



Acoustic discrimination by hosts favours vocal trickery in fledglings of the brood-parasitic screaming cowbird

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Abstract

Agonistic interactions between obligate avian brood parasites and their hosts can lead to the coevolution at any stage of the nesting cycle, yet adaptations and counter-adaptations at the fledgling stage are poorly known. Young of the host-specialist screaming cowbird (*Molothrus rufoaxillaris*) closely resemble those of its greyish baywing (*Agelaioides badius*) host in appearance and begging calls. This overall similarity has shown to be adaptive to escape host discrimination after leaving the nest, but the role of acoustic signals in host deception remained unclear. We examined whether baywing parents are able to distinguish between begging calls of mimetic and non-mimetic fledglings and whether screaming cowbirds can trick host parents by vocally resembling host young. We conducted a field playback experiment using fledgling calls of screaming cowbird (mimetic), shiny cowbird (*M. bonariensis*; non-mimetic) and baywing (conspecific control) in the absence of any visual stimuli. Baywings were significantly less responsive to non-mimetic shiny cowbird calls than to the other call types and more responsive to screaming cowbird calls than to conspecific calls. The results support the idea that baywings cue in on species-specific acoustic signals for fledgling recognition and that vocal similarity to host young in screaming cowbirds plays a role in host deception. The observed host preference for screaming cowbird over conspecific calls further suggests that vocal mimicry in brood parasites could be reinforced by the expression of acoustic features that either act as a supernormal stimulus or exploit host's pre-existing sensory biases.

Significance statement

Brood-parasitic screaming cowbird juveniles closely resemble those of its primary host, the greyish baywing, in plumage appearance and vocalizations. Using a field playback experiment, we studied the ability of adult baywings to discriminate against foreign juveniles based on vocal cues, in the absence of any visual stimuli. Baywings responded differentially to own-species and non-mimetic calls, and even more, they were more attracted to screaming cowbird calls than to those of conspecific juveniles. The study supports the idea that baywings use acoustic signals to distinguish between their own and foreign fledglings, thus favouring the evolution of vocal mimicry in its specialist brood parasite. Moreover, the results suggest that screaming cowbird fledglings would be even more effective than host's own young in attracting parental attention through their begging calls.

Keywords Brood parasitism · Coevolution · Mimicry · Begging calls · Fledglings · Cowbird

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Introduction

Obligate avian brood parasites exploit the parental care of heterospecific hosts to raise their progeny. This reproductive strategy imposes fitness costs to the foster parents, as these often suffer partial or total brood losses at parasitized nests. The antagonistic interactions between brood parasites and their hosts can lead to coevolutionary processes in which adaptations on one side favour reciprocal adaptations to counter them on the other (Rothstein 1990; Davies 2000; Soler 2014). The best studied example is the evolution of host rejection behaviours towards foreign eggs and egg mimicry in parasitic females (Davies 2000; Spottiswoode et al. 2011; Spottiswoode and Stevens 2012). However, host–parasite coevolution can occur throughout the nesting cycle, from egg-laying to post-fledging (Davies and Brooke 1989; Langmore et al. 2003; Davies and Welbergen 2008; De Mársico et al. 2012; Grim and Rutila 2017; Noh et al. 2018).

In the last two decades, evidence has accumulated of ongoing arms races between brood parasites and their hosts beyond the egg stage. A well-studied example came from Australian bronze-cuckoos (*Chalcites* spp.) and some of their hosts, which are able to reject foreign nestlings by abandoning the nest (Langmore et al. 2003) or dragging them out (Sato et al. 2010; Tokue and Ueda 2010). Feeding discrimination by hosts has also been reported against nestlings of African brood-parasitic finches (*Vidua* spp.) that were cross-fostered to a non-host species (Payne et al. 2001; Jamie et al. 2021) or had their phenotype manipulated (Schuetz 2005). In all these parasite species, nestlings exhibit visual and/or vocal mimicry of host young, presumably driven by host discrimination (Langmore et al. 2003, 2008a, 2011; Noh et al. 2018; Jamie et al. 2020, but also see Anderson et al. 2009).

