



Learning about construction behaviour from observing an artefact: can experience with conspecifics aid in artefact recognition?

Andrés Camacho-Alpízar¹ · Tristan Eckersley¹ · Connor T. Lambert¹ · Gopika Balasubramanian¹ · Lauren M. Guillette^{1,2}

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Abstract

Observation of or interaction with the enduring products of behaviour, called ‘social artefacts’ (e.g. an abandoned nest) is a potential source of social information. To learn from an artefact, that artefact needs to be recognized as the product of a behaviour that can provide relevant information (i.e. the artefact should be recognized as a nest). We used zebra finches (*Taeniopygia guttata*) to experimentally test whether observing a conspecific using a nest facilitates recognition of a future artefact as a source of social information. We manipulated the opportunity to form an association between a conspecific and their nest: half the subjects observed a pair of birds incubating eggs in a nest, the control subjects did not get this opportunity. Then, subjects observed an artefact made of their non-preferred colour and finally were allowed to build a nest. We predicted that the subjects given the opportunity to associate a nest with conspecifics would copy the colour of the artefact (i.e. use social information). We found that subjects who had the opportunity to learn what a nest is used social information obtained from the artefact by increasing their use of the artefact-material colour after artefact observation, while control birds did not. These data suggest that forming an association between conspecifics and their nest facilitates recognition of an artefact as a nest affecting how first-time builders use social information. This finding is important because it demonstrates that social learning is not limited to observing behaviour, but rather inferring behaviour from an artefact.

Keywords Animal construction · Artefact · Decision making · Material preference · Nest construction · Social learning · Zebra finch

Introduction

Animals can acquire information about their local environment from observing the behaviour of others (i.e. social information; Mesoudi et al. 2016). Social information can take several forms; for example, a conspecific eating a novel food provides information about which food is safe to eat (e.g. Galef and Whiskin 2004; Guillette and Healy 2014) or a vocalization produced by an individual informing the listener about the presence of predators (e.g. Seyfarth et al. 1980; Magrath et al. 2015). Social information can also be gathered by observing or interacting with

the *products* of another individual’s behaviour, such as scratch marks on bear (*Ursus americanus*) rubbing trees informing the presence of a potential predator/competitor (Preston Taylor et al. 2015), or excavations made by burrowing animals like giant armadillos (*Protonotaria maxima*) indicating the presence of potential prey (Desbiez and Kluyber 2013). Other examples include scats informing the presence of potential prey, predator or competitor (Rothman and Mech 1979), and ant-made foraging trails in deserts informing colony members of novel food sources (*Acromyrmex versicolor*; Gamboa 1975). Two examples of social learning (i.e. learning from social information *sensu* Heyes 1994) via observing or interacting with the products of others’ behaviour are black rats (*Rattus rattus*) that learn to remove pine seeds from cones by interacting with discarded, but partially opened cones (Terkel 1996; Zohar and Terkel 1996) and black-capped chickadees (*Poecile atricapillus*) that learn to open cream tubs by interacting with a previously opened tub (Sherry and Galef 1984).

✉ Lauren M. Guillette
guillett@ualberta.ca

¹ Department of Psychology, University of Alberta,
Edmonton, AB T6G 2R3, Canada

² School of Biology, University of St Andrews, St Andrews,
UK

These products of another individual's behaviour (e.g. half-eaten pine cone or opened cream tub) are behavioural or social artefacts (*sensu* Fragaszy et al. 2013).

Some types of enduring behavioural artefacts (e.g. discarded tools, abandoned animal-made structures) may also aid conspecifics in learning how to make and/or use a tool or how to build a structure. For example, juvenile chimpanzees (*Pan troglodytes*; Humle et al. 2009), tufted capuchin monkeys (*Sapajus* spp.; Coelho et al. 2015) and New Caledonian crows (*Corvus moneduloides*; Holzhaider et al. 2010) manipulate previously used and discarded tools which might allow them to learn different aspects about tool manufacture and use (Fragaszy et al. 2013). Animal constructions such as nests that persist in the environment after they are discarded could also act as artefacts that serve as a source for tactile and visual exploration about nest location, material selection, material use, and/or structural morphology of the nest. Chimpanzees, for example, construct a new nest each night in which they sleep and seem to choose where to build their nests based on the presence of use-wear scars from other individual's previous nesting activity, which could indicate the branch's structural integrity (Stewart et al. 2011).

Learning from the observation or interaction with an artefact would require that the learner recognizes such artefacts as the product of a conspecific's behaviour that can potentially provide useful information for the task at hand (Borgo et al. 2013). In the context of nest-building behaviour for example, learners would need to recognize an artefact as a nest built by another individual.

How do animals know that an artefact contains relevant to-be-learned information? Recognizing an artefact as the product of another's behaviour that is relevant for a given task could be achieved through associative learning by viewing a conspecific using that specific object or other objects of the same functional category (e.g. flat stones that can be used as anvils). Observational evidence from studies in the field shows that learners usually have experienced observing conspecifics using artefacts before they themselves interact with an artefact (Coelho et al. 2015; Fragaszy et al. 2013; Holzhaider et al. 2010; Humle et al. 2009; Ottoni et al. 2005). Experimental laboratory data on zebra finches (*Taeniopygia guttata*) show that observing a nest built by another male (the social artefact) affects material selection in first-time nest builders (Breen et al. 2019), but not to the same extent as if the birds were observing the behaviour of nest building (Guillette et al. 2016). Unlike the current experiment, the focal birds in Breen et al. (2019) were not afforded the opportunity to first form an association between a conspecific nest and the builder of that nest. In fact, the only previous experience the subjects in Breen et al. (2019) had with a nest was with their natal nest, and evidence shows that zebra finches do not copy the material colour of their natal nest and use that experience to inform future nest-building

decisions (Breen et al. 2020; Muth and Healy 2012; Sargent 1965).

