful (black triangles) groups. The grey line represents the regression curve for the Successful group (McFadden's $R^2 = 0.01$), the black line represents the regression curve for the Unsuccessful group (McFadden's $R^2 = 0.09$).

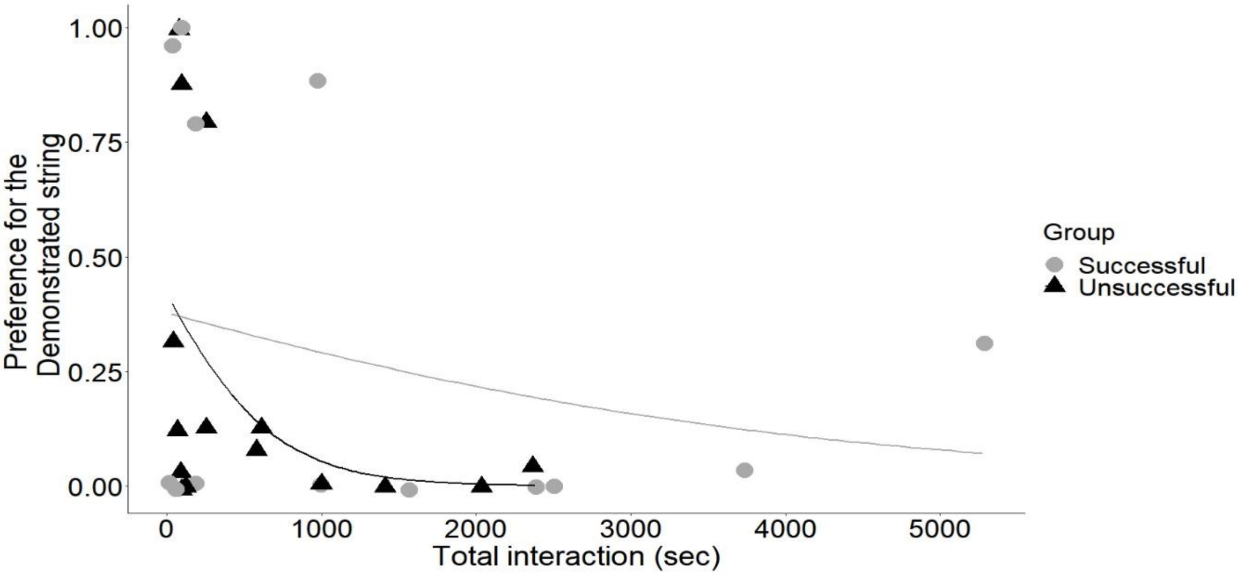

Figure 31. **The preference for the Demonstrated string predicted by the amount of interaction with the novel material in the initial preference test.** The *Observers* preference for the Demonstrated string during the final preference test (y-axis) where 1 indicates all of the first 25 pieces of string deposited were the Demonstrated string and 0 indicates that none of the first 25 pieces of string deposited were of Demonstrated string, correlated with the amount of time (sec) that each male spent interacting with the tied down bundles of string during the initial preference test (x-axis). Preference for the Demonstrated string is shown for males in both the Successful (grey dots) and Unsuccessful (black triangles) groups. The grey line represents the regression curve for the Successful group (McFadden's $R^2 = 0.13$), the black line represents the regression curve for the Unsuccessful group (McFadden's $R^2 = 0.17$).

