ORIGINAL PAPER

Sex differences in the use of spatial cues in two avian brood parasites

Jimena Lois-Milevicich[1] · **Alex Kacelnik**[2] · **Juan Carlos Reboreda**[1]

Abstract

Shiny and screaming cowbirds are avian interspecific brood parasites that locate and prospect host nests in daylight and return from one to several days later to lay an egg during the pre-dawn twilight. Thus, during nest location and prospecting, both location information and visual features are available, but the latter become less salient in the low-light conditions when the nests are visited for laying. This raises the question of how these different sources of information interact, and whether this reflects different behavioural specializations across sexes. Differences are expected, because in shiny cowbirds, females act alone, but in screaming cowbirds, both sexes make exploratory and laying nest visits together. We trained females and males of shiny and screaming cowbird to locate a food source signalled by both colour and position (cues associated), and evaluated performance after displacing the colour cue to make it misleading (cues dissociated). There were no sex or species differences in acquisition performance while the cues were associated. When the colour cue was relocated, individuals of both sexes and species located the food source making fewer visits to non-baited wells than expected by chance, indicating that they all retained the position as an informative cue. In this phase, however, shiny cowbird females, but not screaming, outperformed conspecific males, visiting fewer non-baited wells before finding the food location and making straighter paths in the search. These results are consistent with a greater reliance on spatial memory, as expected from the shiny cowbird female's specialization on nest location behaviour.

Keywords Brood parasitism · Cognition · *Molothrus bonariensis* · *Molothrus rufoaxillaris* · Spatial memory · Spatial orientation

Introduction

Interspecific avian brood parasites such as cuckoos and cowbirds lay eggs in nests of other species, the hosts, which then provide care for the parasite's eggs and chicks (Spottiswoode et al. 2012). Unlike birds that build their own nest and therefore only need to know its location, brood parasites must first locate nests of potential hosts and then return to parasitize them at the right time. During the breeding season, individual cowbirds search for host nests within relatively constant areas (Hahn et al. 1999; Scardamaglia and Reboreda 2014). After locating a nest, they visit it repeatedly to monitor its

progress and return to parasitize it during the laying period of the host (Scardamaglia et al. 2017). Parasitism (egg laying) occurs before sunrise (Peer and Sealy 1999; Gloag et al. 2013; Scardamaglia et al. 2017, 2018), with cowbirds flying directly from the roost where they spent the night to the nest they are going to parasitize (Scardamaglia et al. 2018). During the rest of the day, they prospect previously located nests and search for new ones that they may parasitize the following days (Rothstein et al. 1986; De Mársico and Reboreda 2008; Gloag et al. 2013; Scardamaglia et al. 2017).

This parasitic behaviour makes special demands on information processing, which have been labelled 'book-keeping' (Clayton et al. 1997), as cowbirds must remember and update the location and stage of multiple nests as they progress in the breeding cycle (i.e., construction, laying, early or late incubation). Therefore, when the parasitic female is ready for laying an egg, she faces choices among an inventory of multiple potential host nests, each at a different stage, and must select the most appropriate nest, flying directly to it in the low-visibility, pre-dawn conditions. The navigation

✉ Jimena Lois-Milevicich
jime.loism@bg.fcen.uba.ar

1 Departamento de Ecología, Genética y Evolución & IEGEBA - CONICET, Facultad de Ciencias Exactas y Naturales, Universidad de Buenos Aires, Ciudad Autónoma de Buenos Aires, Argentina

2 Department of Zoology, University of Oxford, Oxford, UK

cannot be guided by visual local cues respect to the target nest because they are not in sight when the parasite leaves its roosting site. The demand for memory of the precise location and nesting stage of multiple host nests correlates with an enlargement of the hippocampus [i.e., a dorsomedial forebrain structure which plays an important role in memory and spatial orientation (Sherry and MacDougall-Shackleton 2015)] when this demand is present, namely in the sex (or sexes) that locates and prospects host nests: females in the brown-headed (*Molothrus ater*) and shiny (*M. bonariensis*) cowbirds, and females and males in screaming cowbirds (*M. rufoaxillaris*), but only in the reproductive season (Sherry et al. 1993; Reboreda et al. 1996; Clayton et al. 1997; Nair-Roberts et al. 2006; Guigueno et al. 2016). Moreover, adult hippocampal neurogenesis is greater in female than in male brown-headed cowbirds, but no sex differences are found in a non-parasitic related species (Guigueno et al. 2016), supporting the hypothesis of hippocampal specialization in brood parasitic cowbirds (Guigueno and Sherry 2017; Sherry and Guigueno 2019).

