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Imprinting in an interspecific brood parasitic bird

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Many animals learn to recognize conspecifics after an early experience with them through sexual imprinting. For brood parasitic birds, it is not possible to develop conspecific recognition using cues provided by their foster parents. One solution is that a unique species-specific signal triggers the learning of additional aspects of the conspecific's phenotype. It has been proposed that for brood parasitic cowbirds, this signal is an innate vocalization, the chatter. This vocalization might act in a cross-modal learning process through which juveniles that listen to the song learn to recognize the visual characteristics of the song's producer. We trained two groups of juvenile shiny cowbirds (*Molothrus bonariensis*). In one group, individuals listened to the chatter or a heterospecific call while they observed a stuffed model of the corresponding species. In the other group, individuals listened to the call of one species (cowbird or heterospecific) while they observed the stuffed model of the other species. In the preference test, juveniles chose the model associated with the chatter, regardless of whether the model was a cowbird or a heterospecific. These results show how the auditory system through a species-specific signal can lead to cross-modal learning of visual cues allowing conspecific recognition in brood parasitic cowbirds.

1. Introduction

Imprinting is a process by which animals, after an early experience with individuals or a specific class of objects, learn their characteristics and restrict their social preferences to them [1,2]. This type of learning has been described in insects [3], spiders [4], fishes [5] and mammals [6] including humans [7], but it has been mostly studied in birds [8,9].

Under natural conditions, imprinting allows individuals to recognize and prefer conspecifics and is adaptive in different social contexts [2]. In birds, imprinting early in life allows chicks to develop a social attachment with their parents (filial imprinting) [10,11]. Imprinting also allows individuals to limit preferences that are expressed later in life to form sexual or mating pairs (sexual imprinting; [9,12]). In addition to learning through experience with the stimulus, the recognition or social attachment may involve visual and auditory predispositions [13]. These predispositions are considered a perceptual preference developed in young animals without the need for a previous experience with the stimulus [13].

Many works have found that precocial birds like domestic chicken (*Gallus gallus*), ducklings (*Anas* spp.) and young geese (*Anser* spp.) and quails (*Coturnix coturnix*) imprint on objects of different colours, sizes and forms, as well as with stuffed models of ducks or fowl [1,14] (for review see [9]). Also, Martinho & Kacelnik [15] showed that ducklings can imprint on a logical relationship between stimuli (same or different colour or form).

Evidence of imprinting in altricial bird species is more limited than for precocial ones. Studies of sexual recognition in zebra finches (*Taeniopygia guttata*) found that males bred in captivity preferred individuals with the mother's plumage and bill morph [16,17]. Also, Slagvold *et al.* [18] studied sexual imprinting

in the wild through cross-fostering experiments in which nestlings of great tit (*Parus major*) or blue tits (*Cyanistes careuleus*) were raised either by conspecifics or heterospecifics. They found that cross-fostered great tits became mis-imprinted and failed to pair with conspecifics, whereas no such effect was seen for cross-fostered blue tits. Their results showed that bird species can differ in the effect that early learning has in conspecific recognition.

Imprinting can be based not only on visual cues but also on acoustic ones. Clayton *et al.* [19] showed that the early acoustic social environment of zebra finch nestlings influences the production of songs of males and the recognition learning of females. Moreover, Riebel *et al.* [20] also found that male and female zebra finches preferred the father's song to which they were early exposed, over an unfamiliar one. Furthermore, when females of the two zebra finch subspecies were cross-fostered, they presented more sexual displays during the playback of songs of the foster species than those of their species [21]. Nevertheless, although male and female zebra finches prefer familiar vocalizations [20,22], juveniles that were not exposed to adult conspecific songs prefer zebra finch songs to control songs [23,24]. These results indicate that other factors besides imprinting might be involved in conspecific recognition.

