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

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Abstract

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

KEYWORDS
aggressive, directed social learning, Network-Based Diffusion Analysis, personality, relationships, social learning strategies

1 | INTRODUCTION

Social learning (learning from others) is widespread across the animal kingdom and can be adaptive in a variety of biological contexts, from foraging to mate choice (Galef & Laland, 2005). This is because social learning permits the spread of adaptive behaviours without the higher risk and energetic costs associated with asocial (independent) learning. However, if individuals are indiscriminate as to when and from whom they learn, social learning can lead to the spread of maladaptive behaviours or outdated information (e.g. Laland &

Williams, 1998). Evolutionary theory, therefore, predicts that natural selection will favour individuals that are selective in how they use social information over those that learn indiscriminately from others (Boyd & Richerson, 1985, 1988).

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

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

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

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

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

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

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

2 | METHODS

2.1 | Study system

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

2.2 | Data collection of social interactions

We collected data on four types of interactions between individuals as follows (for a more detailed account of this data collection, see Appendix S1, Section S1).

2.2.1 | Feeding associations

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

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

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

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

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

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

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

2.2.2 | Aggressive interactions

To record aggressive interactions, we presented the birds with a small, 6.9 cm × 6.7 cm platform (Figure 1a) on which a sprig of millet was placed. The platform was small enough so that only a few birds could fit on it at one time and so would encourage expression of natural aggressive behaviours over food in an area that could be monitored closely (zebra finches generally engage in aggressive interactions with those who are 5–15 cm from themselves; Evans, 1970). The platform was present in the aviary during 19 days between 23rd November 2018 and 19th March 2019 and was reconstructed halfway through the experiment due to poor weather conditions causing it to break. The sprig of millet was secured to the platform initially using two crossed nails and, after reconstruction, using an elastic band. When the millet became depleted or fell off the platform, the researcher entered the aviary to replace it once all birds had dispersed from the platform. A single GoPro camera was used to record activity on the platform—in total, we recorded approximately 27.7 h of video footage over 20 days (average: 1.3 h per day; range: 0.8–2.6 h per day). We analysed the entire footage, recording the ID of each visiting bird, the times at which they landed on and left the platform and all aggressive interactions they engaged in. This included biting but was mostly in the form of “beak fencing” (two birds clashing their beaks together). (Note that we did not include displacements as displays of aggression, because they occurred infrequently and because it was difficult to determine whether they were intentional, or simply a case of individuals losing balance when there were too many birds on the platform). As previous studies have demonstrated an influence of an individual's dominance rank on who learns from whom, we were also interested to know whether the outcome of aggressive interactions influenced the direction of information transfer between aggressors. Thus, when an aggressive behaviour occurred, we recorded the ID of both birds involved and the winner of the fight. A bird was said to have “won” the fight if the other bird fell or jumped off the platform. If two birds stopped fighting without one falling off, the fight was considered to have no winner. We then calculated the overall tendency of bird *i* to win a fight against bird *j*—bird *i* was considered the “winning aggressor” of the pair and bird *j* the “losing aggressor” if the two engaged in at least one fight and *i* won more fights than it lost against *j*.

