Lack of response to conspecific juvenile vocalizations in two avian brood parasites

Rocío Prieto, M. Cecilia De Mársico, Juan C. Reboreda, Romina C. Scardamaglia*

Departamento de Ecología, Genética y Evolución and IEGEBA-UBA-CONICET, Facultad de Ciencias Exactas y Naturales, Universidad de Buenos Aires, Pabellón II Ciudad Universitaria, C1428EGA Buenos Aires, Argentina

*Address correspondence to Romina C. Scardamaglia. E-mail: rscardamaglia@ege.fcen.uba.ar

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Abstract

Juveniles of interspecific avian brood parasites need to locate and recognize conspecifics to continue their life cycle after being reared by individuals of another species. However, little is known about the recognition mechanisms and cues involved in this critical stage of their lives. It has been proposed that adult parasites could show some kind of parental behavior by actively searching and interacting with conspecific young, which in turn could serve the juveniles to learn and/or reinforce the learning of conspecific characteristics. Since acoustic communication is one of the main channels used by birds, if such form of parental behavior by adult avian brood parasites does exist, adult cowbirds should recognize and respond positively to vocalizations of conspecific juveniles. We experimentally tested whether adult shiny Molothrus bonariensis and screaming M. rufoaxillaris cowbirds respond positively towards acoustic signals of conspecific juveniles using two playback experiments, one conducted in semi-captivity and the other in the field. In both cases, we presented three types of playbacks to adults of both cowbird species: vocalizations of shiny cowbird juveniles, vocalizations of screaming cowbird juveniles, and white noise as a control. In the experiment in semi-captivity, no significant differences were found between treatments. In the field experiment, no conspecifics approached the playback area, but hosts of the species whose playback was played were attracted to the loudspeaker. In conclusion, our results do not support the predictions we tested from the parental behavior hypothesis and indicate that adult shiny and screaming cowbirds do not respond positively to acoustic signals of conspecific juveniles, at least not to the type of signals used in our experiments.

Key words: parental behavior hypothesis, Molothrus, vocal recognition, brood parasitism, fledglings

The juvenile stage represents a critical period in the life of birds during which individuals must develop the flight and feeding abilities that will allow them to survive as adults (Naef-Daenzer & Grüebler 2016). At this stage, young birds also learn the characteristics of their species that are necessary to recognize conspecifics and potential sexual partners in the future (Oetting et al. 1995; Ten Cate & Vos 1999). In most bird species, this learning process occurs at a very young age, usually using their parents or siblings as models (Grant & Grant 1997; Irwin & Price 1999; Slagsvold & Hansen 2001; Grant & Grant 2018; Slagsvold 2019). However, in interspecific avian brood parasites, where females lay their eggs in the nests of other species and avoid all parental care, this learning process would lead to misimprinting on the host species. Obviously, a different process must be at play in brood parasites to avoid imprinting on heterospecifics, but little is known about the mechanisms and cues involved in conspecific recognition in these taxa (but see Hauber et al. 2001 and Crudele et al. 2023 for a possible mechanism in brood parasitic cowbirds). Examining the mechanisms of recognition and association with conspecifics is thus particularly relevant in this group (Göth & Hauber 2004). Despite the importance of early social development for the success of the brood-parasitic strategy, data on interactions of young parasites with conspecifics are lacking for most parasite lineages (i.e., most Cuculidae species, the South American black-headed duck Heteronetta atricapilla or the African honeyguides). The scarce available data comes mainly from studies on the great spotted cuckoo Clamator glandarius and cowbirds (Kennerley et al. 2022). At first, it was suggested that interactions between young parasites and adult conspecifics began in foraging grounds once independence was achieved (Woodward, 1983). However, later studies showed that young parasites can recognize and/or interact with adult conspecifics from earlier stages of development (Crudele et al. 2022; Hauber et al. 2001; Hauber 2002; Soler & Soler 1999). For example, adult great spotted cuckoos may occasionally visit nests of its magpie Pica pica host during the last days of the nestling period and maintain contact with conspecific fledglings later, interacting with them vocally or even occasionally feeding them (Soler & Soler 1999). In cross-fostering experiments of cuckoo chicks to host nests outside the cuckoo's breeding range, where visual or acoustic communication with adult parasites was not possible, young cuckoos learned to recognize conspecifics only when reared alongside another parasite chick in the nest, which would indicate that recognition is not innate but must be learned (Soler & Soler 1999). Interestingly, in another crossfostering experiment in a host population sympatric with the cuckoo but with no records of parasitism, parasitic fledglings aggregated with conspecifics in the presence of an adult cuckoo, suggesting the adult facilitated this recognition (Soler & Soler 1999). Furthermore, a great spotted cuckoo female was recorded interacting with her own fledglings, even though interactions between adults and fledglings would not be limited to related individuals (Soler & Soler 1999). These observations have led to the proposal of the parental behavior hypothesis, which suggests that adult parasites could visit nestlings/fledglings as a parental behavior that allows imprinting to occur.