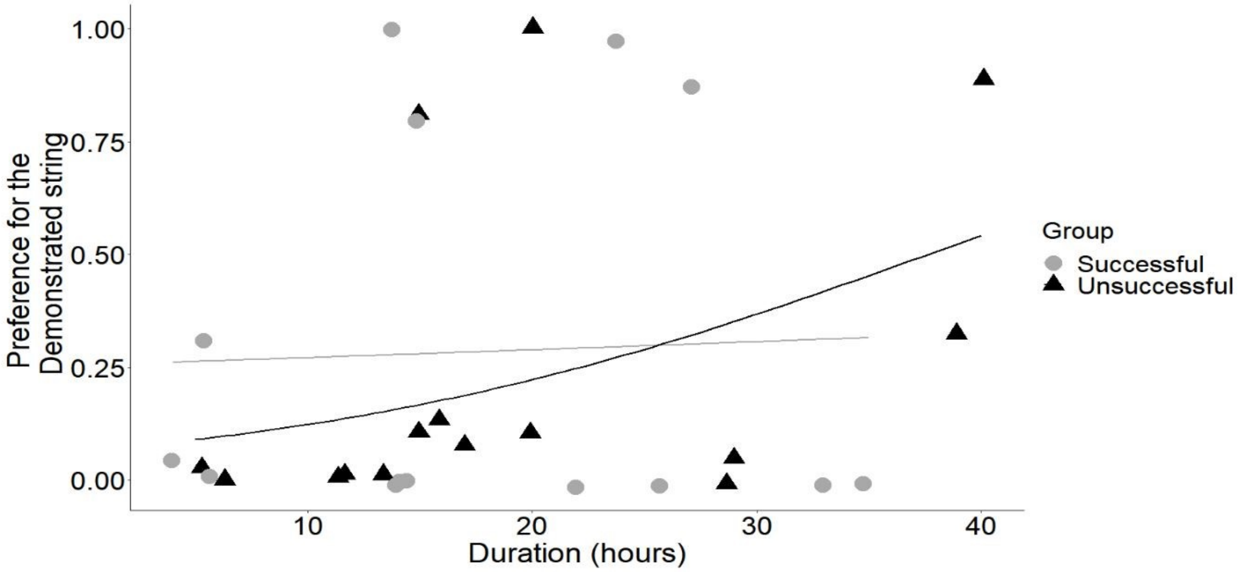

Figure 32. **The preference for the Demonstrated string predicted by the duration of the pre-observation phase.** The *Observers* preference for the Demonstrated string during the final preference test (y-axis) where 1 indicates all of the first 25 pieces of string deposited were the Demonstrated string and 0 indicates that none of the first 25 pieces of string deposited were of Demonstrated string, correlated with the duration of the pre-observation phase experienced by each pair (x-axis). Preference for the Demonstrated string is shown for males in both the Successful (grey dots) and Unsuccessful (black triangles) groups. The grey line represents the regression curve for the Successful group (McFadden's $R^2 = 0.01$), the black line represents the regression curve for the Unsuccessful group (McFadden's $R^2 = 0.07$).

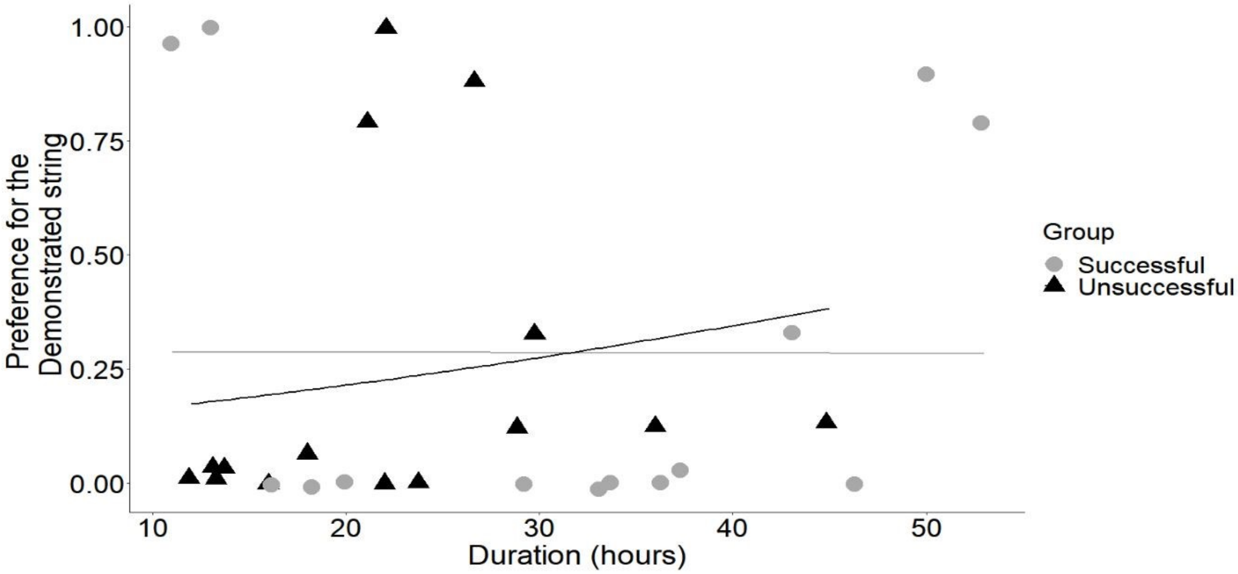

*Figure 33*. **The preference for the Demonstrated string predicted by the duration of the observation phase.** The *Observers* preference for the Demonstrated string during the final preference test (y-axis) where 1 indicates all of the first 25 pieces of string deposited were the Demonstrated string and 0 indicates that none of the first 25 pieces of string deposited were of Demonstrated string, correlated with the duration of the observation phase experienced by each pair (x-axis). Preference for the Demonstrated string is shown for males in both the Successful (grey dots) and Unsuccessful (black triangles) groups. The grey line represents the regression curve for the Successful group (McFadden's $R^2 \leq 0.01$), the black line represents the regression curve for the Unsuccessful group (McFadden's $R^2 \leq 0.01$).

