



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 ± 1.6 g; mean \pm SEM) and 6 males (51.8 ± 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

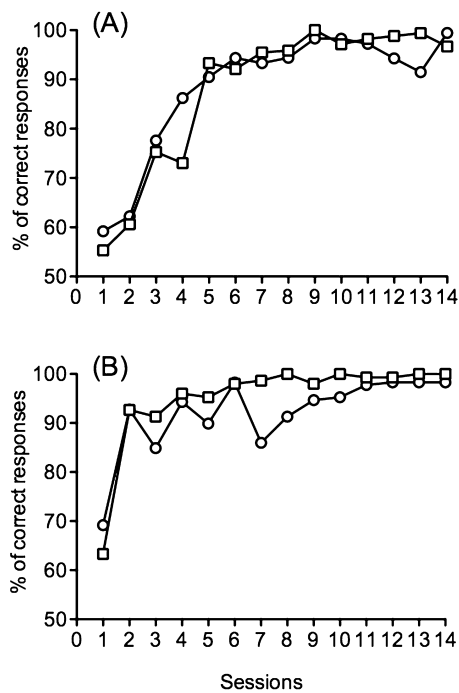


Fig. 1. Performance (percentage of correct responses per session) of 6 female (circles) and 5 male (squares) shiny cowbirds (*Molothrus bonariensis*) during the phase of acquisition in a visual (A) and a spatial (B) discrimination learning task.

of the stimulus, the seeds were delivered immediately after pecking. After the delivery of the reward, the stimulus went off during an intertrial interval (ITI) of 40 s. At the end of this training phase the birds pecked the response key when it was illuminated in more than 95% of the trials and none of the birds showed side or color preferences (binomial tests = ns).

2.4. Experimental procedures

After the pre-training phase, all birds were tested in a visual and in a spatial discrimination learning task. In the visual discrimination task, the stimulus associated with the reward (S+) was the color of the light (green or red, counterbalanced between subjects and sexes), while the position of S+ (left or right) was associated with the reward with $P=0.5$. In the spatial discrimination task, S+ was the position of the light (left or right, counterbalanced between subjects and sexes), while the color of the light was associated with the reward with $P=0.5$. Each discrimination task included three consecutive phases: (1) acquisition (14 sessions, 30 trials per session, one session per day), (2) reversal (14 sessions, 30 trials per session, one session per day), and (3) extinction (6 sessions, 30 trials per session, one session per day at days 1, 3, 7, 15, 31 and 50 after the last session of the phase of reversal). During the phase of reversal S+ was the stimulus that had not been associated with the reward during the phase of acquisition. During the phase of extinction the birds were exposed to the same stimuli of the phase of reversal, but pecking any of the response keys when they were illuminated was not rewarded.

All the birds experienced the visual discrimination task first and then the spatial discrimination task. Because at the end of the phase of extinction in the visual discrimination task the birds were responding in less than 50% of the trials (see Section 3.3), before starting the spatial discrimination task the birds received 20 sessions of instrumental training (we trained the birds to peck the response key when it was illuminated to get a reward of five millet seeds). After this training all the birds pecked the response keys

in more than 95% of the trials per session and none of the birds showed side or color preferences (binomial tests = ns).

2.5. Statistical analysis

We used general linear mixed models (GLMM) to evaluate differences between sexes during acquisition, reversal and retention after extinction. The dependent variable was the percentage of correct responses for each session, which was arcsine transformed to normalize the data. We included sex, session and their interaction as fixed factors and the subject ID as a random factor. When the interaction term was significant, we calculated the simple effects (i.e., contrasts between the levels of one factor for each level of the other factor in the interaction) to evaluate differences between groups and applied the Bonferroni correction to control the global error rate ($\alpha=0.05$). For the acquisition and reversal phases we pooled the data in blocks of two sessions to avoid having too many repeated measures in relation to the number of birds tested. Because one of the males died between the visual and the spatial discrimination tasks, we excluded it from the analysis (final sample size = 6 females and 5 males). We checked for normality of the residuals for all the models. We conducted the analyses using the nlme package (Pinheiro et al., 2013) in R 3.0.1. All statistical tests are two-tailed. Additionally, we calculated partial eta-squared values as a measure of effect size.

3. Results

3.1. Acquisition

Fig. 1 shows the percentage of correct responses by female and male shiny cowbirds during the phase of acquisition in the visual (Fig. 1A) and in the spatial (Fig. 1B) discrimination learning task. In both sexes the percentage of correct responses increased over the sessions (visual task: $F(1, 64) = 112.9, p < 0.0001$; spatial task: $F(1, 64) = 60.3, p < 0.0001$), but there were no sex differences in either task (visual: $F(1, 9) = 0.1, p = 0.75$; spatial: $F(1, 9) = 0.9, p = 0.34$).

