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Specializations in cognition generalize across contexts: cowbirds are consistent in nest prospecting and foraging tasks

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Recently we have found that when prospecting for nests, brood-parasitic female cowbirds (*Molothrus ater*) vary in their use of personal and social information when selecting a nest (White, Davies, Agyapong, & Seegmiller, 2017, *Proceedings of the Royal Society B: Biological Sciences, 284*, 1–8), with females that are most accurate at using personal information relying least on social information and vice versa. Here, using these same female subjects, we studied whether their strategies of using social and personal information would generalize to other cognitive tasks. In two experiments we investigated whether females would attend to others when selecting a foraging site. We varied the amount of social information present and the degree of conflict that existed between personal and social information about the location of mealworms hidden in soil. We found consistency in performance within females across nest-prospecting and foraging tasks: females that were most accurate at using personal information when prospecting for nests were also most accurate at using personal information when locating food sites. Also, similar to nest prospecting, the most personally accurate females were the least dependent on social information when personal information was present. Surprisingly, however, when no personal information was present, these accurate females were most responsive to social information. Taken together, these studies suggest that females weigh the relative value of social and personal information for decisions they make and they use the most valuable information for action.
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Animals can acquire information about local conditions in a variety of ways. They can learn from personal experiences, through trial and error, by learning the relationships between their behaviour and environmental outcomes. Alternatively, they can attend to social information, learning relationships between others' behaviour and the consequences of their behaviour. Often, these two sources of information are not equally valuable and can even conflict with one another. A large literature has amassed detailing the circumstances in which one source of information (personal or social) might be prioritized over another (Danchin, Giraldeau, Valone, & Wagner, 2004; Feldman & Laland, 1996; Galef, 1995; Heyes & Pearce, 2015; Laland, 2004; Laland et al., 1993, 1996; Miller, Garnier, Hartnett, & Couzin, 2013; Valone, 2007; Webster & Laland, 2008).

In many species, individuals differ in their propensity to use social versus personal information. Many social animals exhibit producer–scrounger relationships, where some individuals prioritize independently acquired information ('producers'), whereas others depend on observing others ('scroungers'). Producer–scrounger models have been used most often in foraging contexts to assess the costs and benefits of the different strategies for food acquisition, as well as for understanding forces that promote group living in general (Barnard & Sibly, 1981; Dumke, Herberstein, & Schneider, 2016; Templeton & Giraldeau, 1996). Less is known, however, about why individuals use different strategies of information acquisition and choose to use or prioritize one type of information over another. If there are consistent differences in how individuals depend on social learning, it could have important consequences for social structure, information flow and cultural transmission (Sih, Bell, & Johnson, 2004).

Recently we have examined individual differences in social information use in obligate brood-parasitic female cowbirds' nest-prospecting patterns. Locating and selecting suitable nests to parasitize can be a challenging cognitive task for cowbirds (Evans & Gates, 1997; Friedmann, 1963; Hoover & Robinson, 2007; Louder, Schelsky, Benson, & Hoover, 2014), and since accurate choices are directly related to successful reproduction, it stands to reason that

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the cognitive skills related to making these choices would be subject to selection (Sherry, Forbes, Khurgel, & Ivy, 1993). We have been studying some of the cognitive skills associated with nest selection and have found that females evaluate nests by examining the number of eggs present (White, Ho, de los Santos, Godoy, 2007, White, Ho, Freed-Brown, 2009). Nests containing more eggs are more attractive for parasitism than nests with fewer eggs (within the range of 0–3 eggs). Also, nests in which the number of eggs increases across days are more attractive for parasitism than nests in which the number of eggs remains constant (White et al., 2009). This latter source of information is of more importance to females' parasitism decisions than merely the number of eggs present (for example, a nest containing two eggs that had increased from one egg the day before would be more attractive than a nest that had contained three eggs but had not changed from the day before). Tracking the change in egg number is more cognitively challenging for females than merely evaluating the total number of eggs present, as it requires memory about time, space and number (i.e. 'what-where-when memory'; Clayton & Dickinson, 1998).

