2017

A comprehensive study of personal and social information use in female brown-headed cowbirds, Molothrus ater

Hayden Davies
davi8520@mylaurier.ca

David J. White
dwhite@wlu.ca

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PS699 THESIS

HAYDEN B. DAVIES

Contents

Abstract

Brood parasites face considerable cognitive challenges when locating and selecting host nests for their young. One aspect of this challenge is determining how to use different sources of information to make decisions regarding the quality of a prospective nest. Here we investigate how female-brown-headed cowbirds, *Molothrus ater*, use information when prospecting for nests, and then expand upon this to investigate decisions related to foraging. In chapter 1, we demonstrated female could use social information acquired from observing the nest prospecting patterns of conspecifics to influence their own patterns of nest selection. Furthermore, we found a negative relationship between a female's accuracy at using personal information and her tendency to copy others. In chapter 2, we found the females were able to use social information in a foraging setting as well. The female's accuracy using personal information remained consistent across nest prospecting and foraging contexts however, the relationship between accuracy and tendency to copy others drastically reversed. A follow up experiment revealed the likely possibility that the differing relationship between personal and social information use depended on the degree of conflict that existed between the two types of information. In chapter 3, we redeveloped and implemented a new RFID tracking technology allowing us to investigate how the cognitive strategies from chapters 1 and 2 translated to a naturalistic, socially complex breeding environment. We found female cowbirds who spent more time prospecting, produced a greater quantity of eggs and demonstrated high accuracy scores during chapter 1 and 2, whereas females who relied on copying others spent significantly less time prospecting and demonstrated lower laying accuracy scores. By demonstrating how individuals' cognitive strategies relate across context and translate to a socially complex setting, we have demonstrated the importance of examining behaviour in both of these settings and our RFID tracking technology provides researchers with the framework to effectively study this in the future.

Chapter 1: Female brown-headed cowbirds 'parasitize' public information when prospecting for nests.

David J. White, Hayden B. Davies, Samuel Agyapong and Nora Seegmiller

Introduction

Gregarious animals are exposed to a wealth of information generated by the conspecifics around them. This 'public' [1] or 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 [2-5]. 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 payoff varying by context and by individual [15]. The cognitive demands associated with using social information to make decisions therefore can be pronounced.

Generalist obligate brood parasitic brown-headed cowbirds may be subject to such a trade-off in using social information when prospecting for nests. Finding nests 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, females may vary in the amount of information they have about a nest. Information acquired from the behaviour of knowledgeable prospecting females could inform naïve females about the location of nests and the suitability of a nest for parasitism. In contrast, however, copying other females could also lead to resource competition. 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 with one another around nests and will displace one another [27, 28]. In addition, in aviary experiments, adult female cowbirds show a very strong aversion to lay eggs in nests that already contain a cowbird egg [18].

The experiment by White et al. [18] suggests that female cowbirds do indeed use public information in modifying their nest-selection decisions (the presence of a cowbird egg is a piece of public information produced by the first laying cowbird) and use it to avoid nests that other cowbirds have parasitized, presumably in order to avoid the costs of multiple parasitism. 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 use social information when making a nest selection decision. These hypotheses include: (1) *individual assessment*: females may depend only on individual information and ignore the behaviour or other females, (2) *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, (3) *social learning*: females may use observations of other females prospecting for nests in order to acquire information about good nests and thus be attracted to nests where other females are seen, and (4) *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 payoffs of using social versus personal information.

We devised three experiments to test among 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 mock nests. While the characteristics and behaviour of hosts are certainly important for nest selection decisions [31-33], we have found that cowbirds will also examine the eggs already in a nest in the absence of a host 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 one egg, she will reliably show a strong preference to spend time on, and subsequently lay in the three-egg nest (likewise, females tend to prefer a three-egg nest over a two-egg nest, but the preference is not as pronounced). 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. We have interpreted this result as females are 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 egg number has priority over information about nest number from any given day [19]. This type of information, however, is more cognitively challenging to acquire and 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 manipulated the number of eggs present in mock nests within and across days. Then, by giving different females different opportunities across days to investigate the nests, provided a controlled means to change the type of information the females had about the same nests. We gave some females (referred to as 'naïve 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 naïve 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, naïve 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, one year later 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. 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 public information provided in the nests (other cowbird eggs) to influence their egg laying decisions.

EXPERIMENT 1: Social learning about nests

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

Subjects

12 female cowbirds, wild caught in spring 2014 in West Flamborough County, Ontario, Canada served as subjects throughout the two experiments. After trapping and prior to experimentation, we housed females in a large 12 x 6 x 4 m outdoor aviary with 12 wild-caught males. Throughout testing, birds were provided with *ad lib* 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 individually unique combinations of coloured leg bands to permit individual identification. All subjects were experimentally naïve prior to testing.

Apparatus

We conducted tests in a 2.5 x 2.5 x 6 m flight cage containing grass, six overhead perches, food, water and two bamboo canary nests (Kaytee Products, Chilton, WI, USA). Nests contained grass and either two or three plaster of Paris mock eggs. The mock 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 naïve females. Two opaque

Figure 1: **Experimental Apparatus**
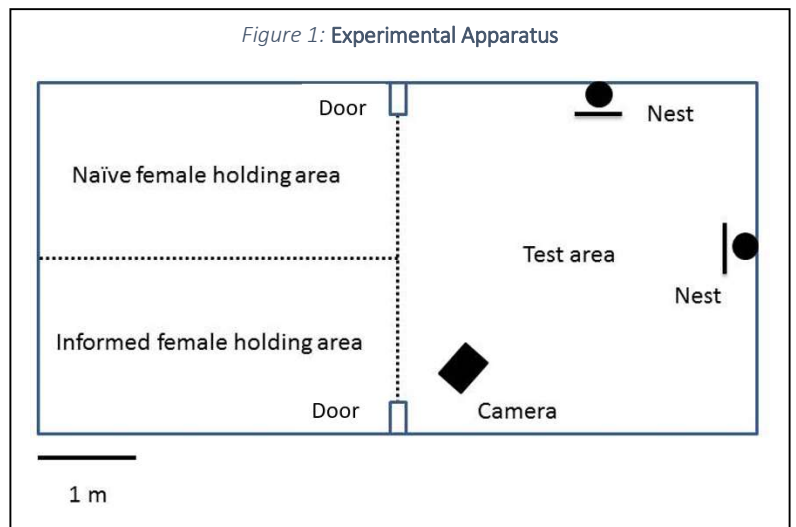
blinds between holding areas and the testing area could be raised or lowered to obscure birds' sight of the other area. Small (20 x 20 cm) doors at the top of the hardware cloth dividers could be opened to allow birds to fly from one area to the other.

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 (approximately 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].

Procedure

All females served as naïve 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 counterbalanced running order within and across females for condition and made sure at least four days elapsed before a female was tested again.

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 three hours to investigate the two nests. One of the nests contained one egg and one nest contained three eggs. Naïve females were not allowed to observe the nests or any of the actions of the informed females on this day.

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: naïve females could see the behaviour of the informed females) or rolled down (Blind condition: naïve 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 naïve female to enter the testing chamber. Each naïve female was allowed to investigate nests for 15 min. During this time, we rolled down the blind so that the other naïve females could not view the testing area. At the end of each 15 min, the naïve female was flushed out of the test area and another naïve female was flushed in. Four naïve females were tested for each informed female pair.

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. We compared for naïve females the proportion of time they spent on the nest that contained two eggs (which was the nest that changed in egg number from pretest to test change nest: hereafter referred to as the change nest) in the Blind and Visible condition. Because we tested several naïve birds with each demonstrator pair, this raises the concern of pseudoreplication: that some demonstrators might have a larger influence than others, thus to examine this issue we used a general linear mixed model comparing time spent investigating the change nest in the visible vs blind condition using the demonstrator pair as a fixed factor.

Results

When in the View condition, all naïve females observed informed females spend the majority of their time on the change nest during the observation phase (mean proportion of inspection time spent on change nest = 0.57 ± 0.016, 6 of 8 informed females spent more time on the change nest).

During the test phase, 11 out of 12 naïve females spent significantly more time on the change nest when they were in the View condition (mean proportion time spent on the change nest = 0.59, ± 0.10) compared to when they were in the Blind condition (mean = 0.30 ± 0.08) (Figure 2). Since we could cluster females into three groups based on which pair of informed demonstrators they experienced, we compared the proportion of time spent on the change nest in view vs blind condition using the identity of the demonstrator pair as a fixed factor. We found a significant main effect of treatment condition ($F_{(1,9)} = 11.98$, $p<.01$) and a significant interaction between the demonstrator pair and the treatment ($F_{(2,9)} = 4.93$, $P<.05$). The three pairs of informed females did not differ substantially in the time they spent investigating the nests when demonstrating. The significant interaction however suggests that some demonstrators are more effective than others at influencing naïve observers.

Figure 2: Mean Time Prospecting Blind & View Condition
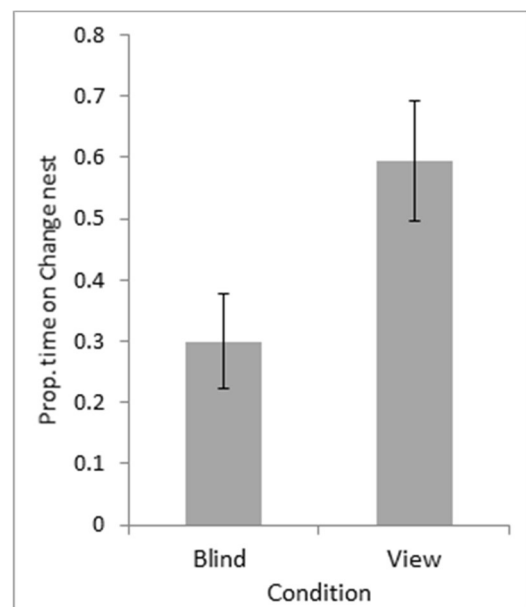
Experiment 2: Group dynamics in nest selection

In experiment 2 we allowed all females – naïve and informed – simultaneous access to the nests. We varied the amount of 'informed' social information present by changing the ratio of naïve to informed females present.

Procedure

We had two different conditions, one where informed females were in the majority in a six-bird prospecting group (four informed and two naïve females: 4Inf condition) and one where the naïve females were in the majority (four naïve and two informed females: 2Inf condition). We assigned females to the two conditions such that after all trials were completed, every female served as naïve 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 counterbalanced 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 these cases we averaged the individual's scores.

Pretest day: Informed females were treated the same as in experiment 1 except that they were tested in groups of four. Thus, four females were given three hours to investigate the one-egg and the three-egg nests

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 naïve 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 videotaped 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.