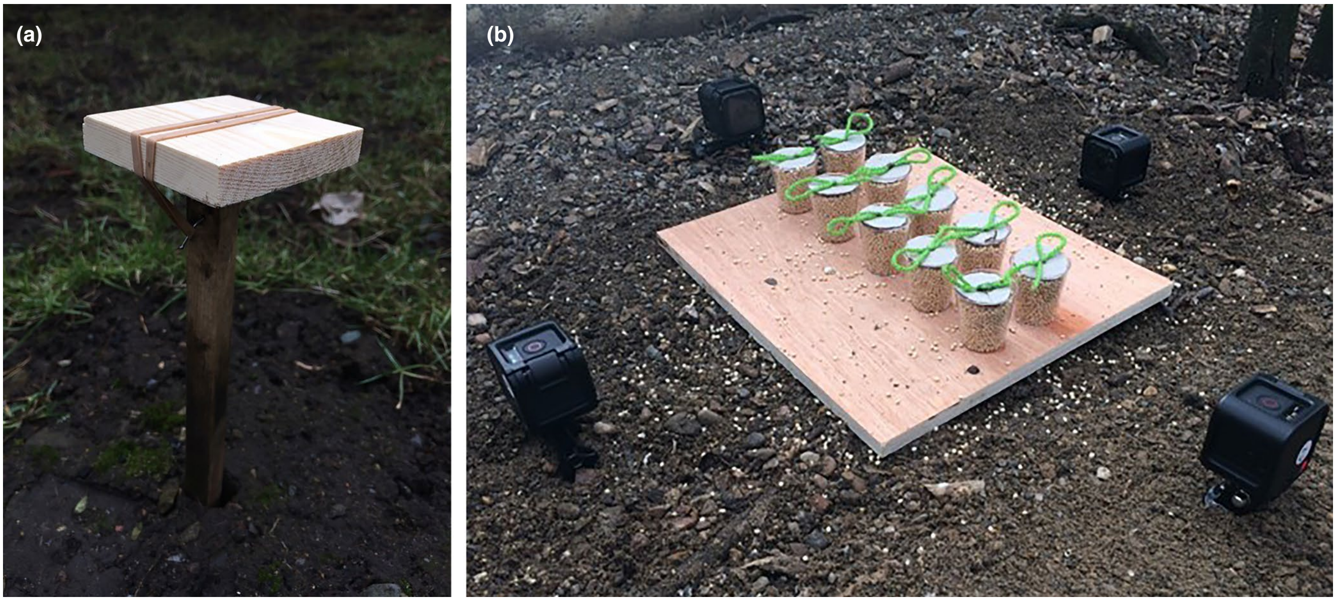


FIGURE 1 (a) The platform used to monitor pairwise aggressive interactions in finches. Millet spray was held onto the platform using an elastic band. (b) The foraging task presented to the finches, along with the placement of four GoPro cameras. The task consisted of 10 transparent plastic cups stuck to a wooden board. Each glass contained millet seed and was covered with a cardboard lid which birds needed to remove to solve the task and access the seed

2.2.3 | Positive interactions and mating pairs

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

2.3 | Generation of social networks

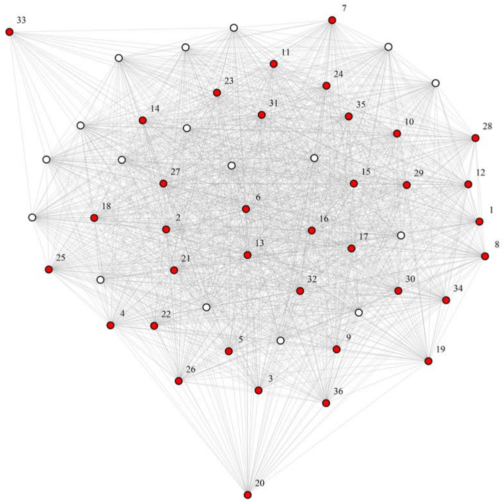
We constructed nine social networks based on the pairwise social interactions described above (Table 1; Figure 2). Each network represents a different social learning pathway and so a different hypothesis concerning how individuals learn from each other based on their social relationships. In the “feeding associations” network, connections between dyads were equal to F_{ij}, reflecting the hypothesis that birds learned from all other birds in proportion to their propensity to feed together. For the remaining types of social interaction (aggressive, positive, mates), we constructed two versions of the social network that made different assumptions about the influence of feeding associations on learning opportunities—a binary version, where a connection of a particular type either existed or did not exist between two individuals, and a feeding association-weighted version (henceforth, shortened to “feeder version”), where any nonzero connection between individuals was equivalent to F_{ij}. The binary version reflects the hypothesis that the finches learned from those they share particular relationships with, for example, individuals learning from their mates. The feeder version reflects the hypothesis that birds learned from those they share particular relationships with at a rate proportional to their propensity to feed together. In the case of aggressive interactions, we additionally considered that information flow may be directional (i.e. transfer from the winning aggressor to the losing aggressor of the dyad, or vice versa) and so divided both versions of this network into two—a “winning to losing aggressor” network and a “losing to winning aggressor” network.

2.4 | Individual-level variables (ILVs)