Previous studies that examined the association between the enlargement of the female hippocampus in cowbirds and a better performance of females in solving tasks that demand the use of spatial memory have shown somewhat conflicting results (reviewed in Guigueno and Sherry 2017). Shiny cowbirds showed no sex differences in the ability to solve a task in which they had to learn to find a well baited with food whose location remained constant between trials, but opposite to the expectation, females learnt to recover food faster than males when the bait was signalled by a colour cue but not by its position (Astié et al. 1998). Similarly, Astié et al. (2015) did not find sex differences during acquisition and reversal discrimination learning task using either colour or location cues. In the latter study, retention after switching to extinction was higher in females than males, which is consistent with female shiny cowbirds having better long-term memory than males for both colour and position cues (Astié et al. 2015). In brown-headed cowbirds, sex differences in spatial memory seem to depend on the type of task, with females performing better than males on 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 performing equal to 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).

As mentioned above, cowbirds locate and prospect host nests in daylight and return to parasitize them up to several days later under poor visibility at the pre-dawn twilight. Thus, during nest searching and prospecting, spatial cues (i.e., information from free-standing visual landmarks other than the target) and visual cues (i.e., characteristics associated with the target, such as its colour or shape) are available, but visual cues become less salient during parasitic visits before sunrise and cannot help in the longer distance navigation from the roost to the target nest's location. This poses the question of how these different sources of sensory information interact and whether there are sex differences in the reliance to different kinds of visual information.

In this work, we studied sex differences in the use of spatial and local visual cues in shiny and screaming cowbirds. We trained females and males of both species to locate a food source with both spatial and colour cues being present and evaluated their performance after displacing the colour cue but not the location of the food. Sex differences were expected in shiny cowbirds, because in this species females search, prospect and parasitize host nests alone and have a seasonally larger relative hippocampus than males. Any sex difference, if present, should be weaker in screaming cowbirds, because in this species, both sexes search, prospect and parasitize host nests together, and no differences in hippocampus size have been reported.
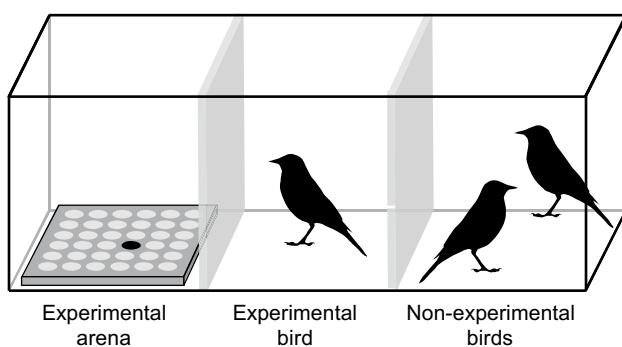
Materials and methods

Subjects

The subjects were six females and four males of screaming cowbird, *Molothrus rufoaxillaris*, and six females and seven males of shiny cowbird, *M. bonariensis*. Screaming cowbirds were captured using mist nets and walk-in traps at Magdalena county, Buenos Aires Province, Argentina (35° 80′ 80″ S, 57° 82′ 30″ W), and Ciudad Universitaria, Buenos Aires city, Argentina (34° 32′ 33″ S 58° 26′ 25″ W), during January 2017, while shiny cowbirds were captured at Ciudad Universitaria, Buenos Aires city, Argentina during August–October 2017. After capture, they were housed in wire cages of $120 \times 40 \times 40$ cm (length × width × height) in groups of up to three birds per cage. Cages were visually but not acoustically isolated. Birds were kept under natural light cycle at room temperature (range 18–30 °C) and fed with an enriched-vitamin seed mix for canary birds containing canary grass (*Phalaris canariensis*), flax (*Linum usitatissimum*), and rapeseed (*Brassica napus*) seeds. They also were fed with *Tenebrio molitor* larvae and pupae (three times per week, five insects per bird). Birds were maintained in captivity at least 15 days before the start of training (shiny cowbirds: 87–97 days, screaming cowbirds: 15–27 days). During the experiments, food was removed from the cages from 05:00–06:00 PM until the start of each session at 08:00–09:00 AM the following morning. After each experimental session (they ended at 11:30 AM–12:00 PM), they had access to food ad libitum. The weight of the birds remained stable over the course of the experiment.

Experiments were conducted during the breeding season of South American cowbirds, in December 2017 (shiny cowbirds) and February–March 2017 (screaming cowbirds). After we completed the experiments, the birds were released.

Experimental arena and procedures

The experimental arena was a wooden board of $40 \times 40 \times 2$ cm (length × width × height) with 36 wells of 1 cm in diameter and 0.5 cm in depth distributed regularly in a 6×6 array. A sliding wooden disk (2 cm in diameter and 0.2 cm of thickness) covered each well. The experiments were conducted in their home cage. Each daily session consisted of two trials of 5 min each with an inter-trial interval of 8 min. Before the start of the session, the cage was divided into three parts of $40 \times 40 \times 40$ cm. One of the lateral parts was used to test the bird, the middle part to keep the bird being tested before the first trial and during the inter-trial interval, and the other lateral to keep the remaining cage mates (Fig. 1). Testing order was randomized within and between cages. We video-recorded each session using a microcamera placed above the experimental arena and connected to a PVR recorder (PV-500 ECO, LawMate Int., TW).

