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Behavioural Processes

Sex differences in learning flexibility in an avian brood parasite, the shiny cowbird

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A B S T R A C T

Females of brood parasitic shiny cowbirds, *Molothrus bonariensis*, search and prospect host nests, synchronizing parasitism with host laying. This behavior is sex-specific, as females perform this task without male's assistance. Host nests must be removed from the female's memory "library" after being parasitized, to avoid repeated parasitism, or when they become unavailable because of predation. Thus, females must adjust their stored information about host nest status more dynamically than males, possibly leading to differences in learning flexibility. We tested for sex differences in a visual (local cues) and a spatial discrimination reversal learning task, expecting females to outperform males as an expression of greater behavioral flexibility. Both sexes learned faster the spatial than the visual task during both acquisition and reversal. In the visual task there were no sex differences in acquisition, but females reversed faster than males. In the spatial task there were no sex differences during either acquisition or reversal, possibly because of a ceiling effect: both sexes learned too fast for differences in performance to be detectable. Faster female reversal in a visual but not spatial task indicates that the greater behavioral flexibility in females may only be detectable above some level of task difficulty.

1. Introduction

Most animals face frequent and unpredictable changes in their biotic and abiotic environment and therefore it is adaptive for them to develop strategies to cope with this variability. One of such strategies is behavioral flexibility, which allows animals to adjust their behavior in response to environmental changes (Bond et al., 2007). Behavioral flexibility includes the ability to inhibit learned behaviors favoring novel learning to better match the requirements of new situations (Shettleworth, 2010; Wright et al., 2010). The level of behavioral flexibility varies widely between species (Fragaszy, 1981; Bond et al., 2007; Gaalema, 2011; Rayburn-Reeves et al., 2011, 2013; Laude et al., 2016; Fuss and Witte, 2019). Furthermore, some studies in fishes (Lucon-Xiccato and Bisazza, 2014, 2017), birds (Rogers, 1974 but see Brust et al., 2013), and rats (Guillamón et al., 1986) indicate that, in a variety of species, females are more flexible than males. These differences seem to be mediated by the effects of testosterone in the early male's life (Guillamón et al., 1986), that increments the persistence of previously

learned contingencies (Rogers, 1974). One may expect these differences to be exaggerated in species where their life history requires major behavioral differences between the sexes.

One of the protocols frequently used to test behavioral flexibility is the discrimination-reversal learning task (Shettleworth, 2010). In this paradigm, animals are trained to discriminate between two stimuli, and after the task is fully acquired, the reward contingency is reversed, asking subjects to ignore the stimulus previously reinforced, inhibiting what they have just learned. This procedure has been widely studied in birds (Bond et al., 2007; Range et al., 2008; Boogert et al., 2010, 2011; Rayburn-Reeves et al., 2011, 2013; O'Hara et al., 2015; Laude et al., 2016; Croston et al., 2017; Guido et al., 2017; McMillan et al., 2017), but only rarely in the context of sex differences in flexibility (i.e., Brust et al., 2013).

Cowbirds (*Molothrus* spp.) are obligate interspecific brood parasites that lay eggs in nests of other species, the hosts, which provide care for the parasite's eggs and chicks (Ortega, 1998). During the breeding season, female shiny (*M. bonariensis*) and brown-headed (*M. ater*)

cowbirds search for host nests without male's assistance within relatively constant areas (Hahn et al., 1999; Scardamaglia and Reboreda, 2014). Once they find a potential nest, they visit it repeatedly the following days, presumably to monitor its progress, and return to parasitize it during the laying period of the host (Scardamaglia et al., 2017; White, 2019). This behavior has been called 'book-keeping' (Clayton et al., 1997), as female cowbirds must remember and update the location and stage of multiple nests as they progress in the nesting stages and avoid parasitizing nests that they have already parasitized to reduce competition between their own siblings (Hahn et al., 1999; Ellison et al., 2006; Gloag et al., 2014; Scardamaglia et al., 2017). Female cowbirds should also eliminate potential host nests from their availability "library" if they are destroyed by predators.

Previous studies have shown that in brown-headed and shiny cowbirds there are sex- and species-specific associations between nest searching and neuroanatomy: in cowbird species showing sexually dimorphic behavior, females have a larger hippocampus than males during the breeding season (Sherry et al., 1993; Reboreda et al., 1996; Clayton et al., 1997; Guigueno et al., 2016). Moreover, in brown-headed cowbirds, adult hippocampal neurogenesis is greater in females than in males (Guigueno et al., 2016) and females have a more accurate spatial memory than males (Guigueno et al., 2014).