In the present study, we aim to explore the role that the experience of observing social demonstrators using a potential artefact plays in the recognition of an artefact as an object that provides relevant information for a given task. We designed an experiment to determine whether associating a nest with its builder (a conspecific) via observation of a conspecific breeding pair using, but not building, a nest allows zebra finch males to recognize an artefact as a nest in future encounters. If observing a conspecific using a nest allows zebra finch males to recognize artefacts they encounter afterwards as nests, then males that have such experience should, in a subsequent nesting event copy the material colour of an artefact, while birds that did not have the opportunity to potentially form an association between a nest and its builder should not. Research on zebra finches has also found evidence that males who had access to material or adults as juveniles, built their first nest faster than males without such experience (Breen et al. 2020). Therefore, observing a conspecific using a nest prior to building a first nest, may have a similar effect and result in faster nest-building speed. Therefore, we also predict that males who observe conspecifics using a nest should build a nest faster than males who did not get such opportunity.

Materials and methods

Subjects and housing

Eighty-two zebra finches (41 male, 41 female) either bred at the University of Alberta ($n=62$) or obtained from a breeder in Quebec, Canada ($n=20$) were housed in same-sex cages ($165 \times 66 \times 184$ cm) in colony rooms on a 14:10 light:dark cycle with overhead fluorescent full spectrum lights (Standard, 32 W, T8 Daylight). Room temperature ranged from approximately 20–23 °C and humidity from 35 to 50%. Birds were given free access to mixed seeds (Hagen Canada), grit (Pacific Pear Oyster Shell and Hartz Grit 'n Gravel) and cuttlefish bone (Canadian Lab Diet). Birds' diets were supplemented with vitamin water (Hagen Canada) and greens (e.g., parsley, spinach) three times a week and spray millet (Hagen Canada) once a week.

Apparatus

Experience and test cages ($100 \times 50 \times 50$ cm, Kings Cages) each contained six perches, two food bowls, two water bowls, grit and cuttlefish bone (Fig. 1). The cage floors were lined with brown paper (U-line Kraft paper). Experimental rooms were kept under the same lighting, temperature and humidity conditions as the colony room. Each cage was provided

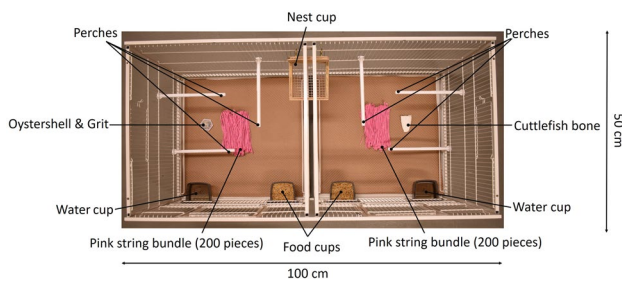


Fig. 1 Top-down photo of the experience/test cage layout specifically used for artefact building, which includes a nest cup and two bundles of pink string (200 pieces each)

food, water and supplements with the same frequency as the colony rooms. Each pair that was building a nest was given egg mix daily (CeDe-Finches).

Experience rooms Two rooms contained experience cages: in one room pairs of zebra finches built nests that would be used as artefacts in the observation phase of the test (see below), in the second room pairs of zebra finches observed conspecifics using a nest, called the experience phase (see below). The birds in the experience cages had auditory, but not visual contact with one another, except when observing a live nesting demonstrator as part of the experimental treatment (see below).

Test rooms The test rooms contained two test cages placed in the center of the room. These test cages were placed back-to-back, 10 cm apart from each other, separated by an opaque barrier made of corrugated plastic, to prevent the observer pair from seeing the contents of the other cage. Each test cage contained three mini-BNC cameras (OSY CAMS): one tied to the roof at the center-top of the 100 cm side of the cage; and two tied at the center-top of each 50 cm sides of the cage, facing opposite directions.

Subjects

31 male–female adult pairs participated in the experiment as observer pairs. Each observer pair was naive about nest building: their only previous experience with a nest was their natal one which was made of coconut fiber (Aves Canada). An additional six male–female adult pairs built nests that served as artefacts in the social artefact observation phase (see below). Finally, four additional male–female pairs acted as live-nesting demonstrators in the experience phase (see below).

