



# Conspecific and heterospecific social learning in shiny cowbirds

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We tested whether shiny cowbirds, *Molothrus bonariensis*, can improve the acquisition of a feeding response by observing a demonstrator of their own species or a species with which they share roosts and foraging flocks. We trained birds to peck a transilluminated response key using a classical conditioning procedure (the key was transilluminated for 10 s and then food was delivered to a hopper). We compared the efficiency in acquiring the pecking response in four experimental groups: (1) birds that could observe a conspecific demonstrator peck the key and then eat the food, (2) birds that could observe a heterospecific demonstrator (a screaming cowbird, *Molothrus rufoaxillaris*) peck the key and then eat the food, (3) birds that could observe the apparatus working automatically ('ghost' demonstrator) and (4) birds that learned the task alone. Birds in the conspecific demonstrator group required fewer trials to learn to peck the key than did birds in the groups with a ghost demonstrator or without a demonstrator. Birds in the group with a heterospecific demonstrator also required fewer trials to learn the task than did birds in the group without a demonstrator. There were no differences between the groups with a conspecific and a heterospecific demonstrator. Our results show that shiny cowbirds can acquire behaviour by observing other individuals, and that they learn from heterospecifics with which they share roosts and foraging flocks as readily as they do from conspecifics.

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Animals can acquire behaviour by individual (asocial) learning or by social learning. Asocial learning refers to behaviour acquired as the result of the animal's own experience of the rewards or punishments contingent upon its acts, and social learning occurs when the acquisition of behaviour is influenced by observation of, or interaction with, another animal or its products (Galef 1988; Heyes 1994).

Social learning can benefit an animal (the observer) by allowing it to copy what another member of the group (the demonstrator) has learned individually (Giraldeau 1997). Social learning may take different forms. In some cases, the demonstrator's behaviour increases the probability that the observer will attend to the stimuli with which the demonstrator interacts (local enhancement or area copying; Thorpe 1963), or it increases the probability that the observer will interact with stimuli of the same physical type as those with which the demonstrator interacts (stimulus enhancement or object copying; McQuoid &

Galef 1992). In other cases, the observation of novel behaviour in a demonstrator increases the probability that the observer will acquire that behaviour (imitation or behaviour copying; Akins & Zentall 1996; Lefebvre et al. 1997).

The ability to learn from the foraging activities of others may be especially beneficial to animals that live in groups, such as birds that feed or roost in flocks (Galef & Giraldeau 2001). A bird could increase its foraging efficiency by travelling to and feeding in locations where it can see conspecifics feeding (e.g. de Groot 1980; Gotmark 1990), by including in its diet novel food types that it has seen conspecifics eating (Mason & Reidinger 1981; Mason et al. 1984; Fryday & Greig-Smith 1994) or by acquiring behavioural techniques for accessing food shown by conspecifics (Fritz & Kotschal 1999; Fawcett et al. 2002).

Although several studies have shown that birds can learn by observing conspecifics (e.g. Mason & Reidinger 1981, 1982; Fritz & Kotschal 1999; Templeton et al. 1999), few studies show evidence of their social learning from heterospecifics. As an example of this, when red-winged blackbirds, *Agelaius phoeniceus*, and common grackles, *Quiscalus quiscula*, observe a demonstrator (either a red-winged blackbird or a common grackle) that has been trained to avoid food paired with a colour, the

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observers also acquire aversion to food paired with that colour (Mason et al. 1984). Likewise, zenaida doves, *Zenaida aurita*, and carib grackles, *Quiscalus lugubris*, learn from conspecifics as readily as they do from heterospecifics with which they scramble-compete in foraging flocks (a carib grackle or a zenaida dove, respectively; Carlier & Lefebvre 1997; Lefebvre et al. 1997). Dolman et al. (1996) found that two populations of zenaida doves can learn a novel foraging task more readily when it is demonstrated by either a conspecific or a heterospecific, depending on the species with which they compete in foraging flocks, and suggested that the type of competitive feeding interaction in the field may predict the pattern of social learning better than species identity.

Shiny cowbirds, *Molothrus bonariensis*, congregate in large foraging flocks during the day, generally with other cowbird and blackbird species with which they scramble-compete for food. Gregarious foraging occurs throughout the year and foraging flocks may contain up to thousands of individuals (Hudson 1874). At night they roost communally in large numbers either in single- or mixed-species groups (Cruz et al. 1990). Shiny cowbirds are omnivorous ground foragers, consuming a wide variety of insects and seeds. They inhabit open and semiopen habitats and are common in disturbed habitats like farmlands, stockyards and agricultural fields (Lowther & Post 1999).