Data analysis: Similar to experiment 1, we examined the change in the amount of time naïve 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). We hypothesized that naïve females would spend more time investigating the change nest in the 4Inf condition compared to the 2Inf condition because there would be more social information

available about the change nest for naïve 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 naïve 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 'naïve' 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 naïve 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.

Results

Overall, birds spent on average 1.62 minutes visiting nests during trials. This time was broken up in numerous brief visits. We measured the number of times more than one bird visited a nest simultaneously. 63 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 naïve compared to when they were informed (naïve = 1.4 ± 0.2 min, informed = 1.22 ± 0.25 min, t(11) = 0.64, P>0.53).

Informed females in aggregate spent more time on the change nest in the 4Inf condition (mean=2:33± 0.23 min) compared to the 2Inf condition (mean=1:21 ± 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 vs 4Inf condition (mean time spent on change nest in 2inf condition = 0.6 min ± 0.25 min, 4Inf condition = 0.52 ± 0.17 min; t(7)=0.32, P>0.76), nor did they differ in their

relative patterns of visiting the two nests across conditions (t(7) = 0.54, P>.62). Thus, overall, informed females behaved in similar ways across conditions.

*Figure 3:* **Mean Time Propsecting when Naive**

The nest visit patterns of naïve females, however, were different across conditions. Naïve females spent more time investigating the change nest in the 4Inf condition (mean proportion of time on change nest = 0.72 ± 0.08), than when they were in the 2Inf condition (mean = 0.32 ± 0.09; t(11) = 3.22, P<.01; Figure 3).

Conformity measures. Naïve females' conformity scores did not differ between conditions (mean 2Inf conformity = 0.61 ± 0.05, mean 4Inf conformity = .59 ± 0.04). This indicated that their responsivity 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 naïve than when they served as informed (mean conformity naïve = 0.60 ± 0.05, mean conformity informed: 0.44 ± 0.07, Binomial test, p<.01).

We examined whether naïve females were more likely to conform to the nest visit patterns of informed females over the visiting patterns of other naïve females in order to determine whether informed females were behaving in a way that was providing more salient social information to the naïve females. We computed conformity measures for each naïve female based on the behaviour of either the informed females, or the other naïve females. We collapsed these measures across all trials and conditions. There were no significant differences in the conformity scores toward informed or naïve females (average conformity: to informed females = .64, ± .06, to naïve females: .67 ± .04; paired t-test (t(11)=.05, NS). This suggests that all females provided similar amounts and quality of social information, but the naïve females were more influenced by it than were the informed females.

Within-individual patterns. Because most subjects served as both informed and naïve subjects across trials, we were able to compare their nest visits in trials when were informed to nest visits when naïve. To get a measure of each female's accuracy in using personal information to select a nest, we used the proportion of time they spent on the change nest when they were informed in the 2Inf condition. This is the more cognitively challenging task and the condition in
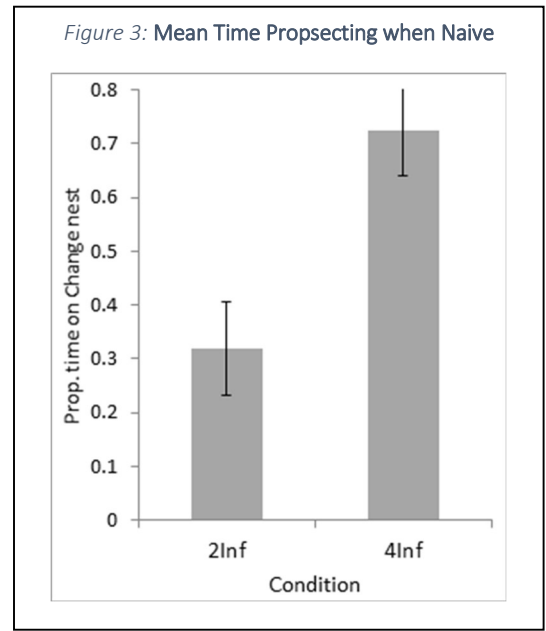
which they had the least amount of social information available to them. Thus we considered females who spent more time on the change nest in this condition as being better able to make nest selection decisions using personal information. We took this measure of individual accuracy and compared it to the degree to which their nest visits were modified by social experience when they were naïve (in the 4Inf condition: the situation where they had little personal information and the most social information available). There was a strong negative relationship between these two scores (r(8) = -.817, p<.02), 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 accuracy in using personal information, the less likely she was to conform to the behaviour of other females when serving as a naïve female in the 4Inf condition (r(8) = -0.85, P<.02).

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 experiment 1 and experiment 2. For experiment 1, we used the difference between naïve females' performance in the View and Blind condition as a measure of the degree to which they were influenced by social information. For experiment 2, we used conformity scores in the 4Inf condition as their measure of social influence. These two measures of social influence were highly correlated (R=.84, N=12, P<.001). Thus the degree to which individuals were socially influenced stayed consistent across experiments.

We then examined the consistency across experiments in individual accuracy. 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. Their accuracy across experiments was consistent (R=0.67), but because not every female served as an informed subject in the two experiments, the low sample size may potentially have kept the correlation from reaching statistical significance (N= 6, P=.07). Since there were more subjects that served as informed females in the 4Inf condition, we compared informed females' accuracy from experiment 1 to their accuracy in the 4Inf condition, here there was a statistically significant correlation (r = 0.61, N=12, P<.05), suggesting that individual accuracy was also consistent across experiments.

Experiment 3: Egg laying patterns

Experiments one and two 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 one year with adult males and then in the next breeding season we investigated their patterns of egg laying in mock nests within the aviary.

Procedure

We manipulated 12 nests in the aviary in two ways. 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.

In phase one, we set up half the nests with one egg and half with three eggs. Each day we would add an egg to the initial one-egg nest until both nests contained three eggs. We would then reset nests, move them to new locations and run the phase again. This manipulation, as used in past experiments [19], was used to determine how accurate each female was at laying in a changing nest versus an unchanging nest. We repeated phase 1 eight times.

In phase 2 we set half of the nests with three white eggs (3W), and the other half with two white eggs and one speckled egg (2W1S). We have used this manipulation in the past to simulate nests that have already been parasitized by another cowbird [18]. Females typically show an aversion to a nest containing one speckled egg. The next morning we reset the nest, moved them to new locations in the aviary and repeated the phase (again, four times total).

We collected eggs each morning at approximately 7 am. 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.

Results

One female died prior to the breeding season, leaving 11 females to examine egg laying. Of the 11, 10 laid at lease one egg during the breeding season (mean laid per female = 6.6 ± 1.83) across the six week breeding season. There was no significant correlation between our accuracy or conformity measures from experiment 1 or 2 and total egg production (r= -.15 for accuracy, r= .10 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 two days. Thus irrespective of our measures of individual accuracy or social conformity scores from experiments 1 and 2, all females showed very high accuracy at laying in changing nests.

In phase 2, overall, females laid 13 eggs in 3W nests and 7 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 ($r=-.70$, $p<.05$) and a significantly positive correlation between the number of eggs laid in the 3W nests and her individual accuracy score from experiment 2 ($r=0.88$, $p<.02$). Thus, those females most influenced by social information in experiments one and two were more likely to lay in already-parasitized (2W1S) nests. Those females most accurate in using personal information in the prospecting experiments were more likely to avoid already-parasitized nests.

Finally, we examined patterns of egg removal by females in the breeding season. Mock nests were affixed into the nests, but females occasionally removed real cowbird eggs laid by other females. There was a significant correlation between females' social conformity score from experiment 2 and the number of eggs they removed ($r=0.82$, $p<.002$). Thus, the most socially influenced females from experiments one and two 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.

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 naïve females evaluated the nests independently (when there was a delay imposed between their observation of the informed females and inspection of the nests: 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 accuracy and tendency to conform to others - were stable properties of individual females across time, trials, different group mates, and experiments. This pronounced negative relationship between females' accuracy 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 individually accurate 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 another cowbird's 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 vs their social information: an hypothesis to be tested in the future.

Some of the patterns of information use in these experiments fit models of social learning strategies. For example, models and empirical data have shown that the propensity to attend to social over individually-acquired information increases when subjects are 'unsure', that is, when personal information is lacking or not particularly valuable [4]. Our finding- that conformity varied *within females*- being more marked when females were naïve compared to when they were informed, supports this idea. Copying when unsure seems to be a general phenomenon, seen in a variety of birds, fish and mammals [41-43]. The variation we found *across females* - some females being more likely than others to be influenced by social information – is more difficult to fit into Laland's [4] framework. It is possibly an example of 'copying when asocial learning is difficult'. Those individuals who were least accurate may have found the task most difficult and thus relied more on social information. This is different than what is usually considered to fit under the 'copy when asocial learning is difficult' models because the difficulty of asocial learning is typically related to aspects of the task itself, not based on the relative learning abilities of the individuals.

There is, in fact, not a large literature connecting individuals' cognitive abilities with social information use [44]. While some work has characterised a connection between individual learning and sociality in general [45] and there is an extensive literature on animal personalities revealing that certain types of consistent behavioural propensies relate to the likelihood of using social information (29,46-50), only Katsnelson et al. [30] has 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

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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 [51] and ultimately the opportunities for and pathways of cultural evolution.

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Chapter 2: Female brown-headed cowbirds vary in their strategies for using social information

Hayden B. Davies and David J. White

Introduction

Gregarious animals live in highly dynamic environments where the behavior of group mates generates an abundance of information. Making use of this information can be beneficial: it can lead an individual to valuable resources [1–6], it can provide a means for evaluating potential mates [6–18], it can improve the speed an individual learns a new task while avoiding the costs of independent discovery [19–24]. Attending to, processing, and placing value on this information can be cognitively demanding [25–31] and it may benefit some individuals more than others. Furthermore, information use by a small number of individuals may have significant effects on the groups behaviour [32]. Thus it is possible that the degree to which an individual uses social information is highly variable and context dependent.

Research investigating social influences on cognition has traditionally focused on the mechanisms underlying social learning [19,20,33], and more recently the strategies that promote social learning [21,34]. Less work has investigated individual differences in social information use. Though some notable early work identified distinct strategies of social and personal information use in foraging animals. In these producer-scrounger models [35], some individuals find most of their food by actively foraging ('producers'), whereas others obtain their food by observing others ('scroungers'). These models have been used across a variety of species and has even expanded to include a third type of individual, 'opportunistic foragers', who can both produce and scrounge [36]. Understanding individuals differences in information use has provided insight into the mechanisms driving these individual differences in information use [37,38]. Some other more recent work has been done to examine the role individual differences in behaviour play in shaping information use and to what degree these behaviours remain consistent across different contexts [39–42]. Overall however there is still much to understand about how individual animals choose to use social information. If there are pronounced and consistent differences in how individuals depend on social learning, it could have important consequences for social structure, information flow and cultural transmission.