Interspecific brood parasites lay their eggs in nests of other species that provide all the parental care. These species confront an interesting problem to learn conspecific cues as they are raised in the nest of heterospecifics, typically without any exposure to conspecifics. Yet, they must later find and recognize conspecifics in order to mate and reproduce successfully. Birds typically learn to recognize conspecifics through early experience, and in most cases could learn features of their parents (visual, auditory or potentially other stimuli) as the template for recognizing conspecifics. This information is not available for interspecific brood parasites and a few other 'non-parental' species such as megapodes [25].

Few works have studied imprinting in brood parasites. Payne *et al.* [26] investigated host imprinting (preference of the parasite for the host species that reared it) in the village indigobird (*Vidua chalybeata*). They found that females reared by their normal host (red-billed firefinch *Lagonosticta senegala*) preferred to parasitize red-billed nests whereas those reared by experimental Bengalese finch, *Lonchura striata*, preferred to parasitize Bengalese nests. Regarding conspecific recognition in brood parasites, King & West [27] found that brownheaded cowbird females raised in auditory and visual isolation from adult cowbirds showed a copulatory response when they listened to the song of male cowbirds during the breeding season. They proposed this response is a mechanism that ensures species identification and induces sexually appropriate behaviour. Nevertheless, this mechanism does not explain how juvenile cowbirds first come to recognize conspecifics [27] as at the time of independence from their foster parents, cowbirds join them in foraging flocks. Hauber *et al.* [28] proposed that conspecific recognition is initiated when young encounter some unique species-specific signal or 'password' (e.g. a vocalization, behaviour or other characteristics) that triggers the learning of additional aspects of the password-giver's phenotype. They proposed that for brown-headed cowbirds (*Molothrus ater*), the password is the chatter call, an innate species-specific vocalization. They found that cowbird nestlings begged significantly more frequently to playbacks of chatters than to other avian sounds and hand-reared fledglings

approached playbacks of chatters faster than to vocalizations of heterospecifics [28]. Also, free-living cowbird fledglings and adults approached playbacks of chatters more often than playbacks of control sounds [28]. In addition, neurobiological studies found indirect evidence supporting the password hypothesis. Lynch *et al.* [29] showed that in brown-headed cowbirds, the auditory forebrain region expresses greater densities of the protein product of the immediate-early gene ZENK in response to the chatter than to control sounds of mourning dove (*Zenaida macroura*) indicating that when cowbirds listen to the conspecific song, they exhibit a specific neural response in brain regions that are key for social recognition. Besides, Louder *et al.* [30] found that the chatter call enhanced song production learning in males and induced a neurogenomic profile of song familiarity in females, even for heterospecific songs, when acoustically naive juvenile male and female cowbirds were exposed to songs paired with chatter calls.

Cross-modal learning refers to the adaptive, synergistic integration of complex perceptions from multiple sensory modalities, such that the learning that occurs within any individual sensory modality can be enhanced with information from one or more other modalities [31]. According to the password hypothesis, the chatter call triggers a cross-modal learning process through which juveniles that listen to the song learn to recognize visual characteristics of the song's producers. In the non-parasitic white-crowned sparrow (*Zonotrichia leucophrys antiantha*), it was found that speciesspecific vocalizations serve as a cue for species recognition and act as a relevant factor in preparation for learning to sing [32]. Different works [32,33] that studied the effect of the introductory whistle of the white-crowned sparrow on song learning found that this introductory whistle serves as a call to attention that in young birds appears to stimulate to attend to and memorize the phrases that follow [33]. Interspecific brood parasites are an ideal model to test for cross-modal learning because in these species the confounding effects of exposure to parental care are naturally eliminated. Thus, they would serve as one of the cleanest tests of cross-modal learning to show if the acoustic cues directly facilitate cross-modal learning of visual cues.