This hypothesis has also been suggested for the brown-headed cowbird *Molothrus ater*, but the evidence supporting it is indirect (Hahn & Fleischer 1995; Hauber 2002). Early DNA fingerprinting studies revealed that brown-headed cowbird females associate with their own juvenile offspring at feeding sites more often than would be expected by chance (Hahn & Fleischer 1995). Moreover, the probability of detecting female brown-

headed cowbirds near host nests was higher during the early fledgling stage than during the incubation and nestling stages, and higher near parasitized than non-parasitized nests (Hauber 2002). White et al. (2002) found an effect of the presence of conspecific adults on the social behavior of parasitic juveniles in a set of experiments that showed that young brown-headed cowbirds were sensitive and responded to the presence of conspecific adults. The juveniles aggregated more with other juveniles and sang more often when they were in the presence of adults than when housed without adults. Some of the benefits for juvenile cowbirds of joining conspecifics soon after becoming independent can include lowered risk of predation by foraging in groups, facilitation in locating food sources and communal roosts, settlement of dominance hierarchies at an earlier age, and learning of a greater repertoire of vocal and courtship features (Freeberg et al. 1999; Freeberg et al. 1995; Hauber et al. 2001; Hauber et al. 2000; O'Loghlen & Rothstein 1995; Smith et al. 2002; West & King 1988; West et al. 1996; White et al. 2002).

There are two possible non-mutually exclusive mechanisms for conspecific recognition in brood parasites. Recognition and initiation of socialization could be started by adults approaching juveniles and/or by juveniles recognizing and approaching adults. Most studies on conspecific recognition in brood parasites have focused on the second mechanism (i.e., recognition of adults by juvenile parasites) and have involved cowbird juveniles raised or kept in captivity (Crudele et al. 2023; Hauber et al. 2001; King & West 1977; Miller et al. 2006; White et al. 2002), and showed that the cowbird's 'chatter call' might serve as an initial password that unambiguously identifies the chatterer as a conspecific, since cowbird nestlings and fledglings preferentially respond to chatters but not to other conspecific and heterospecific vocalizations. On the other hand, only one previous study (Hauber 2002) has investigated whether there is recognition of juveniles by adults as a possible mechanism to learn conspecific characteristics. Hauber (2002) showed that brown-headed cowbird adults preferentially associate with conspecific juveniles when given a choice between a conspecific or a heterospecific individual. In the present work, we studied recognition of juvenile vocalizations by adults in another two cowbird species where this type of recognition has not been studied yet.

In birds, acoustic signals represent the main communication channel. Birds vocalize to communicate with conspecifics, mainly to attract mates or establish a territory, but avian vocalizations can serve other purposes, such as maintaining group contact or signaling about food or danger (Catchpole & Slater 2008; Gil & Llusia 2020). In cowbirds, recognition of certain stereotypical, species-specific vocalizations is innate in juveniles and adults (Crudele et al. 2022; Hauber et al. 2001; Hauber 2002; King & West 1977), so, if adult cowbirds actively contact juveniles, it is expected that adult parasites respond positively to conspecific juvenile vocalizations.

In this study, we experimentally evaluated whether adults of shiny *M. bonariensis* and screaming *M. rufoaxillaris* cowbirds can recognize conspecific juveniles based on acoustic signals. The shiny cowbird is a generalist brood parasite that lays its eggs in nests of over 250 host species, with at least 102 of them raising them successfully to fledglings (Lowther 2023; Ortega 1998). During the reproductive season, females lay their eggs before sunrise and spend the rest of the day feeding and searching for potential host nests to parasitize (Gloag et al. 2013; Scardamaglia & Reboreda 2014; Scardamaglia et al. 2017). They are socially promiscuous,

and females search for host nests without male assistance (Gloag et al. 2013; Kattan 1997; Scardamaglia & Reboreda 2014; Wiley 1988). On the other hand, the screaming cowbird is one of the most specialized brood parasites, using the grayish baywing *Agelaioides badius* as its primary host throughout most of its distribution (De Mársico et al. 2010). They are socially monogamous, with males and females searching for host nests together (Mason 1987; Scardamaglia et al. 2022; Scardamaglia & Reboreda 2014).

