

## Research



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# Nest prospecting brown-headed cowbirds 'parasitize' social information when the value of personal information is lacking

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Brood parasites face considerable cognitive challenges in locating and selecting host nests for their young. Here, we test whether female brown-headed cowbirds, *Molothrus ater*, could use information acquired from observing the nest prospecting patterns of conspecifics to influence their own patterns of nest selection. In laboratory-based experiments, we created a disparity in the amount of personal information females had about the quality of nests. Females with less personal information about the quality of two nests spent more time investigating the nest that more knowledgeable females investigated. Furthermore, there was a strong negative relationship between individual's ability to track nest quality using personal information and their tendency to copy others. These two contrasting strategies for selecting nests are equally effective, but lead to different patterns of parasitism.

## 1. Introduction

Gregarious animals are exposed to a wealth of information generated by the conspecifics around them. This social information can be used to the advantage of those willing and able to attend to it, allowing them to learn tasks faster and avoid the costs of independent discovery [1–5]. Often, however, there can be substantial costs associated with group living that exist concomitant with these benefits. For example, social competition can lead to resource depletion, aggressive interactions or increased predation risk, which can influence the effectiveness of foraging, breeding ground selection and mate selection [6–14]. Thus, there are trade-offs associated with using social information, with the net pay-off varying by context and by individual. Such trade-offs can select for different strategies in favouring personal versus social information [15].

Generalist obligate brood parasitic birds, like brown-headed cowbirds, provide a clear example of the challenges of using social information when prospecting for nests. Brood parasites do not build their own nests. They instead deposit their eggs in other species' nests and leave their young to be raised by the host. Finding a nest and selecting a suitable one—one belonging to an appropriate host species whose nest is ready for parasitism—may be a challenging cognitive endeavour, involving acquiring and evaluating many different types of information [16–24]. At any given moment, female cowbirds may vary in the amount of personal information they have about a nest. Information acquired from the behaviour of other prospecting females could inform naive females about the location of nests and the suitability of a nest for parasitism.

There may, however, be a down-side to copying other females. Nestling cowbirds are vigorous beggars and acquire a high proportion of the host parents' forage [25,26]. Thus an already-parasitized nest is a highly competitive environment for young. Reports in the wild support the idea that female cowbirds defend against this cost. At breeding, females become aggressive around nests and will displace one another [27,28].

Laboratory-based experiments [18] suggest that female cowbirds avoid laying in nests that already contain a cowbird egg. This provides evidence that females use social information to avoid nests other females have found attractive. There

was, however, another intriguing finding from the same set of experiments suggesting that females may also use the presence of a cowbird egg in a nest in order to learn about characteristics of nests and/or their hosts. In contrast to the strong aversion adult female cowbirds showed to an already-parasitized nest, juvenile female cowbirds (experiencing their first breeding season) showed a preference to lay in already-parasitized nests [18]. Presumably, for these less-knowledgeable females, the benefits of selecting a suitable nest outweigh the cost of laying in a highly competitive environment.

The countervailing costs and benefits of selecting a nest in a social context lead to several competing hypotheses about how female cowbirds might prioritize personal and social information when making a nest selection decision. These hypotheses include: (i) *individual assessment*: females may depend only on personally acquired information and ignore the behaviour or other females; (ii) *competitive displacement*: females may use social information in order to avoid nests in which other females are interested, or actively displace other females from their preferred nests; (iii) *social facilitation*: females may be attracted to nests where other females are seen; and (iv) *a mixed strategy*: the amount and quality of personal information an individual has may influence whether or not to use a copying or avoiding strategy [4]. In addition, the characteristics of the individual—their personality [29] or learning skills [30]—might influence the pay-offs of using social versus personal information.