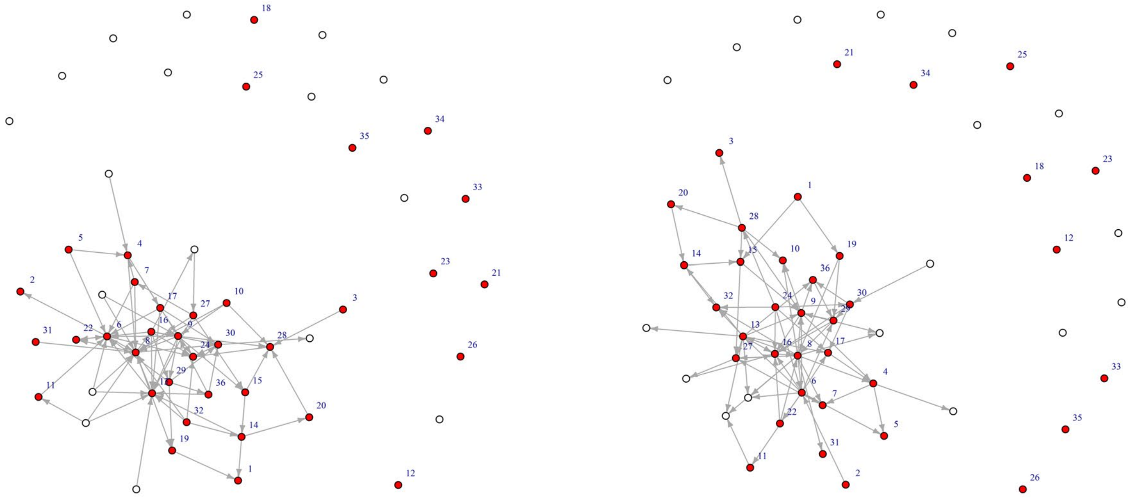
In our analysis, we considered five ILVs which may have influenced individual rates of asocial and/or social learning. (i) The total time (seconds) each individual was recorded at the regular feeders was used as a measure of motivation to feed. (ii) A measure of the individual's overall tendency to win aggressive encounters was calculated based on the total number of fights won minus the total number of fights lost while on the introduced platform. (iii) The total number of fights engaged in while on the platform was used as a measure of aggression. (iv) Solving of a former task was used as a measure

TABLE 1 Descriptions of the social networks used in the analysis, constructed from five types of social interaction between zebra finch individuals

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

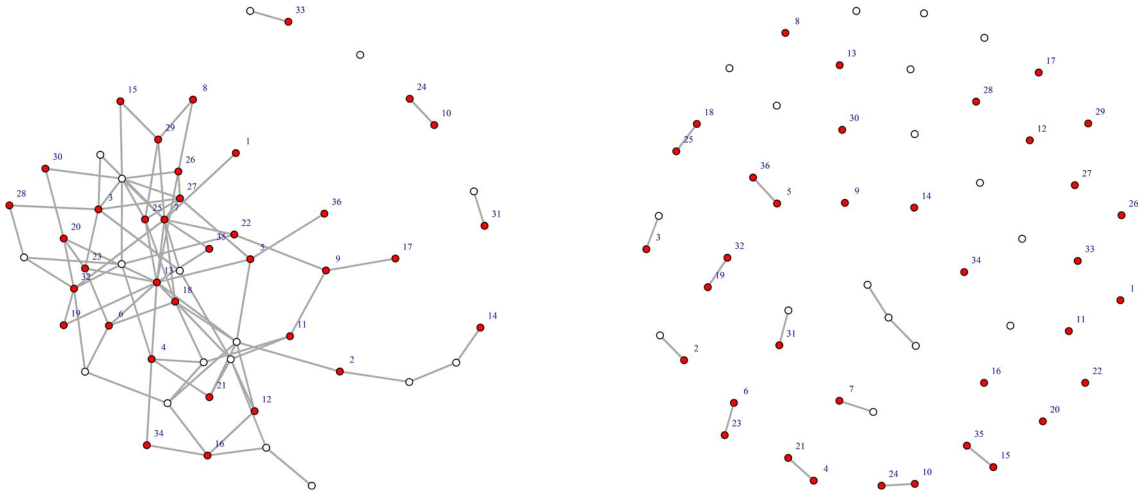


(a) Feeding association network



(b) Winning to losing aggressors network

(c) Losing to winning aggressors network



(d) Positive interactions network

(e) Mates network

FIGURE 2 Legend on next page

FIGURE 2 The five types of network used in our analysis. (a) Feeding association-based network. (b) Winning to losing aggressor network. (c) Losing to winning aggressor network. (d) Positive network. (e) Mates network. Networks b-e are shown in their binary forms. All networks are spring embedded. White nodes represent individuals that did not solve the task. Shaded (red) nodes represent individuals that did solve the task, and are numbered according to the order at which they first solved the task. Lines represent undirected connections between individuals (networks a, d and e). Arrows represent directed connections between individuals (networks b and c). Unconnected dyads were not observed interacting in the manner represented by that network

of learning proficiency and past experience. This was a binary ILV describing whether or not each individual solved a puzzle box task (by either lifting a lid or pulling a door) introduced to the same population during a previous, unpublished study that took place between 31st October 2017 and 20th January 2018 (see Appendix S1, Section S1 for details). (v) Suspected sex. In the absence of genetic information, this was based on morphological differences and singing behaviour and was used as a general indicator of differences in sex.