3.2. Reversal

Fig. 2 shows the percentage of correct responses by female and male shiny cowbirds during the phase of reversal in the visual (Fig. 2A) and in the spatial (Fig. 2B) discrimination learning task. In both sexes the increase in the percentage of correct responses over the sessions was significant (visual task: $F(1, 64) = 176.3, p < 0.0001$; spatial task: $F(1, 64) = 72.9, p < 0.0001$), but there were no sex differences either in the visual ($F(1, 9) = 1.5, p = 0.22$) or in the spatial ($F(1, 9) = 0.06, p = 0.81$) discrimination learning tasks.

3.3. Extinction and retention

Fig. 3A and B shows the percentage of trials with response during the phase of extinction in the visual and in the spatial discrimination learning task, respectively. Birds started this phase responding in most trials but after two sessions the percentage of trials with response decreased to less than 40% in both tasks (visual task: $F(1, 53) = 33.5, p < 0.001$; spatial task: $F(1, 53) = 60.3, p < 0.001$). Regarding the trials with response, females outperformed males in the visual learning discrimination task ($F(1, 9) = 4.1, p = 0.05$, partial eta-squared = 0.31). In regards to the trials with response in the spatial discrimination task, there was a significant effect of the interaction sex \times session ($F(1, 53) = 5.5; p = 0.02$; partial eta-squared = 0.16), but the simple effects were not significant (Fig. 4D). The performance of females was higher than expected by chance up to fifty days after the last session at which they were rewarded, both in the visual (95% CI [74.1, 98.6 %]) and in the spatial task

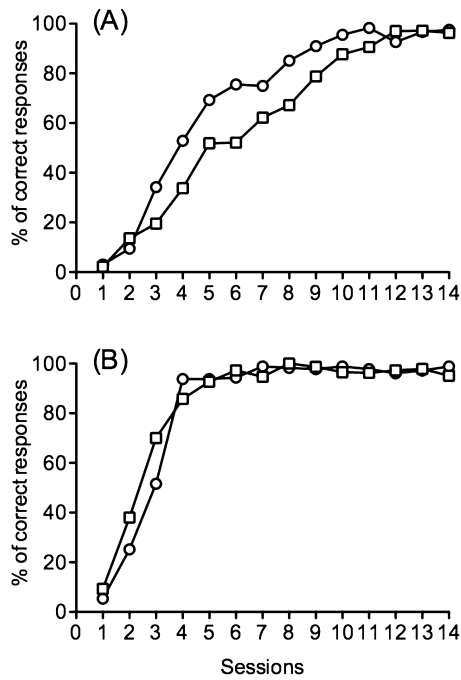


Fig. 2. Performance (percentage of correct responses per session) of 6 female (circles) and 5 male (squares) shiny cowbirds during the phase of reversal in a visual (A) and a spatial (B) discrimination learning task.

(95% CI [78.9, 100 %]). In contrast, the performance of males fifty days after the last rewarded session did not differ than expected by chance (visual task: 95% CI [49.6, 71.1 %]; spatial task: 95% CI [40.9, 100 %]).

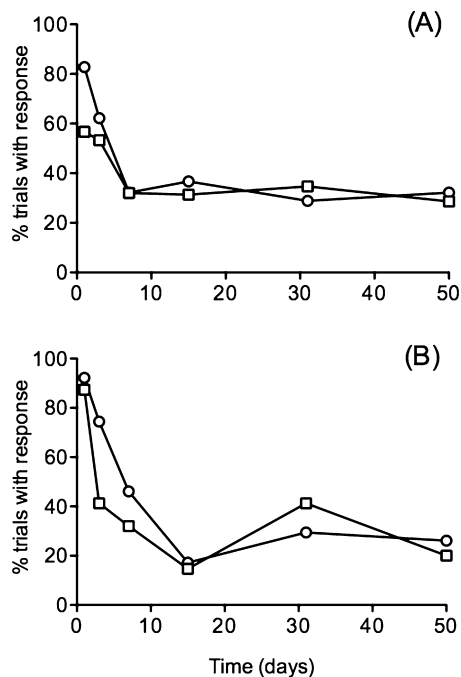


Fig. 3. Performance (percentage of trials with response) during the phase of extinction of 6 female (circles) and 5 male (squares) shiny cowbirds in a visual (A) and a spatial (B) discrimination learning task. This phase consisted in sessions in which the birds were not rewarded after responding. Extinction sessions were conducted at 1, 3, 7, 15, 31 and 50 days after the last session of the phase of reversal.

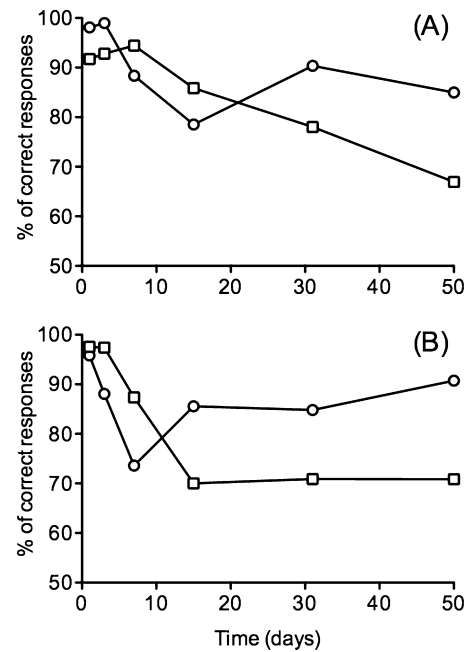


Fig. 4. Performance (percentage of correct responses per session) in the trials with response during the phase of extinction for a visual (A) and a spatial (B) discrimination learning task.