In theory, similar coevolved adaptations could arise at the fledgling stage, but host–parasite interactions during this critical period are rather poorly known (Soler et al. 2014; De Mársico et al. 2017; Tyller et al. 2018; Kysučan et al. 2020). This is likely due to the difficulty of conducting direct behavioural observations during and after the transition to the post-fledgling period and of following individual fledglings in the field. The increasingly available technology for animal tracking is helping to fill this gap (Soler et al. 2014; De Mársico et al. 2017; Tyller et al. 2018; Kysučan et al. 2020), but experimental studies of putative adaptations in brood-parasitic fledglings are scarce (Soler et al. 2014; De Mársico et al. 2017; Tyller et al. 2018; Kysučan et al. 2020).

Visual mimicry of host fledglings has been shown to occur in the screaming cowbird (*Molothrus rufoaxillaris*), a non-evictor parasite that uses the greyish baywing (*Agelaioides badius*; hereafter baywing) as its primary host. Baywing parents accept non-mimetic nestlings, but they stop

providing parental care to them as soon as they leave the nest, provided that they fledge alongside host young (Fraga 1998; De Mársico et al. 2012; Rojas Ripari et al. 2019a). Screaming cowbird fledglings closely match the appearance of host young to a naked human eye (Fraga 1998), and quantitative analyses using avian visual modelling provided further evidence of mimicry from a bird's perspective (De Mársico et al. 2012). This resemblance allows screaming cowbirds to circumvent host discrimination and continue receiving parental care until their independence (Fraga 1998; De Mársico et al. 2012). The striking similarity between host and parasitic young extends to their begging calls, suggesting that fledgling recognition by adult baywings involves both visual and vocal cues (Fraga 1998; De Mársico et al. 2012). Prior studies demonstrated that begging calls of baywing and screaming cowbird nestlings elicit higher provisioning rates compared with non-mimetic begging calls when broadcast at baywing nests (Ursino et al. 2018), but whether vocal similarity could play a role in host manipulation by screaming cowbird fledglings remained unclear.

Acoustic signals are central to parent–offspring communication in birds. Thus, it is not surprising that brood parasites exhibit begging call features that serve to influence host behaviour in their own benefit (e.g. Kilner and Davies 1999; Gloag and Kacelnik 2013). In some host-generalist parasite species, nestlings rely on non-specific acoustic traits such as louder, rapid or repetitive calls to stimulate a variety of host species (Kilner et al. 1999; Peer 2006; Anderson et al. 2009; Gloag and Kacelnik 2013; Samaš et al. 2020; Li and Hauber 2021). In other species, parasitic nestlings produce begging calls that match the acoustic structure of those of their hosts, although in most cases the function of this similarity has not been established (Jamie and Kilner 2017). Begging call similarity can arise as a coevolved defence in response to host rejection (Langmore et al. 2003, 2008), or alternatively, it can result from other processes that do not involve coevolution. These include shared ancestry, tuning into host's pre-existing sensory preferences to stimulate adequate provisioning levels, competition with host nest mates for parental feedings or parallel evolution driven by environmental factors (Grim 2005; Jamie and Kilner 2017; Jamie et al. 2020). Evaluating host behaviour towards apparently mimetic and non-mimetic begging calls is, therefore, a critical step to understand the function of call similarity in parasitic nestlings and fledglings, and disentangling its evolutionary causes (Grim 2005, 2008, 2013; Jamie and Kilner 2017).

So far, the most compelling evidence of begging call mimicry in response to host rejection comes from Horsfield's bronze-cuckoos (*C. basalis*), which seem to be engaged in an “acoustic arms race” with its superb fairywren (*Malurus cyaneus*) host (Langmore et al. 2003; Colombelli-Négrel et al. 2012). Horsfield's bronze-cuckoo

nestlings match innately the begging call structure of fairy-wrens and are more likely to be accepted by fairy-wren parents than shining bronze-cuckoo (*C. lucidus*) nestlings, which do not match this host's begging calls (Langmore et al. 2003, 2008). However, it is important to note that the specific function of call structure for chick recognition has not been tested without the potentially confounding effect of visual cues (Colombelli-Négrel et al. 2012). Indeed, in the vast majority of begging call experiments that tested host response to playbacks, calls were broadcast directly at host nests, supplementing the visual and acoustic signals of chicks themselves. Moreover, to our best knowledge there are no published studies to date that have examined the function of begging call similarity between brood parasitic and host fledglings (Jamie and Kilner 2017; Rojas Ripari et al. 2021).