In chapter 1, we discovered individual differences in social information use in obligate parasitic brood parasitic female cowbirds' nest prospecting patterns. Locating and selecting suitable nests to parasitize can be a challenging cognitive task for cowbirds [43–51]. For example, female cowbirds track the laying patterns of potential hosts over multiple days [51] as well as hosts' reproductive success with other cowbird nestlings over multiple years [50]. We tested whether females would use social information to mitigate these demands. We gave females various opportunities to evaluate nests for parasitism in the presence of other females. Overall, all females showed an enhanced preference for nests in which other females showed interest. In addition, when we varied the amount of information females had about

the suitability of the nests for parasitism, females were more likely to use social information when they had less information about the nests than when they had more. Finally, and most significantly, there were individual differences in social information use depending on how effective females were at evaluating nests on their own. That is, females who were the most proficient at independently prospecting were the least influenced by social information when naïve, and vice versa. This inverse relationship between personal skill and dependence on social information suggests females value personal and social information differently and it may represent a specialized producer-scrounger prospecting strategy that has evolved specifically for selecting appropriate nests, similar to how selection has favoured cognitive specializations for spatial memory [52,53] [54,55]. Alternatively, the patterns seen in nest selection decisions might be reflective of a more general strategy for acquiring and depending on social information across a wide variety of contexts and circumstances.

Another context in which gregarious birds face cognitive demands that could be mitigated by attending to others around them is in locating foraging sites. Again, there is an abundance of evidence that social foragers use social information to select feeding sites, and compete for food [56]. Brown-headed cowbirds aggregate in large mixed flocks for most of the year and forage in small groups on the ground, often among grazing livestock who aid in flushing out grassland insects, a primary source of food along with seeds [57,58]. Previous work shows they have wide fields of visions allowing them to forage and scan conspecifics simultaneously [59] and their foraging behaviour is heavily influenced by their flock size and their distance to other conspecifics [60,61]. Given this information, we believed the female cowbirds have the potential to use social information to influence their forging patterns, possibly in patterns like the ones we found in chapter 1.

Using the same females and a similar methodology from the nest prospecting experiment, we investigated whether the social learning strategies used by female cowbirds in a foraging setting are similar to the strategies used when prospecting for nests. Groups of females were provided two foraging patches and females were either naïve and informed about the quality of the patches. We predicted, similar to the prospecting experiments, that (1) females would use social information to assist them in selecting foraging sites, and (2) females would be more likely to use social information when they had less personal information about the foraging sites than when they had more personal information. Finally, since we worked with the same females from the nest prospecting experiments, we could ask whether there was any consistency in females' (1) proficiency to select appropriate nests and appropriate foraging sites, and (2) in their tendency to use social information to adjust their behavior in the two different contexts.

General Methods

Subjects

11 female cowbirds, wild caught in spring 2014 in West Flamborough County, Ontario, Canada served as subjects throughout the two experiments. After trapping and prior to experimentation, we housed females in a large 12 x 6 x 4 m outdoor aviary with trees, grass and shelter containing 12 wild-caught males. The birds were provided with ad lib access to water and outside of the time we ran the experiments each day, they also had ad lib access to a mix of white millet, red

millet and a modified version of the Bronx zoo diet for omnivorous birds. All birds wore individually unique combinations of coloured leg bands to permit individual identification.

Apparatus

We conducted all tests in a 2.5 x 2.5 x 6 m flight cage containing grass, perches, food, water and two grey plastic foraging bowls (Dynamic Design, Camp Hill, PA, USA).

The flight cage was divided in two sections, an experimental area and a holding area. The experimental area was 1.25 x 1.25 x 3m and the holding area had two compartments, each 0.625 x 0.625 x 3 m (Figure 4). To prevent side biases and carryover from previous trials, we counterbalanced which holding area held the informed and naïve females. A removable opaque canvas screen blocked the view between experimental and holding areas. Small (20 x 20 cm) doors at the top of the hardware cloth dividers could be opened to allow the birds to fly from one area to another. The two foraging bowls were placed inside the experimental area approximately 1.25 m apart. Between each trial, foraging bowls were moved on a 45 and 90-degree axis while maintaining a 1.25-meter separation.

Figure 4: Flight Cage Design
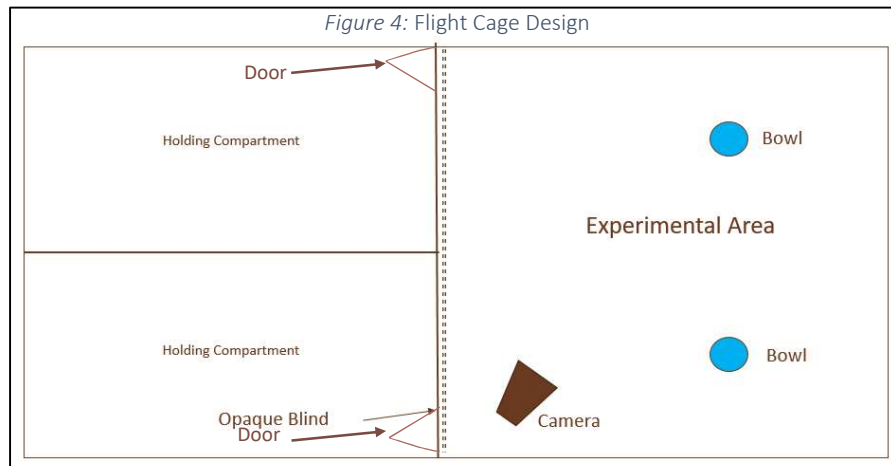
Training Phase: Prior to beginning experiments, all females were trained to forage for worms in the foraging bowls for approximately 4 hours a day over two weeks. All foraging bowls were filled with approximately 3.5 cm of soil. Both bowls had soil in it and each contained 10 mealworms hidden underneath the soil. 20 worms were enough to allow all subjects to forage for worms without overfeeding them resulting in decreased motivation to forage later in the experiment.

Pretest Phase: The purpose of the pretest was 'inform' some females about the value of two foraging locations. We placed two bowls in the experimental area, both contained soil, but only one also contained mealworms. This bowl was designated the 'pretest food' (PF) bowl. The bowl with no mealworms was designated the 'pretest empty' (PE) bowl. We released four females into the experimental area and, in order to keep them from depleting the mealworms, we gave them only 15 minutes to investigate both bowls. Timing commenced when a female made contact with a bowl. After 15 min, we moved the informed females back into their holding area. After 45 min, we restarted the pretest. We refilled the PF bowl with more worms and placed the foraging bowls in the same location. The pretest was repeated three times

however, in cases where an experiment was interrupted by an outside influence or a majority of females had not foraged in the PF bowl, we repeated the pretest between one and two more times.

Experiment #1 (No Private Information)

Methods

In this experiment, a set of six females entered the flight cage. Some of these females were informed about where mealworms were located (experienced during pretest) and the others were naïve. Naïve females did not enter the flight cage in the pretest, thus they had no information about where mealworms were located. There were two conditions in this experiment. In the first ('2Inf') condition, the six female group contained two informed females and four naïve females. The second ('4Inf') condition consisted of four informed females and two naïve females. Across the entire experiment, all females served as both a naïve and an informed female in each of the two conditions. We counterbalanced running order across trials to ensure no female was tested in consecutive trials under the same condition or subject type.

Both PE and PF bowls were placed in the same position as in the pretest. They contained fresh soil, but neither bowl contained mealworms. The females were given seven minutes to investigate both foraging bowls starting from when the first female made contact with either bowl. We ran 17 trials in total.

Data Analysis: We video recorded all trials. We measured the amount of time each female spent on the foraging bowls, as well as the time in the trial when she made her visits. In addition to the seven-minute cut off, we also set a threshold requiring females to forage for at least 20 seconds in order to count as a data point. Furthermore, if in any given trial, more than half the females from either group did not meet this threshold, the entire trial was scrubbed and re-tested on a different day. Because of this, to get usable data we had to re-run many of the females. Thus, some females served in the same condition and subject type multiple times. In these cases, we averaged the female's data. Finally, conformity scores were calculated using the same method as we did in chapter 1.

Results

Females spent 1.12 minutes per trial visiting the foraging bowls. We found no difference in visiting time between the 4Inf and 2Inf conditions (4Inf: mean 1.12 minutes ± 0.2, 2Inf: 1.16 minutes ± 0.27; $t(9)=-0.125$, $p>0.05$) suggesting the time females spent foraging was not significantly impacted by the ratio of informed-to-naïve subjects. We did find a trend suggesting naïve females spent more time visiting the bowls compared to informed females but it was not significant (Naïve: mean 1.28 minutes ± 0.31; Informed: mean 0.74 ± 0.1; $t(10)=2.1$, $p=0.06$).