2.5 | Diffusion experiment

The finches were given a novel foraging task during 23 days between 5th February 2019 and 21st March 2019. The task (Figure 1b) consisted of 10 transparent plastic cups (volume 50 ml) glued to a wooden base. Each glass was filled with millet seed and covered with a round cardboard lid. Each lid had a loop of green string attached to make it easier for the birds to remove. We were interested in the diffusion of lid-removing behaviours through the population. We, therefore, defined a solve as an individual removing or partially removing the lid from one of the cups, regardless of whether the bird fed from the cup afterwards. Presentation of our task and platform was alternated so that the two were never in the aviary at the same time. This is because the platform attracted a lot of attention from the finches and so may have distracted the birds from the task. During the task presentation, birds were allowed to solve and feed from the task freely. In order to avoid interrupting possible learning events, the researcher would only go into the aviary and replace any removed lids either when the birds had completely dispersed from the task or if all lids had been removed. Four GoPro cameras were used to record the task from all sides (positions of the cameras are shown in Figure 1b). We collected a total of 47.1 h video footage for the task across the 23 days (average: 2.0 h per day; range: 1.2–2.4 h per day). We studied the entire footage and documented each solve (i.e. when a bird removed or partially removed a lid from one of the cups), noting the time of solve and the identity of the bird. Solve times were recorded as cumulative times across the entire set of videos.

2.6 | Statistical analysis

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

TABLE 2 Summed Akaike weights across all models with and without the inclusion of each ILV

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

Note: NumberOfFights and *NetFightWin* were treated as a three-way either/or variable and so models without either of these variables are grouped together.

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

All models were generated using the "AICtable" function of the NBDA package.

Models were compared using the corrected Akaike information criterion (AICc), where lower values indicate better-fitting models. Akaike weights were calculated giving a measure of support for each model. Due to the large number of individual models considered, we obtained a measure of support for each network combination and for each ILV by summing the Akaike weights across any models which included that network or variable (while accounting for differences in model number to allow fair comparison, as explained in the Appendix S1, Section S2).

For our best social network combinations (those with the highest Akaike weights), we obtained model-averaged estimates for the social learning parameter (*s*) for each of the social networks included. The social learning parameter represents the increase in the rate at which a naïve individual will learn the novel behaviour per unit of association with informed individuals, relative to the baseline asocial rate of learning. The *s* parameter can, however, be difficult to interpret for proportional networks (as is the case for our feeding association-based networks) because it is scaled relative to the scale of the network itself (Hasenjager et al., 2021). This also means that *s* parameters estimated from networks of different scales cannot be directly compared (e.g. our binary and feeding association-based networks cannot be compared directly from the estimated *s* parameters). Therefore, to facilitate comparison between binary and feeding association-based networks, which were modelled separately, we also calculated the estimated proportion of learning events to have occurred via social transmission (propST) via each network in our best network combinations (Hasenjager et al., 2021). This was calculated as a model-weighted average across all models for each network combination. We also calculated lower limit estimates for both *s* and propST parameters. For further information on the lower limit estimates and additional calculations involving propST estimates, see Appendix S1, Section S2.

Note that we also ran a number of additional analyses (available in the Appendix S1, Section S6) to test the robustness of our findings and to explore some alternative explanations for the observed patterns of information transmission. The results of these analyses are referred to only briefly in the main text and so we refer the reader to the Appendix S1 (Section S6) for the full discussion.

2.7 | Ethical note

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

3 | RESULTS

3.1 | General observations

The task was solved a total of 207 times (at an average rate of 4.4 times per hour) by 36 of the 53 zebra finches. Each solver solved the task an average of 5.75 times, but this was highly skewed, with only 4 birds solving more than 10 times. The task was solved the most times by individual "CrL," who solved the task 39 times over the course of the study period. Behaviours used to remove or partially remove the lid included pulling the cardboard or string with the beak, removing lid with feet while standing on top of the task, and wedging beak into a small gap at the side of the lid. Solvers fed from the cup (within 10 seconds after solving) during only 55 of the 207 solve events.

3.2 | Presence of social learning

There was strong evidence that social learning occurred in our study group. Our best social model (AICc = 236.48) fit the data substantially better than our best asocial model (AICc = 243.72) (ΔAICc = 7.24, corresponding to 37.3x more support for the best social learning model). In addition, the total Akaike weight (summed across all ILV combinations) of the best-performing social network combination (Akaike weight = 0.107) was over 80x that of the asocial model set (Akaike weight = 0.001) (Table 3). Across the top 15 best-performing network combinations, the average summed propST estimate across all included networks was 0.498 (±0.16 SD) and the average summed propST lower limit estimate was 0.179 (±0.07 SD). This suggests that, on average, approximately half of the learning events in the study occurred due to social learning via the included learning pathway(s). This not only provides further evidence for the presence of social learning in the study population but also suggests that a large proportion of learning occurred either asocially or socially via a pathway not included in our analysis.