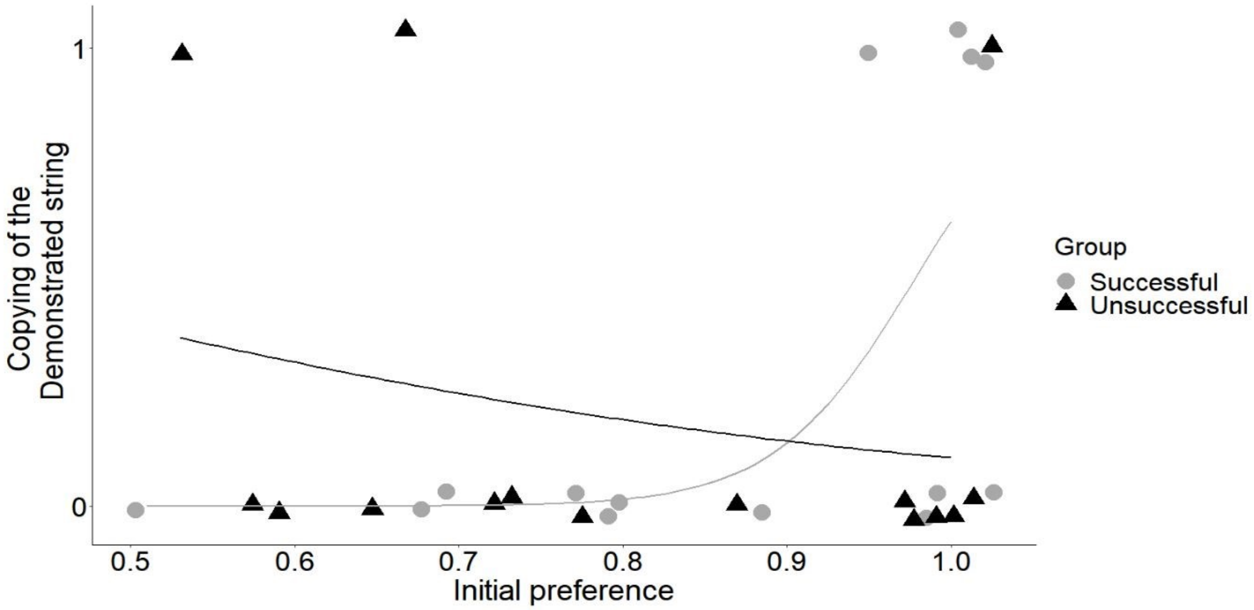

*Figure 34*. **Whether males in either the Successful or Unsuccessful group copied the Demonstrated string as predicted by the strength of the male's initial colour preference.** Copying of the Demonstrated string (y-axis) in the final preference test by males in either the Successful or Unsuccessful group. 1 indicates an *Observer* male copied the Demonstrated string (17 or more of the first 25 pieces of string deposited were the Demonstrated string) and 0 indicates an *Observer* male did not copy (16 or less of the first 25 pieces of string deposited were the Demonstrated string) correlated with the strength of the *Observer* males initial colour preference for the non-demonstrated string (x-axis) for both the Successful (grey circles) and Unsuccessful (black triangles) groups. Each male is represented by a single dot. The grey line represents the regression curve for the Successful group (McFadden's $R^2 \leq 0.37$), the black line represents the regression curve for the Unsuccessful group (McFadden's $R^2 \leq 0.53$).

| | | | |
|---|---|---|---|
| Preference for the Demonstrated string in test final preference test ~ Time with coconut fibre + Nest size + Time before initial preference test | | | |
| Predictor | $\chi^2$ | $p$ | Holm-Bonferroni adjusted $p$ |
| Time with coconut fibre | 0.02 | 0.88 | 1.00 |
| Nest size | 3.11 | 0.08 | 0.62 |
| Time before initial preference test | 0.30 | 0.58 | 1.00 |
| Preference for the Demonstrated string in the final preference test ~ Number of initial preference test trials + Duration of male interaction with string + Number of initial preference test trials * Duration of male interaction with string | | | |
| Predictor | $\chi^2$ | $p$ | Holm-Bonferroni adjusted $p$ |
| Number of initial preference test trials | 0.13 | 0.72 | 1.00 |
| Duration of male interaction with string | 2.07 | 0.15 | 1.00 |
| Number of initial preference test trials * Duration of male interaction with string | $\leq 0.01$ | 0.97 | 1.00 |
| Preference for the Demonstrated string in the final preference test ~ Pre-observation phase duration + Observation phase duration | | | |
| Predictor | $\chi^2$ | $p$ | Holm-Bonferroni adjusted $p$ |
| Pre-observation phase duration | 1.12 | 0.29 | 1.00 |
| Observation phase duration | 0.11 | 0.73 | 1.00 |
| Did copy ~ Initial colour preference | | | |
| Predictor | $\chi^2$ | $p$ | Holm-Bonferroni adjusted $p$ |
| Strength of initial colour preference | 0.58 | 0.45 | 1.00 |

*Table 1.* **Results from logistic regression models.** Table 1 shows the results from four logistic regression models evaluating how variation in the *Observers* experience throughout the various phases of the experiment is related to copying in the final preference test. Each model is shown, followed by its corresponding test statistic(s), non-corrected p-value(s) and Holm-Bonferroni adjusted p-value(s).

## Discussion

In the current study, I asked whether zebra finches with nest-building experience (*Observers*) would copy the colour of the nest-building material used by conspecific *Demonstrators*. The *Observers'* behaviours in the final preference test indicate that when zebra finches have experience building a nest, they do not copy the colour of nest-building material used by the *Demonstrators*. Specifically, the *Observers* preference for the Demonstrated string did not change from the initial to the final preference test. These data indicate that there was no evidence of social learning about the nest-building material choice. In addition, the results showed that variation within the *Observers* experiences in the initial nest-building experience, initial preference test, pre-observation and observation phases did not affect their copying of the Demonstrated string. Furthermore, the results showed that the *Observers* had a pre-existing groupwise preference for orange string.