We found no difference in the mean time spent foraging by the informed females on the PF bowl across conditions (4Inf: 0.47 minutes ± 0.05; 2Inf: 0.64 minutes ± 0.13; $t(6)=-1.0$, $p>0.05$), nor did we find a difference in time spent foraging regardless of the foraging bowl (4Inf: 0.72 minutes ± 0.08; 2Inf: 0.74 minutes ± 0.12; $t(7)=-0.14$, $p>0.05$). This suggests informed females behave consistently across both conditions. However, comparing between the two
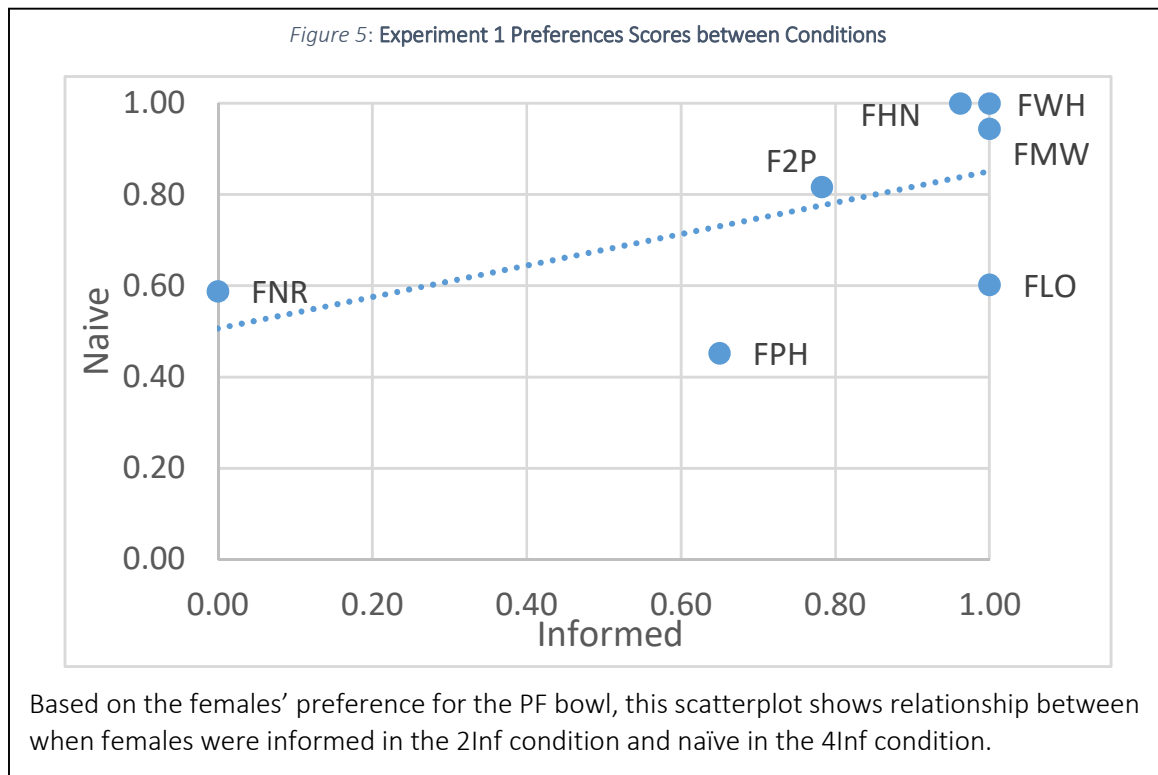
foraging bowls, we found informed females spent significantly more time on the PF bowl compared to the PE bowl, a difference that was significant both in aggregate (PF: 1.37 minutes ± 0.19; PE: 0.35 minutes ± 0.08; t(9)=5.86, p<0.01) and mean times across conditions (PF: 0.67 minutes ± 0.08; PE: 0.18 minutes ± 0.04; t(9)=5.36, p<0.01).

Naïve females demonstrated a preference for the PF bowl over the PE bowl in the 4Inf condition (PF: 1.06 minutes ± 0.26; PE: 0.45 minutes ± 0.18; t(8)=3.66, p<0.01) but not in the 2Inf condition (PF: 0.58 minutes ± 0.18; PE: 0.84 minutes ± 0.32; t(9)=3.66, p>0.05). Comparing relative preferences for the PF bowl compared to the PE bowl was also statistically significant (4Inf: 0.76 ± 0.07; 2Inf: 0.48 ± 0.07; t(8)=3.69, p=0.01).

Eight out of 9 naïve females conformed more in the 4Inf condition than in the 2inf condition (two-sided binomial at 0.5, p=0.04). Comparing the conformity scores across conditions revealed a similar trend (4Inf: mean 0.67 ± 0.05; 2Inf: mean 0.53 ± 0.03; t(8)=2.27, p=0.05). There is no difference in how naïve females conformed to each other or to informed females in both conditions (To Naïve: 0.42 ± 0.07; To Informed: 0.42 ± 0.09; t(10)=0.004, p>0.05). Similar to our previous findings, naïve females conformed more in the presence of 4 informed females however, they show no preference to whom they conformed.

To examine how individual accuracy related to social information use, we needed measures for each of these variables. For individual accuracy, we used each females' preference score for the PF bowl when she was informed, and serving in the 2inf condition. This is the condition where she has individual information about the food bowls form the pretest, and the least amount of social information present. For social information use, we used each female's preference for the PF bowl when the female was naïve in the 4inf condition. This was the condition in which the females had no personal information from the pretests and the most valuable social information present. These measures related directly to the scores we used to compare females in the nest prospecting experiments. There was a moderately positive correlation between the two measures that was not significant (r(7)=0.564, p>0.05; Figure 5). This positive relationship was surprising because it was significantly different from the nest prospecting relationship between these variables (r=-817) (Fisher transformation: z=-2.53, p=0.01). That is, for nest prospecting, the most accurate nest prospectors were the *least* socially influenced, here for foraging, the most accurate foragers were the *most* socially influenced.

Informed females' accuracy in the 2Inf condition across foraging and nest prospecting experiments was strongly correlated (r(5)=0.88, p=0.05). However, there was no significant correlation in their social information use scores (naïve 4Inf condition preference scores, nest vs foraging; r(11)=-0.56, p>0.05). In fact, this correlation was negative and trending toward significance. This suggests individual accuracy was consistent between nest selection and foraging contexts, but tendency to use social information was not.

Figure 5: Experiment 1 Preferences Scores between Conditions

Based on the females' preference for the PF bowl, this scatterplot shows relationship between when females were informed in the 2Inf condition and naïve in the 4Inf condition.

Discussion

Similar to nest prospecting, female cowbirds were socially influenced in their food site selection patterns and they were more socially influenced when they were naïve compared to when they were informed about the location of mealworms from the pretest.

Opposite to the results from nest prospecting however, foraging females who were most accurate at using their own information from the pretest were the ones most socially influenced when they were naïve. One possible reason for this discrepancy is that in the nest experiments, unlike in the foraging experiment, public and private information was always in conflict with one another. Naïve females did not have personal information about how nests had changed in egg number from one day to the next, but they could still see eggs in nests on the test day and this personal information was in conflict with what the social information was providing. In the foraging experiment, there was no conflict between personal and public information. Informed females had information about where mealworms were located in the pretest, but naïve females had no information at all about where to find food. Thus conflict was present in the nest experiment but absent in the foraging experiment. Conflict between information types can play an important role in directing social behaviour (MILLER ref). Thus the purpose of experiment 2 was to develop a foraging procedure to put personal and social information about foraging sites directly in conflict with each other to make it more closely resemble the nest selection experiments.

Experiment #2 (Conflicting information)

Methods

In order to create a conflict between public and private information, we replicated experiment 1 with one change: instead having some females be naïve to events in the pretest, all females instead were given pretest experience where they learned which of two bowls contained mealworms. Here, however, half of the females learned worms were located in one bowl, but the other half of the females learned the worms were in the other bowl. During the test, we manipulated the six-female group such that individual females experienced either high levels of conflict between public and private information (4 other females with pre-training to the opposite food bowl, 1 other female with concordant information) or low levels of conflict (three other females with concordant pre-training, two with opposite training). We ran 14 trials in total during this experiment.

Procedure: All females participated in trials such that they were in high or low conflict with the rest of the group. During the pretest, we followed the same procedure from experiment #1 except we trained two groups of four females consecutively for equal amounts of time and neither group could see the other group in the experimental chamber nor come in direct physical contact during the pretest. One group of females was given mealworms in one of the bowls and not the other while the other group of females had the contents of the bowls reversed such that the two groups of females learned the opposite relationship between the location of the bowls and their contents. We counterbalanced which group started the pretest after each trial. The test phase also followed the same procedure from experiment one. All four females from one of the pretest groups and two randomly selected females from the other pretest group entered into the experimental chamber together. Both bowls contained no worms and the group of six were given 7 minutes to investigate the bowls. The bowl to which the four females were trained was called the Pretest four (P4) bowl and the bowl to which the two females were trained was called the Pretest two (P2) bowl.

Data Analysis: We used the same data analysis methods from the first experiment, comparing the amount of time birds spent on the P4 bowl.