Social artefacts

Six male–female pairs built nests that served as social artefacts in the social artefact observation phase (see below). Each male was paired with a non-related female in an

experience cage for three days before being given 400, 15 cm long, pieces of jute craft twine (James Lever Co., Bolton, UK) and a wooden nest cup (12.5 × 12 × 12 cm). All 400 pieces were the same colour (orange or pink). Once a pair had used all the provided material, the nest was considered finished and removed. A nest was considered suitable for the experiment if it had the species-typical shape (domed nest), for which 400 pieces of 15 cm string is enough material (Breen et al. 2019). Then, we provided the pair 400 pieces of material of the other colour and a new nest cup. Therefore, each pair contributed two artefacts, one pink and one orange (Fig. 2). If a pair failed to construct a domed nest, it was given a new nest cup and string, until producing a domed nest of each colour. Only one pair failed to build a species-typical nest of one colour and was, thus, removed from the experiment. After building a suitable nest of each colour (five pairs) or failing to do so (one pair), these pairs participated in another experiment.

Live-nesting demonstrators

Four male–female pairs that had previously built a nest acted as live-nesting demonstrators. Each pair was given 400 pieces (15 cm long) of white cotton string (polished cotton twine, James Leaver Co., Bolton, UK) and a nest. After building a domed nest using all of the provided material (Fig. 3), we allowed each pair to proceed with their breeding (i.e. laying eggs and incubating). To extend the incubation period, we replaced each egg laid with plastic zebra finch eggs (DummyEggs, Florida, USA). After a live-nesting demonstrator pair participated in one or two live nesting observation events (see below), the nest was removed, and that live-nesting demonstrator pair would wait for at least five days before being provided a new nest cup and nesting material (white cotton string again) to build another nest and repeat the process of being a live-nesting demonstrator.

Procedure

Each observer male ($n = 31$) was randomly paired with a non-related female in the experience room at least four days prior to the start of the experiment to allow for a pair bond to form. During pairing, each observer pair had auditory but not visual contact with other birds in the room. Each observer pair was randomly assigned to one of two treatment groups: (1) birds that observed live-nesting demonstrators during the incubation period of breeding—hereafter nesting observers, and (2) birds who did not observe any live-nesting demonstration—hereafter control birds. The rationale is that information acquired via associative learning during the live-nesting demonstration would allow the observer birds in the nesting observer group to identify future nests as objects that provide relevant information for nest building.



Fig. 2 Photographs of the social artefacts—nests built by five different males. Each column shows two nests built by the same male, one using 400 pieces (15 cm long) of pink string and another using 400 pieces (15 cm long) of orange string



Fig. 3 Example of a dome-shaped nest built by a live-nesting demonstrator male using 400 pieces of white string (15 cm long)

The experiment consisted of four phases: (2) experience phase (2) initial colour preference test, (3) social artefact observation and (4) final preference test (Fig. 4):

1. *Experience phase* After forming a pair bond, each observer pair was moved to an experience cage in which they either had visual access to a live-nesting demonstrator pair (nesting observers; see Fig. 4i) or did not have visual access to any birds (control). The experience phase lasted five days, which is enough time for zebra finches in the wild to acquire social information about the breeding stage of their conspecific neighbours

to synchronize their breeding (Brandl et al. 2019), and it has been also shown to be enough time for first-time nest builders to acquire information on building-material selection from observing a conspecific building a nest (Guillette et al. 2016). In the afternoon of the last day of the experience phase, each observer pair was moved to a test room.

2. *Initial colour preference* The initial colour preference test started two hours after the lights came on in the morning after an observer pair had been moved to the test room. We placed two bundles of 15 cm long string (25 pieces each), one bundle of pink string and one orange, in the observers' cage, one on each side of the cage in front of the food cups (side randomized across observer pairs). The coloured string was tied to one of the long sides of the cage, so birds could interact with the string, but not use it to build a nest (Fig. 4ii). Each observer pair was allowed to interact with the string for four hours, after which we removed the material. Once the material was removed, we scored the video recordings using BORIS v. 7.8 (University of Turin) to determine the time the male spent interacting (i.e. touching the material with his beak, feet or body) with each string colour. If a male spent at least 30 s interacting with one or both bundles of string, we then assessed initial colour preference as the proportion of time the male interacted with each string colour ($n = 22$). However, if a male spent less than 30 s interacting with one or both bundles of string during the first four hours ($n = 8$), his colour preference would be tested again the following day (up to three days for a total of 12 h). If a male did not interact for at least 30 s with the string after three days