In the present study, we investigate sex differences in behavioral flexibility in shiny cowbirds. Because in this species only females locate and prospect host nests (Gloag et al., 2013; Scardamaglia and Reboreda, 2014; Scardamaglia et al., 2017), females face greater demands to respond to changing information, making it reasonable to expect greater learning flexibility in general. We explore the presence of sex differences in behavioral flexibility by quantifying speed of acquisition and of reversal in two tasks: one based on the location of, and the other on local visual cues next to the pecking key paired with a food reward ('spatial' and 'visual' tasks respectively). Flexibility should be evidenced by performance during the reversal phase of the experiment.

2. Methods

2.1. Subjects

We captured adult shiny cowbirds using mist nets at Ciudad Universitaria, Buenos Aires city, Argentina (34° 32′ 33″ S 58° 26′ 25″ W) during August-October 2017. We selected adults based on plumage characteristics (Ursino et al., 2012). After capture, birds were housed for at least a month in wire cages of 120 × 40 × 40 cm (length x width x height) in groups of up to three birds per cage. Cages were visually but not acoustically isolated. They were kept under a natural light cycle at room temperature (range 18−30 °C) and fed with an enriched-vitamin seed mix and insects. A week before the experiment began, birds were moved to a room with a controlled 11:13 h light:dark cycle, with white light switched on from 07:00 AM to 06:00 PM and black light (used as moonlight) switched on from 06:00 PM to 07:00 AM. During this period birds were kept in pairs in the experimental cages (120 × 80 × 80 cm, length x width x height).

During the experiments, we removed the food from 05:00−06:00 PM until the end of the experimental session the following day (11:00 AM-12:00 PM), when they had access to food ad-libitum. The weight of the birds remained stable over the course of the experiment. We conducted the experiments during the breeding season of this species, from September 2017 to February 2018. After we completed the experiments,

the birds were released in the same place where they had been captured.

2.2. Procedures and apparatus

Before the start of every daily session, each experimental cage was divided into three sections of 40 × 80 × 80 cm (length x width x height) using metal divisions. In each of the two laterals, there was an operant panel (Campden Instruments, Loughborough, Leicestershire, UK) attached to the center of the wall. Operant panels had three faces (10 cm wide), a middle one, facing the cage, and two lateral faces attached to the cage at a 70-degree angle (see Shapiro et al., 2008, Fig. 1; and Supplementary video). Each face had one square response key (4 × 4 cm, 9 cm above the floor of the cage) that could be illuminated with different patterns and/or colors by a 4 × 4 array of LED lights. Additionally, the middle face had an open square window of 3 × 3 cm where the birds received the reward. Each panel was connected to a pellet dispenser (Campden Instruments).

Birds were randomly assigned to one of the laterals of the cage for the whole experiment. They experienced two sessions per day of 30 trials each. A trial consisted of a 10 s presentation of one stimulus in the central response key during pre-training, or two stimuli in the lateral response keys during discriminations. If the bird pecked the correct key within the 10 s time window, it received 6.2 ± 1.1 (mean ± SD, n = 60) millet seeds and continued to an intertrial interval of 40 s. If the bird pecked the incorrect key or did not respond during the 10 s window, it moved directly to an intertrial interval. Each session lasted approximately 30 min, depending on how long it took to complete 30 trials, and the interval between the two daily sessions lasted 60 min. Rewards, intertrial intervals, number of trials per session, number of sessions per day and interval between sessions were the same for every phase of the experiment (pre-training, acquisition, and reversal).

The contingencies were programmed using Microsoft Visual Studio 2008. Panels were connected to a BehaviourNet Controller (MkII, Campden Instruments) via WhiskerServer v.3.5 (https://www.whiskercontrol.com).

2.3. Pre-training and discrimination tasks

Each pre-training trial started with the illumination of the central response key with white light. After 10 s, the reward was delivered independently of whether the bird had pecked the key or not (i.e., by autoshaping). Once birds pecked consistently for at least two sessions, they were advanced to a conditional schedule where the reward was only delivered if the bird pecked the response key during the presentation of the stimulus. The criterion to finish the pre-training phase was that birds pecked in more than 80 % of the trials during four consecutive sessions.