The shiny cowbird (*M. bonariensis*) is a Neotropical generalist brood parasite that lays its eggs in nests of more than 250 hosts [34]. Similarly to the closely related brown-headed cowbird, shiny cowbird nestlings reared by one of its hosts (the chalk-browed mockingbird, *Mimus saturninus*) begged more intensively in response to playbacks of conspecific chatter calls than to host calls, indicating that they have speciesspecific perceptual response [35]. After fledging, shiny cowbird young remain associated with their foster parents for approximately 30–40 days, and, at that time, they join foraging flocks of conspecifics and start roosting with them (I.C., J.C.R. and V.D.F. 2017–2019, unpublished data).

Until now, studies of brown-headed cowbirds indicate that nestlings and juveniles recognize the chatter call, and this vocalization produces a specific neural response associated with social recognition. Nevertheless, there is no evidence showing that after cowbirds are exposed to the chatter call, they show a visual preference for the phenotype associated with the chatter producer. The aim of this work was to experimentally test if the chatter call of the shiny cowbird is the cue that triggers learning of visually perceived morphological aspects of the producer, driving future social preferences for conspecifics (i.e. sexual imprinting).

2. Materials and methods

To carry out the experiment, shiny cowbirds were collected as nestlings during the breeding seasons of 2019, 2020 and 2021 in 'Reserve El Destino', near the town of Magdalena (35°80'80" S, 57°82'30" W). They were removed from nests of chalk-browed mockingbirds ($N = 9$ chicks) and house wrens (*Troglodytes aedon*) ($N = 18$ chicks) at 10 ± 0.2 days of age (they usually fledge when they are 12–13 days old). Chicks were maintained for 4–5 days visually isolated in containers of 12 cm in diameter and 18 cm in height. They were fed with a wet paste of premium insect food (CéDé) and Nestle Infant Cereal, 5 Cereals, once per hour until satiation. When they were 13–14 days old and they were able to remain standing on the perches, we transferred them to cages of $120 \times 40 \times 40$ cm where they continue to be visually isolated. When individuals were 30 days old, we offered them millet seeds and water ad libitum which they started to consume when they are approximately 40 days old.

We trained two groups of captive shiny cowbird juveniles. In one treatment (direct), during training, the individuals ($N = 14$) listened to the call and observed the model of the same species (chatter of the cowbird paired with the model of a cowbird and call of a heterospecific paired with the model of a heterospecific). In the other treatment (crossed) individuals ($N = 13$) listened to the call of one species but observed the model of the other (chatter of the cowbird paired with the model of a heterospecific and call of a heterospecific paired with the model of a cowbird). The conspecific models were three shiny cowbird females while the heterospecific models were one rufous-bellied thrush (*Turdus rufiventris*), one rufous hornero (*Furnarius rufus*) and one chalk-browed mockingbird. These heterospecific species were chosen because they were common species in the study area and we could obtain models of them from the Natural Science Museum 'Bernardino Rivadavia'. The number of shiny cowbird juveniles that were trained with each heterospecific model, for the direct and crossed treatments respectively, were eight and six for the rufous-bellied thrush model, four and five for the rufous hornero model, and two and two for the chalk-browed mockingbird model. We were careful to not use the heterospecific mockingbird model for cowbird nestlings collected from mockingbird nests to avoid a potential bias for early exposure to chalk-browed mockingbirds.

Playbacks used during training were built from vocalizations with RMS (root mean square) amplitude standardized within and between samples. This standardization allows for scaling different sound files to approximately equal loudness. To build the playbacks of each species (cowbird and heterospecifics), we used vocalizations from six individuals of each species that were randomly ordered to generate six different sequences of one minute, with one vocalization every 30 s. Vocalizations were obtained from our own recordings and from the xeno-canto website (https://www.xeno-canto.org). Training started when cowbirds were 16.9 ± 0.4 days of age (range 13–19 days). They received approximately 15 blocks of two sessions (one session per day on consecutive days) with an interval of 2 days between blocks. Each session lasted 1 h, and during this time the individuals listened to the playback and could observe a stuffed model located next to the cage at the same height as the perches. In each treatment, the training was repeated until the juveniles were 94.5 ± 3.6 days old (range 76–119 days) resulting in 15.3 ± 0.5 block sessions (range 12–18 blocks). The timing of the final session of training was determined based on our observations of shiny cowbirds and prior studies on brown-headed cowbirds which indicate that in the wild, juveniles at this age are observed with adults [36] (I.C., J.C.R. and V.D.F. 2017–2019, unpublished data).