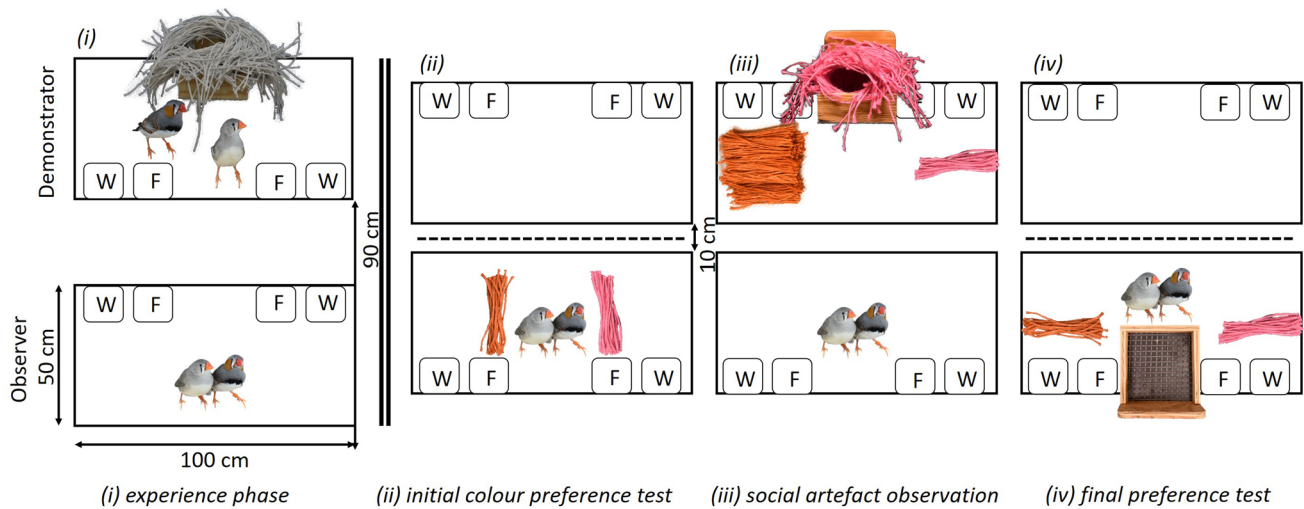


Fig. 4 Top-down schematic view of the experimental setup during the four experimental phases. The observer cage is shown on the bottom and the demonstrator cage on the top. **i** Each observer pair of the experimental group could see a pair of live-nesting demonstrators using a nest made of 400 pieces of white string, during the incubation period of breeding. Observer and demonstrator cages were 90 cm apart. Each observer pair in the control group had no visual contact with any birds during this phase. The remaining phases took place in a test room (represented by the double vertical lines). **ii** Each observer male was tested for his initial colour preference. During this phase, each male was able to interact with two bundles of 15 cm long string (25 pieces each), one pink and one orange, placed on each side of the cage in front of the food cups (randomized across observer pairs). The string was tied to one of the long sides of the cage, so a male could interact with the string but not use it to build a nest. The observer pairs were not able to see the contents of the demonstrator

cage because of an opaque barrier placed in between the observer and demonstrator cages (dotted horizontal line). **iii** During the observation phase, the opaque barrier was removed, and each observer pair was able to see the content of the demonstrator cage (10 cm apart) for 35 daylight hours. The demonstrator cage contained a nest of the observer male’s initially non-preferred colour (pink in this example), and two unsecured 15 cm material bundles of the initially preferred colour (orange in the present example: 425 pieces) and the initially non-preferred/demonstrated colour (pink in the present example: 25 pieces), placed on opposite ends of the cage floor. **iv** In the final preference test, we returned the opaque barrier and gave each observer pair a nest cup and 25 unsecured pieces (15 cm long) of each material colour, placed in the same relative position of the observation phase. The position of each material colour with respect to cage side (left or right) was randomly chosen between observer pairs but remained consistent within observer pairs. *W* water cup, *F* food cup

of testing, he would be removed from the experiment ($n = 1$).

3. *Social artefact observation phase* Once an observer pair finished the initial colour preference, a randomly chosen nest (the social artefact) of the observer male non-preferred colour was moved into the demonstrator cage in the test room (Fig. 4iii). We also placed two bundles of coloured (pink and orange) string on opposite ends of the cage floor, midway along the 50 cm sides of the cage. Each colour bundle mirrored the side they were placed during the initial colour preference phase for that observer. Field studies on various bird species have revealed that relative abundance of raw materials in the environment may affect animal construction decisions, namely that the proportion of different kinds of material found in nests corresponds to the relative abundance of those materials in the environment (e.g. Wang et al. 2009; Álvarez et al. 2013; Cantarero et al. 2015; Briggs and Deeming 2016). For this reason, the bundle of the initially preferred colour contained more pieces of string (425 pieces) than the demonstrated colour bundle (25 pieces) so the total amount of string (nest + bundles) in

the demonstrator cage was equal between colours, signalling equally material abundance in the environment. Having an equal number of each string typed controlled for a potential effect of demonstrated material abundance on material selection. The current experiment was thus designed so that observing individuals could not select their nesting material based on that material’s abundance in the environment, because material abundance was equal. The observation phase started the same day as the initial colour preference phase, immediately after the colour preference of the observer male was determined. We removed the opaque barrier between the observer and the demonstrator cage, allowing each observer pair to view the contents of the demonstrator cage for 35 daylight hours (Breen et al. 2019; Guillette et al. 2016).

4. *Final preference test* Immediately after the observation phase, we returned the opaque barrier so the observers could no longer see the social artefact. We also provided the observer pair with 25 pieces of each material colour (pink and orange—15 cm long) and a nest cup hung in the middle of the cage’s front wall (Fig. 4iv). We placed

the bundles of string on opposite ends of the cage floor, midway along the 50 cm sides of the cage, each colour on the same side as previous phases. Each observer pair was then checked remotely via streamed video, every morning and afternoon until all of the material was deposited into the nest. Once all material was deposited, the final preference test phase ended, and the observer pair was moved to a different room for breeding.

Behavioural scoring

Using BORIS v7.8, we scored the order of deposits of each colour and calculated the proportion of material colour deposited into the nest that was each colour (first 25 deposits only) for each observer male during the final preference test. A deposit was defined as material being brought to and placed into the nest. We also scored the latency to start nest construction (by depositing the first piece of material into the nest) and latency to deposit all 50 pieces of string, while accounting for time during which lights were turned off. Behavioural scoring was carried out blind to the treatment group. One pair in the nesting observer group was removed from the experiment due to experimenter error leaving final $n = 14$ in the nesting observer group and $n = 15$ in the control group.