We tested if adult shiny and screaming cowbirds are attracted by acoustic signals from conspecific juveniles through playback experiments. We predicted that adult cowbirds should: 1) spend a higher proportion of time near the loudspeaker when conspecific juvenile calls were broadcast than when heterospecific juvenile calls or a control sound were broadcasted; 2) approach the loudspeaker faster (i.e. shorter latency) when conspecific juvenile calls were broadcasted than when heterospecific juvenile calls or a control sound were broadcasted; and 3) approach the loudspeaker more frequently in response to conspecific juvenile calls than heterospecific juvenile calls or a control sound.

Materials and Methods

Study site

The study was conducted at Reserva El Destino (35°08′S, 57°23′W), near the town of Magdalena, in the province of Buenos Aires, Argentina, from December 2018 to January 2019, during the reproductive season of shiny and screaming cowbirds. At this site, the shiny cowbird uses as its main hosts the chalk-browed mockingbird (*Mimus saturninus*; frequency of parasitism 89%, Gloag et al. 2013) and the house wren (*Troglodytes aedon*; frequency of parasitism 60%, Tuero et al. 2007). Screaming cowbirds parasitize baywing nests with a frequency close to 100% (De Mársico et al. 2010).

Experimental design

The study consisted of playback experiments in semi-captivity and in the field. All experiments were video recorded and later analyzed using BORIS (Behavioral Observation Research Interactive Software) version 7.4.7 (Friard & Gamba, 2016).

Playback sequences

Calls for broadcasts were obtained from audio recordings of hand-reared fledglings (13-20 days after hatching) performed under standardized conditions during a previous study (De Mársico et al. 2012). All recorded vocalizations consisted of begging calls (i.e., calls uttered by juveniles during food solicitation displays). To avoid pseudoreplication, we used vocalizations of at least seven different individuals per species (seven screaming cowbirds and ten shiny cowbirds). Each recording was converted to a spectrogram using default

settings in Raven Pro 1.4 (K. Lisa Yang Center for Conservation Bioacoustics, 2014). Spectrograms were then visually inspected to extract 10-20 good-quality calls per individual. With the selected calls, we created 3-min broadcast sequences (one per individual) using Raven Pro 1.4 editing tools. The sequences consisted of 18 bouts of five calls each, standardized at a call rate of 1 call per second and separated by 5 sec of silence. The amplitude of calls used during playbacks was standardized with Root mean square (RMS) within and between samples. As a control sound we used white noise samples created using version 2.2.1 of Audacity® recording and editing software (Audacity Team 2017). We generated 20-msec pulses of white noise (i.e., a random signal of constant power density) with the default settings of the noise generator tool, and then used these pulses to create the playback sequences in the same manner as the experimental call stimuli. White noise playbacks therefore consisted of 18 bouts of 5 pulses of white noise each, broadcast at a rate of 1 pulse per second and separated by a 5-sec silence period.

Semi-captivity experiment

We captured 9 shiny cowbirds (4 females and 5 males) and 13 screaming cowbirds (8 females and 5 males) using mist nets and walk-in traps baited with millet. Each bird was banded with a unique color-ring combination and a metal ring with a unique identification number. Blood samples (20-30 I) were drawn from the brachial vein to confirm the sex of screaming cowbird individuals by molecular sexing, since they show low sexual dimorphism (for details see De Mársico et al. 2010). After capture, birds were transferred to a laboratory in the field site and were housed in $120 \text{ cm} \times 40 \text{ cm} \times 40 \text{ cm}$ cages with food and water ad libitum until the next morning, when experiments were carried out.

Playback experiments were conducted in a 7 m \times 1 m (length \times width \times height) experimental arena constructed with a steel frame and covered by nylon anti-bird garden netting. The experimental arena (Figure 1) was divided into 3 areas: a neutral area located in the center (3 m length, containing 6 equidistant perches) and 2 response areas (right and left, 2 m length each, containing 4 equidistant perches each). A loudspeaker (model Philips BT2500B), from which the stimuli were broadcast using a wav/mp3 audio player (Zoom N4H, Zoom, Hauppage, NY, USA), was placed at the corner of each response area and food and water were available in the neutral area.

All experiments were carried out between 8:00 AM and 1:00 PM. Each trial began with the release of the bird inside the experimental arena, where it was left to habituate for 40 min. Three different treatments were presented sequentially, each consisting of 3-min broadcast sessions, preceded by a 10-min period of silence. Each treatment was played from one of the two loudspeakers placed in the response areas. Broadcast treatments consisted of 1) vocalizations of shiny cowbird juveniles; 2) vocalizations of screaming cowbird juveniles; and 3) white noise as a control. Each bird was tested only once, using a randomly selected sequence of each treatment. The order of presentation of treatments and the location of the active speaker (right/left) in the experimental arena were counterbalanced between individuals. We quantified the intensity of response

to playbacks using the following variables: 1) the time elapsed until the bird entered the active speaker area ('latency'), 2) the number of times the bird approached (i.e., made contact with) the loudspeaker ('approaches'), and 3) the proportion of time that the bird spent in the active speaker area ('duration').