We tested the individuals when they were 95 ± 2.3 days old (range 75–124 days). Three days before testing, we moved the birds to an experimental arena for acclimatization. The arena was an acoustically and visually isolated room of $3 \times 3 \times 3$ m, with three perches located at 1 m in height. Two perches were on opposite sides of the room, at 50 cm from two small platforms of 10×10 cm where we located the models during the test. The third perch (neutral) was placed in the middle of the room. During the morning of the test day, we placed the cowbird and the heterospecific models on opposite sides of the aviary concealed by sliding curtains. When the bird was perched on the neutral perch, we moved the curtains slowly to allow it to see both models simultaneously and the test session started. No playbacks were emitted during the test session. We filmed the session for 15–30 min. We used two variables to determine the preference of individuals for one of the models: (i) the identity of the model to which the bird approached first and (ii) the proportion of time the bird was on the perch closer to each model. Sample sizes were 14 birds (10 females and 4 males) for the 'direct' treatment and 13 birds (6 females and 7 males) for the 'crossed' treatment.

(a) Statistical analyses

We compared the number of juveniles that first approached the model paired with the chatter in each treatment through a Fisher Exact test. To determine if the proportion of time juveniles spent with the model paired with the chatter (response variable) differed between treatments (predictor variable), we performed a GLM with beta error distribution and log link function [37]. To determine if in each treatment the proportion of time juveniles spent with the model paired with the chatter differed from 0.5, we evaluated the P of the intercept when it included one or the other level of the treatment. We transformed the response variable (y) following [38] as $y \times (n - 1) + 0.5)/n$, where n is the number of observations. We used the R software, version 3.4.0 [39], and the R Studio, version 1.0.143 [40]. The analysis of data was conducted using the betareg package (betareg package v. 3.1-4 (1) [41].

3. Results

In both treatments during the preference test individuals first approached the model that was associated during training with the chatter call (table 1). In the 'direct' treatment, 12 of 14 individuals first approached the cowbird model whereas in the 'crossed' treatment 12 of 13 individuals first approached the heterospecific model (Fisher exact test, $p < 0.0001$). There were no differences between treatments in the proportion of time birds spent near the model associated during the training with the chatter (figure 1, GLM with beta error distribution and log link function, intercept: estimate ± s.e. = 1.20 ± 0.32, $Z = 3.77$, $p = 0.0002$, 'crossed' treatment: estimate ± s.e. = 0.06 ± 0.42, $Z = 0.15$, $p = 0.88$). In both treatments, the birds spent more time near the model associated during training with the chatter call than near the model associated with the heterospecific call (figure 1, 'direct' treatment: $X = 0.77$, IC 95% = 0.54–0.80, $p = 0.0002$, 'crossed' treatment: $X = 0.78$, IC 95% = 0.53–0.81, $p = 0.0001$).