I also asked whether copying of the Demonstrated string would differ between zebra finches who were Successful in their previous nest-building attempt (pairs that produced and fledged chicks) compared to pairs who were Unsuccessful (they failed to produce chicks). Contrary to my prediction – that Unsuccessful pairs would more readily copy the Demonstrated string than Successful pairs – neither the Successful nor the Unsuccessful group showed evidence of copying the Demonstrated string. Further, the results indicate that social learning did not differ between the Successful and Unsuccessful groups with respect to the nest-building material selection (touching, picking up, and carrying) and nest building (depositing) behaviours, in addition to preference for the Demonstrated string. These data suggest that despite experiencing what was intended to be a dissatisfying experience in the initial nest-building experience, the Unsuccessful group did not more readily use social information from

Demonstrators compared to the Successful group, as would be predicted by the *copy-when-dissatisfied* social learning strategy (Laland, 2004).

**The influence of *Observers* previous experience on subsequent nest-building behaviours**.

The *Observers'* choice to not copy the Demonstrated string is indirectly supportive of the *copy-when-uncertain* strategy. The *copy-when-uncertain* strategy predicts that when an individual is uncertain (meaning the animal has no relevant knowledge to drive their behaviour), they are more likely to socially learn from the behaviours of others (Laland, 2004). This was the case in Guillette et al. (2016), as the naïve zebra finches copied the nest-building material choice of the familiar Demonstrators. Whereas when an individual's personal experience decreases their uncertainty, it is predicted that they will disregard social information (Kendal et al., 2005). As the *Observers* in the current study built a nest during the initial nest-building experience before watching the *Demonstrators* nest building, this experience would be expected to decrease the *Observers* uncertainty regarding future nest building behaviours because they now have relevant experience that they can recall to inform future attempts. As such, the *Observers* would not meet the criteria under which the *copy-when-uncertain* strategy would predict them to copy (Laland, 2004). The *Observers* behaviour indirectly supports this social learning strategy as here the *Observers* are in the opposite state (being certain rather than uncertain) of which this strategy predicts social learning, so then we would expect the negative finding of social learning or not copying. In other words, these data reveal that when an Observer has an experience that makes them certain (i.e., they have relevant experience), then the Observer does not copy. Similar findings, where individuals who have acquired reliable information from a previous asocial experience tend to disregard social information, have been found in the foraging domain (Kendal, Coolen, & Laland, 2004; Leadbeater & Florent, 2014; Van Bergen, Coolen, & Laland, 2004; Wood, Kendal, & Flynn, 2013). These data suggest that the effects of a relevant personal experience on an animal's choice to disregard social information is a finding that can be replicated in multiple domains and across different species.

In providing support for the *copy-when-uncertain* strategy, the data from the current study provides evidence contrary to the prediction that the choice of nest-building material in zebra finches is a culturally driven behaviour (Guillette et al., 2016). Behaviours that are considered evidence of culture in animals are those perpetuated by the transmission of social information by individuals who live in the same group (Hoppitt & Laland, 2013; Laland & Hoppitt, 2003). Experimental findings indicate that culturally transmitted behaviours can (but do not always) produce a fitness benefit, such as allowing an individual to quickly adapt to a new environment via acquiring the behavioural norms of local individuals (Franz & Matthews, 2010; Laland & Williams, 1998; Van De Waal, Borgeaud, & Whiten, 2013). For instance, vervet monkeys (*Chlorocebus aethiops*) were found to disregard their previous experience about the palatability of differently coloured maize corn, instead adopting the preference for the colour of maize corn preferred by local individuals when joining a group (Van De Waal et al., 2013). In this study, naïve vervet monkeys (naïve due to either migrating from one group to another or naïve because the monkeys were maturing juveniles) were tested for their preference of either pink or blue maize corn after being trained to find maize corn in one of these colours distasteful. In the training, groups were presented with both the blue maize corn and the pink maize corn, one of which was made distasteful, while the other was unaltered. Groups were then provided with these diets for three months. After the presentation of these diets, van de Waal and colleagues (2013) tested whether the naïve individuals would adopt the same maize corn colour preference as the local group. During the test, individuals were presented with both coloured maize corn options (neither of which was distasteful at this point), recording both the colour of corn first consumed and the proportion of their diet that matched the local preference. Juveniles were tested to see whether they would copy the preferences of their mothers. In contrast, males who migrated from one group to another were tested to see if they would copy the local preference (most males traversed to a group trained to prefer the maize of the opposite colour to that of the migrating males, the rest had not been trained before). If the juvenile vervet monkeys copied their mothers' food choice, that would suggest that the groups maintained a food preference based on its colour even when the associated consequence (being distasteful) is no longer relevant. Whereas if the migrating male vervet monkeys adopted the diet of the group they joined, this would be indicative of the cultural transmission of a behaviour as the arriving individuals are acquiring a food preference based on social information contradictory to their personal experience. Van de Waal and colleagues (2013) found that the naïve vervet monkeys acquired the food preference of the local groups, supporting the above predictions.

The *Observers'* behaviours in the current study are contradictory to these discussed that would be indicative of culture. Had all the *Observers* copied the Demonstrated string, this would provide evidence of culture in the nest-building material selection of zebra finches as despite being certain about how to build a nest, the *Observers* would be disregarding their initial preference to match that of familiar individuals already in the process of nest building. As such, the *Observers* would be copying the nest material choice of the *Demonstrators* despite any apparent cost or benefit to using one colour of string over the other, instead opting to copy because they had been presented with this social information. However, as the *Observers* showed no evidence of social learning, while naïve individuals copy the nest material of familiar

*Demonstrators*, it appears as though social learning about nest-building material is only of benefit when a zebra finch has no relevant information to guide their behaviour (Laland, 2004).