Birds were trained to retrieve food (millet seeds) from the experimental arena following the training scheme shown in Table 1. If they failed to retrieve food in one session, we repeated the same training scheme in the following session, and if they failed in two consecutive sessions, we went back to the previous stage of the training scheme. During the training phase, all disks covering the wells were the same colour (light brown). After the birds completed the training, we started the following phase in which only one well was baited, always in the same position for each bird, and identified both by its position and

Table 1 Scheme used for training shiny and screaming cowbirds to retrieve food from the experimental arena

Session	Wells with food	Seeds per well	Uncovered wells	Semi-covered wells	Covered wells
1	16	2	36	0	0
2	16	2	18	18	0
3	16	2	0	18	18
4	16	2	0	0	36
5	8	5	0	0	36
6	4	10	0	0	36
7	2	20	0	0	36
8	1	40	0	0	36

by a covering disk of a different colour (red). The position of the baited well was randomized across subjects. Therefore, in this phase, birds could learn to locate food using redundant location and colour cues (cues associated). The criterion to finish this phase was that the bird retrieved the food in three consecutive trials with three or fewer visits to non-baited wells. After completing this phase, the spatial and colour cues were dissociated (the food remained in the same location, but the red disk varied its location randomly).

Data analysis

For each trial, we recorded the latency until the bird retrieved the food and the number of visits to non-baited wells before finding the food. We considered it a visit if the bird opened the well or attempted to move the covering disk even if it was a well that the bird had previously touched. Therefore, in some trials, the number of visited wells exceeded the number of wells in the experimental arena (36). For the phase with cues associated, we computed the number of sessions until the birds reached our learning criterion. For the first trial after the colour and spatial cues were dissociated, we analysed the number of non-baited wells visited and the latency to find the well with food. For this trial, we also calculated the straightness index of the path to reach the well with food. This index was estimated as the length of a straight line between the first well visited and the well with food, divided by the observed minimal path length, defined as the sum of the linear distances between each consecutive pair of wells visited (Benhamou 2004). This index helps to understand better how animals move along the arena and if the opened wells were close to (shorter path) or far away from (longer path) the well with food. This estimate ranges from near 0 (long and tortuous path) to 1 (the straightest path). If the bird went directly to the baited well, the index was assigned a value of 1.

Fig. 1 Schematic representation of the cage where the birds were kept, and the experiments conducted. One of the laterals was used to test the bird in the experimental arena (wood board with 36 wells). In the middle part, we kept the bird that was tested before the start of the session and during the inter-trial interval, while other birds remained in the other lateral

Statistical analyses

We analysed each species independently since they were tested at different times. We examined differences in the number of sessions to reach the learning criterion when location and colour cues were associated using general linear models (GLM) with negative binomial distribution (log link function). Similarly, we used GLM with negative binomial distribution to analyse differences in the number of non-baited wells visited until reaching the well with food during the first trial after the cues were dissociated. We also examined differences in the latency and the straightness index to reach the well with food using GLM, with gamma distribution (inverse link function) to model latencies and beta distribution (logit link function) to model indexes. Sex was included in all the previous models as a fixed factor. We performed GLM using R package glmmTMB (Brooks et al. 2017). 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). To evaluate if after cues were dissociated birds found the well with food visiting fewer non-baited wells that expected by chance, we generated 1000 samples with replacement from the set of numbers of non-baited wells visited for each species in this trial. The sample sizes were the same as the number of individuals tested in each group. We pooled data from both sexes for this test. We calculated the mean of each bootstrapped sample and generated a distribution for those mean values. We calculated the 95% confidence interval (CI95) of the real sample mean as a 0.025–0.975 quantile interval of the bootstrapped distribution. Finally, we checked if the expected value of a negative hypergeometric distribution with the same parameters as our experiment ($E(X) = \mu = 18.5$) was included in the calculated CI95s. This distribution assumes performance by chance and if the calculated CI95s include the value 18.5, then we cannot exclude the possibility that birds found the baited well by chance. This distribution describes a search without replacement, but birds usually revisited some wells multiple times. In this case, the expected value of the distribution would be 36. We performed all statistical analyses using R 3.6.3 (R Core Team 2020).

Results

All the birds learnt to find the food when the spatial and colour cues were associated. The number of sessions to criterion ranged between 2 and 11 (shiny cowbirds) and 3 and 7 (screaming cowbirds), with no significant sex differences in either species (GLM, shiny cowbirds: $p = 0.944$; screaming cowbirds: $p = 0.082$) (Fig. 2).

During the first trial after the cues were dissociated, shiny cowbird females visited fewer non-baited wells than males to find the well with food (GLM, $p = 0.03$), but there were no sex differences in screaming cowbirds (GLM, $p = 0.78$) (Fig. 3a). Shiny cowbird females also followed straighter paths than conspecific males to find the well with food (GLM, $p = 0.04$) but these sex differences were not found in screaming cowbirds (GLM, $p = 0.48$) (Fig. 3b). There were no sex differences in the latencies to find the baited well (GLM, shiny cowbirds: $p = 0.831$; screaming cowbirds: $p = 0.189$). For both species, the number of non-baited wells visited before finding the well with food was lower than expected by chance (Bootstrapped CI95, shiny cowbirds: 3.36–8.46; screaming cowbirds: 3.78–15.78).