4. Discussion

Contrary to our original prediction, females did not outperform males in the spatial discrimination learning task in either the acquisition or the reversal phases. Likewise, there were no sex differences in acquisition and reversal in the visual discrimination learning task. The only sex difference observed was during extinction. In this phase, the performance of females in the visual and in the spatial discrimination learning task was better than expected by chance up to 50 days after the last rewarded session, but the performance of males at that time did not differ from chance. This last result indicates that female shiny cowbirds can remember information learned using visual or spatial cues for longer periods than males.

Our results differ partially from those obtained in two previous studies that tested if the larger volume of female's hippocampus in cowbirds is correlated with a better performance in solving tasks demanding the use of spatial memory. Astié et al. (1998) found that females learnt to find food faster than males when the location was associated with visual cues, but in the present study we did not detect sex differences in the acquisition and the reversal phases of the visual discrimination learning task. Similarly to Astié et al. (1998), we did not find sex differences in the acquisition and the reversal phases of the spatial discrimination learning task either. In regards to the study of Guigueno et al. (2014), these authors found that brown-headed cowbird females outperformed males in a delayed-matching-to-sample spatial memory task in which birds re-located a single covered cup containing food among 25 cups after a retention interval of 1 or 24 h. One explanation for the differences between Guigueno et al. (2014) study and the present one could be that the task used to test spatial memory capabilities in the former was more difficult and this allowed detecting sex differences in spatial memory. In agreement with this interpretation, we only detected sex differences in the phase of retention during extinction and after a long retention interval.

The association between sex differences in hippocampus volume and spatial cognition has been extensively studied in food-hoarding birds (Hampton and Shettleworth, 1996; Biegler et al.,

2001; Shettleworth and Westwood, 2002). For example, Biegler et al. (2001) have found that food-storing species remembered information for longer than did non-storing species. Similarly, studies comparing the performance of migratory vs. non migratory species showed that memory of a particular feeding site persisted for longer periods in a long-distance migrant than in a closely related non-migrant species, and that this difference is associated with an increase in relative hippocampal size from the first to the second year of life in the migrant, but not in the non-migrant species (Mettke-Hofmann and Gwinner, 2003).

In contrast, it has been more difficult to demonstrate that the sexual dimorphism in the relative hippocampal size of brood parasitic cowbirds (Sherry et al., 1993; Reboreda et al., 1996) is associated with sex differences in spatial memory abilities (Astié et al., 1998; Guigueno et al., 2014, this study). In addition, there have been no studies comparing the performance in spatial memory tasks of closely related parasitic and non-parasitic species.

One possibility to explain the failure to detect sex differences in spatial memory performance in our study is that captivity during the experiment affected females' hippocampus volume and this masked sex differences in spatial cognitive abilities. Day et al. (2008) proposed that preventing brown-headed cowbirds from nest searching by holding them in captivity would selectively decrease the volume of the female, but not the male hippocampus. Consistently, these authors found that captive females, but not males, had a smaller hippocampus than their wild counterparts. Although we kept the birds with a light:dark cycle corresponding to that of the breeding season, we cannot rule out that captivity had affected the volume of females' hippocampus, thus concealing sex differences in spatial memory.

During the phase of extinction the performance of females was higher than expected by chance up to 50 days after the last rewarded session, with females responding correctly in ~85–90% of the trials and outperforming males in the visual and spatial discrimination learning tasks. These results are consistent with other studies showing that during extinction, the subjects learned that their response is no longer rewarded, but they did not forget the original learning (Vaughan and Greene, 1984; Bouton, 2004).

Relatively few studies have investigated the longevity of spatial memory in birds and most of these studies have been conducted on scatter hoarding birds of two families (Corvidae and the Paridae) that use spatial memory to relocate their caches (i.e., Balda and Kamil, 1992; Brodin and Kunz, 1997; Roth et al., 2012), or in migratory species (Mettke-Hofmann and Gwinner, 2003). As regard retention of a discrimination task using appearance cues, Bogale et al. (2012) showed that jungle crows (*Corvus macrorhynchos*) have a high retention capacity for learned information of a color stimulus, making no or very few errors after up to a 10-month retention interval. While other studies in birds have investigated sex differences in learning using visual or spatial cues (Vallortigara, 1996; Hodgson and Healy, 2005), to the best of our knowledge, our study is the first to investigate and show sex differences in retention in a visual and a spatial discrimination learning task.

To summarize, we showed that female shiny cowbirds can remember information learned using visual or spatial cues for longer periods than males. Whether these sex differences are related with differences in nest searching behavior requires further study.

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