



## Sex differences in retention after a visual or a spatial discrimination learning task in brood parasitic shiny cowbirds



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### ABSTRACT

Females of avian brood parasites, like the shiny cowbird (*Molothrus bonariensis*), locate host nests and on subsequent days return to parasitize them. This ecological pressure for remembering the precise location of multiple host nests may have selected for superior spatial memory abilities. We tested the hypothesis that shiny cowbirds show sex differences in spatial memory abilities associated with sex differences in host nest searching behavior and relative hippocampus volume. We evaluated sex differences during acquisition, reversal and retention after extinction in a visual and a spatial discrimination learning task. Contrary to our prediction, females did not outperform males in the spatial task in either the acquisition or the reversal phases. Similarly, there were no sex differences in either phase in the visual task. During extinction, in both tasks the retention of females was significantly higher than expected by chance up to 50 days after the last rewarded session (~85–90% of the trials with correct responses), but the performance of males at that time did not differ than that expected by chance. This last result shows a long-term memory capacity of female shiny cowbirds, which were able to remember information learned using either spatial or visual cues after a long retention interval.

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### 1. Introduction

Avian brood parasites, like cuckoos and cowbirds, lay their eggs in nests of other species, the hosts, which provide all parental care for the parasite's eggs and chicks (Rothstein and Robinson, 1998; Spottiswoode et al., 2012). One of the consequences of this breeding strategy is that brood parasites must locate host nests and then decide whether to parasitize them. As an example, brown-headed cowbirds (*Molothrus ater*) and shiny cowbirds (*Molothrus bonariensis*) discover nests using host behavior as a cue (Wiley, 1988; Banks and Martin, 2001), although they may also find nests by thoroughly searching the habitat (Fiorini and Reboreda, 2006). Then, they return to parasitize nests, mainly during host laying (Astié and Reboreda, 2009; Fiorini et al., 2009). Cowbird parasitism occurs just before sunrise (Scott, 1991; Peer and Sealy, 1999; Gloag et al., 2013) and during the rest of the day cowbird females search for nests they may parasitize on subsequent days (Norman and Robertson, 1975; Gloag et al., 2013). Cowbirds search for nests within

relatively constant areas throughout the breeding season (Hahn et al., 1999; Scardamaglia and Reboreda, 2014), which would facilitate monitoring over time and synchronization of parasitism with host laying. In shiny cowbirds, females fly directly from the roost to the nest they will parasitize, which is located within the area the female has visited previously (Scardamaglia and Reboreda, 2014) suggesting that, at the time a female departs from the roost, she knows the location of the nest to parasitize. Besides, cowbird females do not return to lay eggs in nests that they have already parasitized, probably to avoid competition between their own offspring (Alderson et al., 1999; McLaren et al., 2003; Ellison et al., 2006; Gloag et al., 2014).

This parasitic behavior makes special demands on information processing. The cowbird female locates host nests within her home range and these nests are at different stages (i.e., construction, laying, early or late incubation). Therefore, at the time she is ready for laying an egg she may face choices among several potential host nests at different stages. Then, she must choose the nest at the most appropriate stage and return to this nest in a short time-window before sunrise. Besides, a female cowbird should remember all the nests in which she has laid eggs to avoid repeat parasitism and therefore competition between her offspring. This cowbird's

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demand for remembering the precise location and nesting stage of multiple host nests correlates with a relative enlargement of the hippocampus (Sherry et al., 1993; Reboreda et al., 1996), a brain region involved with spatial information processing in all vertebrates (O'Keefe and Nadel, 1978; Bingman et al., 2009). This enlargement is present in the sex that locates host nests: females in shiny and brown-headed cowbirds and females and males in screaming cowbirds, *Molothrus rufoaxillaris* (Sherry et al., 1993; Reboreda et al., 1996). In addition, in shiny and screaming cowbirds the relative hippocampal volume is larger during the breeding than during the non-breeding season and in shiny cowbirds the sexual dimorphism present in summer is not found in winter (Clayton et al., 1997), which suggests neuroanatomical plasticity associated with seasonal changes in spatial memory demands for searching host nests. The interpretation of the observed sexual dimorphism and seasonal changes in hippocampus volume is that ecological pressures, like remembering the precise location of multiple host nests, has imposed on female cowbirds higher spatial memory demands that selected for the modification of the neural substrate for spatial memory abilities (Sherry et al., 1993; Reboreda et al., 1996; Clayton et al., 1997). Thus, brain and cognition would be adaptively specialized to solve specific ecological problems (i.e., adaptive specialization hypothesis, Sherry, 2006).