We devised three experiments to test these hypotheses using methods that have previously been successful in evaluating the cognitive processes associated with nest selection decisions in cowbirds [18,19]. These methods involve manipulating egg numbers in experimental nests. While the characteristics and behaviour of hosts are certainly important for nest selection decisions [31–33], we have found that in the laboratory, cowbirds will also examine the eggs in a nest in the absence of a host and use them to make decisions about the nest's suitability for parasitism. For example, female cowbirds adjust their nest visitation patterns and subsequent laying patterns based on the types of eggs present (size, colour and pattern) [18,19]. In addition, they show distinct preferences for certain numbers of eggs in nests [18,19]. For example, if a female is given a choice between a nest that contains three eggs and a nest that contains two eggs, she will show a preference to spend time on, and subsequently lay in the three-egg nest. The relative numbers of eggs in nests however, is less important to females than is information acquired about the nest from the day before. Females who can investigate nests across multiple days show strong preferences for nests that increase in egg number and will show a strong aversion for nests whose egg numbers do not change. This preference is remarkably strong. We have now documented preferences for changing nests in laboratory studies in Canada and the USA, in over 10 years of study, comprising over 600 female cowbirds ([18,19], D. White 2017, unpublished observations). We have interpreted this result as females timing the readiness of a nest for incubation. Hosts typically commence incubation once the penultimate or ultimate egg has been laid and thus a non-changing nest is one where incubation has already begun and is a poor choice for parasitism because the cowbird baby would be at a developmental disadvantage to the host young. For prospecting females, information acquired across days about the change in eggs has priority over information about egg number from any given day [19]. This type of information, however, is more cognitively challenging to acquire and to use

effectively as it requires memory for the contents of nests, their location, and the time they were encountered (so-called, episodic-like, or 'what-where-when' memory [19,34]).

In the first two experiments, we varied the personal and social information females had about nests to examine how females would weigh them when prospecting for nests. To do so, we manipulated the number of eggs present in nests within and across days. Then, by giving females different opportunities across days to investigate the nests, we could control the type of information females had about the same nests. We gave some females (referred to as 'naive females') information about nest contents for only the current day, for example, they would get to encounter a nest containing three eggs and another nest containing two eggs, but they were naive to the status of the nests from the day before. Other (informed) females, however, got more valuable information; they were given the opportunity to visit the nests on the day prior to the test. On that prior day, the nest containing two eggs on the test day had contained only one egg, while the three-egg nest from the test day contained three eggs on the prior. Thus, on the test day, informed females had information indicating that the two-egg nest had changed while the three-egg nest had remained constant. If the females evaluated these nests without being influenced by the behaviour of other females, naive individuals should show a preference for the three-egg nest because, all else being equal, nests containing three eggs are preferred over nests containing two eggs [18,19], while the informed females should show a preference for the two-egg nest because it is a changing and thus active nest.

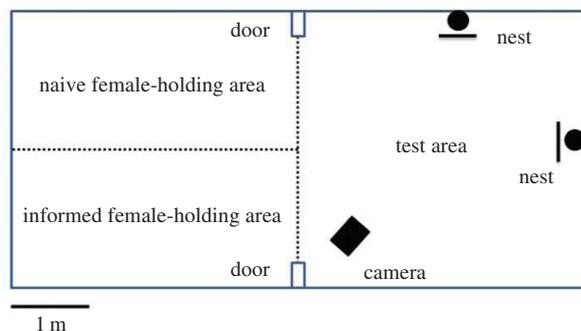
Finally, 1 year later we conducted the third experiment in which we allowed the same set of females to live and breed in a large outdoor aviary where they had access to a variety of nests. Here, we were able to examine whether the patterns of information females used in experiments 1 and 2 related to actual egg-laying decisions. We manipulated the number and types of eggs in the nests to examine each female's accuracy at laying in changing nests, as well as whether they would use social information provided in the nests (other cowbird eggs) to influence their egg-laying decisions.

## 2. Experiment 1: social influences on nest prospecting

In the first experiment, naive females observed two informed females investigating two nests. After informed females left the area, the naive females entered, one at a time and investigated the nests.

### (a) Subjects

Twelve female cowbirds, wild-caught in spring 2014 in Flamborough County, Ontario, Canada served as subjects throughout the experiments. All females were adults, experiencing at least one breeding season in the wild. After trapping and prior to experimentation, we housed females in a large 12 × 6 × 4 m outdoor aviary with 12 wild-caught males. Throughout testing, birds were provided with ad libitum access to water and a mix of white millet, red millet and a modified version of the Bronx zoo diet for omnivorous birds. All birds wore unique combinations of coloured leg bands to permit individual identification. All subjects were experimentally naive prior to testing.