3.3 | ILVs

There was little evidence that any of the ILVs included in this analysis had an effect on individual learning (Table 2). Models performed better without the inclusion of *FeederTimes*, *LastYearSolves* and *SuspectedSex* and the fights-based ILVs had little effect on the total Akaike weight. The estimated proportion of social learning events via each network were also largely unaffected by the inclusion

TABLE 3 Total Akaike weight (summed across all ILV combinations) for our top fifteen network combinations, as a percentage of the summed Akaike weights across all network combinations in the analysis, along with *s* parameter estimates for each network in each combination

Network combination	Social networks present									Summed Akaike weight (%)
	Feeder networks					Binary networks				
	FeedingAssociations	*WinningToLosingAggressor*	*LosingToWinningAggressor*	*Positive*	*Mates*	*WinningToLosingAggressor*	*LosingToWinningAggressor*	*Positive*	*Mates*	
1		0.28	0.28							15.86
2						1.46	1.46		1.46	14.87
3						1.11	1.11			10.61
4		0.26	0.38							5.97
5	48.9	721.2	1,600.67							4.70
6						0.89	1.66			4.38
7		0.39								3.61
8		0.17	0.17		0.17					2.59
9							1.75			2.55
10						1.63			1.63	2.01
11						1.53				1.96
12		0.31	0.43		0.04					1.96
13	0.04	1.21								1.88
14						1.29	2.02		0.85	1.84
15			0.44							1.78
NA	*Remaining 68 social model sets*									23.21
43										0.20

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

of different ILV combinations (Table S3). Additional analysis also showed that social networks based on these five ILVs did not convincingly explain the observed patterns of social transmission between individuals (Table S15).

3.4 | Social learning pathways

Table 3 shows the support, measured by summed Akaike weights, for the 15 best-performing social network combinations (see also Table S1). The top 15 network combinations accounted for >75% of the summed Akaike weights across all 84 network combinations used in our analysis, beyond which the summed Akaike weights dropped below 0.012 (~1/10 the support of the best model set) (Figure S1). The full set of network combinations is available in (Table S6).

Of all the network combinations we tested, that which included the *WinningToLosingAggressor* and *LosingToWinningAggressor* networks (feeder versions), with the *s* parameters of each network constrained to be the same, received the most support (total Akaike weight = 0.107; 15.9% of best model set weights; Table 3). This corresponds to the hypothesis that individuals were most likely to learn from those with whom they shared aggressive interactions (at a rate proportional to their propensity to feed together) and that the rate of learning was unaffected by the direction of the aggressive interaction within a dyad. The model-averaged *s* parameter estimate was 0.28 (95% C.I. lower limit estimate = 0.08) for both networks, meaning that a naïve individual learned the task an estimated 0.28x faster (relative to the baseline asocial rate of learning) per unit of connection to an informed aggressor, proportional to their feeding associations. Since the *s* parameter can be difficult to interpret for proportional networks (Hasenjager et al., 2021), the propST estimate offers a more intuitive measure of social transmission via each included network. The model-averaged propST estimate is 0.277 (±0.017 SD) for the *WinningToLosingAggressor* network and 0.183 (±0.01 SD) for the *LosingToWinningAggressor* network (Table S2). In other words, an estimated 28% of learning events involved individuals learning from those who generally won against them during aggressive encounters and an estimated 18% involved individuals learning from those who generally lost to them during aggressive encounters. The propST lower limit estimate is 0.133 (±0.031 SD) for the *WinningToLosingAggressor* network and 0.090 (±0.02 SD) for the *LosingToWinningAggressor* network, providing further evidence that social transmission occurred via both networks.

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

Overall, out of all the networks we tested, we found the strongest evidence for social transmission between individuals that shared aggressive interactions, in that every one of the top 15 network combinations included either the *WinningToLosingAggressor* or *LosingToWinningAggressor* network and 9 of the 15 included both (Table 3). This includes the top two network combinations described above, which account for 31% of the model support over the 84 tested network combinations and, after which, model support rapidly drops (Figure S1). Additional analyses clarified that simple associations on the aggression platform did not explain this pattern of social transmission (Tables S12–S13), suggesting that the pairwise connections between aggressors were important in predicting the pattern of task solves. In addition, the removal of pretask recordings of aggression had little impact on the explanatory power of these networks, suggesting that aggressive relationships were relatively stable in this population (Table S14).