Statistical analyses

All statistical analyses were performed using R v4.0.2 (R Core Team 2020). Goodness-of-fit of every model was assessed using the “DHARMA” package (Hartig 2020). Each model significance was tested using Type II Wald chi-square tests with the “car” package (Fox and Weisberg 2019). The final colour preference of the observers was measured as the proportion of the first 25 pieces of deposited string that were of the social artefact colour. Therefore, a score of 0 means that the male deposited first all of the 25 pieces of string from his initially preferred colour, a score close to 0.5 means the male deposited an equal number of pieces of each colour (initially preferred or demonstrated colour), and a score of 1 means the male deposited first all of the 25 pieces of string of the demonstrated colour.

To test whether demonstrated colour preference changed between the initial and final colour preference test, we built a within-subject generalized linear mixed model using the “lme4” package in R (Bates et al. 2015). The response variable was preference for the demonstrated colour (proportion chosen by each individual) and the predictor variables were the testing phase (initial vs final preference phase), experimental treatment (nesting observers vs control birds), demonstrated colour (orange vs pink), and the interaction between these terms initial preference strength (initial proportion preference for non-demonstrated colour). We also

included individual ID as a random factor to account for the repeated measures on each individual. We included the initial preference proportion of the demonstrated colour in our model to test whether males with a stronger initial colour preference (i.e. initial preference for preferred material closer to 1.0) were less likely to change their material-colour preference after social artefact observation than males with a weaker initial colour preference (i.e. initial preference for preferred material closer to 0.5). We also conducted Wilcoxon signed-rank tests to determine whether the final preference for the demonstrated colour differed from chance level (0.5) in each experimental group. Finally, we used Wilcoxon rank-sum tests to determine whether nesting observers differ from control birds in their initial colour preference.

To analyze nest construction speed, we used linear models to determine whether observing a live-nesting demonstrator influenced the time it took males to (1) initiate (deposit first piece of material), (2) complete (deposit last piece of material), and (3) build (time from nest initiation to completion) their first nest. The predictor variable in all models was live nesting observation (yes or no). We calculated the effect size (standardized coefficient) using the *effectsize* function from the “effectsize” package (Ben-Shachar et al. 2020).

Results

Material colour preference

We found an overarching initial preference for the orange material colour (25 out of 29 individuals), which might have hindered copying. The distribution of birds that initially preferred pink, and therefore observed an orange artefact was equal between treatment groups ($n = 2$ each). Despite this overarching preference for orange, demonstrated colour preference significantly increased between the initial and the final preference tests in birds from the nesting observer group, but not in control birds (phase \times treatment, $X^2 = 11.5$, $n = 29$, $p < 0.001$) supporting our hypothesis that observing nesting conspecifics would affect material selection following artefact observation (Fig. 5). The two individuals that observed an orange artefact in the nesting observer group increased their preference for the demonstrated colour, while none of the two control birds who observed an orange artefact increased their preference for the demonstrated colour, resulting in a significant three-way interaction between phase, treatment and demonstrated colour (Supp. Figure 1; phase \times treatment \times demonstrated colour, $X^2 = 9.9$, $n = 29$, $p = 0.002$). Overall, six individuals switched colour preferences. Two observed an orange artefact and four observed a pink artefact. Increase in preference for the demonstrated colour was also influenced by the initial preference strength for the non-demonstrated colour (phase \times initial preference

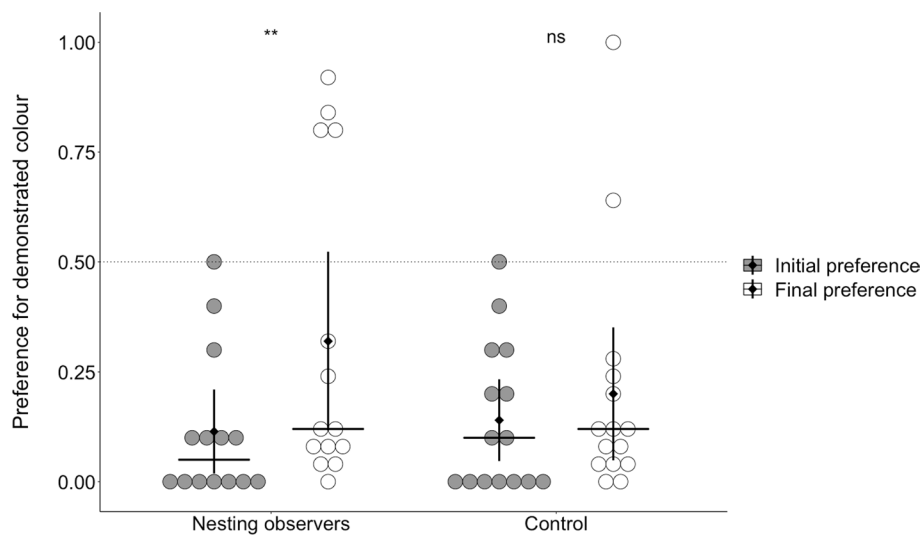


Fig. 5 The preference for demonstrated colour (y axis) selected by birds in the nesting observer group and the control group (x axis) in both the initial preference test (filled circles) and the final preference test (open circles). In between the initial and the final preference tests, birds observed a nest (i.e. social artefact) made of their initially non-preferred colour for three days. Black horizontal lines indicate the