The discrimination tasks had two phases: acquisition and reversal. During the acquisition phase, individuals had to learn to respond to two stimuli of different shapes (an X and an O produced by eight LED lights) that appeared in the lateral response keys. In the visual discrimination task, the correct stimulus (S+) was associated to one of the two shapes (X or O) and was presented with equal probability in the left or right response keys, while the other shape appeared in the alternative key. In the spatial discrimination task, S+ was associated to one of the sides (left or right) while the two shapes could appear on either side with equal probability. For each individual we randomly assigned which stimulus was S+ in the acquisition phase. The learning criterion was two

consecutive days (four sessions) with > 80 % of correct responses in each session. Once birds reached the criterion, the stimulus associated to reward reversed. After completing the reversal phase (same criterion as for acquisition), birds received four sessions of conditional pre-training and then, they shifted to the other task. The order of the tasks was counterbalanced between subjects. The color of the stimuli used in the second task was different from that used in the first one (some birds started with green light stimuli and continued in the second task with yellow stimuli while the others had the opposite combination).

2.4. Data and statistical analyses

Nine females and seven males completed the pre-training and started a discrimination task, but only six females and four males completed both acquisition and reversal in the two tasks. The number of birds that completed each phase and task were as follows. Visual task: eight females and five males in acquisition, and seven females and four males in reversal. Spatial task: nine females and seven males in acquisition, and six females and five males in reversal.

To analyze if there were sex differences in number of sessions to criterion during pre-training, we used a generalized linear model (GLM) with a Poisson distribution (log link function) because of the discrete nature of the response variable, with sex as a fixed factor. To analyze sessions to criterion during acquisition and reversal phases in both tasks we used a generalized linear mixed model (GLMM) with task, phase, sex, and task order as fixed factors and individual as a random factor. Due to overdispersion, we used a Negative Binomial distribution (log link function) to model this discrete response variable. Estimations were done using maximum likelihood; therefore, z values are reported. We conducted the analysis using R package glmmTMB (Brooks et al., 2017). Pairwise post-hoc comparisons and effect sizes (Cohen's d) were performed using R package emmeans (Lenth, 2020). For each model, we assessed residuals diagnostics by plotting residuals vs. predicted values and checking for a non-significant dispersion in the QQ plot of residuals using R package DHARMa (Hartig, 2020). All statistical analyses were performed in R 4.0.2 (R Core Team, 2020). Models' fit, statistical details, post-hoc, and effect size comparisons are presented in the Supplementary data.

3. Results

There were no sex differences in number of sessions to criterion during the pre-training phase (GLM, $z = -1.26$, $p = 0.21$). Females needed on average 5.9 ± 2.9 sessions (mean $\pm$ SD, n = 9) and males 4.4 ± 1.1 sessions (n = 7). Birds required almost four times more sessions to learn the visual discrimination task (different shapes) than the spatial discrimination task (different sides). Both acquisition and reversal were completed faster in the spatial than in the visual task (GLMM, $z = -6.93$, $p < 0.01$, Fig. 1a,b). In the visual task, the number of sessions to criterion during acquisition did not differ significantly between females and males (GLMM post-hoc comparison, $p = 0.36$, Cohen's $d = -0.03$, 95 % CL [−0.06;0]) but during the reversal, females reached criterion faster (GLMM post-hoc comparison, $p < 0.01$, Cohen's $d = -0.07$, 95 % CL [−0.11;−0.03]) (Fig. 1a). In the spatial task there were no differences between sexes in either acquisition or reversal (GLMM, $p > 0.24$ for all post-hoc comparisons, Fig. 1b).