Field experiment

To study if shiny and screaming cowbird adults are attracted by vocalizations of conspecific juveniles, we conducted a playback experiment in the field. We chose 14 random locations within the study site, where we had seen or heard both species of cowbirds immediately before the onset of the experiment. At each site we presented 3 different treatments sequentially, each consisting of 3-min broadcast sessions, preceded by a 5-min period of silence. Broadcast treatments consisted of 1) vocalizations of shiny cowbird juveniles; 2) vocalizations of screaming cowbird juveniles; and 3) white noise as a control.

Before the start of each trial, a loudspeaker (model Philips BT2500B) was placed in a tree branch. The loudspeaker was connected to a wav/mp3 audio player (Zoom N4H, Zoom, Hauppage, NY, USA) from which we played the treatments. We broadcast call treatments from a hide placed 10 m away from the loudspeaker, from which we simultaneously monitored bird behavior in real time using 8 × 42 binoculars. The experiments were carried out in the morning between 10 AM and 12 PM, and in the afternoon between 4 PM and 6 PM. The order of presentation of treatments was counterbalanced between sites. We quantified the response to playbacks using the following variables: 1) species of the first individual to respond (i.e., approaching within a 5 m radius of the speaker), 2) number of individuals of each species that responded, and 3) emission of vocalizations and identity of the individuals that emitted them.

The protocol and procedures employed were ethically reviewed and approved by the Provincial Organism for Sustainable Development (Disp. N° DI-2019-48, OPDS, Buenos Aires, Argentina) and comply with current laws of Argentina.

Statistical analysis

We tested for differences in latency among treatments for each species using a stratified Cox proportional hazard model, as suggested by Jahn-Eimermacher et al. (2011), using the coxph function from survival library (Therneau 2015) in R 3.6.0 (R Core Team 2020). The model included treatment and treatment order as fixed factors, and bird identity as a random effect. The frequency to approach the active loudspeaker was not analyzed statistically because approaches were too few to make comparisons (see Results). We used Wilcoxon tests to analyze whether the proportion of time spent by the birds in the response area during each treatment did not differ from that expected by chance (0.29), which would indicate no response to treatments, or

whether it was higher or lower, which would indicate attraction or aversion to playbacks respectively. The proportion of time expected by chance at each of the response areas was 0.29 (= 2/7) since the total length of the experimental arena was 7 m, and each response area was 2 m long. Furthermore, to analyze whether the duration of the response varied across treatments for each species, we used generalized linear mixed models (GLMMs) with beta distributions. Models were fitted using the glmmTMB function included in package glmmTMB in R version 3.6.0 (R Core Team, 2020). We included treatment (type of playback: conspecific, heterospecific, control), and treatment presentation order as fixed factors, and bird identity as a random effect. Due to the type of data obtained (see below) results from the field experiment were analyzed qualitatively.

Results

Semi-captivity experiment

For shiny cowbirds, the latency to respond to playbacks did not differ either between treatments ($\chi^2 = 2.39$, P = 0.30) or the order of presentation of treatments ($\chi^2 = 0.62$, P = 0.43). Similarly, for screaming cowbirds, the latency to respond to playbacks was not associated with treatment ($\chi^2 = 1.87$, P = 0.39) nor the order of presentation of treatments ($\chi^2 = 0.02$, P = 0.88).

Regarding the number of approaches to the loudspeaker, none were recorded for shiny cowbirds, while only two screaming cowbirds approached the loudspeaker, four and three times respectively during the conspecific vocalization treatment.

Duration in the response area during treatments did not differ from that expected by chance in any of the cases (all tests P > 0.05). Furthermore, response duration did not differ between treatments for shiny cowbirds (Figure 2A, Table 1A) or screaming cowbirds (Figure 2B, Table 1B). The order of presentation had no effect on the response in either species.

Field experiment

In seven out of the 14 trials, playback of juvenile vocalizations attracted birds, yet not conspecific adults. In all cases the individuals that approached the loudspeaker were of a host species of the cowbird whose playback was being played (Table 2). All these birds vocalized in response to the juvenile vocalizations broadcast.

Discussion

In this paper we studied if adults are attracted by conspecific begging calls in two avian brood parasites, testing some predictions of the parental behavior hypothesis in both semi-captivity and field playback experiments. Contrary to our predictions, adult cowbirds did not respond differentially to conspecific vocalizations of juveniles in the semi-captivity experiment. Moreover, no conspecifics were attracted during the field experiment, despite being present in the area while the playbacks were being played, reinforcing our result that adult parasites do not respond to conspecific juvenile vocalizations.