As regards the cue preference of birds during the dissociation trial, we did not find a clear tendency as some birds touched the colour cue before the spatial cue (shiny cowbirds: females 4/5, males 4/6; screaming cowbirds: females 4/6, males 3/4) while the others went directly to the spatial cue.

Discussion

We found no sex or species differences in learning to locate well with food when it was signalled by colour and position cues. When the colour cue was displaced to a misleading well, birds of both species visited fewer non-baited wells than expected by chance, indicating that they remembered the location of the well with food. In this phase, shiny but not screaming cowbird females outperformed conspecific males, by visiting fewer non-baited wells and making straighter paths to the baited well. Our results show a better spatial performance by shiny cowbird females than conspecific males, as expected from their specialization on nest location behaviour. Our result is consistent with previous results by Guigueno et al. (2014) showing that in brown-headed cowbirds, a species with a similar sex-specific parasitic behaviour than shiny cowbirds, females outperformed males in a spatial memory task. It is important to note that our hypothesis and interpretation, as well as that of Guigueno et al. (2014), assume that food location tasks recruit similar cognitive mechanism as that used for remembering the location of host nests. This assumption is supported by a study of Davies and White (2018) that shows consistency in performance in brown-headed cowbirds females across nest-prospecting and foraging tasks.

Avian brood parasites show highly specialised nest searching behaviour. In cowbirds, this behaviour involves identifying suitable host nests as potential targets for parasitism under daylight and returning to lay their eggs one or several days later in the pre-dawn twilight, flying directly to it in the low visibility, pre-dawn conditions (Peer and Sealy
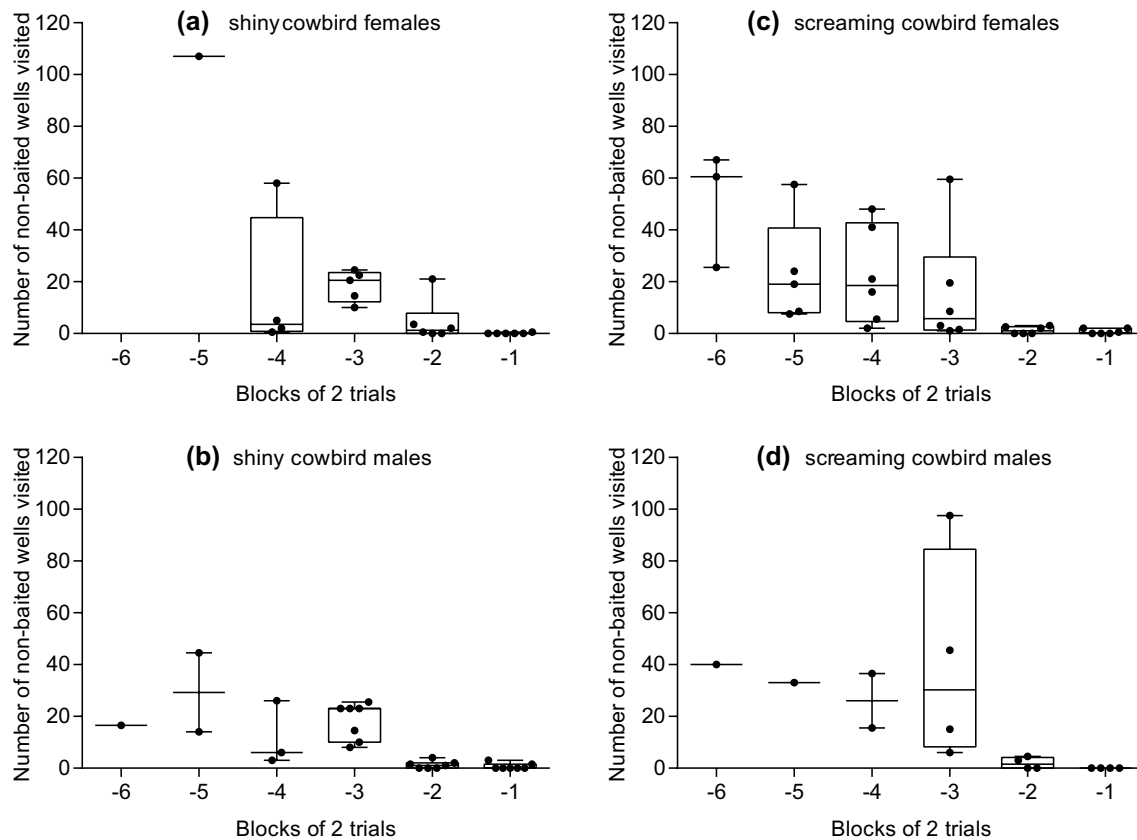
Fig. 2 Number of non-baited wells visited before finding the baited well. Left: shiny cowbird females (**a**) and males (**b**); right: screaming cowbirds females (**c**), and males (**d**) during learning to find a well with food. The position of the well did not change between trials and was indicated by a colour cue. Each point represents an individual's mean across two consecutive trials. The x-axis indicates blocks preceding the trial when spatial and colour cues were dissociated (day 0). For comparative purposes, data from days − 11 to − 7 are not shown. Boxplots show medians, interquartiles and ranges