**Figure 1.** Experimental apparatus. (Online version in colour.)

### (b) Apparatus

We conducted tests in a  $2.5 \times 2.5 \times 6$  m flight cage containing grass, six overhead perches, food, water and two bamboo canary nests (Kaytee Products, Chilton, WI, USA). Nests contained grass clippings and either two or three plaster-of-Paris eggs. These eggs were made from molds of real cowbird eggs and painted white. Each egg had a plastic-coated paperclip affixed into it that descended through the bottom of the nest. The paperclip served to secure the egg in the nest so that the birds could not remove it. It could not be seen by the birds.

The flight cage was divided in half, creating a 'holding' area and a 'testing' area (figure 1). The holding area was divided in half with hardware cloth to separate informed and naive females. Two opaque blinds between holding areas and the testing area could be raised or lowered to obscure birds' sight of the other area. Small ( $20 \times 20$  cm) doors at the top of the hardware cloth dividers could be opened to allow birds to fly from one area to the other.

We affixed nests on the walls of the testing side of the cage approximately 1 m from the ground and approximately 1 m away from one another. Small sticks (approx. 30 cm) were positioned in front of the nests allowing birds to alight and investigate nests. After every trial, we moved nests to new locations (keeping the above-mentioned dimensions consistent). In past work, we have found that females consider nests moved to new locations to be different nests [18,19].

### (c) Procedure

All females served as naive subjects in each of two conditions: the view and blind conditions. Also, eight of the females were randomly assigned to serve as informed females. We counter-balanced running order within and across females for condition and made sure at least 4 days elapsed before a female was tested again.

#### (i) Pretest day (the day prior to testing)

To make females informed, we placed them in the testing area, two at a time and gave them 3 h to investigate the two nests. One of the nests contained one egg and one nest contained three eggs. Naive females were not allowed to observe the nests or any of the actions of the informed females on this day.

#### (ii) Test day

The next day, we put two informed females into the testing area and gave them 15 min to investigate the two nests. Prior to the informed females entering the testing area, we added an egg to the nest that contained one egg during the pretest and we added no eggs to nest containing three eggs during the pretest. The only difference between view and blind conditions was

whether the opaque blind that separated the holding areas from the test area was rolled up (view condition: naive females could see the behaviour of the informed females) or rolled down (blind condition: naive females could not see the behaviour of the informed females). After the 15 min, we removed the informed females and then opened the door in the divider allowing a single naive female to enter the testing chamber. Each naive female was allowed to investigate nests for 15 min. During this time, we rolled down the blind so that the other naive females could not view the testing area. At the end of each 15 min, the naive female was flushed out of the test area and another naive female was flushed in. Four naive females were tested for each informed female pair.

#### (iii) Data analysis

We captured all nest visits on video. For each female, we recorded her landing and departure times on each nest and on the sticks adjacent to the nests, a measure we have used in the past that predicts females' preferences to lay in a nest [18,19]. We compared for naive females the proportion of time they spent on the nest that contained two eggs on the test day (we refer to this nest as the 'change nest' hereafter because it was the nest that changed in the number of eggs it contained between pretest day and test day) in the blind and view condition. Owing to small sample sizes, indeterminate values and the risk of non-normality in proportion data, we used repeated-measures non-parametric statistics (Wilcoxon *T*-tests and Spearman-ranked correlation coefficients) throughout.