median. Diamonds and vertical lines indicate mean \pm 95% Confidence Intervals, respectively. ** $p < 0.01$, ns indicates $p > 0.05$ for Wilcoxon signed-rank tests (paired) used to determine whether birds of each group changed their colour preference between the initial and final preference test

strength, $X^2 = 12.1$, $n = 29$, $p < 0.001$). Specifically, birds with stronger initial preference (closer to 1.0) were less likely to increase their preference for the demonstrated colour after artefact demonstration than birds with weaker initial preference (closer to 0.5; Supp. Figure 1).

During the final preference test, preference for the demonstrated colour in nesting observers was not significantly different from chance ($n = 14$, median = 0.1, mean = 0.3, lower = 0.1, upper = 0.5 95% CI; $V = 23$, $p = 0.07$), but preference for the demonstrated colour was significantly lower than chance for control birds ($n = 15$, median = 0.1, mean = 0.2, lower = 0.05, upper = 0.4 95% CI; $V = 15$, $p = 0.01$; Fig. 5). A power analysis revealed that the lack of a significant difference from chance level in nesting observers could be owed to the fact that our analysis had low power ($\beta = 0.46$), therefore, this result must be taken with caution. During the initial preference test, the males' preference for the demonstrated colour did not differ between nesting observers ($n = 14$, median = 0.05, mean = 0.1, lower = 0.02, upper = 0.2 95% CI) and control birds ($n = 15$, median = 0.1, mean = 0.1, lower = 0.04, upper = 0.2 95% CI; $W = 96.5$, $p = 0.7$).

Nest construction speed

Our linear models for (1) nest initiation speed and (3) nest building speed were not good fits for our data and did not achieve goodness-of-fit ($p < 0.05$), for which we log-transformed the data and achieved goodness-of-fit. Associating

a nest with conspecifics did not affect the speed at which zebra finch males (1) initiated the construction of their first nest (nesting observers: mean = 5.1 h, median = 2 h, lower = 2.2, upper = 7.9 95% CI; control birds: mean = 2.9 h, median = 2.3 h, lower = 1.6, upper = 4.2 95% CI; $X^2 = 0.7$, $n = 29$, $p = 0.4$; Fig. 6a); (2) completed the construction of their first nest (nesting observers: mean = 6.1 h, median = 4.6 h, lower = 3.3, upper = 9.0 95% CI; control birds: mean = 4.2 h, median = 3.5 h, lower = 2.5, upper = 5.8 95% CI; $X^2 = 1.7$, $n = 29$, $p = 0.2$; Fig. 6b); nor (3) built their first nest (nesting observers: mean = 1.1 h, median = 0.4 h, lower = -0.3, upper = 2.5 95% CI; control birds: mean = 1.3 h, median = 0.8 h, lower = 0.5, upper = 2.1 95% CI; $X^2 = 1.1$, $n = 29$, $p = 0.3$). One male of the nesting observer group took longer (9.6 h) to build its first nest than the rest of nesting observers (mean including outlier male = 1.1 h; mean without outlier male = 0.4 h). Removing that particular outlier male resulted in live-nesting observation affecting the speed at which males built their first nest (mean = 0.4 h, median = 0.4 h, lower = 0.3 h, upper = 0.6 95% CI; $X^2 = 4.3$, $n = 28$, $p = 0.04$; $\beta = 0.7$; Fig. 6c). Data for the model that excludes the outlier male fit the data properly ($p > 0.05$), therefore data did not require to be log-transformed.