Results

The females spent on average 1.3 minutes per trial visiting the foraging locations. We did not find a significant difference in the mean time spent foraging when females were in high conflict (HC) and when they were in low conflict (LC) (LC: 1.05 minutes ± 0.15; HC: 1.51 minutes ± 0.47; $t(8)=-1.14$, $p>0.05$). We also compared the mean time spent by females in this experiment to the times they spent foraging when they were in the previous foraging experiment and found no significant difference (Conflict: 1.06 minutes ± 0.25; Experiment 1: 1.06 minutes ± 0.26; $t(9)=-0.7$, $p>0.05$). Similar to previous results, time spent foraging is consistent regardless of group or experiment conditions.
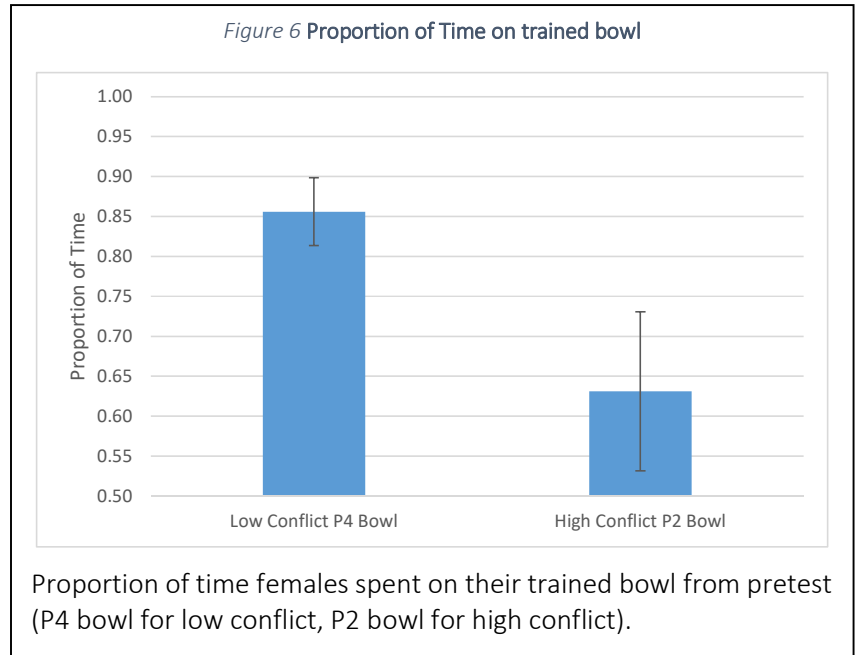
When females were in low conflict, they spent a significantly higher proportion of their foraging time on the P4 bowl than they spent on the P2 bowl when they were in high conflict (8 out of 9 females spent more time on the P4 bowl when they were in low conflict than they spent on P2 when in high conflict; two-sided binomial at 0.5, $p=0.04$ proportion
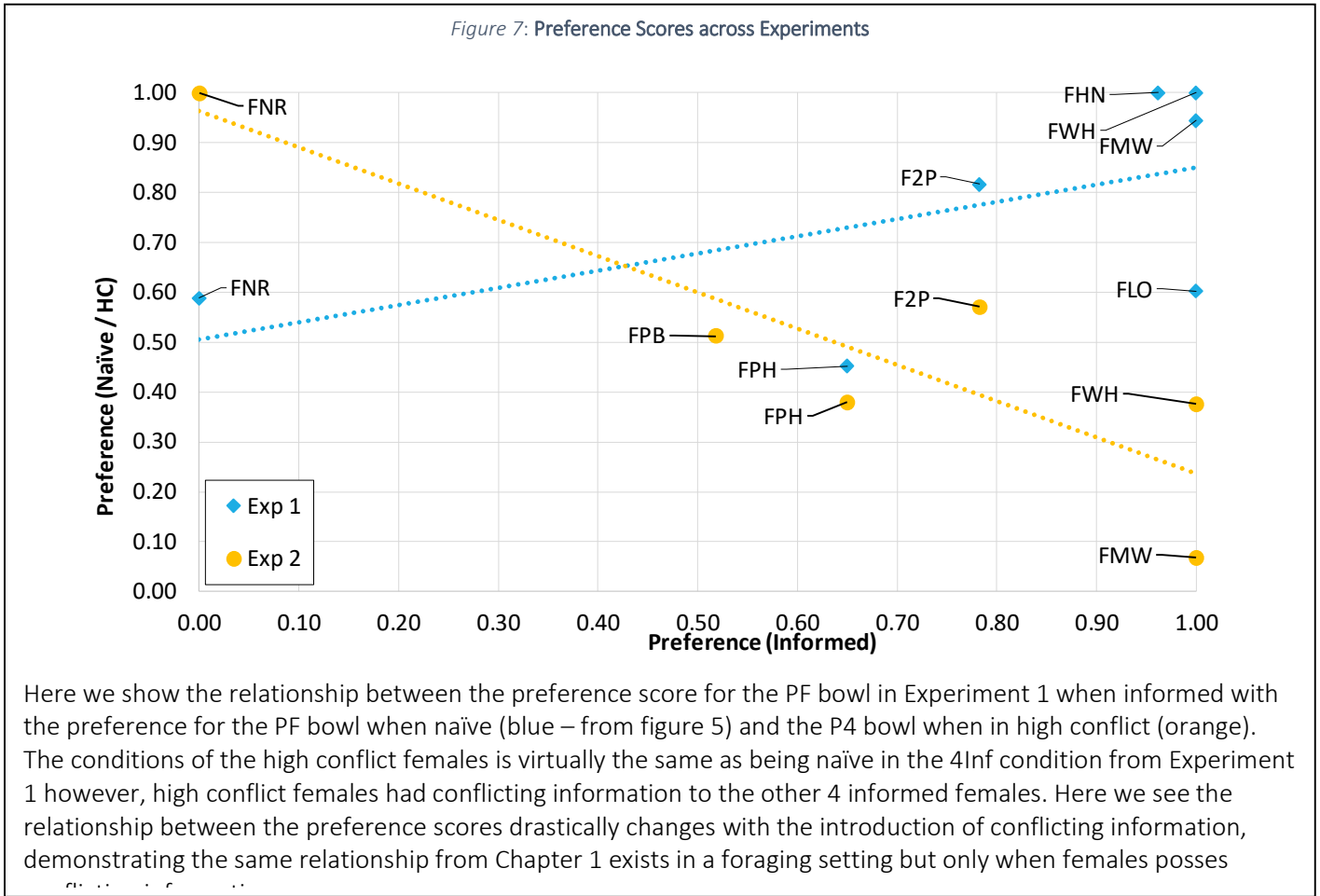
of time spent on the bowl to which they were trained (LC: 0.86 ± 0.04; HC: 0.63 ± 0.1; t(8)=2.47, p=0.04, Figure 6). That is, they spent more time on the bowl where they were trained to find worms when there were more females present who were also trained on the same bowl.

In experiment 1, naïve females in the 4Inf condition had no information regarding either foraging location whereas the informed females did. In experiment 2, serving in the high conflict condition replicated this 4Inf condition however, the naïve females now had conflicting

Figure 6 Proportion of Time on trained bowl

Proportion of time females spent on their trained bowl from pretest (P4 bowl for low conflict, P2 bowl for high conflict).

information to the other four females. When the females were in high conflict, they conformed less than when the females were serving as naïve females in the 4Inf condition from experiment 1 (HC: 0.47 ± 0.05, Naïve: 0.68 ± 0.06; t(6)=2.48, p= 0.05). There was no difference in conformity between low conflict females and informed females in the 4Inf condition (LC: 0.57 ± 0.04; Informed: 0.57 ± 0.06; t(8)=0.05, p>0.05). These results demonstrate when naïve females are provided with conflicting information, they significantly reduce their conformity yet the introduction of conflicting information had a minimal effect on the informed females.

Finally, we examined the relationship between individual accuracy and susceptibility to social information once again to determine whether adding conflict changed the relationship between these variables back towards the relationship seen in the nest prospecting experiments. For this experiment, as a measure of social influence, we used the proportion of time females spent on the P4 bowl when they were in high conflict. Thus this measure is the degree to which they shifted from their training to the majority decision during testing. We compared this to their individual accuracy score we used from experiment 1 (preference score from 2Inf PF bowl). There was a strong negative relationship between these two scores ((r(6) = -0.89, p=0.02; Figure 7), suggesting that females who were proficient at foraging independently, were less likely to copy others. This was significantly different from the relationship in experiment 1 (Fisher's transformation: z=2.70, p = 0.007), and not differentiate from the relationship in the nest prospecting experiments (r(8) = 0.36; Fisher's transformation: z= 0.38, p > 0.05). Thus, introducing conflict between private and public information, it drastically changed the proclivity of females to use social information to influence their decisions.

Figure 7: Preference Scores across Experiments

Here we show the relationship between the preference score for the PF bowl in Experiment 1 when informed with the preference for the PF bowl when naïve (blue – from figure 5) and the P4 bowl when in high conflict (orange). The conditions of the high conflict females is virtually the same as being naïve in the 4Inf condition from Experiment 1 however, high conflict females had conflicting information to the other 4 informed females. Here we see the relationship between the preference scores drastically changes with the introduction of conflicting information, demonstrating the same relationship from Chapter 1 exists in a foraging setting but only when females posses conflicting information

Discussion

Female cowbirds were influenced by the foraging patterns of other females when making a choice about two potential food sites. The degree to which females used social information depended on the amount of personal information they had previously acquired about the food sites, and the number of other individuals providing social information. Finally, there were individual differences in the females' proclivities to use social information to modify their behavior. The individual differences in social information use depended on the degree of conflict that existed between their personal information and the public information. When provided with no personal information, females who were most proficient at using personal information were also most influenced by social information. However, when personal information conflicted with social information, females most proficient at using personal information were the least influenced by social information.

Females were remarkably consistent in their behavior between the contexts of foraging and nest prospecting: Females displaying the most accuracy at selecting the best nests were also the females most accurate at locating a food site that had been previously associated with mealworms, and it was those individually accurate females who were least likely to be socially influenced (provided both personal and public information were present).

The negative relationship between individual accuracy and the degree of social influence found in the nest prospecting experiments was suggestive of the existence of two distinct strategies comparable to producer-scrounger models where individuals either attend to (scroungers), or do not attend to (producers) social information when making decisions[35]. Those who are best able to acquire and use information individually were least dependent on others to influence their decisions and those least able to make use of individual information overcame this challenge by copying others, with the two strategies potentially existing as adaptive alternatives, with no one strategy being superior than the other. This work however has provided an important new insight to the relationship between individual accuracy and social information use that challenges the producer-scrounger interpretation. When faced with no individual information, those individual who are typically the least socially influenced switch to become the most socially influenced. Thus they are not merely producers that are insensitive to social information but are instead choosing the information that provides the best payoff under specific circumstances. This result suggests that there are not two adaptive alternative strategies, but one more cognitively complex process that requires an 'informational cascade' [62,63] where personal and social information is not based a dichotomous decision making process but instead based on both sources of information where the relative value of each source determines the preference of the individual. The individual variation we find thus reflects variation in female quality that should be measureable in terms of fitness and reproductive success.

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Chapter 3: Using RFID (radio frequency identification) to study behavioural variability in socially complex environments

Hayden B. Davies, David J. White & Gregory M. Kohn

Introduction

One of the most vibrant areas of study in the life sciences is in understanding the underlying mechanisms and ultimate function of the mind. Investigations into how evolution may have acted to shape cognitive processes have begun to examine the workings of the animal mind [1]. These investigations, typically conducted in highly controlled conditions with artificial stimuli, have provided a wealth of information about how the animal mind may acquire, process, store and use information, but have not provided critical information about how cognition works in nature [2]. Especially important for an evolutionary analysis is how individuals' cognitive skills relate to social competency and reproductive success. To study this relationship, researchers are faced with the challenging task of providing subjects with a socially complex environment while maintaining the necessary experimental controls and efficiently collect a sufficient sample of data. We have developed and implemented a research method which addresses these issues, allowing us to easily acquire a wealth of information on individuals' behaviour in a socially complex environment.

We have redesigned and deployed RFID tracking technology to investigate female cowbirds' behaviour while they are engaging in a cognitively challenging task- prospecting for nests for parasitism. RFID technology is being used in the wild and in laboratory settings [3,4] to study group sizes [5], competitive ability [6], spatial memory [7] and social networks [8]. However, this technology has predominately used to track visit numbers and by redesigning the technology, we are now able to incorporate duration of visits into our analysis. Furthermore, by creating an environment where we can maintain both a naturalistic setting and rigorous experimental controls, the data collected can be compared to measures of reproductive success as well as the results of cognitive experiments run in highly controlled environments. This provides a unique insight into how an individuals' behaviour and their cognitive abilities, translate to their interaction in the social environment and ultimately how cognition relates to fitness.

Brown-headed cowbirds, *Molothrus ater*, breed across a large area in the central and lower northern areas of North American including South Ontario typically between April to July, then migrate to southern parts of North American during the winter [9]. Their home range can vary between 4 ha to 4241 ha, averaging between 261 – 845 ha [10]. Females remained in relatively stable groups of 13-16 females during the breeding season and there is moderate overlap in the females breeding territories, averaging between 9.2 and 21.5 ha [11]. Estimates for the number of eggs a female will lay during the breeding season range from five to 10 eggs per year to over 100 egg [12–14]. As gregarious brood parasitic birds, the females are faced with the challenging cognitive task of acquiring and evaluating a variety of personal and social information when investigating potential nests to parasitize [15–18]. In chapter 1, we demonstrated female cowbirds are

able to use social information to determine the quality of a prospective nest. In chapter 2, we demonstrated female cowbirds are also able to use social information in a foraging setting. In the previous chapters, female prospecting behaviour was tested in highly controlled environments, tested either individually or in small groups. In chapter 1 and 2, we learned there was significant variation in how effectively females use personal information and how some females demonstrate significant plasticity in their preference to use social information. However, the remaining question was how their different cognitive strategies related to actual egg laying decisions in a highly complex social setting. Using the same females from chapters 1 and 2, now living and breeding in a large outdoor aviary, we were able to use RFID tracking technology on nests in the aviary to investigate patterns of prospecting, social interactions, egg laying, and reproductive success.