One possible explanation for these negative results is that both acoustic and visual cues are necessary to elicit a response. Hauber (2002) performed choice trials with brown-headed cowbird adults in the laboratory to determine if they approached conspecific juveniles preferentially. Unlike the present work, this study used live birds, thus visual and acoustic signals were simultaneously presented. Two sets of stimulus pairs were presented: the first set composed of a juvenile-plumaged female brown-headed cowbird and an adult male song sparrow *Melospiza melodia*, and the second set composed of a juvenile-plumaged male brown-headed cowbird and an adult male red-winged blackbird *Agelaius phoeniceus*. The results differed from ours since he observed that both brown-headed cowbird females and males associated with conspecific juveniles significantly more than expected by chance. So, it is possible that vocal recognition occurs after visual exposure to the juvenile or that the interaction of both stimuli is necessary for eliciting recognition.

Another possible explanation is that the acoustic signals used in the experiments were not adequate to trigger a response in adult cowbirds. Considering that the recordings used corresponded to begging calls of fledglings between 13 and 20 days of age, it is possible that the stimulus needed to trigger a response is other types of vocalizations or vocalizations of older individuals. Preliminary results of two studies in which juveniles of shiny and screaming cowbirds were radio-tracked after fledging indicate they disperse and leave their host territories at around 38-52 days of age (Crudele et al. unpublished data and De Mársico et al. unpublished data). So, it is possible that fledglings older than 20 days emit other types of vocalizations before the age of dispersion and that those are recognized by adult parasites. Nonetheless, it is important to note that the acoustic signals used in the field experiment were effective in attracting individuals of common hosts of shiny and screaming cowbirds, which indicates that the lack of response was not due to the stimuli being unrealistic or to the experimental design per se. Similarly to what we found in our field experiment, when a stuffed great spotted cuckoo fledgling was presented simultaneously with a cuckoo fledging playback in the field, adult hosts (i.e., magpies) were attracted to the site (Soler et al. 2014). Furthermore, the response of adult magpies to the playback- stuffed cuckoo depended on whether the adults were caring for cuckoo fledglings themselves or caring only for their own magpie fledglings, being willing to feed or attack the model respectively (Soler et al. 2014). In our case, we could not determine whether the hosts that were attracted to the site were caring for parasite fledglings, and since no stuffed model was presented, we observed neither positive nor negative responses from hosts, but just attraction to the playback site.

Finally, a third explanation for our results is that recognition and initiation of socialization depend exclusively on juveniles and not adults, i.e., that juveniles themselves are the ones that respond to vocalizations and/or visual cues of adults. Previous field studies and laboratory choice experiments support an active role of fledglings in their social interactions with conspecific adults. In field observations, juvenile brown-headed cowbirds were seen 'chasing' adults soon after becoming independent from their foster parents (Hauber et al. 2001; Woodward 1983), while in a laboratory choice experiment juvenile cowbirds spent a greater proportion of time in the proximity of a conspecific female adult stimulus (Hauber 2002). Furthermore, Hauber et al. (2001) suggested that cowbirds may use 'passwords' for species recognition. Young parasites could innately recognize certain phenotypic traits that are reliable signs of conspecific identity, such as certain vocalizations produced by the adults. This could in turn trigger additional learning of the phenotypic characteristics of the signaler, such as plumage characteristics or certain behaviors. For example, in the brownheaded cowbird, the chatter call of adult males and females (an innate species-specific vocalization) has been proposed as such a password (Hauber et al. 2001) and this mechanism was confirmed in shiny cowbirds, where conclusive evidence shows that imprinting is the mechanism that allows conspecific recognition and is initiated after juveniles listen to the chatter call (Crudele et al. 2023). A similar mechanism could be at play in parasitic male indigobirds (Vidua spp.) which exhibit mimicry songs that are common to conspecific males that share the same host species and non-mimicry songs that are common to conspecific males from the same local neighborhood (Da Costa & Sorenson, 2014; Payne et al. 1998). Young males who disperse outside their local 'dialect neighborhood' may use mimicry songs to identify conspecifics (Da Costa & Sorenson 2014).

We acknowledge that a potential issue when carrying out studies with birds captured from the wild is that they may not express their natural behaviour in cage. However, two points can be made, which allow us to trust our results. First, previous studies carried out with caged brown-headed cowbird adults testing whether they approached conspecific or heterospecific juveniles, showed differential responses towards the different stimuli (Hauber 2002). Similarly, caged juvenile shiny cowbirds responded to shiny cowbird adults' stimuli (Crudele et al. 2023). Second, the consistency of the results obtained in the semi-captivity experiment with those of the field playback experiment further suggest a true lack of response of the birds tested in cage.