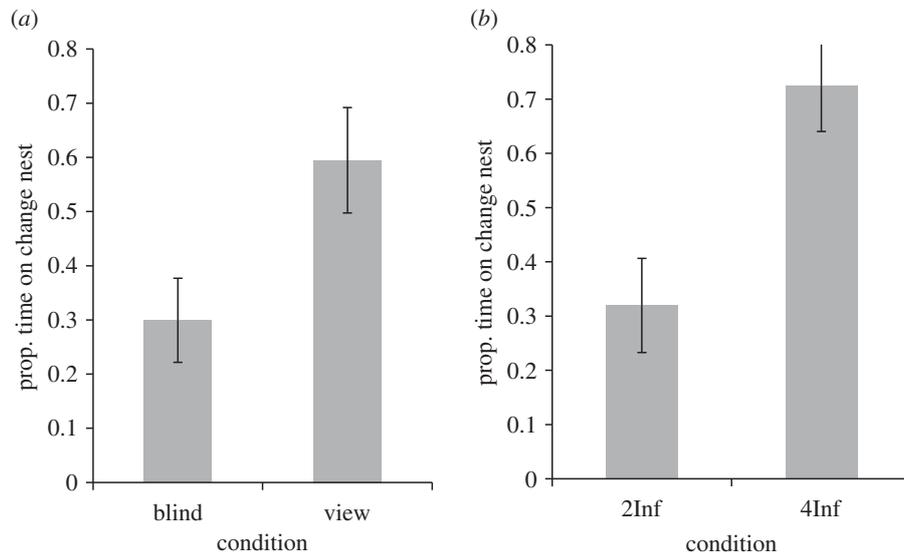
## 3. Results

Overall, informed females spent  $35.4 (\pm 10.8)$  s on the change nest, and  $28 (\pm 6.9)$  s on the static nest. While this was not statistically significant for individual females (Wilcoxon *T*-test,  $T_7 = 14$ , n.s.), examining the pairs of informed females that naive females observed revealed that all pairs of informed females spent a higher proportion of time (mean =  $0.57 \pm 0.016$ ) on the change nest.

During the test phase, 11 out of 12 naive females spent significantly more time on the change nest when they were in the view condition (mean proportion of time spent on the change nest =  $0.59 \pm 0.10$ ) compared to when they were in the blind condition (mean =  $0.30 \pm 0.08$ ;  $T_{11} = 8$ ,  $p < 0.05$ ) (figure 2*a*).

## 4. Experiment 2: nest selection with competition

In experiment 1, we found that there was a social facilitation effect: observer females spent more time on the nest that the informed female preferred. However, by allowing the naive females to inspect nests alone, experiment 1 could not test whether there might also be a negative effect of prospecting in a nest in which other females showed interest. Perhaps other females might aggress against the naive female, or guard the nest. Thus, in experiment 2, we created a condition where the opportunity to compete over limited nests was extreme—where many females would simultaneously evaluate only two nests. While this might be a more competitive environment than cowbirds would typically encounter in the wild, it would maximize the potential to observe negative social effects on prospecting. We varied the amount of social



**Figure 2.** (a) Mean ( $\pm 1$  s.e.m.) proportion of time spent on change nest in blind and view conditions by naive females in experiment 1. (b) Mean ( $\pm 1$  s.e.m.) proportion of time spent on change nest in 2Inf and 4Inf conditions by naive females in experiment 2.

information about two-egg nests in the prospecting groups by changing the ratio of naive to informed females present.

### (a) Procedure

We created two different conditions, one in which informed females were in the majority in a six-bird prospecting group (four informed and two naive females: 4Inf condition) and one in which the naive females were in the majority (four naive and two informed females: 2Inf condition). We assigned females to the two conditions such that after all trials were completed, every female served as naive in both conditions, and every female served as informed in at least one condition (all females served as informed in the 4Inf condition, and eight females were informed in the 2Inf condition). We counter-balanced running order across trials and ensured that no female was tested in consecutive trials. We ran a total of 10 trials (four 2Inf and six 4Inf trials). Some females served in the same type of trial multiple times. In cases where females were tested multiple times in the same condition, we averaged their scores.

#### (i) Pretest day

Informed females were treated the same as in experiment 1 except that they were tested in groups of four.

#### (ii) Test day

Six females entered the test area simultaneously. Running order for the two conditions was randomized. We randomly selected either two or four females to serve in the naive treatment, and used either four or two randomly selected informed females, depending on the condition being run. On the test day, all six birds were flushed into the testing area and were given 15 min to investigate the two nests. As in experiment 1, one nest contained three eggs (staying the same from pretest to test) and one nest contained two eggs (changing by the addition of one egg from the pretest: thus, again, the 'change' nest). We videorecorded all visits to the nests and measured the amount of time each female spent on the nests or on the perches immediately adjacent to the nests, as well as the time in the trial when she made her visits.

#### (iii) Data analysis

Similar to experiment 1, we examined the change in the amount of time naive females spent investigating the change