Unlike Guillette and colleagues' (2016) previous work, the present *Observers* possessed a pre-existing preference for the orange string. The present *Observers* had never participated in any research before starting this experiment, so the exact reason why the majority of *Observer* males preferred orange string is unknown. Previous work with zebra finches has found that initial colour preferences can impact mate selection, with the colour of plastic leg bands and bill colour affecting mate choice (Burley, Krantzberg, & Radman, 1982; Price, 1996). These data suggest that even if a pervasive colour preference is arbitrary, groupwise preferences for one colour can drive behaviours of interest. Perhaps the *Observers* preference for orange string here is driven by a similar mechanism where the colour of some object the *Observers* were exposed to has led to the development bias towards the colour orange that was strong enough to discourage copying. However, this colour preference developed, the sample did show a groupwise preference for the colour orange rather than an equal preference for orange and pink, which may have influenced the results as if the preference for the colour orange is not based on an arbitrary choice, the *Observers* would have a reason other than their previous nest-building experience which could be driving their decision not to copy.

The results also indicate that variation within the *Observers* experience throughout the experiment is of no consequence to the *Observers* choice to copy the Demonstrated string. The logistic models measuring whether copying in the final preference test was predicted by differences between *Observers* in the (1) initial nest-building experience, (2) initial preference test phase, and (3) the pre-observation and observation phases and (4) how strong the *Observers* preference for the Non-demonstrated string all found that the differences measured were inconsequential to the choice of copying. These findings suggest that after building a nest, zebra finches become more certain about the behaviours involved, which can guide future nest-building attempts (Laland, 2004). Further, neither how the experience of building the first nest manifests, nor variation in the experience between the completion of the first nest to the start of the second nest, affects the certainty provided in that experience. In other words, *Observers* cease to need to acquire new information about nest building after gaining a second experience, even if social information is made readily available (Giraldeau et al., 2002).

### Differences between the Successful and Unsuccessful groups.

When tested separately, neither the Successful nor the Unsuccessful group copied the Demonstrated string just as was the case for the *Observers* as a whole, providing no evidence of social learning. For the Successful group, their choice to not copy the Demonstrated string is in line with the *copy-when-dissatisfied* strategy (Laland, 2004). Given that this social learning strategy predicts that individuals will only copy when the outcome of their behaviour is sub-optimal, the Successful groups' experience does not satisfy this condition. The Successful group's previous experience involved building a nest where they could raise chicks and seek shelter, meaning they achieved the primary functions of a nest (Healy et al., 2008; Laland, 2004). Further, the Successful group relying on their previous experiences to inform their future nest building behaviours would not be a costly behaviour as the personal information they have from their experience is indicative of a behaviour that produces an optimal outcome. Simultaneously, there is no guarantee that copying the Demonstrators would produce as good or a better outcome (Kendal et al., 2005; Laland, 2004; Rendell et al., 2010; Rieucau & Giraldeau, 2011). Similar findings have been produced from research investigating the use of social information in foraging bumblebees (Leadbeater & Florent, 2014). This study demonstrated that bumblebees disregard social information about a rewarding flower species if they had previously acquired personal information about a different flower species being rewarded (Leadbeater & Florent, 2014). These findings show that when an individual's behaviour is satisfied with the outcome, these individuals have no reason to copy the behaviour of another (Grüter, Czaczkes, & Ratnieks, 2011; Laland, 2004; Rendell et al., 2010).

The reason(s) why the Unsuccessful group did not copy the Demonstrated string is unclear. As discussed earlier, the experience of building a nest but failing to produce chicks in that nest was intended to be a dissatisfying experience for the Unsuccessful group as one of the primary uses of a nest is to provide birds with a space in which they can produce and rear young, so failing to do so would make their nest sub-optimal (Healy et al., 2008; Laland, 2004; Muth & Healy, 2011). We know that birds can associate their ability to produce chicks with both their nesting site (Dow & Fredgat, 1983; Herlugson, 1981) and nest-building material (Muth & Healy, 2011). For these reasons, I predicted that the Unsuccessful group would copy the Demonstrated string as their experience fits the conditions under which the *copy-when-dissatisfied* strategy predicts social learning will occur (Laland, 2004). As social learning by the Unsuccessful group did not occur, I will attempt to provide some rationale that might explain the Unsuccessful group's behaviour.

One possible factor that might have contributed to the Unsuccessful groups' choice not to copy the Demonstrated string is that failing to produce chicks during the initial nest-building experience was not an outcome sub-optimal enough to warrant social learning (Kendal et al., 2005; Laland, 2004). As discussed in the introduction, social learning can provide an Observer with benefits; however, it is not without its costs. In social learning theory, the occurrence of social learning is thought to occur when the costs of acquiring or relying on asocial information are greater than the costs that could be incurred through social learning (Giraldeau et al., 2002; Kendal et al., 2005; Rendell et al., 2010; Rieucau & Giraldeau, 2011). Along these lines, perhaps the behaviour of the Unsuccessful group indicates that the cost of relying on their previous experience to guide their future nest-building behaviours is not greater than the perceived risk of copying the *Demonstrators* material choice. While yes, the Unsuccessful group did fail to produce chicks in their initial nest, the nest still provided the pairs with shelter. Further, the experience that the Unsuccessful group had when interacting with the two types of string provided had no negative consequence as they were able to interact with it and then it was removed, which would not constitute a costly acquirement of asocial information.