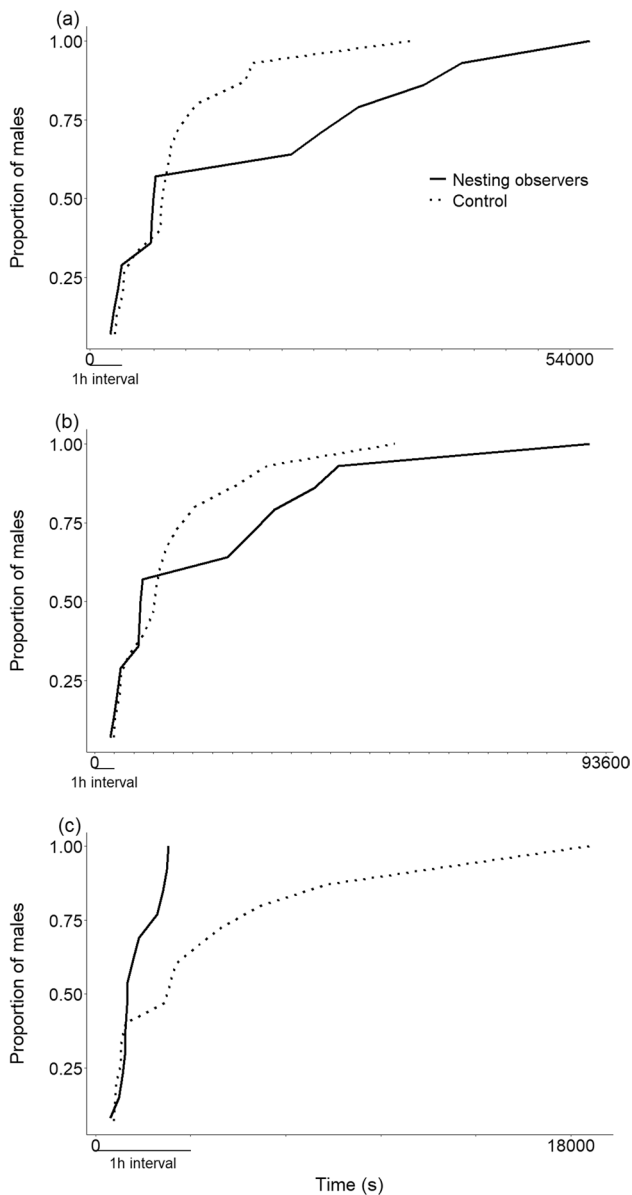


Fig. 6 Cumulative proportion of males (y axis) at different times (x axis) to **a** initiate (deposit first piece of material), **b** complete (deposit last piece of material), and **c** build (time from nest initiation to completion) their first nest. Nesting observers are represented by the continuous line and control birds by the dashed line. **c** shows data excluding one outlier in the nesting observers group. A steeper slope indicates faster construction speed

Discussion

Birds that were given the opportunity to associate a nest with a conspecific subsequently used social information from an artefact while birds in the control group did not. Our results show that although most birds did not change colour preference for the demonstrated colour in the final preference test, initially non-preferred material selection significantly increased after observing a social artefact only for birds that

had observed live nesting demonstrators. Material colour preference did not change between their initial and final preference tests for birds in the control group who did not get an opportunity to associate a nest with conspecifics. These results show that observing an artefact influenced future nest building decisions only in birds that recognized the observed artefact as a nest via associative learning. While nest building initiation for first-time builders was not affected by the opportunity to associate a nest with conspecific, the speed at which the nest was built was affected: birds that observed live-nesting demonstrators took less time to build their nest. These results suggest that the experience of observing live nesting demonstrators allows zebra finch males to recognize an artefact as a nest, thus affecting to a degree how nesting observer birds use the social information that the artefact provides, and how fast nesting observer birds complete their first nest.

Recognition of an artefact as a nest, appears to be a crucial step towards learning from artefact observation. The mechanism behind such recognition could be associative learning, which would be possible thanks to the experience of observing conspecifics using an object of the same functional category of an eventual artefact. Evidence from primates suggests that artefact recognition is also important in tool use learning via artefact observation and manipulation (Borgo et al. 2013). Field studies on tool use further suggest that forming an association between an artefact and a conspecific's behaviour makes such artefacts 'attractive' for learners (Fragaszy et al. 2013). Bearded capuchin monkeys (*Cebus libidinosus*), who use stone anvils to crack open seeds prefer to re-use anvils they witnessed being used by others over using other available anvils available they did not see being used (Liu et al. 2011). Stone-handling Japanese macaques (*Macaca fuscata*) were found to preferentially select stones from piles, which is a sign of stone-handling by others, rather than from randomly scattered stones (Leca et al. 2010). These observations show that artefacts potentially associated with conspecifics become relevant for other individuals, thus affording an opportunity to socially learn from these artefacts. Our finding that only the birds who learned that the artefact observed was a nest used the social information from the artefact, provides experimental evidence that recognizing an artefact as the product of others' behaviour plays a key role in social learning via artefact observation or interaction.

The artefacts that subjects in our experiment observed were not the same nests used by conspecifics during the live-nesting demonstration phase. Because of this, our results show that birds can generalize the association made between a nest and conspecifics to other similar artefacts they have not observed before. Such generalization could be achieved because birds might learn to associate objects with a particular physical form (i.e. the domed nest) or located at a specific

place within the cage, with a particular function (in the present experiment a place conspecifics spent time inside). Experiments with mice (*Mus musculus*) have revealed that mice recognize, at the neurological level, different objects as nests by recognizing the functional features of nests (Lin et al. 2007). That is, hippocampal neurons in these mice fire or cease to fire selectively when encountering novel objects with different shapes, sizes and made of different materials, as long as these novel objects had the functional features of nests (Lin et al. 2007). We found that birds used social information provided by the artefact only when they had the opportunity to observe conspecifics using a nest, thus, suggesting that associating an object with its function is crucial for social learning from an artefact. Forming such an association might be important because it allows birds to infer behaviour from an artefact, thus making that artefact relevant for social learning.