Learning events occurring through the aggression-based pathways did, however, appear to occur more often in the winner to loser direction. The average propST estimate for the *WinningToLosingAggressor* network (averaged over the top 15 network combinations in which either the binary or feeder version of this network is present) is 0.297 (±0.06 SD), with an estimated lower limit of 0.121 (±0.08 SD) (Table S2). The average propST estimate for the *LosingToWinningAggressor* network is 0.220 (±0.05 SD), with an estimated lower limit of 0.089 (±0.04 SD). This provides strong support that social transmission occurred via both of these pathways, and suggests that the *WinningToLosingAggressor* pathway was responsible for an estimated 1.35× as many learning events, on average, as the *LosingToWinningAggressor* pathway. The reason for this, despite the equal *s* parameters which indicate equal rates of learning along both pathways, appears to be due to three individuals with a disproportionate number of connections to losing aggressors acting as "hubs" of information. All three successfully learned the task—and also learned the task quickly—giving them the potential to provide their many connected losing aggressors with early learning opportunities and promote information transfer along the *WinningToLosingAggressor* pathway. In addition, one of these highly connected individuals, "CrL," solved the task considerably more times than any other individual, allowing it to act as a particularly strong source of social information. (Tables S8–S11).

In addition to aggression-based social learning, we found some support for social transmission between mates—5 of the top 15 network combinations contained the *Mates* network, including the second-best model. However, propST estimates for the *Mates* network tended to be <0.1, suggesting that very little social information was actually transmitted via this pathway, and social transmission between mates was only apparent when the *Mates* network was included with at least one of the aggression-based networks. In addition, when interactions recorded prior to task introduction were removed from the analysis, the *Mates* networks received less support, suggesting either that finches learned novel behaviours from both past and present mates, or simply that removal of a subset of interactions made the *Mates* networks, which already contained only a few pairwise connections, too sparse to add any explanatory power to our models (Table S14).

We found little to no support for social transmission via pathways based on positive associations (none of the top 15 network combinations included the *Positive* network) or via a purely feeding association-based network (only 2 of the top 15 network combinations included the *FeedingAssociation*s network and *s* parameter and propST estimates were extremely varied). In addition, the binary and feeder versions of the *WinningToLosingAggressor*, *LosingToWinningAggressor*, *Positive and Mates* networks both received a similar level of support (summed Akaike weights of 0.529 ± 0.001 SD for binary versions and 0.471 ± 0.001 SD for feeder versions, when asocial models and models including the full feeder network are disregarded), suggesting that a dyad's propensity to feed together did not greatly influence their likelihood of learning from one another.

4 | DISCUSSION

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

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

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

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

An alternative explanation for social transmission along aggression-based pathways in our zebra finch population, rather than aggression having a direct impact on or acting as an indicator of learning ability, is that aggressive individuals were more likely to observe each other perform the novel behaviour. This may be because aggressive acts were a direct result of close association, and it was these close associations specifically that resulted in increased learning opportunities. This, however, does not seem likely, since none of our other measures of association (including associations on the aggression platform itself, as analysed in the Appendix S1, Section S6) offered a convincing explanation for the observed pattern of social transmission. Perhaps more likely, individuals who are aggressive towards each other may do so because they compete with each other over resources, which may result in context-specific associations between these birds. If this is the case, since our task was a foraging task, aggressors who compete over food may have been more likely to be present at the task at the same time in order to observe each other performing novel behaviours. Since our focus was purely on the importance of relationship-based pathways of social transmission, we did not document the identities of task observers—only task solvers—and so we are unable to comment on whether aggressors actively associated or competed with each other at the task location. Alternatively, rather than competing with one another, individuals may pay more attention to their aggressors in order to avoid or prepare for conflict, making them more likely to witness those aggressors demonstrating novel behaviours.

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

Our results suggested, however, that learning from mates was not the main pathway of social learning, offering additional explanatory power only when combined with the aggression-based social networks. This may be because the mates networks were comparatively small, containing only a few isolated pairwise connections (see Figure 2e), thus restricting the number of possible opportunities for social learning via this pathway. This would explain why the proportion of social learning events attributed to mates learning from one another tended to be low. This result additionally reflects the importance of considering multiple pathways of learning at the same time when studying animal social learning, as the effect of the mates networks may not have been noticeable if they were not combined with the aggression-based networks. Furthermore, research into directed social learning between mates is currently lacking and we encourage further research into such behaviour in zebra finches and other species, keeping in mind that social transmission between mates may be difficult to detect if only a few pairwise connections exist.