nest in the presence of many informed individuals (4Inf condition) and in the presence of fewer informed individuals (2Inf condition) using non-parametric statistics (Wilcoxon *T*-tests and Spearman-ranked correlation coefficients) throughout. We hypothesized that naive females would spend more time investigating the change nest in the 4Inf condition compared with the 2Inf condition, because there would be more social information available about the change nest for naive females to use in the 4Inf condition. This, however, is only a rudimentary measure of social influence. When subjects are able to interact freely in groups, there may be numerous social influences that could obscure the naive females' patterns of nest visits. Social information could vary dramatically depending on the particular behaviours of the group members. Any female who lands on a nest, be they 'informed' or 'naive' as we have defined them, is providing some amount of social information to the rest of the birds in the group and the dynamics of any particular trial might vary dramatically. We thus created a more sensitive measure of social influence; a 'conformity' score for each individual within each trial. Conformity took into account how many times other females (irrespective of informed or naive status) landed on a nest prior to the focal subject's visit. Thus, for each nest visit, a focal female got a conformity score (an index between 0 and 1) that was calculated as: the total amount of time all females in the group spent on a nest prior to the focal's visit divided by the total amount of time spent by all females on both nests up to that moment. At the end of the trial, the focal female's scores for each of her nest visits were averaged to give her an overall conformity score for that trial.

### (b) Results

Overall, birds spent on average 1.62 min visiting nests during trials. This time was broken up in numerous brief visits. We measured the number of times that more than one bird visited a nest simultaneously. Sixty three times a pair of birds visited simultaneously, 10 times a trio of birds visited and there were no instances where more than three birds visited a nest simultaneously. We measured no instances of competitive displacement during the 73 instances of multiple birds on a nest.

Females did not spend significantly different amounts of time investigating nests when they were naive compared to when they were informed (naive =  $1.4 \pm 0.2$  min, informed =  $1.22 \pm 0.25$  min,  $T_{11} = 15$ , n.s.).

Informed females in aggregate spent more time on the change nest in the 4Inf condition (mean =  $2:33 \pm 0.23$  min) compared with the 2Inf condition (mean =  $1:21 \pm 0:10$  min). This was because there were twice as many informed females in the 4Inf condition, not because the informed females did anything differently in the two conditions: informed females did not differ significantly in the amount of time they spent on nests in the 2Inf versus 4Inf condition (mean time spent on change nest in 2Inf condition =  $0.6$  min  $\pm$   $0.25$  min, 4Inf condition =  $0.52 \pm 0.17$  min;  $T_7 = 7$ , n.s.). Thus, overall, informed females behaved in similar ways across conditions.

The nest visit patterns of naive females, however, were different across conditions. Naive females spent more time investigating the change nest in the 4Inf condition (mean proportion of time on change nest =  $0.72 \pm 0.08$ ), than when they were in the 2Inf condition (mean =  $0.32 \pm 0.09$ ;  $T_{11} = 8$ ,  $p < 0.05$ ; figure 2b).

### (i) Conformity measures

Naive females' conformity scores did not differ between conditions (mean 2Inf conformity =  $0.61 \pm 0.05$ , mean 4Inf conformity =  $0.59 \pm 0.04$ ). This indicated that their responsiveness to social information was the same in two conditions, there was just more social information about the change nest in the 4Inf condition.

Eleven out of 12 females had higher conformity scores when they served as naive than when they served as informed (mean conformity naive =  $0.60 \pm 0.05$ , mean conformity informed:  $0.44 \pm 0.07$ ,  $T_{11} = 8$ ,  $p < 0.05$ ).

There were no significant differences in the conformity scores towards informed or naive females (average conformity: to informed females =  $0.64 \pm 0.06$ , to naive females:  $0.67 \pm 0.04$ ;  $T_{11} = 13$ , n.s.). This suggests that all females provided similar amounts and quality of social information, but the naive females were more influenced by it than were the informed females.

### (ii) Within-individual patterns

Because most subjects served as both informed and naive subjects across trials, we were able to compare their nest visits in trials when they were informed to nest visits when they were naive. To get a measure of each female's ability to use personal information, we examined how well they were able to track the changing nest when they were informed in the 2Inf condition. This is the condition in which they had the least amount of social information directing them to the change nest. Thus, we considered females who spent more time on the change nest in this condition as being better able to remember the information acquired personally (from the pretest) and make nest selection decisions during the test. We compared this value to the degree to which their nest visits were modified by social experience when they were naive (in the 4Inf condition: the situation where they had no personal information from the pretest and the most social information directing them towards the changing nest). There was a strong negative relationship between these two scores (Spearman  $r_s = -0.904$ ,  $p < 0.01$ ), suggesting that those individuals who were better able to make individual evaluations of nest quality were the least susceptible to social information and vice versa. This

negative relationship also held for conformity scores. That is, the better the female's ability to track the changing nest using personal information, the less likely she was to conform to the behaviour of other females when serving as a naive female in the 4Inf condition ( $r_s = -0.735$ ,  $p < 0.04$ ; figure 3a).