The association between the relative enlargement of the hippocampus and the ability to solve tasks demanding the use of spatial memory has been broadly studied in food-hoarding birds (i.e., birds that recover stored food by remembering where they have hidden their caches) (for reviews see Healy et al., 2009; Pravosudov and Smulders, 2010; Pravosudov and Roth, 2013). In contrast, few studies have analyzed whether the larger volume of female's hippocampus in brood parasites is correlated with a better performance in solving tasks demanding the use of spatial memory. Astié et al. (1998) tested whether shiny cowbirds presented sex differences in a memory task consisting of finding food in an experimental patch of 64 wells. In this experiment the well with food was indicated either by the color or the spatial location of the covering disk. Contrary to predictions, females learnt to retrieve the food faster than males when food was associated with visual cues, but there were no sex differences when food was associated with spatial cues. More recently, Guigueno et al. (2014) tested for sex differences in spatial memory in brown-headed cowbirds using a foraging task in which birds had to find one rewarded location after 24 h and found that females made significantly fewer errors than males and took more direct paths to the rewarded location than males.

In this study we tested the hypothesis that shiny cowbirds show sex differences in spatial cognitive abilities associated with sex differences in host nest searching. One of the difficulties for testing this hypothesis has been to find a laboratory experimental task similar to that of locating and re-visiting host nests. Ideally, the task used should resemble nest searching, but because males do not search for nests the comparison between males and females requires a task that both sexes can perform and in which possible differences in performance are not due to differences in motivation or motor skills of the subjects. The procedure so far has been to compare the performance of females and males in a memory task requiring spatial vs. visual memory and to assume that the spatial memory task has a common underlying cognitive mechanism to that used by cowbirds to re-visit host nests (Astié et al., 1998; Guigueno et al., 2014). Similarly, the procedure we use in the present study is to compare the performance of females and males in a visual and a spatial discrimination learning task with food as reinforcement. In this task, we do not expect sex differences in motivation or motor skills. We first tested sex differences during acquisition and reversal in a visual and a spatial discrimination learning task and then, we tested sex differences in retention up to 50 days after the last

rewarded session during an extinction procedure. According to the adaptive specialization hypothesis, females of *M. bonariensis* should outperform males in the spatial but not in the visual task.

## 2. Methods

### 2.1. Birds and housing conditions

Subjects were 12 wild-caught shiny cowbirds, 6 females ( $43.3 \pm 1.6$  g; mean  $\pm$  SEM) and 6 males ( $51.8 \pm 1.0$  g). We caught the birds in July (mid winter) near the city of Buenos Aires using mist nets. We housed them in wire cages of  $120 \times 40 \times 30$  cm (length  $\times$  width  $\times$  height) in groups of three same sex individuals. Cages were arranged so that birds in different cages were visually isolated. The birds were maintained on a summer 14:10 h light:dark cycle (light onset at 06:00 h) at room temperature (range: 15–25 °C). Throughout the experiments they were food deprived from 16:00 h until the start of each session at 09:00 h the following morning. Between experiments they had free access to food (millet seeds and balanced food for insectivorous birds). Water was available ad-libitum all the time. Body mass and general condition of all except one bird remained stable throughout the experiments, which lasted 8 months. After we completed the experiments, the birds were released in an area regularly occupied by free-living cowbirds.

### 2.2. Apparatus

To minimize the disturbance of the birds we conducted both the pre-training (see Section 2.3) and the experiments (see Section 2.4) in the home cages. Before the start of each session we divided the cage into two compartments using an opaque plastic partition. We used one of the compartments (experimental,  $40 \times 40 \times 30$  cm) for sequentially training or testing the birds while in the other compartment (housing,  $80 \times 40 \times 30$  cm) we kept the birds that were not trained or tested. The experimental compartment had an operant device of  $16 \times 4.5 \times 4.5$  cm (width  $\times$  height  $\times$  depth) with two response keys 3 cm in diameter on the top of each side of a central food hopper of  $4 \times 3 \times 2.5$  cm (length  $\times$  depth  $\times$  height). 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 illuminated with red and green lights, and when cowbirds pecked them they closed a micro switch connected to an I/O interface (Med Associates, Inc.). A computer running MedPC language (Med Associates, Inc.) controlled the stimulus events and response contingencies and recorded the data. After one bird finished its session we moved the bird to the housing compartment and a new bird to the experimental compartment. The order in which the birds of the same cage were trained and tested each day was randomized.

### 2.3. Pre-training

We trained the birds to peck the response key when it was illuminated to get a reward (five millet seeds). This period lasted 15 sessions (30 trials per session, one session per day). Each trial started with the illumination of the pecking keys, one with green light and the other with red light. In 50% of the trials the green stimulus was presented on the left side and the red stimulus on the right side and in the other 50% of the trials, the opposite. The stimulus was on during 10 s, and after that the food dispenser delivered the reward independently of whether the bird had pecked the key or not (first four "autoshaping" sessions) or contingent to one peck on any of the keys (last 11 "instrumental" sessions). In the "instrumental" sessions, if the bird pecked the key during the presentation

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