The system of the screaming cowbird and its baywing host provides a suitable model to investigate if begging calls of parasitic fledglings can play a role in host deception. A previous study showed that screaming cowbird nestlings experimentally cross-fostered to nests of a non-host species developed begging calls that were similar to those of screaming cowbird and host nestlings reared in baywing nests in both their acoustic structure and effect on host behaviour (Rojas Ripari et al. 2019b). This developmental pattern points towards the existence of genetically fixed vocal mimicry in screaming cowbirds, as it is expected in host-specialist parasites that are under selection to avoid host discrimination (De Mársico et al. 2012; Jamie and Kilner 2017). Following this idea, our aim in this study was to expand on previous studies and evaluate the hypothesis that vocal similarity between screaming cowbird and host fledglings can be an adaptation selected for by the ability of baywings to discriminate between acoustic signals of own and foreign fledglings. To do that, we tested the acoustic discrimination abilities of adult baywings under natural field conditions by presenting them with begging calls of conspecific, screaming cowbird (mimetic) and shiny cowbird (non-mimetic) fledglings in the absence of visual cues of host or parasitic fledglings. We predicted that baywings will behave differentially towards playback of host-like juvenile calls (i.e., conspecific and screaming cowbird calls) compared with non-mimetic begging calls. More specifically, we predicted that baywings would be more attracted to own-species and screaming cowbird begging calls than to shiny cowbird calls, as measured by the latency and intensity of their response, the latter including the frequency and duration of the approaches to the loudspeaker and the number of adults involved in the response. In addition, if vocal resemblance to host fledglings in screaming cowbirds is selected for by host discrimination, we expected that baywings would respond similarly to playbacks of screaming cowbird and conspecific calls.

Methods

Study site and species

The study was conducted between November 2012 and February 2013 at the private reserve El Destino (-35.131° S, -57.387° W), located within Parque Costero del Sur (MAB-UNESCO) in the Province of Buenos Aires, Argentina. Baywings are year-round residents in the area and breed from late November to late February. They rarely build their own nests but use instead domed or closed nests built by other species. They can also occasionally nest in secondary cavities and nest boxes (Fraga 1988; De Mársico et al. 2010). Baywings are single-brooded and facultative cooperative breeders (Fraga 1991). On average, 40% of the breeding pairs in the study area have one or more helpers at the nest, mostly after the eggs hatch (range: 1–3 helpers per nest; Ursino et al. 2011). Helpers participate in nest defence and provisioning, and the number of helpers generally increases after the chicks fledge (Fraga 1991; Ursino et al. 2011). Baywing nests are almost always parasitized by screaming cowbirds and, more rarely, by the host-generalist shiny cowbird (parasitism rates: ~90–100% and 15–25%, respectively) (De Mársico et al. 2010).

During the breeding season of 2012–2013, baywing nests were located and monitored every 1–2 days until young fledged or the nest failed (due to predation or abandonment). The contents of the nest were recorded during each visit. Eggs and nestlings were individually marked with Sharpie markers for identification (see De Mársico et al. 2010 for more details). Screaming and shiny cowbirds had slightly higher growth rates than baywings, but nestlings of the three species reach their asymptotic mass at a similar age (~10–11 days post-hatching). Baywing and parasitic nestlings typically remain in the nest for 12 to 16 days, with a mean fledging age of 14 days post-hatching (De Mársico et al. 2010).