Additionally, unlike zebra finches in the wild, the Unsuccessful group did not face the same breeding challenges and risks associated with breeding, including predation and difficulty finding food and water (Zann, 1996). With these factors in mind, the Unsuccessful group faces little relative costs in breeding failure as they are safe from predation and are provided with enough food, water and supplements that may negate the energy and caloric costs of producing eggs to no avail. Similar findings, where an animal provided with social information continue to behave based on previously acquired asocial information rather than change their behaviour based on the social information, even when the social information may reduce costs for the animal, has been found in bees. Work done with honeybees (*Apis mellifera*) found that they continue to rely on previously learned information rather than socially learn even when continuing to rely on previous experience would be costly (Grüter, Segers, & Ratnieks, 2013). Grüter and colleagues (2013) trained honeybees to forage at a food source either near or far from their hive. Both the near food source trained group and the far food source trained group then observed a Demonstrator performing a waggle dance with information about a new food source equidistant from the hive as the near food source but in the opposite direction. After being provided with the opportunity for social learning, both groups of bees were then tested for their choice of foraging site to determine whether they would make use of the social information provided or rely on the information acquired from their own experience. Grüter and colleagues (2013) predicted that honeybees trained to go to the further food source would be more likely to use social learning, which would constitute an example of the *copy-if-asocial-information-is-costly* strategy (Laland, 2004). Contrary to the researcher's predictions, the bees trained to forage at the further food source continued to rely on their previously acquired and more costly asocial information (Grüter et al., 2013). Through relying on their previous experience over the newly provided social information, the bees incurred an energy cost, but at the same time may be choosing to behave on the more reliable information (Grüter et al., 2013).

Another possible explanation for why the Unsuccessful group did not copy the Demonstrated string during the final preference test might be that these birds did not transfer their association from the nest-building material used in the initial nest-building phase to the novel material provided during the test phases. In the previously discussed Muth and Healy (2011), the authors found that zebra finch males changed their preference after a successful breeding attempt. In their study, after zebra finch pairs built a nest out of coconut fibre of their non-preferred colour and successfully raised chicks to nutritional independence, the males changed their preference from their initially preferred colour of coconut fibre to that of the colour used to build their nest in which they produced chicks. However, the same study found that after failing to produce chicks (in a similar manner used in the current study), males maintained their preference for their initially preferred coconut fibre regardless of nest success. After these findings, the authors posited that perhaps the reason for the maintenance of the initial material preference after an unsuccessful breeding attempt is that perhaps strong initial preferences are difficult to change after using this material to build a nest (Muth & Healy, 2011). While the current study involved testing zebra finches' preference between two novel nest building materials after an initial nest building experience, I did test whether the strength of the initial preference affected copying of the Demonstrated string. As I found null results, these eliminate the explanation that it is the strength of the initial preference that influence a change in the initial preference. These data suggest, going back to the *copy-when-uncertain* strategy, that it is simply acquiring experience that reduces uncertainty that impacts social learning about nest-building material regardless of whether that experience is satisfying. Alternatively, the *Observers* may not have transferred the association of nest failure or success to the material provided in the test phases. We know that the *Observers* did learn to associate the nest-building material in the initial nest-building attempt with nest success, thanks to a follow-up study which examined in a subsequent nest-building attempt would the *Observers* use more coconut fibre or a third novel nest-building material (Camacho-Alpízar et al., 2021). We found that the Successful group used more coconut fibre than the third novel material in their nest, suggesting a learned association (and therefore preference) between the initial nest-building material and their initial nest's success. Whereas the Unsuccessful group used an equal amount of the coconut fibre and the novel nest-building material, suggesting not so much an avoidance of the initially used material, but rather a willingness to incorporate new materials in their nest. As the initial nest-building material was not present during any of the testing phases, the *Observers* never had a chance to interact with it again during the present study, forcing them to make a choice between novel material, neither of which they had experience with. Further the string differed in not just colour, but in composition, rigidity, and other physical properties. As such it may have been that the

*Observers* evaluated this novel material in a novel environment as being different enough to not warrant transferring the association from the initial nest-building material to this new material and without a cost associated with this material there may not be a reason to copy the Demonstrated string.

Across the initial nest-building experience, the initial preference test, the pre-observation phase, and the observation phase, the only experience that differed between the Successful and Unsuccessful groups was the manipulation of their nest success in the initial nest-building experience. As there were no differences in the experience of *Observers'* other than the nest success, we can say that any differences (or lack thereof) in copying between the Successful and Unsuccessful groups was due only to the success of their previous nest. The results suggest that the impact of the success of the previous nest on social learning by *Observers* when building a second nest was null, as (1) the preference for the Demonstrated string did not change for either the Successful or Unsuccessful group from initial to final preference tests, (2) there was no difference in the number of Successful versus Unsuccessful males who used the Demonstrated string for their nest selection and nest-building behaviours (touch, pick up, carry or deposit) and (3) the latency to begin nest construction did not differ between the Successful and Unsuccessful groups.