Methodology

14 female cowbirds and 13 male cowbirds, wild caught in the spring of 2014 in West Flamborough Country, Ontario, Canada served in all experiments in the spring of 2015. Of the females, 10 were adults and four were juveniles, none of the juveniles took part is Chapter 1 and 2. Only 1 male was a juveniles, the rest were adults. After trapping and during experimentation, we housed females in a large 12 x 6 x 4m outdoor aviary with trees, grass, perches and shelter. Throughout testing, birds were provided with ad lib 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 individually unique combinations of coloured leg bands to permit individual identification.

General Apparatus

We conducted all tests using eight bamboo canary breeding nests (Kaytee Products, Chilton, WI, USA). Nests contained grass and either one, two or three white, plaster of Paris mock eggs or one spotted mock egg. The mock eggs were made from molds of real cowbird eggs. 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 the egg. It could not be seen by the birds.

The nests were attached to a variety of small pine trees, larger dead trees or small perches approximately 1 m from the ground. After every trial we moved the 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 [15,18].

SMARTNest System (Figure 8)

Affixed to the outside edge each nest, so as not to interfere with the nest, was a circular RFID Antenna made from enamel-coated magnet wire, sealed with black electrical tape and connected to an RFID tracking system (SMARTNests). The tracking system consists of a 125 kHz RFID module (Seeedstudio), a microcontroller (Ardiuno Mega 2560) and a data logger (ADAfruit). Attached to each female birds coloured leg band was a 12x2 Unique 125 kHz RFID glass pit tag (CynTag) that could be read by the RFID module. When the pit tag came within range of the magnetic field of the antenna the unique code for the pit tag would be recorded along with the date, time and nest location. This information would repeat for every 3-5 seconds until the pit tag was no longer within the antenna's field. The antenna's magnetic field was designed

to be approximately 5cm above and below the inside area of the circular antenna, only registering females in direct contact with the nests. In addition, all nests were recorded by a surveillance system (Geo-vision GV-1480, Irvine California) with motion-sensitive, low-light, closed circuit cameras mounted near each nest.

Figure 8: SMARTNest Diagram
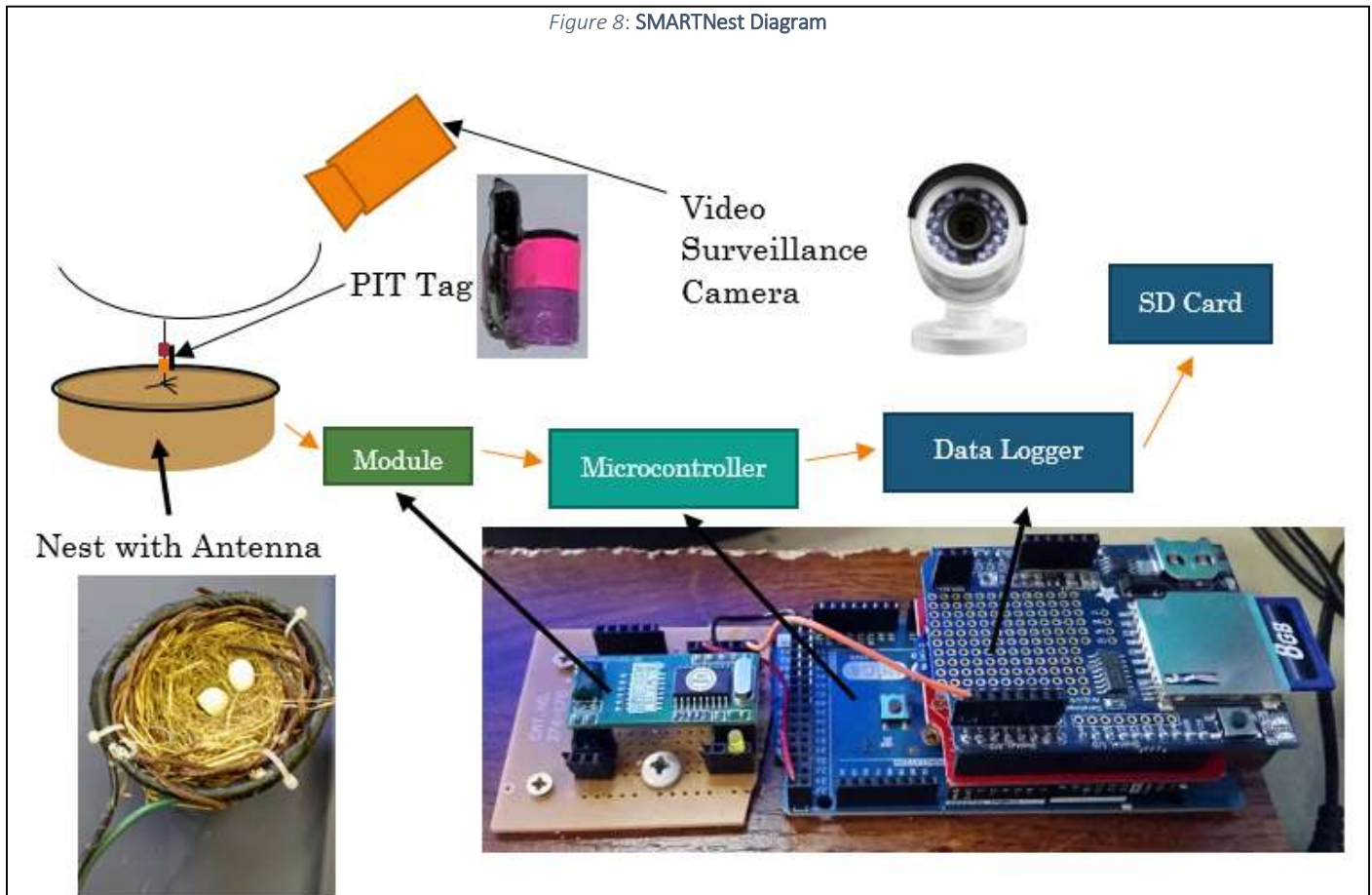
SMARTNest Visit Determination

From May 8th to July 1st, the SMARTNest system recorded 67,644 data points. Since one nest visit may consist of multiple RFID data points, we grouped each female's data points together to determine nest visitation length. If a female's data point was followed by a data point at a new location, this would split those into two different nest visits. Also, anytime two sequential data points for one female at one location was separated by another female's data point at the same location, we would record the female as having two nest visits. For instances where females triggered data points repeatedly at the same nest, we used a 15 second threshold above which we considered the points to be different visits. Pilot testing revealed that females shuffling around nests caused the system to miss a data point occasionally, and the data points triggered at varied times. A 15 seconds threshold was the most accurate grouping threshold. Therefore, by grouping data points in this fashion, the first data point in the group was used as the nest visit start time and the last data point in the group was the end time.

Data Collection & Experiments

We recorded all nest visitations from May 8th to July 1st. From May 15th to June 30th, we manipulated the eggs within the nests in two different ways, similar to the ones outlined in Chapter 1, Experiment 3. In phase 1, we

manipulated the number of eggs added to nests across days and in phase 2, we manipulated whether the nests were parasitized or not using a speckled mock egg placed in the nest.

Phase One: We set up half the nests with one egg and half with three eggs. Each day we would add an egg to the initial one-egg nest until both nests contained three eggs. We would then reset nests, move them to new locations and run the phase again. This manipulation, as used in past experiments [18], served to determine how accurate each female was at laying in a changing nest versus an unchanging nest. We repeated phase 1 eight times.

Phase Two: We set all nests with two white eggs. On the following day we added a white egg to half of the nests giving them three white eggs (3W). The other half we added one speckled egg giving the nest two white eggs and one speckled egg (2W1S). We have used this manipulation in the past to simulate nests that have already been parasitized by another cowbird [15]. Females typically show an aversion to a nest containing one speckled egg. The next morning, we reset nests, moved them to new locations in the aviary and repeated the phase nine times in total.

During both phases, the day was broken into two blocks of time. The first (laying block) ran from approximately 5:30 am until 7:30 AM. This period covered the time when females laid eggs and we used 7:30AM as the cut-off as this was the time at which the last egg was laid by a female during the breeding season. The second (investigative block) ran from the time when we added an egg to the nest each day to the end of the day. The time between the end of the laying block and the start of the investigative block was not used when making any calculations related to either phase.

In addition, we also collected eggs each morning at approximately 7 am. We used the surveillance footage to record the identity of each laying female. Using an established method for collecting behavioural data, we sampled the aviary over the course of the breeding season and collected male songs directed towards females using voice-recognition software [19].
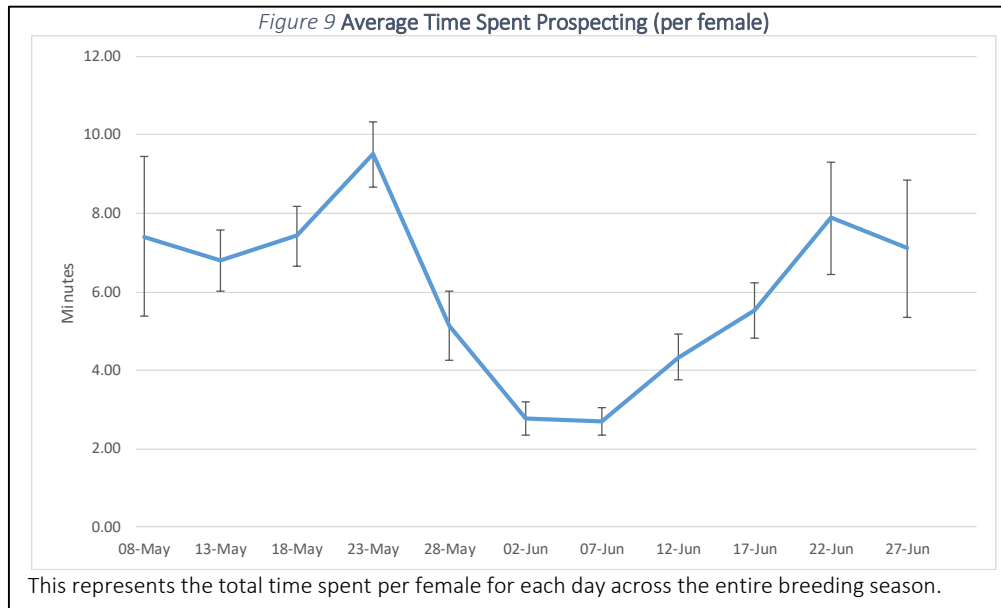
Results