Playback experiment

To assess the ability of adult baywings to vocally discriminate between their own and foreign fledglings, we conducted a playback experiment under field conditions. Ideally, the function of vocal similarity to host young in screaming cowbirds should be tested during the post-fledging stage, which is at the time when discrimination against non-mimetic young is at play in baywings (Fraga 1998; De Mársico et al. 2012). However, we found that setting up a controlled playback experiment at this stage was unfeasible for practical reasons. Baywings with recently fledged young are highly alert and easily disturbed by human presence, and they often move unpredictably within their breeding territory. These

behaviours made it impossible for us to anticipate for how long our focal subjects will settle at any given location, thus precluding the standardization of exposure to the stimuli within and among playback treatments. Also, we could not avoid interferences due to the presence of host's own fledglings (see Kysučan et al. 2020 for similar field constraints). Given these limitations, we opted for conducting the experiment during the late nestling stage. We already knew from our own experience working with baywings, that breeding adults seldom leave the nests unattended during the nestling stage, and that they quickly resume their normal parental activity once we walked away from the nests after inspecting the nest contents or placing recording equipment (e.g. Ursino et al. 2018; Rojas Ripari et al. 2019b). Hence, we reasoned that by conducting the playback experiment near nests that were close to the fledging age we could test the acoustic discrimination abilities of baywings under more controlled conditions. Our experiment therefore allowed us to assess the general response to the acoustic stimuli of all baywings attending the focal nests.

It can be argued that host response to fledgling begging calls at the end of the nestling stage does not necessarily reflect how hosts will behave to the same stimuli after fledging their own brood. Nonetheless, we believe that the timing of the experiment has not critically biased the results nor invalidates the conclusions, based on the following arguments. First, fledgling begging calls can be considered a stimulus distinct from nestling calls for nesting baywings because the acoustic structure partially differs between them (Table SI 1), and host response pattern is qualitatively different between playbacks of fledgling calls (this study) and nestling calls (Ursino et al. 2018; Rojas Ripari et al. 2019b). In particular, baywings exposed to playback experiments during the late nestling stage (9–14 days post-hatching) behaved similarly in response to calls of screaming cowbird and conspecific nestlings (Rojas Ripari et al. 2019b), but responded differentially towards fledgling begging calls (see Results), as measured with the same protocol. Second, baywings are able to discriminate against non-mimetic young after having reared them to fledging (Fraga 1998; De Mársico et al. 2012; Rojas Ripari et al. 2019a) and, indeed, they showed stronger discrimination when non-mimetic fledglings were reared in mixed broods than when they were reared alone (Rojas Ripari et al. 2019a). Therefore, our estimates of host response to fledgling calls can be regarded as conservative, since baywings appear to improve their discrimination abilities after having experience with their own fledglings. Considering all this, it seems reasonable to assume that if baywings are able to distinguish between calls of mimetic and non-mimetic fledglings a few days before fledging their own brood, they will also do so after fledging, i.e., at the time when fledgling discrimination actually occurs. Lastly, it is worthwhile to note that our experiment

resembled natural events of asynchronous fledging, which occur occasionally at baywing nests due to hatching asynchrony in parasitized broods (CAU pers. observ.). Hence, we are confident that our experiment provides a reliable test of baywings' discrimination abilities towards fledgling calls, despite having been conducted prior to fledging.

We did the experiment during days 9–11 post-hatching to assess host response to playbacks at a time as closest to the fledging age as possible, but without risking causing forced-fledging events with our manipulations. We tested the response of adult baywings at 13 nests that survived to that age. Sample size was small because baywings in our study area breed at low densities, and nest failure rates are high due to nest predation and brood parasitism (De Mársico et al. 2010). We used a repeated-measures design to statistically account for among-nest variation in intrinsic and extrinsic factors that could influence the effect of playbacks on host behaviour, such as the presence of helpers, the breeding experience of individuals or microhabitat characteristics. The attending adults at each nest were therefore treated as a "block" that received sequentially three playback treatments, each consisting of a 3-min broadcast of begging calls of screaming cowbird ("mimetic"), shiny cowbird ("non-mimetic") and baywing (control) fledglings, separated by a 10-min resting interval. A previous study using the same experimental design showed that this resting period was sufficient to avoid carry-over effects in baywing response to subsequent call treatments (Rojas Ripari et al. 2019b). Treatments began when the broadcast was first detected by one or more of the attending adults, as inferred by sudden changes in behaviour (i.e. becoming alert or restless, vocalizing repeatedly and/or moving towards the sound source). The order of treatments was randomly assigned to each nest. We numbered all possible sequences of playbacks of the three species (from 1 to 6) and randomly assigned a sequence to each nest using a dice.