4. Discussion

In the preference test, shiny cowbird juveniles preferred the model associated with the playback of the chatter call during training, approaching this model first and spending
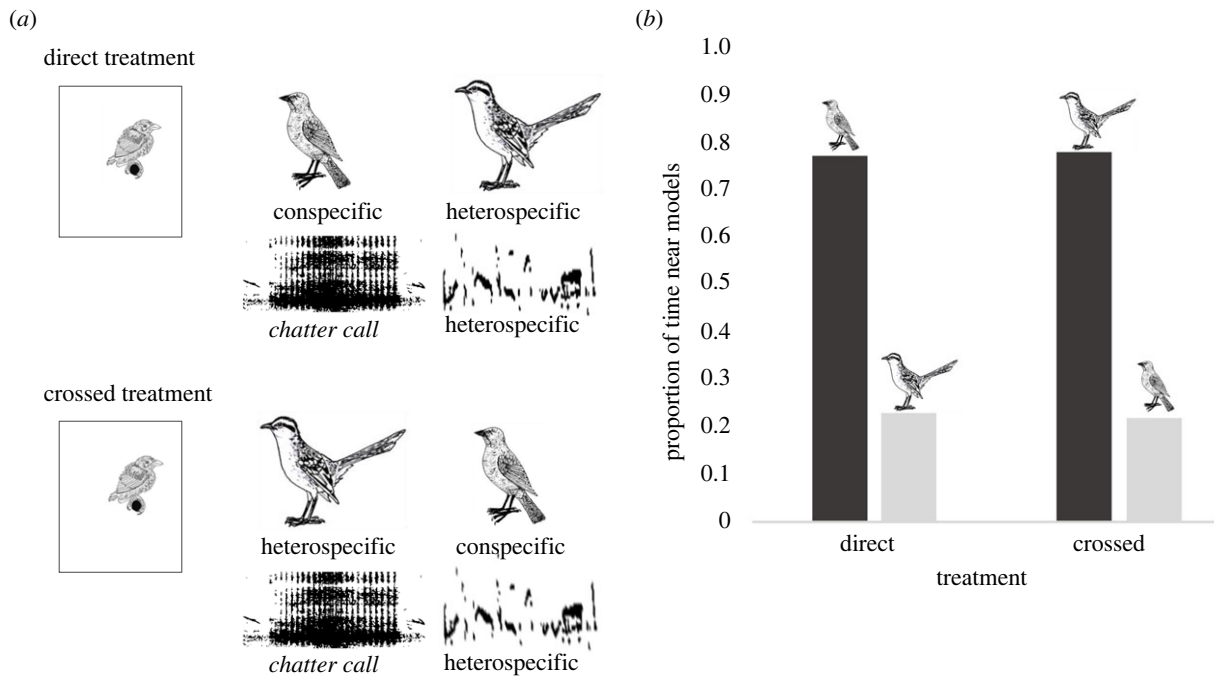
Figure 1. Treatments and results of the experiment. (a) To test if shiny cowbird juveniles use the chatter call as the cue that triggers the learning of some morphological aspects of the producer, we trained two groups of captive cowbirds. In the 'direct' treatment, during the training, cowbirds (N = 14) listened to the call and observed the stuffed model of the same species, while in the 'crossed' treatment, during the training, cowbirds (N = 13) listened to the call of one species but observed the stuffed model of the other species. In the figure are represented the juvenile shiny cowbird inside the rectangle (individual cage), the conspecific model above the sonogram of the chatter call and one of the heterospecific models (the mockingbird) above the sonogram of one of its calls. Each cowbird juvenile was trained with only one heterospecific model and its corresponding calls. For clarity, the other heterospecific models and the sonograms of their calls used in the experiment are not shown. (b) Proportion of time that juvenile shiny cowbirds of direct and crossed treatments spent near the conspecific and heterospecific models during the preference test. Black bars correspond to models paired with chatter call and grey bars correspond to models paired with heterospecific call.

Table 1. Experimental design and results of the preference test. In both treatments, juveniles received 15 blocks of two sessions (one session per day on consecutive days) with an interval of 2 days between blocks. In the 'direct' treatment, 14 cowbirds received in one session playbacks of the shiny cowbird chatter call associated with a stuffed model of a cowbird, and in the other block session, playbacks of a heterospecific call associated with the stuffed model of a heterospecific (rufous-bellied thrush *Turdus rufiventris*; rufous hornero, *Furnarius rufus*, or chalk-browed mockingbird *Mimus saturninus*). In the 'crossed' treatment, 13 cowbirds received, in one session, the playbacks of the cowbird chatter associated with a stuffed model of a heterospecific, and in the other block session, the playbacks of a heterospecific call associated with the stuffed model of a shiny cowbird. The training was conducted since juveniles were 17 days old until they were 94 days old. The column on the right indicates the number of individuals that first approached the model associated with the playback in the preference test conducted when juveniles were 95 days old.