1999; Gloag et al. 2013; Scardamaglia et al. 2017, 2018). Also, at the time of parasitism, cowbirds must decide among multiple potential host nests at different stages of the nesting cycle and select the most appropriate one to parasitize it. To accomplish this, female cowbirds prospect host nests and track information of nest progress, which allows them to time parasitism with host laying (Scardamaglia et al. 2017; White 2019). In addition, female cowbirds that lack information about nest availability can eavesdrop on nest selection decisions of other females (Gloag et al. 2013; White et al. 2017).

Since cowbird parasitism occurs during pre-dawn, under very low visibility conditions, flying from the roosting site to the host nest must be guided by memory, rather than by direct sensory detection of the target nest. Although colour visual cues may serve to identify a host nest while prospecting in daytime, they cannot be used as beacons to reach target nests at laying time. The most plausible scenario is that upon discovery of a suitable target, the prospecting bird places its finding in a pre-existent cognitively represented map (O'Keefe and Nadel 1978) of its home range, ready for

later use, and at laying time widely distributed landmarks allow the subject to navigate towards the position of its target using spatial memory. This contrasts with locating a target using visual sensory stimuli as navigational beacons (Gray et al. 2005; Pearce et al. 2006; Kelly 2010; Feenders and Smulders 2011; Hornsby et al. 2014; Hurly et al. 2014; Pritchard et al. 2015; see Gould et al. 2010, for a review).

Sex differences in the use of spatial cues have been extensively studied in mammals (i.e., Gaulin and FitzGerald 1986, 1989; Gaulin et al. 1990; Galea et al. 1996; Bettis and Jacobs 2013; see Coluccia and Louse 2004, for a review). As regards birds, several studies investigated the preferences for the use of spatial or visual cues in species with high spatial memory demands, like food-storing or nectar-feeding birds, and found that these species prefer to use spatial over colour cues (Brodbeck 1994; Clayton and Krebs 1994; Brodbeck and Shettleworth 1995; Hurly and Healy 1996, 2002; but see Fenders and Smulders 2011). In contrast, species which do not have high spatial memory demands do not show a clear pattern in the use of both cue types (Brodbeck 1994; Clayton and Krebs 1994; Mayer and Bischof 2012).
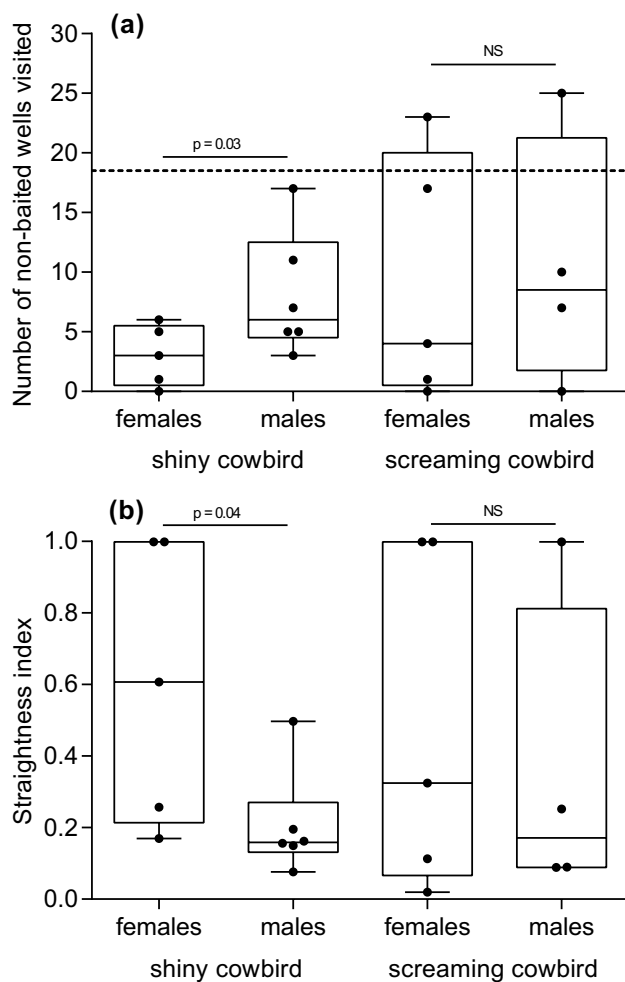
Fig. 3 Number of non-baited wells visited before finding the baited well (**a**) and straightness index (**b**) during the first trial after displacement of the colour cue. Dots indicate individual values. The grey line in the upper graph indicates the number of errors expected by chance (i.e., 18.5). Boxplots show medians, interquartiles and ranges

Sex differences in the preference for the use of spatial or colour cues within bird species have been less investigated (i.e., Vallortigara 1996; Hodgson and Healy 2005). Vallortigara (1996) did not find sex differences in chicks (*Gallus gallus domesticus*) in a learning task when colour and position cues were associated, but when cues were dissociated, females performed better in the colour-learning task and males performed better in the spatial-learning task. In contrast, Hodgson and Healy (2005) find that females and males of great tit (*Parus major*) that learnt to find food with colour and position cues associated preferred to follow the spatial cue when they were dissociated and did not show sex differences in cue use.