Calls for broadcasts were obtained from audio recordings of fledglings (13–20 days old) performed under standardized conditions during a previous study (De Mársico et al. 2012). These individuals were removed from the nest when they were 8–10 days old, taken to the laboratory and hand-reared to nutritional independence (see De Mársico et al. 2012 for details). We could not statistically assess the degree of acoustic similarity between begging calls of hand-reared and wild fledglings due to lack of sufficient samples for comparison. Yet, we assumed that call samples used in this study were representative of the natural fledgling calls of each species based on previous studies that showed a little influence of the rearing environment on the acoustic structure of begging calls in shiny and screaming cowbirds (Tuero et al. 2016; Rojas Ripari et al. 2019b). We used vocalizations of at least seven different individuals per species (eight baywings, seven screaming cowbirds and eight shiny cowbirds)

to avoid pseudoreplication. Each recording was converted to a spectrogram using default settings in Raven Pro 1.4 (Bioacoustics Research Program 2014). Spectrograms were then visually inspected to extract 10–20 good-quality calls per individual. With the selected calls, we created 60-s broadcast sequences (one per individual fledgling) using Raven Pro 1.4 editing tools, standardizing call rate (1 call per second) and root mean square (RMS) amplitude within and between treatments (Fig. 1).

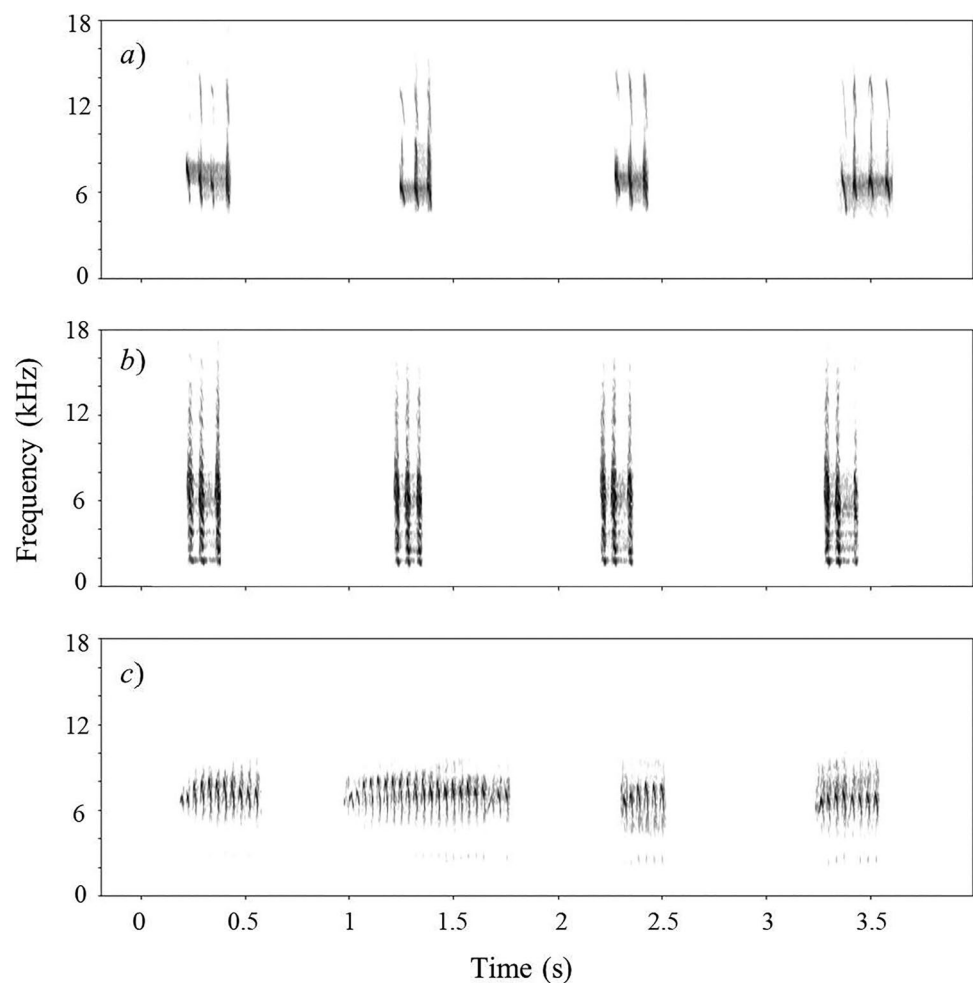
To carry out the playback experiment, we placed a loudspeaker (Ipok, China) 1–2 m away from the focal nest, in order to avoid interference with the begging calls of nestlings (see video SI 2). The loudspeaker was attached to the vegetation with duct tape and connected through a cable to a wav/mp3 audio player (Zoom H4n, USA). A full HD camcorder (Sony Hdr-Cx110) was mounted on a tripod at ~5 m from the nest to record baywings' responses. We placed the equipment as quickly as possible to minimize disturbance at the nests. Then, we allowed the attending adults to habituate to the experimental setting for 15 min before starting broadcast sessions. In all cases,