We also examined whether the tendency to be influenced by social information was consistent within females. We compared the degree to which females were socially influenced in experiments 1 and 2. For experiment 1, we used the proportion of time females spent on the change nest in the view condition and compared these values to their conformity scores in the 4Inf condition. These two measures of social influence were highly correlated ( $r = 0.77$ ,  $n = 12$ ,  $p < 0.01$ ; figure 3b). Thus, the degree to which individuals were socially influenced stayed consistent across experiments.

We then examined the consistency across experiments in individual ability to track the changing nest using personal information. In experiment 1, we measured this by the amount of time females spent on the change nest when they were informed. In experiment 2, we used their time spent on the change nest on the test day in the 2Inf condition. These two scores were significantly correlated ( $r_s = 0.78$ ,  $p < 0.05$ ), suggesting that individual abilities to track the changing nest was also consistent across experiments.

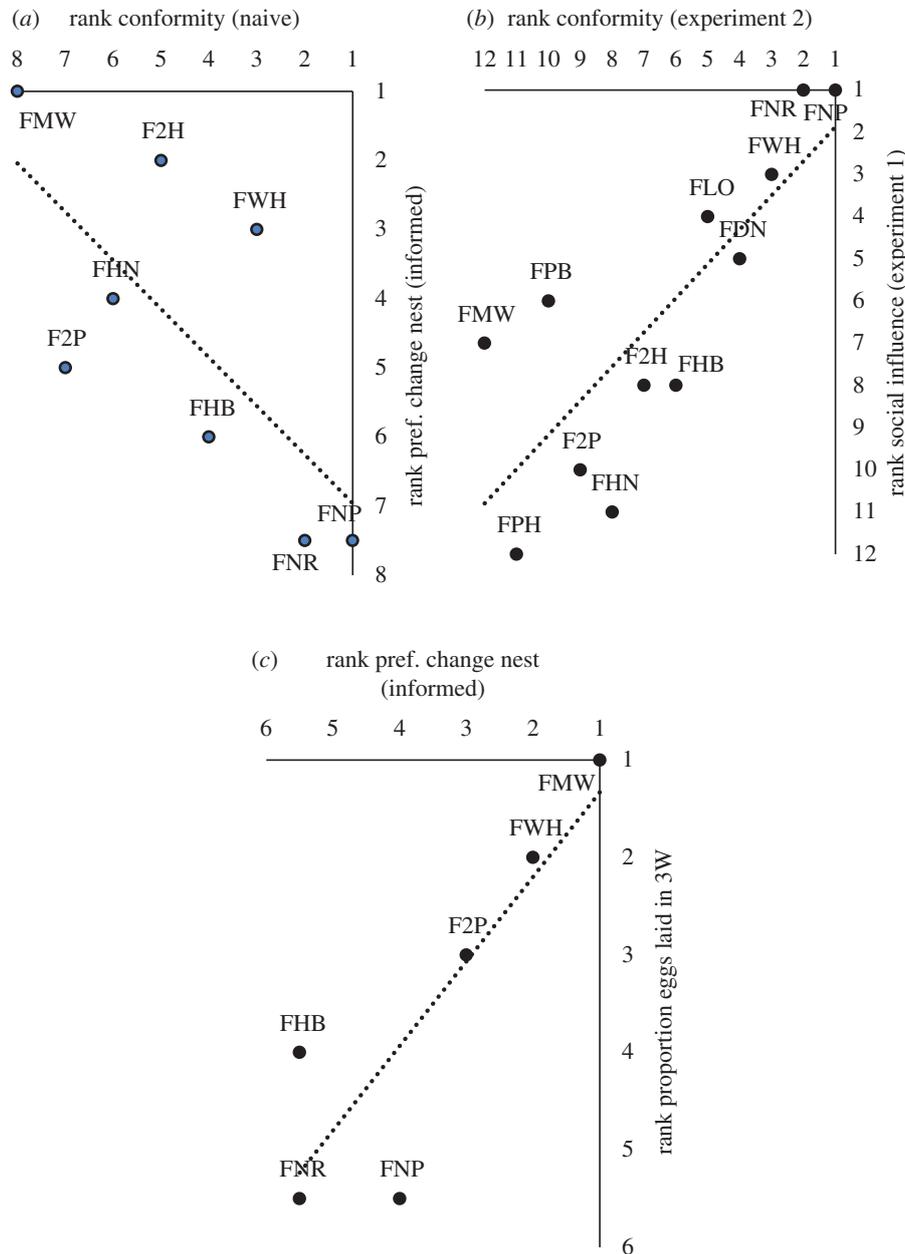
## 5. Experiment 3: egg-laying patterns

Experiments 1 and 2 suggested there were two general strategies being employed by females when prospecting: either rely on personal information if good at making decisions, or else copy others. In experiment 3, we investigated whether these strategies for nest prospecting would lead to any observed differences in egg-laying patterns. Thus, we placed the females from experiments 1 and 2 into the large outdoor aviary for 1 year with 12 adult males and then in the next breeding season we investigated their patterns of egg laying in nests within the aviary.

### (a) Procedure

We placed 12 bamboo canary nests in trees within the aviaries. All nests were secured in the trees approximately 1 m above the ground. We experimentally manipulated the nests in two phases. First (phase 1) to get a measure of each female's laying accuracy, then (phase 2) to measure each female's tendency to use public information when selecting a nest.

Each trial of phase 1 lasted 4 days, at 11.00 of day 1, we secured one plaster-of-Paris egg in each of six randomly selected nests. We secured three eggs in the other six nests. On day 2, at 11.00 we added an egg to the initial one-egg nest, and on day 3 we once again added an egg to the initial one-egg nest such that on this day both nests contained three eggs. We collected all cowbird eggs laid in the nests at approximately 7.00 on days 2–4. We used a surveillance system (Geo-vision GV-1480, Irvine California) with motion-sensitive, low-light, closed circuit cameras mounted near each nest to record the individual identity of each laying female. At the end of the fourth day of testing, we removed the nests and placed new nests in new locations within the aviary and commenced the procedure for phase 1 again. Overall, we repeated phase 1 four times. The manipulation used in phase 1 has been used numerous times in the past [19], to determine how accurate females were at laying in a changing nest versus an unchanging nest.