In conclusion, our results are not consistent with the predictions from the parental behavior hypothesis that we tested (Soler & Soler 1999), as they show that adults of shiny and screaming cowbirds do not respond differentially to acoustic signals of conspecific juveniles, at least not to begging calls of fledglings between 13 and 20 days of age. Therefore, begging calls would not be enough stimulus to attract adult cowbirds, or adults' visits to territories where young are, would not be guided by the presence of nestlings/fledglings but for other reasons (i.e., adults may visit host territories searching for new nests and during these visits, if they find young, they interact with them). The agreement of the results in semi-captivity and field experiments supports this interpretation.

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Conflict of interest statement

The authors declare no conflicts of interest.

References

- Audacity Team, 2017. Audacity(R): Free Audio Editor and Recorder [Computer application].
- Catchpole CK, Slater PJ, 2008. *Bird Song: Biological Themes and Variations*. New York: Cambridge University Press.
- Crudele I, Reboreda JC, Fiorini VD, 2022. Preferential begging responses of shiny cowbirds to the conspecific chatter call. *Front Ecol Evol* 9:725051.
- Crudele I, Reboreda JC, Fiorini VD, 2023. Imprinting in an interspecific brood parasitic bird. *Proc R Soc B*. 290: 20230230
- Da Costa JM, Sorenson MD, 2014. An experimental test of host song mimicry as a species recognition cue among male brood parasitic indigo birds (*Vidua* spp.). *Auk* 131(4):549–558.
- De Mársico MC, Gantchoff MG, Reboreda JC, 2012. Host-parasite coevolution beyond the nestling stage? Mimicry of host fledglings by the specialist screaming cowbird. *Proc R Soc B* 279(1742):3401–3408.
- De Mársico MC, Mahler B, Chomnalez M, Di Giácomo AG, Reboreda JC, 2010. Host use by generalist and specialist brood-parasitic cowbirds at population and individual levels. *Adv Study Behav* 42(C):83–121.
- De Mársico MC, Mahler B, Reboreda JC, 2010. Reproductive success and nestling growth of the baywing parasitized by screaming and shiny cowbirds. *Wilson J Ornithol* 122(3):417-431.
- Freeberg TM, Duncan SD, Kast TL, Enstrom DA, 1999. Cultural influences on female mate choice: An experimental test in cowbirds, *Molothrus ater*. *Anim Behav* 57(2):421–426.
- Freeberg TM, King AP, West MJ, 1995. Social malleability in cowbirds *Molothrus ater artemisiae*: Species and mate recognition in the first 2 years of life. *J Comp Psychol* 109(4):357–367.
- Friard O, Gamba M, 2016. BORIS: A free, versatile open-source event: Logging software for video/audio coding and live observations. *Methods Ecol Evol* 7(11):1325-1330.
- Gil D, Llusia D, 2020. The bird dawn chorus revisited. In: Aubin T, Mathevon N eds. *Coding Strategies in Vertebrate Acoustic Communication*. Cham: Springer, 45–90.
- 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(5):1023–1029.
- Göth A, Hauber ME, 2004. Ecological approaches to species recognition in birds through studies of model and non-model species. *Ann Zool Fenn* 41:823–842.
- Grant PR, Grant RB, 1997. Hybridization, sexual imprinting, and mate choice. Am Nat 149(1):1–28.

- Grant PR, Grant RB, 2018. Role of sexual imprinting in assortative mating and premating isolation in Darwin's finches. *Proc Natl Acad Sci USA* 115(46):E10879–E10887.
- Hahn DC, Fleischer RC, 1995. DNA fingerprint similarity between female and juvenile brown-headed cowbirds trapped together. *Anim Behav* 49(6):1577–1580.
- Hauber ME, 2002. First contact: A role for adult-offspring social association in the species recognition system of brood parasites. *Ann Zool Fenn 39*(4):291–305.
- Hauber ME, Russo SA, Sherman PW, 2001. A password for species recognition in a brood-parasitic bird. *Proc R Soc B* 268(1471):1041–1048.
- Hauber ME, Sherman PW, Paprika D, 2000. The armpit effect in a brood parasite: Self-referenced phenotype-matching in brown-headed cowbirds. *Anim Cogn* 3:113–117.
- Irwin DE, Price T, 1999. Sexual imprinting, learning and speciation. Heredity 82(4):347-354.
- Jahn-Eimermacher A, Lasarzik I, Raber J, 2011. Statistical analysis of latency outcomes in behavioral experiments. *Behav Brain Res* 221(1):271–275.
- Kattan GH, 1997. Shiny cowbirds follow the "shotgun" strategy of brood parasitism. *Anim Behav* 53(3):647–654.
- Kennerley JA, Somveille M, Hauber ME, Richardson NM, Manica A et al., 2022. The overlooked complexity of avian brood parasite host relationships. *Ecol Lett* 25(8):1889-1904.
- King AP, West MJ, 1977. Species identification in the North American cowbird. Science 195(1):1002-1004.
- K. Lisa Yang Center for Conservation Bioacoustics, 2014. Raven Pro: Interactive Sound Analysis Software (Version 1.6.3) [Computer software]. New York: Cornell Lab of Ornithology. Available from: https://ravensoundsoftware.com/
- Lowther PE, 2023. *Lists of Victims and Hosts of the Parasitic Cowbirds (Molothrus)*. Chicago: Field Museum.