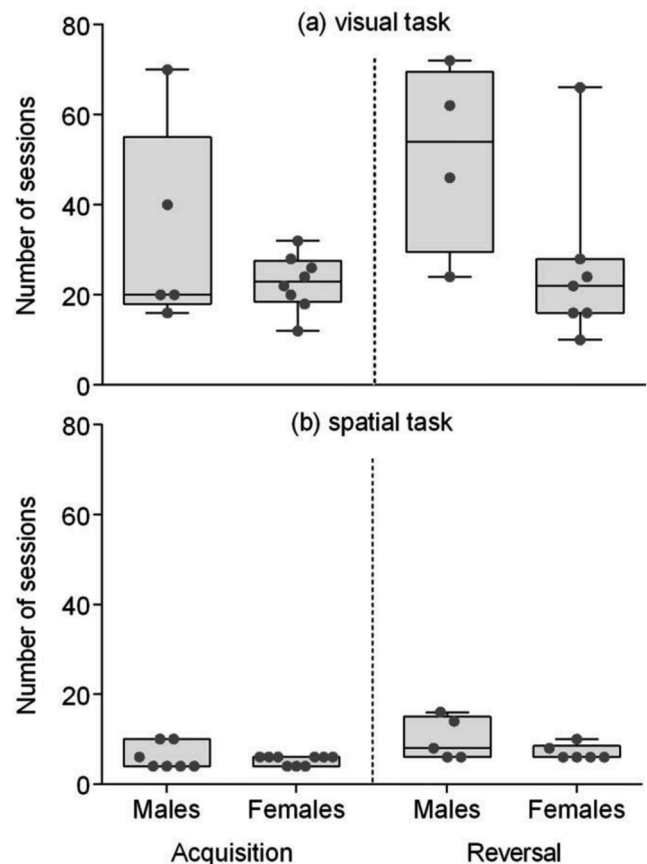We found no general effect of the task order we randomly assigned to

Fig. 1. Discrimination-reversal learning in shiny cowbirds.
Number of sessions to reach the learning criterion during the acquisition and reversal phases by shiny cowbird females and males during: (a) visual task (different shapes) and (b) spatial task (different locations). Boxplots show medians, interquartiles and ranges. Points represent individual data.

individuals (GLMM, $z = -0.11$, $p = 0.91$; Supplementary data Fig. S3).

4. Discussion

We tested whether female and male shiny cowbirds differ in behavioral flexibility using two tasks, each requiring first acquisition of a binary discrimination and then a reversal. In one task (spatial), only responses on one side (left or right) led to reward, regardless of the shape in the stimuli (X or O) while in the other (visual), pecks at one of two shapes (either X or O) were paired with the food reward regardless of location, which varied randomly between trials. Sex differences in flexibility were expected because in this species only females track the location and status of potential host nests (Gloag et al., 2013; Scardamaglia and Reboreda, 2014; Scardamaglia et al., 2017), and this is known to be associated to some learning and neuroanatomical correlates (Reboreda et al., 1996; Lois Milevicich et al., 2021). We found that reaching a performance criterion took longer in the visual than the spatial task for both sexes, and that in the visual (but not in the spatial) task females reversed faster than males. This task-dependent difference in performance corresponds to a sex difference that differs from what

was expected from ecological and neuroanatomical arguments, since the 'book-keeping' behavior typical of females in the field is spatial rather than based on local visual cues. One possible explanation is that ease of acquisition and evidence for sex differences are interrelated: if the task is either too easy or too hard, ceiling or floor effects may mask sex differences. In our case, learning a binary spatial discrimination may have been sufficiently easy for both sexes to conceal differences. This interpretation is consistent with previous evidence showing that acquisition-reversal spatial tasks appear to be intrinsically easier than tasks requiring discrimination of local features such as color or shape of the cues (Bond et al., 2007; Range et al., 2008; Astié et al., 2015). This may be due to how naïve animals experience differential rewarding contingent on their behavior. Typically, naïve animals show some side bias (Diekamp et al., 2005; Versace et al., 2007; Rugani et al., 2015a, b; Fuss and Witte, 2019; Szabo et al., 2019). Thus, in two-choice spatial tasks, naïve subjects might experience either continuous reinforcement or extinction, the former resembling immediate acquisition and the latter forcing the animal to try the alternative. In contrast, in a stimulus shape or color discrimination, a side-biased naïve animal that ignores the programmed contingency receives partial reinforcement whichever side it prefers and can then take longer to attribute differential reinforcement to its own behavior. Another potential reason for false negatives could be the small sample size, a common problem when working with wild-caught animals. As a consequence, our statistical tests have limited power, and differences between groups are difficult to support even when they are true, possibly resulting in false negatives. However, we did find differences in the visual task with the same sample sizes as the spatial task, which suggests that there might be a difference in effect strength, and this could magnify the difficulty caused by ceiling effects.