We have recently examined whether females would use social information to mitigate the cognitive demands associated with tracking nest quality across time (White, Davies, Agyapong, & Seegmiller, 2017). We gave females a variety of different opportunities to evaluate nests for parasitism in the presence of other females. In each of the tasks, they had the ability to use personally acquired information as well as socially acquired information about the status of nests. Overall, all females showed an enhanced preference to examine nests in which other females showed interest. There were, however, individual differences in (1) individual ability to use personal information to track the changing characteristics of nests, with some individuals being reliably better than others at this task, and (2) the degree to which they were influenced by social information. These two characteristics of individuals were negatively related: females who were the most proficient at independently prospecting were the least influenced by social information when naïve, and vice versa (White et al., 2017). The negative relationship between personal skill and dependence on social information may represent a specialized producer–scrounger nest-prospecting strategy that evolved specifically for selecting appropriate nests, similar to how selection has favoured cognitive specializations for spatial memory in this species (Guigueno, Snow, MacDougall-Shackleton, & Sherry, 2014; Sherry et al., 1993). Alternatively, the patterns of prioritization of personal versus social information 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.

Our primary purpose in the current experiments was to examine whether the patterns of information use by cowbirds when prospecting for nests would generalize to their tendencies to use social and personal information in different cognitive tasks. Thus, here we devised experiments to examine foraging site selection using the same cowbird subjects that we tested in the nest-prospecting studies (White et al., 2017).

In the wild, cowbirds aggregate in large flocks for most of the year and forage in small groups on the ground, often among grazing livestock, which aid in flushing out grassland insects, a primary food source for cowbirds, along with seeds (Friedmann, 1929; Lowther, 1993). Previous work has shown that cowbirds have wide fields of vision, allowing them to forage and scan conspecifics simultaneously, and their foraging behaviour is heavily influenced by their flock size and their distance to other conspecifics (Fernández-Juricic et al., 2004, 2007). Thus, while the demands associated with selecting a foraging site may differ substantially from selecting a nest for parasitism, cowbirds have the potential to use social information in both contexts.

In captive conditions, we assembled small groups of females and provided them with two foraging patches. In experiment 1, some females were given prior personal information about the location of mealworms in the patches while other groupmates were naïve to the location of mealworms. In experiment 2, all females were given personal information about the location of the mealworms, but groupmates had different prior information about the location of the food. Thus, in this experiment, personal and social information were in direct conflict. We examined whether females would prioritize personal or social information when foraging and whether their patterns of information use would relate to their nest-prospecting decisions. Specifically, we were interested in whether individuals' accuracy at using personal information for nest prospecting would relate to their personal accuracy at locating mealworms, and whether the negative relationship between personal skill and social conformity found in the nest-prospecting experiments would hold for the foraging experiments.

GENERAL METHODS

Subjects

Eleven 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 × 6 × 4 m outdoor aviary with trees, grass and shelter containing 12 wild-caught males. The birds were provided with ad libitum access to water and a mix of white millet, red millet and a modified version of the Bronx zoo diet for omnivorous birds. All birds wore individually unique combinations of coloured leg bands to permit individual identification. These females had been housed in aviaries for 2 years. They served as subjects in the series of experiments examining nest prospecting and egg laying, detailed in White et al. (2017).

Apparatus

We conducted all tests in a 2.5 × 2.5 × 6 m flight cage containing grass, perches, food and water. The flight cage was divided into two equal sections, an experimental area and a holding area. Two small (20 × 20 cm) doors at the top of the hardware cloth dividers could be opened to allow birds to fly from one area to another. Two, 30 cm diameter grey plastic bowls (Dynamic Design, Camp Hill, PA, U.S.A.) were placed inside the experimental area approximately 1.25 m apart to serve as the foraging patches.

Training Phase

Prior to beginning experiments, all females were trained to forage for worms in the bowls for approximately 4 h per day over 2 weeks. All bowls were filled with approximately 3.5 cm of soil. Both bowls contained soil and each contained 20 mealworms hidden underneath the soil such that birds could not see worms without digging for them. Pilot tests revealed that 20 worms would not be completely depleted by the end of the session.

Pretest Phase

The purpose of the pretest was to 'inform' some females about the value of two foraging locations. We placed two bowls in the experimental area, both containing soil, but with only one also containing 20 mealworms (Fig. 1). 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 gave them 15 min to investigate both

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