 Available from: https://www.datocms-assets.com/44232/1680014702-molothrus-hosts-ver-14jan2023.pdf
- Mason P, 1987. Pair formation in cowbirds: Evidence found for screaming but not shiny cowbirds. *Condor* 89(2):349–356.
- Miller JL, Freed-Brown SG, White DJ, King AP, West MJ, 2006. Developmental origins of sociality in brown-headed cowbirds *Molothrus ater. J Comp Psychol* 120(3):229–238.
- Naef Daenzer B, Grüebler MU, 2016. Post-fledging survival of altricial birds: Ecological determinants and adaptation. *J Field Ornithol* 87(3):227-250.

- O'Loghlen AL, Rothstein SI, 1995. Culturally correct song dialects are correlated with male age and female song preferences in wild populations of brown-headed cowbirds. *Behav Ecol Sociobiol*, 36(4):251–259.
- Oetting S, Pröve E, Bischof HJ, 1995. Sexual imprinting as a two-stage process: Mechanisms of information storage and stabilization. *Anim Behav* 50(2):393–403.
- Ortega CP, 1998. Cowbirds and Other Brood Parasites. Tucson: University of Arizona Press.
- Payne RB, Payne LL, Woods JL, 1998. Song learning in brood-parasitic indigo birds *Vidua chalybeata*: Song mimicry of the host species. *Anim Behav* 55(6):1537–1553.
- Scardamaglia RC, Fiorini VD, Kacelnik A, Reboreda JC, 2017. Planning host exploitation through prospecting visits by parasitic cowbirds. *Behav Ecol Sociobiol* 71(23).
- Scardamaglia RC, Lew AA, Gravano A, Winkler DW, Kacelnik A et al., 2022. Automated radio tracking provides evidence for social pair bonds in an obligate brood parasite. *Ibis* 164(4):1180–1191.
- Scardamaglia RC, Reboreda JC, 2014. Ranging behavior of female and male shiny cowbirds and screaming cowbirds while searching for host nests. *Auk* 131:610–618.
- Slagsvold T, Hansen BT, 2001. Sexual imprinting and the origin of obligate brood parasitism in birds. *Am Nat* 158(4):354–367.
- Slagsvold T, 2019. Social learning in birds studied by cross-fostering in the wild. *Integr J Vet Biosci* 3(2):1–4.
- Smith VA, King AP, West MJ, 2002. The context of social learning: Association patterns in a captive flock of brown-headed cowbirds. *Anim Behav* 63(1):23–35.
- Soler M, Soler JJ, 1999. Innate versus learned recognition of conspecifics in great spotted cuckoos *Clamator glandarius*. *Anim Cogn* 2(2):97–102.
- Soler M, Pérez-Contreras T, Ibáñez-Álamo JD, Roncalli G, Macías-Sánchez E et al., 2014. Great spotted cuckoo fledglings often receive feedings from other magpie adults than their foster parents: which magpies accept to feed foreign cuckoo fledglings? *PLOS ONE* 9(10):e107412.
- R Core Team, 2020. *R: A Language and Environment for Statistical Computing.* Vienna: R Foundation for Statistical Computing. Available from https://www.r-project.org/
- Ten Cate C, Vos DR, 1999. Sexual imprinting and evolutionary processes in birds: A reassessment. *Adv Study Behav* 28:1–31.
- Therneau T, 2015. A Package for Survival Analysis in S. version 2.38. Available from https://cran.r-project.org/package=survival

- Tuero DT, Fiorini VD, Reboreda JC, 2007. Effects of shiny cowbird *Molothrus bonariensis* parasitism on different components of house wren *Troglodytes aedon* reproductive success. *Ibis* 149(3):521–529.
- West MJ, King AP, 1988. Vocalizations of juvenile cowbirds *Molothrus ater ater* evoke copulatory responses from females. *Dev Psychobiol* 21(6):543–552.
- West MJ, King AP, Freeberg TM, 1996. Social malleability in cowbirds: New measures reveal new evidence of plasticity in the eastern subspecies *Molothrus ater ater*. *J Comp Psychol* 110(1):15–26.
- White DJ, King AP, Cole A, West MJ, 2002. Opening the social gateway: Early vocal and social sensitivities in brown-headed cowbirds *Molothrus ater*. *Ethology* 108(1):23–37.