Because of their social behaviour, shiny cowbirds could especially benefit from learning by observing birds that share roosts and foraging flocks with them. Studies in another cowbird species, the brown-headed cowbird, *Molothrus ater*, have shown that experience with different cultural backgrounds influences the patterns of assortative mating, courtship and mate choice in females (Freeberg 1996; Freeberg et al. 1999).

In this study we analysed, in a laboratory experiment, whether shiny cowbirds could improve the acquisition of a feeding response by observing a demonstrator of their own species or a species with which they share roost and foraging flocks (the screaming cowbird, *Molothrus rufoaxillaris*). We tested whether individuals that had observed a conspecific or a heterospecific demonstrator perform the task would acquire the feeding response faster than birds that learned the task alone, and faster than individuals that were exposed to the stimulus-reinforcer sequence ('ghost' demonstrator).

## METHODS

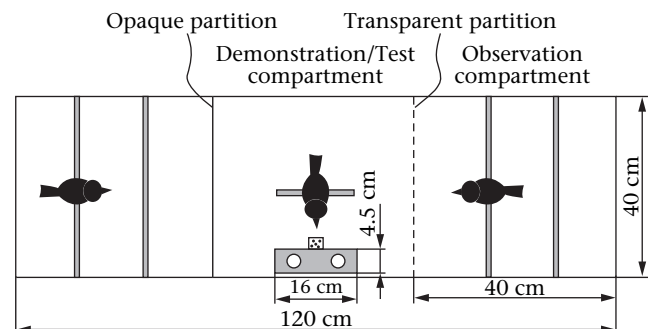
### Subjects

Subjects were 42 wild-caught shiny cowbirds, 22 females ( $\bar{X} \pm \text{SE}$  weight =  $43.6 \pm 1.3$  g) and 20 males ( $53.2 \pm 0.9$  g). We caught the birds near Buenos Aires, Argentina. They were kept in an outdoor aviary of  $3 \times 2 \times 2.5$  m (length  $\times$  width  $\times$  height) in groups of approximately 10–12 birds (males and females) for 3–4 weeks. We then moved the birds into the laboratory, where they were housed in wire cages of  $120 \times 40 \times 40$  cm in groups of three birds per cage. Cages were arranged so that birds in different cages were visually

but not acoustically isolated. The birds were maintained on a 12:12 h light:dark cycle (light onset 0700 hours) at room temperature ( $15\text{--}25^\circ\text{C}$ ). They were food deprived from 1600 hours until the start of each session between 0900 and 0930 hours the following morning. This period of food deprivation is approximately 3 h longer than the one that cowbirds experience in the wild during winter. During the experimental sessions, the birds were rewarded with millet seeds, and from the end of the session until 1600 hours, they received millet seeds and balanced food for insectivorous birds ad libitum. Water was available ad libitum. Body mass and general condition remained stable throughout the experiment. After the experiment was completed, the birds were returned to the outdoor aviary for 3–4 weeks to reacclimatize to outdoor conditions and to gain exercise, especially in flight, and then they were released into the wild into an area regularly occupied by free-living cowbirds.

### Apparatus and Experimental Procedure

To minimize disturbance of the birds, the experiments were conducted in the home cages. Each cage had three birds (one demonstrator and two birds from different experimental groups). Immediately before the beginning of each session (between 0900 and 0930 hours), the cage was divided into three compartments of  $40 \times 40 \times 40$  cm, using either opaque or transparent plastic partitions (Fig. 1). The central compartment was used for the demonstration and test sessions, and the lateral compartments were used to house the experimental birds during the demonstration. The central compartment had an operant device of  $16 \times 4.5 \times 4.5$  cm (width  $\times$  height  $\times$  depth). This device had two response keys 3 cm in diameter on the top of each side of a central food hopper ( $4 \times 3 \times 2.5$  cm; Fig. 1). The food hopper was connected to a food dispenser (Med Associates, Inc., St Albans, Vermont, U.S.A.) filled with millet seeds sieved to an even size. The response keys could be transilluminated with red and green lights, and when they were pecked they closed a microswitch connected to an I/O



**Figure 1.** Schematic of apparatus. The central compartment ( $40 \times 40 \times 40$  cm) was used for the demonstration and test sessions, and the lateral compartments ( $40 \times 40 \times 40$  cm) were used to house the subjects during the demonstration. Central and lateral compartments were divided with either opaque or transparent plastic partitions, depending on the condition.

interphase (Med Associates, Inc.). A computer running MedPC language (Med Associates, Inc.) controlled the stimulus events and response contingencies and recorded the data.