Not only do the Successful and Unsuccessful groups not show evidence of copying, but their behaviour also shows no evidence of social information use at all. The social information provided by the *Demonstrators* does not only include the colour of string chosen to build their nests but also their nest material selection (touching, picking up, carrying) and building behaviour (depositing string). If males in either or both the Successful and Unsuccessful groups had first touched, picked up, carried, or deposited the Demonstrated string and still maintained their initial colour preference, we could say that there is evidence of the males acquiring social information. The evidence of social information here would be that aspects of their second nest-building attempt would mirror that of the social information provided. As *Observers* did not copy any aspect of the social information provided, the question becomes, did the *Observers* acquire any information provided from the *Demonstrators*? Guillette and colleagues (2016) found that naïve nest-building zebra finches will copy the material choice of a familiar individual. However, when the Demonstrator is unfamiliar, the Observer zebra finches will ultimately not copy, yet still, show evidence of social information use as they touched and picked up the material used by the Demonstrator first. As neither the Successful nor Unsuccessful groups copied any nest-building behaviour presented by the *Demonstrators*, it is unclear if they even acquired information from the *Demonstrators*. However, as discussed for all *Observers,* individuals may tend to disregard social information when individuals have relevant previous experience, which these data lend more credence to support (Kendal et al., 2004; Leadbeater & Florent, 2014; Van Bergen et al., 2004; Wood et al., 2013).

The Successful and Unsuccessful groups did not differ in the latency to first touch, pick up, carry, deposit, deposit 25 pieces and deposit 50 pieces of string during the final preference test, indicating that both groups began and completed their nest construction at the same speed. Previous research has found differences in the nest construction speeds of first-time nest builders between zebra finches who had the opportunity to observe conspecifics nesting prior to observing an artefact, compared to individuals who did not have the opportunity to observe conspecifics nesting. Specifically, zebra finches who had the opportunity to observe conspecifics nesting before artefact observation both began and completed building their nest faster than individuals who did not observe nesting familiar conspecifics (Camacho et al., in prep). Similar findings (that nest construction speed differed as a result of experience) has also been found in first time builders, where zebra finches who had access to nest-building material and/or a conspecific adult male, built their nests faster than conspecifics without access to material and/or an adult (Breen et al., 2019). As the present study found no differences between the Successful and Unsuccessful groups nest construction speed, these data suggest that having previous experience building a nest eliminates differences in nest construction speed regardless of whether that nest was successful.

### Future Directions.

Given both the design and results of the current study, there are two follow up questions that could be pursued. First, I would be interested in testing whether making an alternative aspect of the nest-building process dissatisfying might influence the use of social learning in nest material choice. As mentioned previously, according to the *copy-when-dissatisfied* strategy, if an individual's behaviour produces a sub-optimal outcome, it would be considered dissatisfying, which increases the likelihood of social learning (Laland, 2004). In the case of nest building, I thought that in failing to produce chicks, the nest-building experience of my Unsuccessful group would encourage them to socially learn from the nest-building behaviours of others as the primary functions of a nest are to provide a place to raise young and to provide shelter from the environment, one of which their nest failed in (Laland, 2004; Walsh, Hansell, Borello, & Healy, 2011). Perhaps, an alternative way of making the nest-building experience dissatisfying would be to allow the birds to build their nest and then have some birds' nests fail to provide adequate shelter by destroying a part of the nest. After simulating a nest failure through nest destruction, the project would involve running an experiment in a very similar fashion to the present study repeating the initial preference test, pre-observation, observation, and final preference test phases after the destruction of the nest. In having the nest be destroyed in some manner, there may perhaps be a more direct link between the nest's failure to provide protection and the material used as described above, compared to associating the nest material and the removal of eggs.

The second follow up question involves investigating whether there is repeatability in nest-building behaviours across multiple nests. Part of the current project involved the observation phase in which the *Demonstrators* modelled building a nest with a given material. Six *Demonstrators* pairs were used for the observation phase, all of whom built multiple nests. Thus, the other possible project would be examining the behaviours the *Demonstrators* engaged in across trials to look for repeatability in individuals. In doing, so, we have the opportunity to gain new information not about social, but rather asocial learning in nest-building behaviours. Previous research with Southern Masked weaverbirds (*Ploceus velatus*) found that material handling behaviours vary between individuals and that the weaving becomes ‘neater’ as individuals acquire more experience, however, these studies called for more research to be done to examine the effects of experience on nest building (Collias & Collias, 1964; Walsh et al., 2011). Thus, as my *Demonstrators* had multiple attempts (between 2 and 7) to build a nest, the same could be tested. One could investigate the latency to nest completion or the average number of pieces of string deposited per hour and other behaviours pertinent to building the nest that show an increased performance due to experience.

### Conclusions.

I hypothesized that zebra finches that had previously built a nest and failed to produce chicks would be more likely to socially learning about novel nest-building material when choosing material for a subsequent nest than zebra finches whose previous nest did produce chicks. Instead, I found that regardless of the previous nests’ success, experienced nest-building

*Observers* did not copy the material choice of a *Demonstrator* when choosing which material to use in building their second nest. Moreover, there were no differences in social learning between the Successful and Unsuccessful groups, as not only did their preference for the Demonstrated string not differ, neither their choice of nest-building material during the nest-building material selection behaviours (touching, picking up, and carrying) nor their nest construction behaviours (depositing) differed. These findings contradict the ‘when’ social learning strategy known as the *copy-when-dissatisfied* strategy and instead provide support for the *copy-when-uncertain* strategy.