Correlational evidence from field studies suggests an effect of material availability on material selection for nest building. Great tits (*Parus major*) occupying four different Mediterranean habitats, for example, were found to incorporate different amounts of each kind of material in their nest according to different material abundance among habitats (Álvarez et al. 2013). Pied flycatchers (*Ficedula hypoleuca*) incorporate leaves of different tree species into their nests reflecting the different tree species abundance within their territory (Briggs and Deeming 2016). A study on Chinese bulbuls (*Pycnonotus sinensis*) nests, found that the incorporation of anthropogenic nesting materials increased with urbanization (Wang et al. 2009). Previous experimental work found, in a group which was equivalent in experience to the current control birds, a group-level loss of initial preference for material colour in their birds (Breen et al. 2019). It is plausible, based in part on the correlational evidence presented above, that material abundance may have accounted for this social learning effect. That is, in Breen et al. 2019 during the artefact observation phase, there was higher material abundance (~425 pieces of string) that matched the colour of the artefact, while there were only 25 pieces of the observers initially preferred colour. Following the material abundance argument, the birds may have selected, during their first nesting attempt, the colour that was more abundant, which was always the same colour as the artefact. Our laboratory environment in the current experiment allowed us to control for the material abundance available during both the social information gathering phase and first nest-building phase of our focal birds. In this way, we were able to build on the results of Breen et al. (2019) and ask if birds in the current experiment use social information gleaned from the artefact, even when material is equally abundant in the environment. Indeed, we continue to find a social effect—that is a group-level loss of initial material colour preference—even when material abundance is controlled, exclusively in the

experimental group that had the opportunity to learn what a nest is and therefore recognized the artefact as a nest.

We asked whether initial preference strength for the demonstrated colour had an effect on changing colour preference after observing an artefact. We found that the males who increased their preference for the material colour of the artefact had, on average, a weaker initial colour preference (closer to 0.5) than males who did not increase their demonstrated colour preference. Individual variation in their tendency to use social information and possible causes for these individual differences are varied (reviewed in Mesoudi et al. 2016). Causes for individual variation in social information use have been studied in various species. In zebra finches, only females were found to copy the feeder colour of male demonstrators (Guillette and Healy 2014). House sparrows (*Passer domesticus*) that performed better in tests of individual learning in a foraging task showed less social learning while foraging in a group (Katsnelson et al. 2011). Among individual differences in exploratory behaviour was also found to play a role in social information use. In zebra finches, more exploratory females, presumably those that were able to gather more information from their environment, showed less copying in a foraging and a mate-choice context (Rosa et al. 2012). In three-spined sticklebacks (*Gasterosteus aculeatus*) however, more exploratory individuals relied more on social learning when learning about food location (Nomakuchi et al. 2009). Another potential cause for inter-individual differences in social learning is developmental stress. Adult rats who were raised by low grooming mothers, an indicator of stress, were less likely to copy the food preferences from demonstrators (Lindeyer et al. 2013). Our results that individuals with stronger initial preferences, for whatever reason, were less likely to act on the social information provided by an artefact, show that inherent arbitrary preferences also play a role in how individuals differ in their social information use. The role of individual preference strength on social learning, however, could change depending on how the social information is transmitted (e.g. via observation of a female versus a male demonstrator; Guillette et al. 2014; or via artefact observation versus live observation of a familiar conspecific building a nest; Guillette et al. 2016).

The present experiment revealed that observing a live-nesting demonstration increased nest building speed, but not nest initiation speed nor nest completion speed. Once birds started nest construction, males without the experience of observing a conspecific using a nest were slower to finish depositing all the available material into their first nest compared to nesting observers. A decrease in building speed was also found in an experiment comparing nest completion speed between birds that had access to material and/or adults as juveniles, and birds without access to neither (Breen et al. 2020). Our experiment

shows that experience prior to first-time nest construction as adults affects material selection and how fast males deposit material into the nest. These results provide further evidence for the significant role that experience plays in nest-building behaviour and show that latent learning (i.e. acquiring information without receiving an immediate reward; Blodgett 1929) might play a role in structure-building tasks. Latent learning has been found to influence tool-use behaviour in both keas (*Nestor notabilis*) and New Caledonian crows (Lambert et al. 2017). Individuals that were allowed to explore novel objects that could be used as tools in a future tool-use task were found to outperform individuals without prior exploration experience in that future tool-use task. Similarly, first-time nest builders in our experiment benefited from observing live-nesting demonstrators in that these nesting observers build their nest faster than individuals without such observational experience.

In conclusion, our results suggest that first-time nest builders need to recognize the observed artefact as a nest to use social information from it, when controlling for material abundance. Such recognition can be achieved potentially by forming an association between an object of the same functional category as the artefact (a nest) and conspecifics. Moreover, birds seem to be able to generalize the association between a specific nest with conspecifics to other artefacts they have never encountered before. The present study also found supporting evidence for a role of material relative abundance in the environment in nest-building material selection in birds. Observing conspecifics using a nest also increased the speed to complete a nest after depositing the first piece of material, thus suggesting a role for latent learning on structure-building tasks. Overall, our results are important because they demonstrate that animals not only socially learn from observing behaviour, but also from inferring behavior from an artefact.

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Author contributions ACA and LMG conceived and designed the experiment with input from TE, CTL and GBB. ACA collected the data. ACA analyzed the data. ACA wrote the manuscript with input from TE, CTL, GBB and LMG. TE, CTL and GBB provided help with bird husbandry. All authors read and approved the final manuscript.

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Data availability All data generated and analysed for this experiment are included as supplementary material.

Code availability R Code is included as supplementary material.

Declarations

Conflict of interest We declare no conflict of interests.

Ethics approval All procedures were conducted in accordance with the Canadian Council on Animal Care (CCAC) Guidelines and Policies and the ABS Guidelines for the Use of Animals in Research. Procedures also had the approval from the Animal Care and Use Committee for Biosciences for the University of Alberta (AUP 2923), which is consistent with the Animal Care Committee Guidelines for the Use of Animals in Research.

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