To test the accuracy of the system, we compared a random sample of 38 nests visits recorded by the surveillance system to the corresponding data grouping from the SMARTNests data. We found no significant difference in the average visit length across both samples (video footage: mean 12.8 seconds ± 3.6; SMARTNests: mean 12.9 seconds ± 3.6, t(36) = 0.19, p >0.05). Furthermore, visually identifying bands was difficult in the footage and resulted in us being unable to identify 11 females who made brief visits to the nests. Conversely, the SMARTNests only failed to identify 3 visits in total.
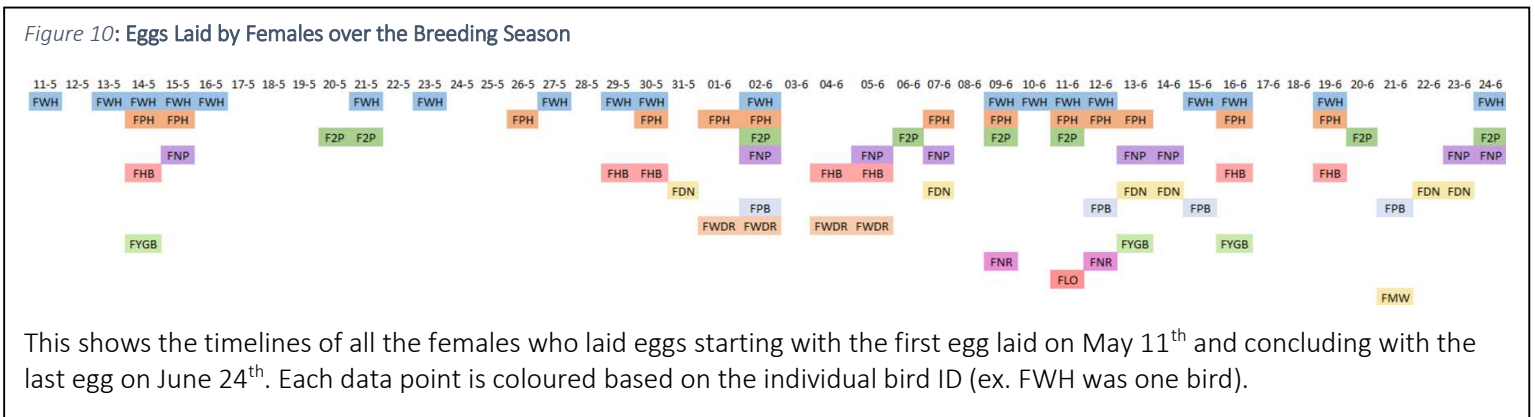
Nest Visits: The 15 second threshold translated the data points into 15,656 nest visits over the entire breeding season. This equated to 67.2 hours of nest visitation time. Approximately 1.2 hours were spent per day by all females and on average, the females spent 15 seconds per visit. Activity varied throughout the breeding season, starting with a peak during the first 20 days, followed by a massive decrease in activity and the activity slowly returning towards the end of the breeding season (Figure 9).

During the investigative blocks, we recorded 6,852 visits with an average visit length of 16 seconds and 32.9 hours of prospecting time. During the laying block, we recorded 1,758 visits with an average visit length of 8.5 seconds and 4.6 hours of prospecting time.

Figure 9 Average Time Spent Prospecting (per female)

This represents the total time spent per female for each day across the entire breeding season.

Eggs: We recorded 76 eggs across the 14 females, averaging 5.43 eggs ± 1.44 per female. 12 out of the 14 females laid at least one egg and the most laid by female was 19 eggs. Eggs were laid between May 11th and June 24th and the egg distribution across time was normally distributed with 68% of the eggs laid between May 26th and June 18th. We calculated the number of days between laying eggs starting with a female's first egg and ending with her last egg, and found a mean standard error 0.56, with values ranging from 0.27 to 0.82. However, it should be noted some females did not have a figure since they laid a small number of eggs and only had 1 gap between eggs. If females laid their eggs relatively equally apart, as we saw with FWH, she had the lowest standard error, whereas FNP, would had large gaps between laying has the highest standard error. A visual observation of Figure 10 shows females mainly lay in clutches however, in cases where females lay a lot of eggs, this was not as prominent.

Figure 10: Eggs Laid by Females over the Breeding Season

This shows the timelines of all the females who laid eggs starting with the first egg laid on May 11th and concluding with the last egg on June 24th. Each data point is coloured based on the individual bird ID (ex. FWH was one bird).

Nest Preference

Phase One: Previous work has demonstrated that females prefer a three-white nest when no other information is available. However, when exposed to nests over two days, females will prefer a nest where the egg count increases each day compared to a nest that remains the same. In chapter 1, females showed strong preferences to lay in changing nests (21 of 22 eggs were laid in a change nest in Chapter 1) and this was consistent with our previous findings [15,18]. Here,

we considered the attractive (A) nests to be the three-white egg nest on day one of Phase 1, and the changing nest on days 2 and 3 of phase 1. The one-egg nest on day 1, and the non-changing nests on days 2 and 3 were considered the unattractive (U) nests.

Past work under controlled conditions found the time a female spends investigating nests on the day before laying accurately predicts the nest in which the female will lay [15,18]. We calculated for each female the proportion of time females spent on A nests compared to U nests for the first hour of the investigative block on each day. All 14 females demonstrated a greater preference for the A nest (two-sided binomial at 0.5, $p < 0.001$). However, when we ran this same binomial test for hours two through four, we found no significant effect (Table 1), suggesting the first hour is the critical period prospecting nests and therefore, continued our investigation based on the first hour of each experiment. Using a repeated measures ANOVA with a Greenhouse-Geisser correction, we found the mean preference score significantly increased across all three days ($F(1.742, 22.646)=3.936$, $p = 0.039$). A post-hoc analysis using the Bonferroni correction revealed there was not significant difference between day 1 (mean 0.596 ± 0.047) and day 2 (mean 0.692 ± 0.054, $p = > 0.05$) but there was for day 3 (mean 0.761 ± 0.026, $p = 0.022$). Furthermore, there was no difference between days 2 and 3 ($p > 0.673$). This demonstrates there is no difference between their inherent preference and a nest increasing by one egg over on the second day. However, after adding a second egg, they demonstrate a significant preference for the changing nest on the third day (Figure 11). Furthermore, an analysis looking at mean time each day also revealed females spent significantly more time on the A nests on each day (Table 2). Together, these results suggest the females demonstrate an overwhelming preference for the A nests and this preference strengthens over the three days.

Table 1: **Binomial Test for Preference from Hours 1 to 4**

Hour	# of Females greater than 0.5 (out of 14)	p-value
1	14	<0.01
2	8	0.79
3	6	0.79
4	6	0.79

Figure 11: Phase 1 Preference Score for Attractive Nest
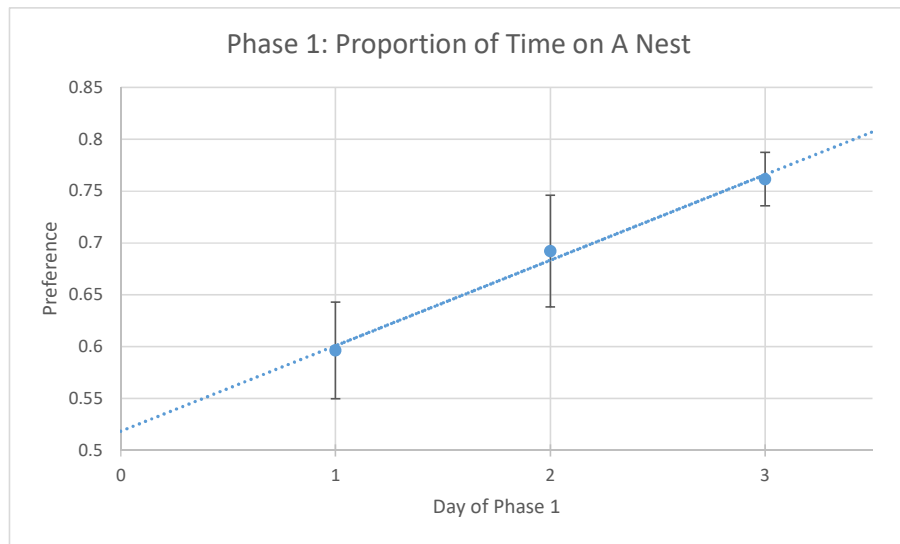
Linear relationship between the mean proportion of time the females spent on the attractive nest each day for all three days of phase 1.

Table 2: Average Total Time spent on each nest per female

Mean Total Time (mins)	A	U	t-test	p-value
Day 1	4.13	3.21	2.88	0.01
Day 2	3.37	1.65	2.66	0.02
Day 3	2.28	0.74	3.80	> 0.01

Phase Two: In chapter 1, females demonstrated a greater preference for the non-parasitized nests over parasitized nests, 13 eggs and 7 eggs respectively, and this is consistent with previous findings [15]. We compared whether there were any differences between prospecting the 3W and 2W1C nests in phase 2. We found there was no significantly difference between mean time prospecting the two nest types (3W: mean 1.18 minutes ± 0.27; 2W1C: mean 0.74 minutes ± 0.19; $t(13) = 1.23$, $p > 0.05$). We found 9 out of the 14 females had a greater preference for 3W nest but this was not significant (two-sided binomial at 0.5, $p > 0.05$).

Laying vs. Investigative Block

Females demonstrated the same preferences in the laying block as they did in the investigative block. However, females spent significantly less time during nest visits in the laying block compared to the investigative block (Table 3). Furthermore, we compared the mean number of visits during the first two hours of the investigative block (mean 1.61 ± 0.11) to the laying block (mean 6.32 ± 0.60) and found a significant difference ($t(13) = 8.895$, $p < 0.001$). This suggests females likely spend more time prospecting nests during the investigative blocks whereas during laying blocks, they are jumping from nest to nest, but not likely carefully investigating the nests.

Table 3: Visit Length Across Both Blocks

Mean Visit Length	Investigative	Laying	t-test	p-value
Overall	13.46 seconds	8.59 seconds	6.314	<0.01
A Nests	15.08 seconds	9.77 seconds	11.674	<0.01
U Nests	11.41 seconds	7.93 seconds	2.795	0.02

Egg Production & Prospecting Behaviour

We found females who laid more eggs spend more time investigating A nests ($r(14) = 0.592$, $p = 0.026$) but not U nests ($r(14) = 0.350$, $p > 0.05$). However, we found no relation between egg laying and the strength of their preference for A nests ($r(14) = 0.178$, $p > 0.05$).