Before the beginning of the experiment, each bird experienced a variable number of training sessions (one session per day, 30 trials per session). During these sessions, the food dispenser delivered five millet seeds to the food hopper every 40 s. The training sessions continued until the bird started to eat the millet seeds from the food hopper immediately after they were delivered.

We trained the birds to peck the response key using a classical conditioning procedure. Each trial started with the transillumination of one of the pecking keys (right or left, alternated) with a combination of green and red lights. The stimulus was on during 10 s, after which the food dispenser delivered the reward (five millet seeds) independently of whether the bird had pecked the key. If the bird pecked the key during the presentation of the stimulus, the seeds were delivered immediately. After the delivery of the reward, the stimulus went off and an inter-trial interval of 40 s started.

We analysed the number of trials elapsed until the birds acquired the pecking response in four conditions: (1) demonstration sessions in which subjects could observe a conspecific peck the response key when it was transilluminated and then collect the food from the hopper (conspecific demonstrator); (2) demonstration sessions in which subjects could observe a bird of a different species peck the transilluminated key and then collect the food (heterospecific demonstrator); (3) demonstration sessions in which subjects could observe the apparatus working automatically (i.e. transillumination of the key for 10 s and then delivery of the food to the hopper; 'ghost' demonstrator); and (4) birds that learned the task alone (no demonstrator).

#### *Conspecific demonstrator condition*

Subjects were 12 birds (six females and six males). In the first phase, the birds experienced six demonstration sessions (30 trials per session, two sessions per day with an intersession interval of 60 min). In these sessions the experimental bird was in one of the lateral compartments, where it could observe the demonstrator performing the task (i.e. pecking the response key when it was transilluminated and then eating the food from the hopper). We physically separated the model from the observer to prevent scrounging, because evidence suggests that individuals who have the opportunity to scrounge do not perform the specific task needed to get access to the food themselves (Giraldeau & Lefebvre 1987).

We used as demonstrators six shiny cowbird males that had been trained to peck the key using conventional shaping techniques and then an instrumental conditioning procedure (they obtained the reward only if they pecked the response key when it was transilluminated). We used six demonstrators: one to tutor three subjects, four to tutor two subjects each, and one to tutor one subject. We treated the birds of the group as independent subjects because the dependent variable (latency to the

first keypeck) was recorded on isolated, separately caged individuals (Lefebvre & Helder 1997).

In the second phase, the experimental birds had 18 demonstration-test sessions (one session per day). Each session consisted of 30 demonstration trials, similar to the ones they had received during the first phase. Immediately after these trials, we withdrew the demonstrator and moved the experimental bird from the observation to the demonstration compartment, where it experienced 20 test trials.

In the demonstration sessions of the first and second phases, the tutors responded, on average, in more than 95% of the trials.

#### *Heterospecific demonstrator condition*

The subjects were eight birds (four females and four males). The procedure was the same as in the conspecific demonstrator condition, except that we used as demonstrators five screaming cowbird males ( $\bar{X} \pm \text{SE}$  weight =  $57.3 \pm 1.4$  g). We used five demonstrators: three to tutor two subjects each, and two to tutor two subjects each. As in the conspecific group, during the presentation of the stimulus in the demonstration sessions of the first and second phases, the tutors responded, on average, in more than 95% of the trials.

#### *'Ghost' demonstrator condition*

Subjects were 12 birds (six females and six males). The procedure was the same as in the demonstrator groups, except that during the first and second phases of the demonstration sessions, the subject, instead of observing a demonstrator peck the key and collect the food, observed the apparatus working automatically (i.e. the pecking key was transilluminated, and after 10 s the food dispenser delivered the millet seeds).

#### *No-demonstrator condition*

Subjects were 10 birds (six females and four males). These birds received no demonstration trials and 360 test trials.