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

5 | CONCLUSION

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

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CONFLICT OF INTEREST

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

AUTHOR CONTRIBUTION

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

DATA AVAILABILITY STATEMENT

The data sets generated during and/or analysed during the current study are available in the FigShare repository, https://doi.org/10.6084/m9.figshare.13570559. Additional information is included in Appendix S1.

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REFERENCES

Aplin, L. M., Farine, D. R., Morand-Ferron, J., & Sheldon, B. C. (2012). Social networks predict patch discovery in a wild population of songbirds. *Proceedings of the Royal Society B: Biological Sciences*, *279*, 4199–4205. https://doi.org/10.1098/rspb.2012.1591

Atton, N., Hoppitt, W., Webster, M. M., Galef, B. G., & Laland, K. N. (2012). Information flow through threespine stickleback networks without social transmission. *Proceedings of the Royal Society B: Biological Sciences*, *279*, 4272–4278. https://doi.org/10.1098/rspb.2012.1462

Avital, E., & Jablonka, E. (2000). *Animal traditions: Behavioural inheritance in evolution*. Cambridge University Press.

Baptista, L. F., & Petrinovich, L. (1984). Social interaction, sensitive phases and the song template hypothesis in the white-crowned sparrow. *Animal Behaviour*, *32*, 172–181. https://doi.org/10.1016/S0003-3472(84)80335-8

Barrett, B. J., McElreath, R. L., & Perry, S. E. (2017). Pay-off-biased social learning underlies the diffusion of novel extractive foraging traditions in a wild primate. *Proceedings of the Royal Society B: Biological Sciences*, *284*, rspb20170358. https://doi.org/10.1098/rspb.2017.0358

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

Benskin, C. M. H., Mann, N. I., Lachlan, R. F., & Slater, P. J. B. (2002). Social learning directs feeding preferences in the zebra finch, *Taeniopygia guttata*. *Animal Behaviour*, *64*, 823–828. https://doi.org/10.1006/anbe.2002.2005

Bonoan, R., Clodius, F., Dawson, A., Caetano, S., & Yeung, E. (2013). Dominance hierarchy formation in a model organism, the zebra finch (*Taeniopygia guttata*), and its potential application to laboratory research. *Bios*, *84*, 201–209. https://doi.org/10.1893/0005-3155-84.4.201

Boogert, N. J., Nightingale, G. F., Hoppitt, W., & Laland, K. N. (2014). Perching but not foraging networks predict the spread of novel foraging skills in starlings. *Behavioural Processes*, *109*, 135–144. https://doi.org/10.1016/j.beproc.2014.08.016

Boyd, R., & Richerson, P. J. (1985). *Culture and the evolutionary process*. University of Chicago press.

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

Brainard, M. S., & Doupe, A. J. (2002). What songbirds teach us about learning. *Nature*, *417*, 351. https://doi.org/10.1038/417351a

Clayton, N. S. (1987). Song tutor choice in zebra finches. *Animal Behaviour*, *35*, 714–721. https://doi.org/10.1016/S0003-3472(87)80107-0

Coelho, C. G., Falotico, T., Izar, P., Mannu, M., Resende, B. D. D., Siqueira, J. O., & Ottoni, E. B. (2015). Social learning strategies for nut-cracking by tufted capuchin monkeys (*Sapajus spp.*). *Animal Cognition*, *18*, 911–919. https://doi.org/10.1007/s10071-015-0861-5

Coolen, I., Ward, A. J., Hart, P. J., & Laland, K. N. (2005). Foraging nine-spined sticklebacks prefer to rely on public information over simpler social cues. *Behavioural Ecology*, *16*, 865–870. https://doi.org/10.1093/beheco/ari064

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

Darwin, C. (1896). *The descent of man and selection in relation to sex* (Vol. *1*). D. Appleton.

David, M., Auclair, Y., & Cézilly, F. (2011). Personality predicts social dominance in female zebra finches, *Taeniopygia guttata*, in a feeding context. *Animal Behaviour*, *81*, 219–224. https://doi.org/10.1016/j.anbehav.2010.10.008

Evans, S. M. (1970). Aggressive and territorial behaviour in captive zebra finches. *Bird Study*, *17*, 28–35.

Farine, D. R., Aplin, L. M., Sheldon, B. C., & Hoppitt, W. (2015). Interspecific social networks promote information transmission in wild songbirds. *Proceedings of the Royal Society B: Biological Sciences*, *282*, 20142804. https://doi.org/10.1016/j.cub.2015.06.071

Farine, D. R., Spencer, K. A., & Boogert, N. J. (2015). Early-life stress triggers juvenile zebra finches to switch social learning strategies. *Current Biology*, *25*, 2184–2188. https://doi.org/10.1016/j.cub.2015.06.071

Franz, M., & Nunn, C. L. (2009). Network-based diffusion analysis: A new method for detecting social learning. *Proceedings of the Royal Society B: Biological Sciences*, *276*, 1829–1836. https://doi.org/10.1098/rspb.2008.1824

Galef, B. G., & Laland, K. N. (2005). Social learning in animals: Empirical studies and theoretical models. *BioScience*, *55*, 489–499.