Our results show that the use of spatial and colour cues by shiny and screaming cowbirds is flexible, as some individuals inspected the well associated with the colour cue

first, and then searched using the location cue, while others went directly to the well with food using location and dismissing the displaced colour cue. Similarly, LaDage et al. (2009) found that food caching mountain chickadees (*Poecile gambeli*) that had learnt to find food in a feeder with spatial and colour cues associated, when colour was dissociated from the spatial location, inspected feeders associated with the correct colour first and then visited the correct spatial locations. These results along with other studies (Healy 1995; Healy and Krebs 1992a, 1992b; Hodgson and Healy 2005; Morandi-Raikova et al. 2020) are not consistent with the view (Brodbeck 1994; Clayton and Krebs 1994; Brodbeck and Shettleworth 1995; Hurly and Healy 1996, 2002) that in species with high spatial memory demands, like food-storing birds or brood parasites, memory of spatial cues always takes priority over non-spatial cues.

To summarize, our results in shiny and screaming cowbirds are consistent with an association between sex-specific adaptations in cognition and neuroanatomy and sex- and species-specific ecological demands, such as remembering the precise location of multiple host nests in brood parasites (Clayton et al. 1997; Sherry 2006; Guigueno and Sherry 2017; Sherry and Guigueno 2019). We showed that shiny and screaming cowbirds can relocate a food source that was learnt using both colour and spatial information using only the latter. Moreover, females performed better than males in shiny cowbird, a species in which females use more spatial information as they search, prospect and parasitize host nests alone and have a larger hippocampus than conspecific males, while no sex difference was observed in screaming cowbirds, a species in which both sexes search, prospect and parasitize host nests together and they do not differ in hippocampus size.

Compliance with ethical standards

References

Astié AA, Kacelnik A, Reboreda JC (1998) Sexual differences in memory in shiny cowbirds. Anim Cogn 1:77–82. https://doi.org/10.1007/s100710050011

Astié AA, Scardamaglia RC, Muzio RN, Reboreda JC (2015) Sex differences in retention after a visual or a spatial discrimination learning task in brood parasitic shiny cowbirds. Behav Process 119:99–104. https://doi.org/10.1016/j.beproc.2015.07.016

Benhamou S (2004) How to reliably estimate the tortuosity of an animal's path: straightness, sinuosity, or fractal dimension? J Theor Biol 229:209–220. https://doi.org/10.1016/j.jtbi.2004.03.016

Bettis TJ, Jacobs LF (2013) Sex differences in memory for landmark arrays in C57BL/J6 mice. Anim Cogn 16:873–882. https://doi.org/10.1007/s10071-013-0619-x

Brodbeck DR (1994) Memory for spatial and local cues: a comparison of a storing and a nonstoring species. Anim Learn Behav 22:119–133. https://doi.org/10.3758/BF03199912

Brodbeck DR, Shettleworth SJ (1995) Matching location and color of a compound stimulus: comparison of a food-storing and a nonstoring bird species. J Exp Psychol Anim Behav Process 21:64–77. https://doi.org/10.1037/0097-7403.21.1.64

Brooks ME, Kristensen K, van Benthem KJ, Magnusson A, Berg CW, Nielsen A, Skaug HJ, Maechler M, Bolker BM (2017) glmmTMB balances speed and flexibility among packages for zero-inflated generalized linear mixed modeling. R J 9:378–400. https://journal.r-project.org/archive/2017/RJ-2017-066/index.html

Clayton NS, Krebs JR (1994) Memory for spatial and object-specific cues in food-storing and non-storing birds. J Comp Physiol A 174:371–379. https://doi.org/10.1007/BF00240218

Clayton NS, Kacelnik A, Reboreda JC (1997) Seasonal changes in hippocampus size in parasitic cowbirds. Behav Process 41:237–243. https://doi.org/10.1016/S0376-6357(97)00050-8

Coluccia E, Louse G (2004) Gender differences in spatial orientation: a review. J Environ Psychol 24:329–340. https://doi.org/10.1016/j.jenvp.2004.08.006

Davies HB, White DJ (2018) Specializations in cognition generalize across contexts: cowbirds are consistent in nest prospecting and foraging tasks. Anim Behav 144:1–7. https://doi.org/10.1016/j.anbehav.2018.07.019