treatment	playback	model associated with the playback	preference for the cowbird model
direct	chatter call	cowbird	12/14
	heterospecific call	heterospecific	
crossed	chatter call	heterospecific	1/13
	heterospecific call	cowbird	

more time close to it than to the model associated with the playback of the heterospecific call, regardless of whether the model associated with the chatter was conspecific or heterospecific. This result indicates that shiny cowbirds use the chatter call as a password to develop a social preference for the phenotype of the individual that produces this vocalization and is the first direct evidence supporting the password hypothesis as the mechanism for explaining how an interspecific brood parasite can learn the phenotypic characteristics of their conspecifics.

Individuals can imprint during a time window called the sensitive period [13,14]. For brood parasites, there is no clear information on when this sensitive period starts and how long it lasts. Unlike other bird species that imprint during the first days of life [11], the sensitive period in brood parasites should be delayed until individuals can receive the correct information [42]. Thus, the sensitive period should start after parasites fledge from host nests and continue until they join conspecific flocks. During this time, parasitic juveniles may interact with conspecific adults that produce the chatter call [27,43] and learn their phenotypic characteristics. On two occasions, we observed shiny cowbird females perched near and soliciting preening from conspecific juveniles of 20–30 days old (I.C., J.C.R. and V.D.F. 2017–2019, unpublished data). Adults of other brood parasitic species also interact with parasitic fledglings in host territories (reviewed in [42,43]). These first interactions during a potentially sensitive period would promote the start of conspecific recognition [42]. Another possibility would be that cowbirds are sensitive to the password since the time they

hatch but develop a conspecific recognition template after they became independent from hosts [28,32,44]. This possibility is supported by studies showing that cowbird's nestlings begged more intensively in response to playbacks of conspecific chatter calls than to host calls [28,35].

Louder *et al.* [30] found that the exposure of brown-headed cowbirds juveniles to the chatter improves their song learning. When hand-raised juvenile males were exposed to playbacks of canaries (*Serinus canaria*) songs followed by a chatter, they reproduced the heterospecific songs better than if they listened to the canary followed by coos of mourning doves (*Zenaida macroura*). Moreover, males exposed to chatter calls expressed more genes related to auditory learning and neuroplasticity, whereas females exposed to chatter calls expressed genes involved in long-term memory [30]. These results would indicate that the chatter call can initiate social learning, increasing song acquisition in males and recognition learning in both sexes.

The results of this work show how the auditory password system through a species-specific signal can lead to cross-modal learning of visual cues allowing conspecific recognition in brood parasitic cowbirds. This resolves a significant puzzle to understanding the learning of conspecific recognition in obligate interspecific brood parasites, but there is potential for this to be a general feature of songbirds. Similar 'password' type systems guide learning of conspecific songs in other, non-parasitic songbirds. Famously, the introductory whistle of white-crowned sparrows serves this purpose (e.g. [32,33]). However, no previous work has tested whether such acoustic cues that 'turn on' learning may also act to initiate cross-modal learning in other songbirds. Generally, researchers assume that exposure to parents during the period of parental care leads to learning of conspecific visual cues. However, after the results of this study, it would be possible to think that acoustic-to-visual cross-modality is a general property of species recognition learning in songbirds.

To summarize, previous studies in brown-headed cowbirds have provided indirect evidence supporting the 'password hypothesis' but until now there was no direct evidence showing that listening to the chatter call triggers the learning of the visual characteristics associated with the producer. In our study, we experimentally showed that the encounter of a parasitic juvenile with an individual that produces the chatter results in the development of a preference for the phenotype characteristics of the individual that produces this vocalization. Thus, our results provide an explanation for how brood parasites, which do not have the opportunity to develop conspecific recognition using cues provided by the adults that raise them, can learn to recognize conspecifics.

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