**Figure 3.** Scatterplots showing relationship between (a) ranks of females' ability to track changing nests using personal information when informed (pref. for change nest) and the ranks of their social conformity score when naive in experiment 2, (b) the ranks of females' preference for the change nest in the view condition of experiment 1 (rank social influence) and the ranks of their social conformity score in experiment 2, (c) ranks of females' ability to track changing nests using personal information when informed (pref. for change nest) in experiment 2, and the ranks of the proportion of eggs they laid in 3W compared to 2W1S nests in experiment 3. Data labels refer to the females' leg band acronyms. (Online version in colour.)

In phase 2, we secured three white eggs into six randomly selected nests (3W nests). In the other six nests, we secured two white eggs and one white egg that had been artificially speckled with brown paint to resemble a cowbird egg (2W1S nests). We have used this manipulation in the past to simulate nests that have already been parasitized by another cowbird [18]. Adult females typically show an aversion to a nest containing a speckled egg. After collecting all eggs laid in the nests the next morning, we removed the nests and conducted phase 2 again with nests in new locations. We repeated phase 2 four times.

## (b) Results

One female died prior to the breeding season, leaving 11 females to examine egg laying. Of the 11, 10 laid at least one egg during the breeding season (mean laid per female =  $6.6 \pm 1.83$ ) across

the six-week breeding season. There was no significant correlation between our measures of personal information use or conformity from experiment 1 or 2 and total egg production ( $r_{10} = -0.12$  for personal information use,  $r_{10} = 0.11$  for conformity).

In phase 1, all females showed remarkably strong preferences for laying in changing nests. Out of the 22 eggs laid, only one egg was laid in a nest that had stayed at three eggs across 2 days. Thus, irrespective of our measures of individual ability or social conformity scores from experiments 1 and 2, all females showed very strong tendencies for laying in changing nests.

In phase 2, overall, females laid 13 eggs in 3W nests and seven in 2W1S nests. Here, the measures from experiments 1 and 2 did relate to egg production. There was a significant negative correlation between the number of eggs a female laid in 3W nests and her social conformity score from

experiment 2 ( $r_9 = -0.725$ ,  $p < 0.03$ ) and a significantly positive correlation between the number of eggs laid in the 3W nests and her individual ability to track changing nests score from experiment 2 ( $r_6 = 0.87$ ,  $p < 0.03$ ; figure 3c). Thus, those females most influenced by social information in experiments 1 and 2 were more likely to lay in already-parasitized (2W1S) nests. Those females most able to track the changing nests using personal information in experiments 1 and 2 were more likely to avoid already-parasitized nests.