De Mársico MC, Reboreda JC (2008) Egg-laying behaviour in screaming cowbirds. Why does a specialist brood parasite waste so many eggs? Condor 110:143–153. https://doi.org/10.1525/cond.2008.110.1.143

Feenders G, Smulders TV (2011) Magpies can use local cues to retrieve their food caches. Anim Cogn 14:235–243. https://doi.org/10.1007/s10071-010-0357-2

Galea LAM, Kavaliers M, Ossenkopp KP (1996) Sexually dimorphic spatial learning in meadow voles *Microtus pennsylvanicus* and deer mice *Peromyscus maniculatus*. J Exp Biol 199:195–200

Gaulin SJC, FitzGerald RW (1986) Sex differences in spatial ability: an evolutionary hypothesis and test. Am Nat 127:74–88. https://doi.org/10.1086/284468

Gaulin SJC, FitzGerald RW (1989) Sexual selection for spatial-learning ability. Anim Behav 37:322–331. https://doi.org/10.1016/0003-3472(89)90121-8

Gaulin SJC, FitzGerald RW, Wartell MS (1990) Sex differences in spatial ability and activity in two vole species (*Microtus ochrogaster* and *M. pennsylvanicus*). J Comp Psychol 104:88–93. https://doi.org/10.1037/0735-7036.104.1.88

Gloag R, Fiorini VD, Reboreda JC, Kacelnik A (2013) The wages of violence: mobbing by mockingbirds as a frontline defence against brood-parasitic cowbirds. Anim Behav 86:1023–1029. https://doi.org/10.1016/j.anbehav.2013.09.007

Gould KL, Kelly DM, Kamil AC (2010) What scatter-hoarding animals have taught us about small-scale navigation. Phil Trans R Soc B 365:901–914. https://doi.org/10.1098/rstb.2009.0214

Gray ER, Bloomfield LL, Ferrey A, Spetch ML, Sturdy CB (2005) Spatial encoding in mountain chickadees: features overshadow geometry. Biol Lett 1:314–317. https://doi.org/10.1098/rsbl.2005.0347

Guigueno MF, Sherry DF (2017) Hippocampus and spatial memory in brood parasitic cowbirds. In: Soler M (ed) Avian brood parasitism. Springer, Cham, pp 203–218. https://doi.org/10.1007/978-3-319-73138-4_11

Guigueno MF, Snow DA, MacDougall-Shackleton SA, Sherry DF (2014) Female cowbirds have more accurate spatial memory than males. Biol Lett 10:20140026. https://doi.org/10.1098/rsbl.2014.0026

Guigueno MF, MacDougall-Shackleton SA, Sherry DF (2015) Sex differences in spatial memory in brown-headed cowbirds: males outperform females on a touchscreen task. PLoS ONE 10(6):e0128302. https://doi.org/10.1371/journal.pone.0128302

Guigueno MF, MacDougall-Shackleton SA, Sherry DF (2016) Sex and seasonal differences in hippocampal volume and neurogenesis in brood-parasitic brown-headed cowbirds (*Molothrus ater*). Dev Neurobiol 76:1275–1290. https://doi.org/10.1002/dneu.22421

Hahn D, Sedgwick J, Painter I, Casna N (1999) A spatial and genetic analysis of cowbird host selection. Stud Avian Biol 18:204–217

Hartig F (2020) DHARMa: residual diagnostics for hierarchical (multilevel/mixed) regression models. v. 0.3.1. https://florianhartig.github.io/DHARMa

Healy SE (1995) Memory for objects and positions: delayed non-matching-to-sample in storing and non-storing tits. Q J Exp Psychol B 48:179–191. https://doi.org/10.1080/14640749508401446

Healy SD, Krebs JR (1992a) Comparing spatial memory in two species of tit: recalling a single positive location. Anim Learn Behav 20:121–126. https://doi.org/10.3758/BF03200409

Healy SD, Krebs JR (1992b) Delayed-Matching-to-Sample by marsh tits and great tits. Q J Exp Psychol B 45:33–47. https://doi.org/10.1080/14640749208401023

Hodgson ZG, Healy SD (2005) Preference for spatial cues in a non-storing songbird species. Anim Cogn 8:211–214. https://doi.org/10.1007/s10071-004-0249-4

Hornsby MAW, Hurly TA, Hamilton CE, Pritchard DJ, Healy DE (2014) Wild, free-living rufous hummingbirds do not use geometric cues in a spatial task. Behav Process 108:138–141. https://doi.org/10.1016/j.beproc.2014.10.003

Hurly TA, Healy SD (1996) Memory for flowers in rufous hummingbirds: location or local visual cues? Anim Behav 51:1149–1157. https://doi.org/10.1006/anbe.1996.0116

Hurly TA, Healy SD (2002) Cue learning by rufous hummingbirds (*Selasphorus rufus*). J Exp Psychol Anim Behav Process 28:209–223. https://doi.org/10.1037//0097-7403.28.2.209