### **Statistical Analyses**

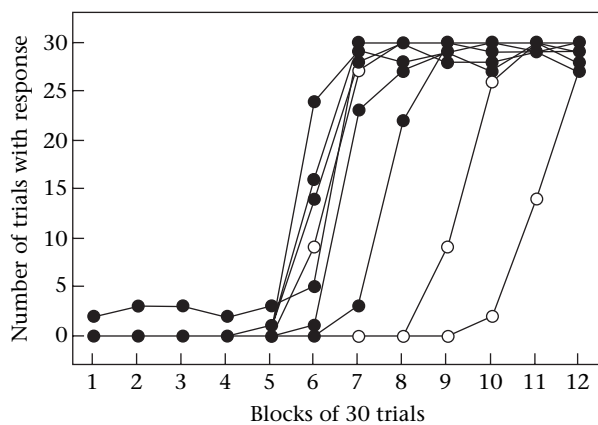
We used nonparametric statistics because of the lack of normality of the data and the small sample sizes of the experimental groups. We tested for sexual differences in the acquisition of the pecking response within the groups with a Mann-Whitney *U* test. For comparison between groups, we used a Kruskal-Wallis test, and when the obtained value was significant, we made multiple comparisons between groups. The critical value of *z* used in the comparisons between groups was adjusted for an  $\alpha$  level of significance of 0.05 (two tailed) and the number of comparisons we made (Siegel & Castellan 1988). Because sample sizes of the groups were relatively small (8–12 subjects), when the comparisons yielded a nonsignificant result we report the confidence intervals (Colegrave & Ruxton 2003). Statistical tests were performed using StatView 5.0 (SAS Institute Inc. 1998) with  $P < 0.05$  (two tailed).

## RESULTS

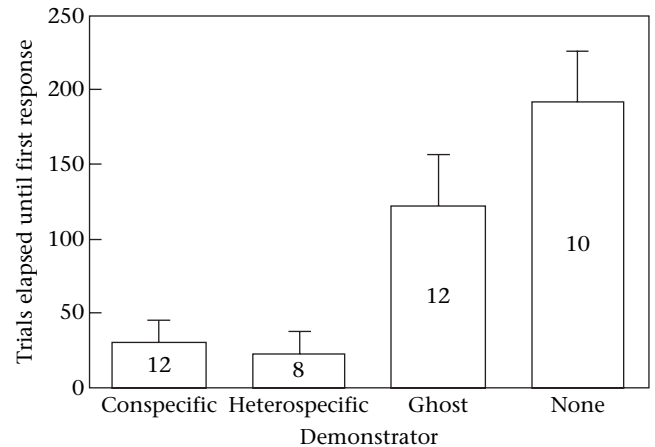
We evaluated whether the observation of a demonstrator resulted in an improvement on the acquisition of the pecking response, using as the dependent variable the number of trials elapsed until the bird pecked the response key for the first time (latency to the first response). Although measures of this variable showed considerable variation between subjects, once a bird started to peck, it reached an asymptotic level of response (more than 80% of the trials with response during the session) within the subsequent two sessions (Fig. 2). Therefore, we considered this variable to accurately estimate how fast the birds acquired the pecking response.

We did not detect sexual differences in the latency to acquire the pecking response in any of the groups (Mann–Whitney  $U$  tests: conspecific demonstrator:  $U = 28$ ,  $N_1 = N_2 = 6$ ,  $P = 0.10$ ; heterospecific demonstrator:  $U = 12$ ,  $N_1 = N_2 = 4$ ,  $P = 0.24$ ; ghost demonstrator:  $U = 21$ ,  $N_1 = N_2 = 6$ ,  $P = 0.63$ ; no demonstrator:  $U = 20.5$ ,  $N_1 = 6$ ,  $N_2 = 4$ ,  $P = 0.07$ ). Therefore, for the comparison between groups, we pooled the data of males and females.

We detected significant differences between groups in the latency to the first response (Kruskal–Wallis test:  $H_3 = 15.3$ ,  $P < 0.001$ ; Fig. 3). Multiple comparisons between groups indicated significant differences between the conspecific demonstrator and both the no-demonstrator group ( $z_{6,0.05} = 2.64$ ,  $N_1 = 12$ ,  $N_2 = 10$ ,  $P < 0.05$ ) and the ghost demonstrator group ( $z_{6,0.05} = 2.64$ ,  $N_1 = N_2 = 12$ ,  $P < 0.05$ ), as well as between the heterospecific demonstrator and the no-demonstrator groups ( $z_{6,0.05} = 2.64$ ,  $N_1 = 8$ ,  $N_2 = 10$ ,  $P < 0.05$ ). There were no differences between the conspecific and heterospecific demonstrator groups (conspecific:  $\bar{X} \pm SD = 30.8 \pm 50.5$ ,  $N = 12$ , heterospecific:  $22.4 \pm 44.1$ ,  $N = 8$ , 95% confidence interval:  $-54.4$ – $37.7$ ) or between the heterospecific and the ghost demonstrator groups (ghost:  $\bar{X} \pm SD = 121.8 \pm 117.8$ ,  $N = 12$ , 95% confidence interval:  $7.3$ – $191.6$ ). The differences between the ghost demonstrator and no-demonstrator groups were marginally significant ( $P < 0.10$ , no



**Figure 2.** Number of trials with response per block of 30 trials during the acquisition of the pecking response in birds of the no-demonstrator group. ●: males; ○: females.