Griesser, M., & Suzuki, T. N. (2016). Kinship modulates the attention of naïve individuals to the mobbing behaviour of role models. *Animal Behaviour*, *112*, 83–91. https://doi.org/10.1016/j.anbehav.2015.11.020

Guenther, A., Brust, V., Dersen, M., & Trillmich, F. (2014). Learning and personality types are related in cavies (*Cavia aperea*). *Journal of Comparative Psychology*, *128*, 74. https://doi.org/10.1037/a0033678

Guillette, L. M., Scott, A. C., & Healy, S. D. (2016). Social learning in nest-building birds: A role for familiarity. *Proceedings of the Royal Society B: Biological Sciences*, *283*, rspb20152685. https://doi.org/10.1098/rspb.2015.2685

Hasenjager, M. J., Leadbeater, E., & Hoppitt, W. (2021). Detecting and quantifying social transmission using network-based diffusion analysis. *Journal of Animal Ecology*, *90*, 8–26. https://doi.org/10.1111/1365-2656.13307

Heyes, C. M. (1994). Social learning in animals: Categories and mechanisms. *Biological Reviews*, *69*, 207–231.

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

Hoppitt, W., & Laland, K. N. (2011). Detecting social learning using networks: A users guide. *American Journal of Primatology*, *73*, 834–844. https://doi.org/10.1002/ajp.20920

Hoppitt, W., Photopoulou, T., Hasenjager, M., & Leadbeater, E. (2019). *NBDA: A Package For Implementing Network-Based Diffusion Analysis*. R package version 0.8.3.

Horner, V., Proctor, D., Bonnie, K. E., Whiten, A., & de Waal, F. B. (2010). Prestige affects cultural learning in chimpanzees. *PLoS One*, *5*, e10625. https://doi.org/10.1371/journal.pone.0010625

Jones, A. E., & Slater, P. J. B. (1996). The role of aggression in song tutor choice in the zebra finch: Cause or effect? *Behaviour*, *133*, 103–115. https://doi.org/10.1163/156853996X00053

Katz, M., & Lachlan, R. F. (2003). Social learning of food types in zebra finches (*Taenopygia guttata*) is directed by demonstrator sex and feeding activity. *Animal Cognition*, *6*, 11–16. https://doi.org/10.1007/s10071-003-0158-y

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

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

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

Laland, K. N., & Williams, K. (1998). Social transmission of maladaptive information in the guppy. *Behavioural Ecology*, *9*, 493–499. https://doi.org/10.1093/beheco/9.5.493

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

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

Payne, R. B. (1981). Song learning and social interaction in indigo buntings. *Animal Behaviour*, *29*, 688–697. https://doi.org/10.1016/S0003-3472(81)80003-6

Schnoell, A. V., & Fichtel, C. (2012). Wild redfronted lemurs (*Eulemur rufifrons*) use social information to learn new foraging techniques. *Animal Cognition*, *15*, 505–516. https://doi.org/10.1007/s10071-012-0477-y

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

Sih, A., & Del Giudice, M. (2012). Linking behavioural syndromes and cognition: A behavioural ecology perspective. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *367*, 2762–2772. https://doi.org/10.1098/rstb.2012.0216

Soma, K. K., Scotti, M. A. L., Newman, A. E., Charlier, T. D., & Demas, G. E. (2008). Novel mechanisms for neuroendocrine regulation of aggression. *Frontiers in Neuroendocrinology*, *29*, 476–489. https://doi.org/10.1016/j.yfrne.2007.12.003

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

Watson, S. K., Reamer, L. A., Mareno, M. C., Vale, G., Harrison, R. A., Lambeth, S. P., Schapiro, S. J., & Whiten, A. (2017). Socially transmitted diffusion of a novel behavior from subordinate chimpanzees. *American Journal of Primatology*, *79*, e22642. https://doi.org/10.1002/ajp.22642

Williams, H. (1990). Models for song learning in the zebra finch: Fathers or others? *Animal Behaviour*, *39*, 745–757. https://doi.org/10.1016/S0003-3472(05)80386-0

Zann, R. A. (1996). *The Zebra Finch: A Synthesis of Field and Laboratory Studies*. Oxford University Press, USA.

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