To determine whether females engaged in different patterns of investigation across the nests in the aviary, we calculated the variance in the time females spent across all eight nests. Thus high variance indicates higher focus on specific nests, whereas lower variance represents equal time spent on the nests. On average, females spent 48% ± 1.93 of their time on their highest nest and only 0.6% ± 0.08 of their time on their lowest nest (Figure 12). Females had a mean variance of 3.62 ± 1.26 and this score was positively correlated with total eggs laid ($r(14) = 0.642$, $p = 0.01$). This suggests the more eggs a female produced, the more focus she had on a smaller number of nests

Figure 12: Percentage of Time Spent on Highest to Lowest Nest
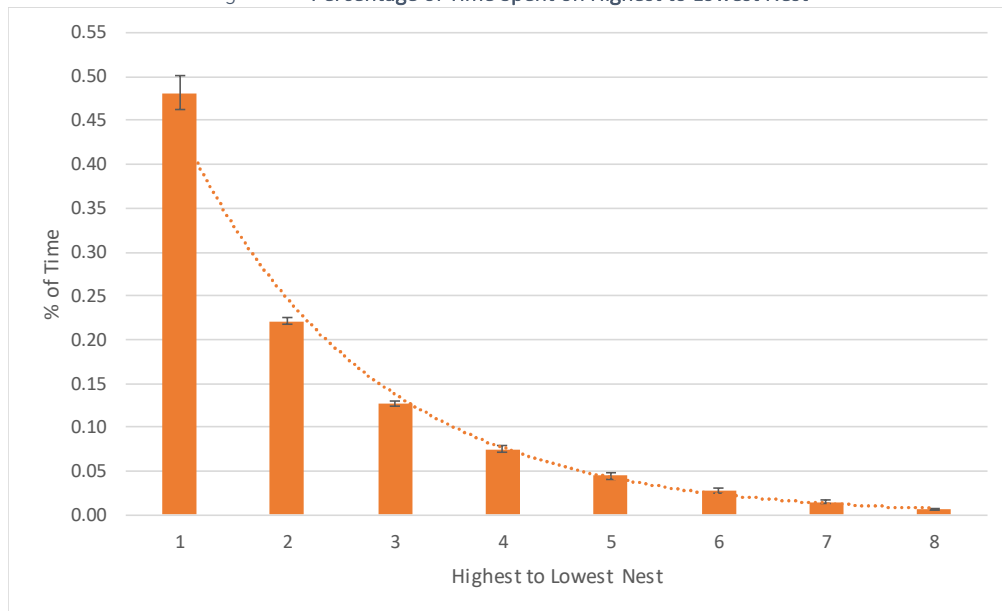
Percentage of time females spent on the nest they preferred the most each day to the nest they preferred the least.

Comparing Results to Previous Experiments

Ten of the females in this experiment were the same females who were tested in chapters 1 and 2. Thus we had the ability to compare their patterns of social information use from the nest prospecting experiment (chapter1) and the foraging experiments (chapter 2) with their actual egg laying patterns.

We found the more socially influenced a female was, the less time she spent prospecting ($r(10) = -0.767$, $p = 0.01$) and demonstrated the smallest nest variance score ($r(10) = -0.717$, $p = 0.02$). Conversely, females who relied more heavily on their personal information, spent the most time prospecting ($r(6) = 0.842$, $p = 0.036$), more time on nests during a visit when investigating nests ($r(6) = 0.835$, $p = 0.038$) and were the most accurate at laying during the breeding season ($r(6) = 0.817$ $p = 0.05$).

In chapter 1 and 2, we found the accuracy scores were highly correlated across experiments as well as both contexts, nest prospecting and foraging. Accuracy and social scores in chapter 1 and 2 were calculated the same way preference scores were calculated this chapter, that is, we divided the time a female spent on the higher quality location (change nest, PF bowl, attractive nest) by the time she spent at both locations, giving us a value between 0 and 1. We averaged the accuracy scores for chapter 1 and 2 in order to get an average accuracy score when tested individually. Although we did not include the juveniles in chapter 1 and 2, during the fall of 2015 where we completed testing for chapter 2, we also gathered accuracy scores for these four females, giving us accuracy scores for all four females. We hypothesized the females with lowest accuracy scores during chapter 1 and 2 would see a drastic improvement in their score when exposed to the complex social group where there is an abundance of social information. We used the accuracy score median to split the females into two groups of 7 females (mean 0.64 ± 0.07, median 0.66) and found all seven females with the lowest accuracy scores had higher scores when exposed to the social group in the aviary setting (two-sided binomial at 0.5, $p<0.01$) and there was a significant difference between the two scores (Aggregate Accuracy: 0.44 ± 0.07; Ch.3 Preference: 0.68 ± 0.3; $t(6)=-3.52$, $p=0.01$). Although regression to the mean could be playing a role in this effect, given the strength of the effect, this suggests females with lower accuracy scores benefit from being exposed to the social group.

Discussion

By redeveloping previous established RFID technology [3], we gained insights into how female prospecting behaviour varied by individual, by nest type and by the time of day. Most importantly, we were able to relate key aspects of their prospecting behaviour with measures of reproductive success. Females with the highest levels of reproductive success prospected the most per day and had the most focus on specific nests.

Looking back on chapters 1 and 2, we know some females were more proficient than others at using personal information, determined by their higher accuracy scores, and also demonstrated a higher propensity to copy others (social information) when provided no personal information. It could be argued that females varied in their ability to *copy when uncertain*, a type of social learning strategy (SLS), since some females demonstrated a significant difference in their use of social information across the two conditions [20]. However, given their SLS related directly to their ability to use
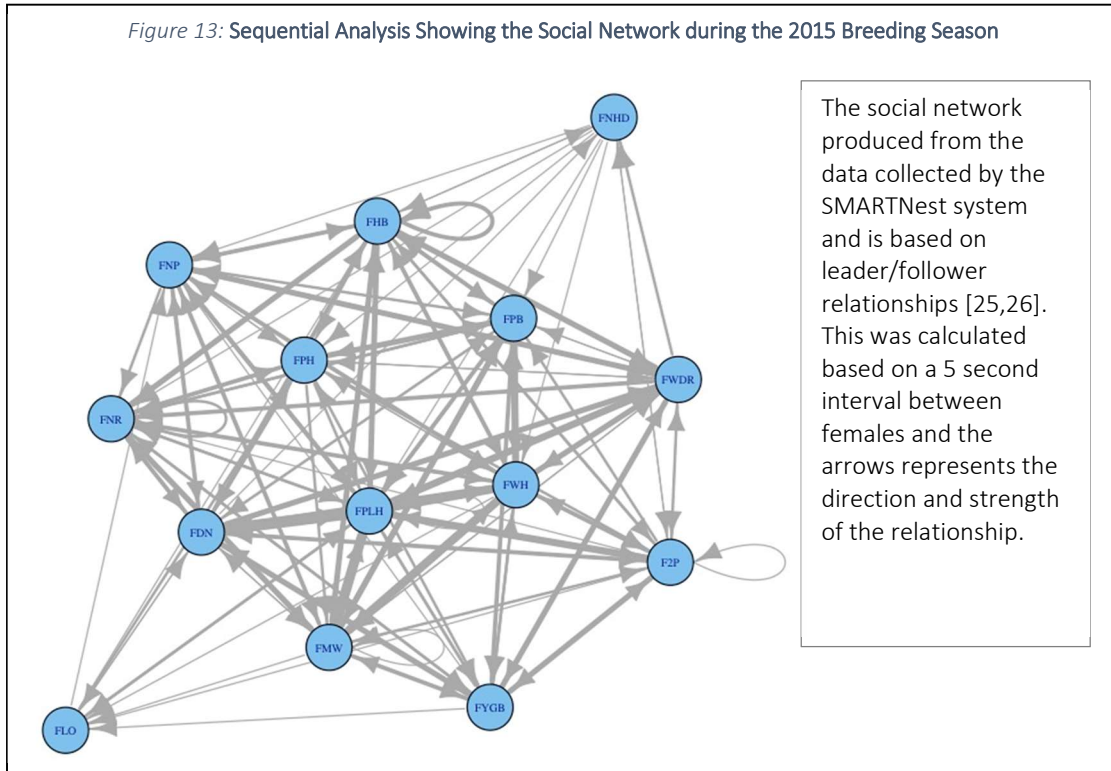
personal information, this may suggest the underlying mechanisms of their SLS may be the same or highly related to the mechanisms driving their ability to use personal information. These findings would more consistent Heyes and Pearce who argue the same associative processes that mediate asocial learning, also mediate social learning [21]. Chapter 3 demonstrates females who were more proficient at using personal, spent more time prospecting and spent more time during each visit, suggesting they were more thoroughly investigating the nests. Furthermore, accuracy scores were highly correlated across both settings. Conversely, the females who relied on social information in chapter 1 and did not demonstrate the same variability in their social information use, spent less time prospecting, varied their time more evenly across all nests and in the end, were significantly less accurate at selecting quality nests. Therefore, it is possible the mechanisms driving a females asocial learning ability, may also be the same mechanism driving their social learning ability and this ability relates to critical factors driving an individual's fitness.

Although this clear demonstration our RFID technology was able to provide unique insights into the females' prospecting behaviour and connect their cognitive strategies to their behaviour in the socially complex environment, our results still suffered from a number of limitations. Using the same females throughout all chapters meant we had a plethora of information on their behaviour, but there is a trade-off between depth of information and breadth. Our sample side was limited, which reduced our statistical power and increases the risks of our study lacking generalizability. Additionally, the females all lived in one group, which raises the risk of pseudo-replication. In the near future, we will extend the RFID technology to test multiple groups of females.

Moving forward, our RFID technology can be modified for use in a variety of settings and to study a number of different behaviours including personality traits and other cognitive skills. In addition, results we captured from our RFID system can be used to construct social network structure, allowing us to investigate how an individual's role in the social group influences their behaviour (Figure 13)[8].

In addition, the recent interest in behavioural and cognitive plasticity across contexts is a perfect area where our technology can be used to expand our understanding of how the social group influences individual plasticity [2,22–24]. Recently, we began modifying our RFID tracking system to study foraging behaviour, with the aim of understanding how an individual's fitness relates to personality traits and different cognitive skills, and how the social group impacts this relationship. More importantly, we hope to understand the role development plays in shaping personality and cognition.

Figure 13: Sequential Analysis Showing the Social Network during the 2015 Breeding Season

The social network produced from the data collected by the SMARTNest system and is based on leader/follower relationships [25,26]. This was calculated based on a 5 second interval between females and the arrows represents the direction and strength of the relationship.

Chapter 3: References

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