Hurly TA, Fox TAO, Zwueste DM, Healy SD (2014) Wild hummingbirds rely on landmarks not geometry when learning an array of flowers. Anim Cogn 17:1157–1165. https://doi.org/10.1007/s10071-014-0748-x

Kelly DM (2010) Features enhance the encoding of geometry. Anim Cogn 13:453–462. https://doi.org/10.1007/s10071-009-0296-y

LaDage LD, Roth TC II, Fox RA, Pravosudov VV (2009) Flexible cue use in food-caching birds. Anim Cogn 12:419–426. https://doi.org/10.1007/s10071-008-0201-0

Mayer U, Bischof HJ (2012) Brain activation pattern depends on the strategy chosen by zebra finches to solve an orientation task. J Exp Biol 215:426–434. https://doi.org/10.1242/jeb.063941

Morandi-Raikova A, Vallortigara G, Mayer U (2020) The use of spatial and local cues for orientation in domestic chicks (*Gallus gallus*). Anim Cogn 23:367–387. https://doi.org/10.1007/s10071-019-01342-6

Nair-Roberts RG, Erichsen JT, Reboreda JC, Kacelnik A (2006) Distribution of substance P reveals a novel subdivision in the hippocampus of parasitic South American cowbirds. J Comp Neurol 496:610–626. https://doi.org/10.1002/cne.20915

O'Keefe J, Nadel L (1978) The hippocampus as a cognitive map. Oxford University Press, Oxford

Pearce JM, Graham M, Good MA, Jones PM, McGregor A (2006) Potentiation, overshadowing, and blocking of spatial learning based on the shape of the environment. J Exp Psychol Anim Behav Process 32:201–214. https://doi.org/10.1037/0097-7403.32.3.201

Peer BD, Sealy SG (1999) Laying time of the bronzed cowbird. Wilson Bull 111:137–139

Pritchard DJ, Hurly TA, Healy SD (2015) Effects of landmark distance and stability on accuracy of reward relocation. Anim Cogn 18:1285–1297. https://doi.org/10.1007/s10071-015-0896-7

R Core Team (2020) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna. https://www.R-project.org

Reboreda JC, Clayton N, Kacelnik A (1996) Species and sex differences in hippocampus size in parasitic and non-parasitic cowbirds. NeuroReport 7:505–508. https://doi.org/10.1097/00001756-199601310-00031

Rothstein SI, Yokel DA, Fleischer RC (1986) Social dominance, mating and spacing systems, female fecundity, and vocal dialects in captive and free-ranging brown-headed cowbirds. In: Johnston RF (ed) Current ornithology. Plenum, New York, pp 127–185. https://doi.org/10.1007/978-1-4615-6784-4_3

Scardamaglia RC, Reboreda JC (2014) Ranging behavior of female and male shiny and screaming cowbirds while searching for host nests. Auk 131:610–618. https://doi.org/10.1642/AUK-14-54.1

Scardamaglia RC, Fiorini VD, Kacelnik A, Reboreda JC (2017) Planning host exploitation through prospecting visits by parasitic cowbirds. Behav Ecol Sociobiol 71:23. https://doi.org/10.1007/s00265-016-2250-8

Scardamaglia RC, Kacelnik A, Reboreda JC (2018) Temporal and spatial patterns of roosting behavior by brood parasitic cowbirds. Ibis 160:779–789. https://doi.org/10.1111/ibi.12587

Sherry DF (2006) Neuroecology. Annu Rev Psychol 57:167–197. https://doi.org/10.1146/annurev.psych.56.091103.070324

Sherry DF, Guigueno MF (2019) Cognition and the brain of brood parasitic cowbirds. Integ Zool 14:145–157. https://doi.org/10.1111/1749-4877.12312

Sherry DF, MacDougall-Shackleton SA (2015) Seasonal change in the avian hippocampus. Front Neuroendocrinol 37:158–167. https://doi.org/10.1016/j.yfrne.2014.11.008

Sherry DF, Forbes MR, Khurgel M, Ivy GO (1993) Females have a larger hippocampus than males in the brood-parasitic brown-headed cowbird. Proc Natl Acad Sci USA 90:7839–7843. https://doi.org/10.1073/pnas.90.16.7839

Spottiswoode CN, Kilner RM, Davies NB (2012) Brood parasitism. In: Royle NJ, Smiseth PT, Kölliker M (eds) The evolution of parental care. Oxford University Press, Oxford, pp 226–243

Vallortigara G (1996) Learning of colour and position cues in domestic chicks: males are better at position, females at colour. Behav Process 36:289–296. https://doi.org/10.1016/0376-6357(95)00063-1

White DJ (2019) Cowbird cognition: examinations of the mental skills of a brood parasite. Adv Stud Behav 51:143–175. https://doi.org/10.1016/bs.asb.2018.12.002

White DJ, Davies HB, Agyapong S, Seegmiller N (2017) Nest prospecting brown-headed cowbirds 'parasitize' social information when the value of personal information is lacking. Proc R Soc B 284:20171083. https://doi.org/10.1098/rspb.2017.1083