Within local cues protocols, it appears that discriminations between colors are easier than between shapes (Range et al., 2008; Lucon-Xiccato et al., 2019). This may be on account of stimulus' color being more salient than shape, at least for taxa for which colors have an important role in foraging and reproduction (i.e., fishes: Lucon-Xiccato et al., 2019). Although we did not compare color vs shape, our birds took almost four times as many sessions to learn the shape than the spatial discrimination, which is twice the difference found by Astié et al. (2015) when comparing color vs spatial performance in the same species. This is consistent with the idea that shape discriminations are more difficult to learn than color-based ones.

While it was the ecological behavioral dimorphism in relation to brood parasitism that led us and other authors to seek for sex differences in learning, memory, and, here, in behavioral flexibility, such differences may recognize other adaptive causes. Studies of behavioral flexibility conducted in other, non-parasitic taxa (fishes: Lucon-Xiccato and Bisazza, 2014, 2017; chickens: Rogers, 1974; rats: Guillamón et al., 1986) have shown a more flexible behavior in females, with males showing greater persistence in behavior. These sex differences have not, to our knowledge, been associated to ecological adaptations, but mechanistically, they could be an example of the proposed trade-off between memory retention and cognitive flexibility, which might be explained by an interference in acquiring new memories linked to pre-existing cues or by a competition of old and new memories during the recall processes (for a review see Tello-Ramos et al., 2019).

The fact that females' flexibility exceeded that of males in the visual but not in the spatial task somewhat contradicts expectations, because the extra demands of host nest bookkeeping appear to be spatial rather than visual. However, a revision of the evidence indicates that the association between hippocampal size and spatial memory in cowbirds (reviewed in Guigueno and Sherry, 2017) is not yet solidly established, and that spatial laboratory tasks give variable results. Astié et al. (1998) did not find sex differences in shiny cowbirds that had to learn the position of a well baited with food in a grid of 64 wells, and Astié et al. (2015) failed to find sex differences in acquisition and reversal in a spatial discrimination task similar to the one in this study, but they found that females have better retention performance than males

specially in spatial memory tasks. More recently, Lois-Milevicich et al. (2021) found that females were more faithful to food location than males in a task where individuals learned the location of food with redundant visual and spatial cues and later had the visual cues placed elsewhere. In brown-headed cowbirds, a species which presents behavioral and neuroanatomical sex dimorphism similar to that of shiny cowbirds (Sherry et al., 2003; Guigueno et al., 2016), sex differences in spatial memory also seem to depend on the type of task: females outperformed males in an open field, spatial, delayed matching to sample task in which subjects had to move through space and remember a location for 24 h (Guigueno et al., 2014), but males performed equally or even better than females on a stationary touchscreen delayed matching to sample task in which they had to remember a location on a screen for up to 60 s (Guigueno et al., 2015).

It is, of course, possible that this complicated picture is present because the hypothesized sex differences in cognitive competences are simply not there, or are too weak to yield consistent results in the laboratory, but an alternative is that they do exist but are only evident when the experimental task is in an appropriate range of difficulty (i.e., delayed matching to sample in Guigueno et al., 2014, retention in Astié et al., 2015; dissociation in Lois-Milevicich et al., 2021), so that they are not masked by ceiling or floor effects. This can also be the case for tests of the association between hippocampal size or neurogenesis and spatial memory. Sex differences in spatial memory in species with a sex dimorphism in hippocampal size, like cowbirds, might not be detected in protocols where the spatial scale is reduced and individuals are observed in a small space using only two or a few locations.

In summary, while we did observe an expression of greater behavioral flexibility in female shiny cowbirds, this was, paradoxically, in a shape discrimination rather than in a spatial test. This result, as well as several previous inconsistent observations, may be due to sensitivity of experimental protocols: sex differences may only appear when the difficulty of the task lies in a Goldilocks range where they are not masked by both sexes performing either too well or too poorly. A parametric study of the interaction between test complexity and behavioral sex difference in memory tasks is thus timely.

Author contributions

Lois-Milevicich, J.: Conceptualization; Data curation; Formal analysis; Investigation; Methodology; Resources; Validation; Visualization; Writing - original draft; Writing - review & editing. Cerrutti, M.: Data curation, Software. Kacelnik, A., Reboreda, J.C.: Conceptualization; Funding; Methodology; Resources; Supervision; Writing - review & editing.

Declaration of Competing Interest

The authors report no declarations of interest.

Appendix A. Supplementary data

Supplementary material related to this article can be found, in the online version, at doi:https://doi.org/10.1016/j.beproc.2021.104438.

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