Wiley JW, 1988. Host selection by shiny cowbird. Condor 90(2):289–303.

Woodward PW, 1983. Behavioral ecology of fledgling brown-headed cowbirds and their hosts. *Condor* 85(2):151–163.

Figure legends

Figure 1 Experimental arena and setup. The arena consisted of two response areas to the sides, each containing 4 perches, and a neutral area in the center, containing 6 perches. Each response area had a loudspeaker from where the stimuli were broadcast

Figure 2 Proportion of time spent in the active loudspeaker area as a function of treatment (playback type: conspecific, heterospecific, and control) for (A) shiny cowbirds and (B) screaming cowbirds



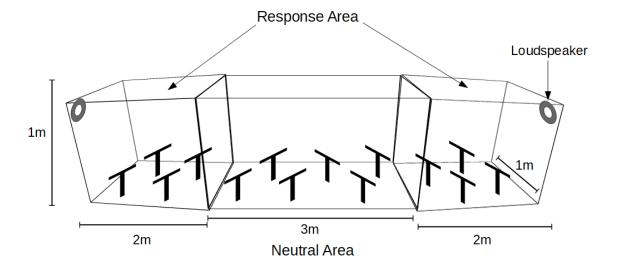
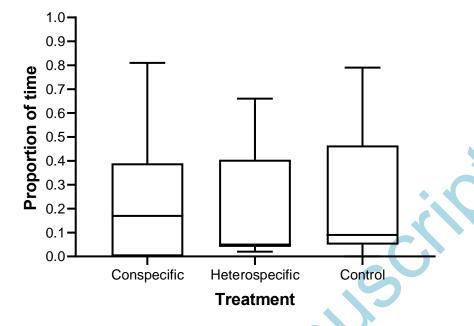


Figure 1



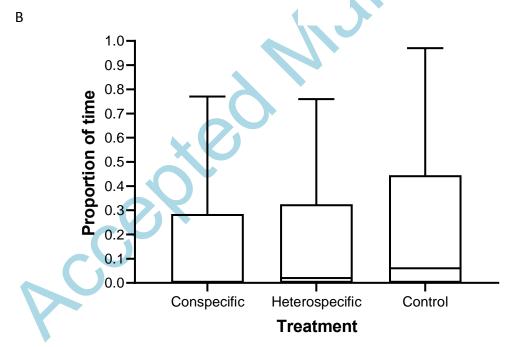


Figure 2

Table legends

Table 1 Results of the generalized linear mixed models for the duration of response that birds spent in the active speaker area as a function of treatment (playback type: conspecific, heteroespecific, and control) and order of presentation of treatments for (A) shiny cowbirds and (B) screaming cowbirds

Table 2 Playback treatment, species, and number of individuals that approached the loudspeaker for experiments where there was a response. The baywing *Agelaioides badius* is the exclusive host to the screaming cowbird in the study area. The house wren *Troglodytes aedon*, the chalk-browed mockingbird *Mimus saturninus*, and the rufous-collared sparrow *Zonotrichia capensis* are common hosts to the shiny cowbird in the study area

Tables

Table 1

Parameters	Coefficients	SE	Z	Р
(A) Shiny cowbirds				<u> </u>
Intercept (Conspecific)	-0.86	0.60	-1.43	0.15
Treatment (Heterospecific)	-0.18	0.48	-0.38	0.70
Treatment (Control)	0.05	0.48	0.11	0.91
Order	-0.06	0.25	-0.25	0.80
(B) Screaming cowbirds	7///			
Intercept (Conspecific)	-1.18	0.50	-2.33	0.02
Treatment (Heterospecific)	0.50	0.43	1.16	0.25
Treatment (Control)	0.73	0.41	1.78	0.08
Order	-0.35	0.22	-1.60	0.11

Table 2

Sample #	Treatment (playback)	Recruited species	# recruited birds
1	Screaming cowbird	Baywing	1
5	Screaming cowbird	Baywing	3
6	Shiny cowbird	House wren	2
7	Shiny cowbird	Chalk-browed mockingbird	2
8	Screaming cowbird	Baywing	4
9	Shiny cowbird	Rufous-collared sparrow	3
12	Shiny cowbird	Chalk-browed mockingbird	2