**Figure 3.** Mean  $\pm$  SE number of test trials elapsed until subjects started to peck the response key. The number of subjects is indicated inside each bar.

demonstrator:  $\bar{X} \pm SD = 191.6 \pm 106.1$ ,  $N = 10$ , 95% confidence interval:  $-170.4$ – $30.9$ ).

## DISCUSSION

Our results show that observing either a conspecific or a heterospecific demonstrator influences the acquisition of a behaviour in shiny cowbirds. Cowbirds that observed a demonstrator perform the task acquired the pecking response faster than those that did not. These differences were not due to the observation of the light–food sequence only, because subjects that observed a demonstrator acquired the pecking response faster than birds that observed the apparatus operate in the absence of a demonstrator. In addition, birds in the group with a ‘ghost’ demonstrator tended to acquire the pecking response faster than individuals that were not exposed to this stimulus–reward sequence. This result suggests that cowbirds may also learn from the observation of the light–food sequence that we used to train demonstrators. Similarly, Biederman et al. (1986) found that pigeons learn a stimulus discrimination task faster when they have previously observed a stimulus that is subsequently used as the stimulus paired with the delivery of food than when they are exposed to the visual discriminative stimuli only.

Heyes (1994) distinguished several varieties of imitative and nonimitative social learning, according to the role of the demonstrator in generating matching behaviour on the observer. Although our study was not designed to distinguish between these different mechanisms, it is unlikely that the observers learned the pecking response by imitation (i.e. that they learned the operant task directly through the observation of the model’s behaviour; Zentall 1996). An important criterion to postulate imitation as the cognitive mechanism involved in social learning is that the probability of occurrence of the behaviour in the group without a demonstrator is very low (Thorpe 1963; Caldwell & Whiten 2002). In our study, cowbirds in the no-demonstrator group also learned the pecking response,

and the observation of a demonstrator only accelerated the acquisition of this behaviour. This result suggests that a nonimitative form of social learning (i.e. local enhancement, stimulus enhancement or observational conditioning) was involved in our study.

Local enhancement refers to cases in which an animal is attracted to a site or object by the current presence of the demonstrator or by residues of the demonstrator's activity, and stimulus enhancement occurs when observation of an action leads the observer to increase the proportion of its behaviour directed towards the location or object of the demonstrator's activity (Heyes 1994). In our study, the demonstrator was not present during the test sessions and there were no residues of the demonstrator activity in the test chamber (except for possible odour cues, which are not very important in birds; Waldvogel 1989; Roper 1999). Thus, the presence of a conspecific or a heterospecific demonstrator may have increased the probability that the observer interacted with the stimulus with which the demonstrator had interacted (stimulus enhancement), or that the observer associated the location or object with the reward obtained by the demonstrator (i.e. observational conditioning; Cook et al. 1985; Heyes 1994).

We did not find sexual differences in observer performance in any of the experimental groups. However, we only used males as demonstrators, so we cannot rule out the possibility of an effect of the sex of the demonstrator on the amount of attention that it attracts from the observer. In zebra finches, *Taeniopygia guttata*, females prefer the colour of food eaten by male demonstrators, whereas males show no preferences between the colour of food eaten by male and female demonstrators (Benskin et al. 2002; Katz & Lachlan 2003). Demonstrator characteristics other than sex, like familiarity with the observer (Benskin et al. 2002) or dominance rank (Nicol & Pope 1999), can also affect the amount of attention that they attract from observers. In our study, observers and demonstrators were familiar, because they shared the same cage during the whole experiment. However, we did not control for the dominance rank of observer and demonstrator, except that shiny cowbird males are dominant over females.

Our study shows that shiny cowbirds improve the acquisition of a feeding task by observing a demonstrator of either their own species or a species with which they share roosts and foraging flocks. Dolman et al. (1996) suggested that the type of feeding interaction (competitive, noncompetitive) might better predict the pattern of social learning than species identity. Our results are consistent with this interpretation, because shiny and screaming cowbirds congregate in large foraging flocks throughout the year where they compete with each other for food. An experiment with a heterospecific demonstrator that does not compete with shiny cowbirds in foraging flocks would be necessary to evaluate Dolman et al.'s (1996) hypothesis more completely.

Future studies are also needed to address whether the ability to acquire information from conspecifics and heterospecifics improves the foraging efficiency of shiny cowbirds and contributes to their survival and reproductive success in natural circumstances. Considering that

this species is a brood parasite, it would also be interesting to evaluate whether cowbirds can also acquire information about the location of host's nests by social learning.

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