Finally, we examined patterns of egg removal by females in the breeding season. The plaster-of-Paris eggs were affixed into the nests with paper clips and could not be removed, but females occasionally removed real cowbird eggs laid by other females prior to when we collected the eggs that morning. There was a significant correlation between females' social conformity score from experiment 2 and the number of eggs they removed ( $r_{12} = 0.82$ ,  $p < 0.002$ ). Thus, the most socially influenced females from experiments 1 and 2 were most likely to lay in nests that already had been parasitized by other cowbirds, and were also the most likely to remove other cowbird eggs from nests.

## 6. Discussion

Females modified their nest inspection behaviour based on the behaviour of other females around them, increasing the time they spent investigating nests that other females investigated. This occurred both when naive females evaluated the nests independently (experiment 1) and when all females investigated the nests at the same time (experiment 2). The degree of this social influence, however, differed across females. Some females were more effective at using personal information, and others were more likely to be copiers. Females who were most accurate at tracking the status of the changing nest across days were least influenced by the behaviour of others. Both of these measures—individual ability to use personal information and tendency to conform to others—were stable properties of individual females across time, trials, different group mates and experiments. This pronounced a negative relationship between females' ability to track the changing nests and their social conformity may indicate that there are two distinct strategies for selecting a nest for parasitism: either prospect individually or copy others.

In experiment 3, we found that these strategies related directly to the females' egg-laying patterns. While all females were able to select changing nests, those females who were most able to track the changing nests in the prospecting tasks were most likely to avoid nests that other females had parasitized (as indicated in 2W1S nests) and females who were most socially influenced in the prospecting tasks were most likely to lay in the parasitized nests. These females were also the most likely to remove other cowbirds egg from a nest. Thus, this strategy could allow those highly socially influenced females to gain the benefits of using social information to select a nest, while

reducing the costs associated with having other cowbird chicks compete with their baby for the host's food. While here we have measured egg laying in captivity, there is some evidence that these patterns may also exist in the wild [35,36]. These distinct strategies are reminiscent of producer/scrounger strategies seen in many socially foraging animals [37–40]. Alternatively, however, there may be a single cognitive mechanism underlying the decision to use or not use social information, requiring, for each female in each instance, an evaluation of the value of their personal versus their social information: a hypothesis to be tested in the future.

There have been numerous theoretical and empirical studies on how group composition and behaviour can influence personal information use and conformity [41–46]. Much of this work focuses on how the benefits of being in a group may conflict with the immediate needs of individuals within the group and thus promote multiple strategies for using or avoiding social information. Female cowbirds show distinct variability in tendencies to be social throughout their lifetimes and sociability might be a consistent trait that relates to a variety of decision processes that includes, but is not limited to nest prospecting.

There is not a large literature connecting individuals' cognitive abilities with social information use [47]. While some work has characterized a connection between individual learning and social behaviour in general [48], and there is an extensive literature on animal personalities revealing that certain types of consistent behavioural propensities relate to the likelihood of using social information [29,49–53], only Katsnelson *et al.* [30] have connected learning ability and social information use: showing that individual learning ability related to the use of a producer foraging tactic in house sparrows. The distinction between personality traits and cognitive abilities as they relate to social information use may be an important one. If ability varies naturally in a population, as does social information use, it has consequences for information flow, social dynamics, the emergence of keystone individuals [54] and ultimately the opportunities for and pathways of cultural evolution.

**Ethics.** All work on animals adhered to the CCAC guidelines for research on animals and was approved by the Institutional Animal Care Committee at Wilfrid Laurier University (protocol no. R13000).

**Data accessibility.** Data supporting this work are available at <https://sites.google.com/site/whitesocialbehaviourlab/home/white-lab-research>.

**Authors' contributions.** All authors contributed to the design and execution of the experiment. S.A., N.S. and H.B.D. conducted all data collection; D.J.W. conceptualized the study and wrote the manuscript. D.J.W. and H.B.D. conducted data analysis.

**Competing interests.** We declare we have no competing interests.

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