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## Appendices

### Appendix 1: Table of methods to experimentally test social learning in animals.

| | |
|---|---|
| Multiple Demonstrators | In this experimental method of testing social learning, the researcher will present a single Observer with multiple Demonstrators performing a behaviour and record whom the Observer chooses to copy. In this design, the researcher can test questions regarding who an Observer chooses to copy based on characteristics of the Demonstrator (i.e., age, sex, size) |
| Multiple Observers | In this experimental method of testing social learning, the researcher will present a single Demonstrator performing a behaviour to multiple Observers and test which Observers choose to copy the Demonstrator. In this design, the researcher can test differences between Observer groups that might affect who chooses to copy or not, based on features of the Observer or the context regarding the behaviour (i.e., familiarity or naivety) |
| Linear Transmission Chain | In this experimental method of testing social learning, the researcher will first train an initial individual to perform a behaviour. The trained individual becomes a Demonstrator for an Observer. Upon the Observer learning the behaviour from observation, the Observer then becomes a Demonstrator for another Observer and so on. In this design, a researcher can test how a behaviour changes over Observer/Demonstrator combinations. |
| Replacement Transmission Chain | In this experimental method of testing social learning, a group of individuals are trained to perform a behaviour and then are gradually replaced with naïve individuals rather than just having one individual be trained and then act as Demonstrator for an Observer as in the linear transmission chain. In doing so, social learning (and thereby copying) can be seen in the |

| | |
|---|---|
| | behaviour of the replacement group members. The advantage to the replacement transmission chain method is that this method still maintains some experimental control, but the social interactions and environment appear more akin to those found in the wild |
| Open Diffusion | In this experimental method of investigating social learning, an initial individual will be trained in a behaviour by the researcher. After which, the trained individual will be placed into a population that does not have training in that behaviour. Then the researcher will observe how the behaviour is ‘diffused’ through the group from the initially trained individual and so on. |

## Appendix 2: General Husbandry tasks – Required daily for all birds in Tristan's Experiment.

Supply locations:

1. 419A – On the cart for transporting supplies: food, supplements, and water supplies
    a. Extra grit'n'gravel, oyster shells, cuttlebones, spray millet, and vitamin mix can all be found on the bookcase in the southeast wall of 419A
    b. The broom, dustpan and squeegee are located against the southwest wall

2. 419R – Demineralized water line, transport containers for cups and tubes to be washed
    a. For vitamin-enriched water; mix 20 grams of vitamin powder for every 3600mL

3. P-108 – In the fridge: spinach

4. 419T – clean water cups and vitamin mix tubes, brooms, mop, squeegee, replacement Kraft paper and cutting station, drying racks

Daily Care tasks:

1. Gather cart with supplies from 419A

2. Check health and status of birds visually (i.e., loss of feathers, check for blood)
    a. If there is a problem, report to PI/Supervisor and SASS immediately

3. Do all steps below for each cage before moving to the next cage
    a. Top up food
    b. Top up Petri dish with grit'n'gravel and Oyster shells if necessary (approximately 75% oyster shells, and 25% grit'n'gravel)
    c. Water
        i. M/W/F –fill watering tubes up to about halfway (2 per cage) and empty and wash out water cups using the sink in 419T just rinsing in water then place in racks to dry on M/F

        ii. Tu/Thu/Sat – empty watering tubes of excess vitamin mix into a bucket and place tubes into another bucket and put two water cups into each cage filled about 75%. Rinse the tubes in the 419T sink on Tu/Sat and place them on the drying rack
        iii. Sun – replace water from cups again to 75% full
        iv. W – leave the cups out in the large container from SASS located in 419R for SASS to wash
        v. Thu – retrieve the cups from 419R cleaned by SASS and provide them with the tubes in the small container located in 419R for SASS to wash
    d. Supplements
        i. Spinach MWF (a few leaves) in each cage
            a. If deplenished, ask appropriate grad student to by more
        ii. Spray millet Th one piece in each cage
            a. If deplenished, as SASS for more
        iii. Cuttlebone when depleted
            a. If deplenished as SASS for more
        iv. If nest building/incubating/breeding/raising fledglings/or there are juveniles, provide egg mix in a Petri dish 1-2 times a day

4. Check temperature and humidity
    a. Report min-max and current for both on room checklist sheet and clear thermo-hydrometer

5. Sign checklist sheet

6. Clean up and disposal
    a. Dirty water is to be poured down the sink in 419T using the strainer located on the cart, any waste caught in the strainer is to be thrown in the trash bins in the hallway
    b. Using the sink in 419T, rinse both the inside and outside of any tubes or cups collected while doing care on every day except W/Thu and place them in the

drying racks located on the table by the sink. When done, lay one rack over the sink to drain and hang the other over the table edge with a bucket below to drain into.

c. The hallway from 419R to 419A is to be swept daily using the brooms in 419T

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

1. Sweep floor in the room using the broom and dustpan located in 419T and deposit waste into a trash can in the hallway specifically labelled for our laboratory
2. Kraft paper replacement if necessary

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June 19th, 2019 – Tristan Eckersley created
Jun 25th, 2019 – Tristan Eckersley added revisions
November 15th, 2019 – Tristan Eckersley added revisions