there was at least one adult baywing perched near the focal nest when the playback started. Playback was done from a hide placed 5–10 m away from the nest, and at the same time, focal observations were conducted in real time using 10×50 binoculars. Playback volume was adjusted by ear to match the natural sound level of host and parasite fledglings and kept constant at each nest. Likewise, the distance between the loudspeaker and the nest was the same for the three call treatments within each “block”. It was not possible to record data blind because our study involved focal animals in the field.

Data analysis

To quantify baywings' responses to each begging call type, we extracted four variables from video recordings and focal observations: 1) “latency”, measured as the time elapsed in seconds from the beginning of the playback treatment until the first baywing perched within a radius of 50 cm from the speaker; 2) “frequency”, defined as the number of times at least one adult baywing entered a radius of 50 cm around

Fig. 1 Representative spectrograms of the begging calls used in the playback experiment corresponding to *a*) baywing, *b*) screaming cowbird and *c*) shiny cowbird fledglings (13–20 days old)



the speaker during the 3-min playback period; 3) “recruitment”, defined as the ratio between the maximum number of baywings that approached the speaker simultaneously during the treatment (within a radius of 50 cm) and the total number of attending adults at the time of the playback period; and 4) “duration”, defined as the total time in seconds during which there was at least one adult baywing within a radius of 50 cm from the speaker.

We tested for differences among treatments in the latency to respond using Cox proportional hazard models, as suggested by Jahn-Eimermacher et al. (2011) for right-censored data. Models included playback treatment (baywing, screaming cowbird, shiny cowbird), treatment order (first, second, third) and brood composition (host chicks only, host and screaming cowbird chicks, host and shiny cowbird chicks) as fixed categorical factors, and nest identity as a random effect to account for repeated measures on each nest. We checked model assumptions of proportional hazards and ran the models using the R CRAN packages *survival* (Therneau, 2020a) and *coxme* (Therneau 2020b).

To analyse the effect of playback type on the frequency and recruitment variables, we used generalized linear mixed models (GLMM) with playback treatment and treatment order as explanatory variables and nest identity as a random effect. Given that nests varied in brood composition, which was manipulated as part of a different study (Ursino 2016), we also included this variable as a fixed factor in the models. We applied the experiment to baywings that were rearing broods with host chicks only ($n=5$ nests), with host chicks plus a screaming cowbird chick ($n=5$ nests) and with host chicks plus a shiny cowbird chick ($n=3$ nests). Models were fit by a Laplace approximation (Bolker et al. 2009) using the *lme4* package (Bates et al. 2015), with Poisson distribution and log link for frequency, and binomial distribution and logit link for recruitment. These models consistently estimated random-effect variance as exactly zero, suggesting that among-nest variance was negligible relative to residual (i.e., within treatment) variance. Therefore, following Pasch et al. (2013), we dropped the random variance component from the model, which has no effect on any other estimated parameter. Model fitting was checked by visually inspecting diagnostic plots and using likelihood ratio (LR) tests against the null model (i.e., the model without predictor variables).

The effect of playback treatment on the duration of the response was analysed using a hurdle negative binomial model. Hurdle models allow accounting for zeros due to lack of response by modelling separately the binary (yes/no) response process and response duration (zero-truncated count data). Models were fitted using the package *glmmTMB* (Brooks et al. 2017) with playback treatment, treatment order and brood composition as explanatory variables. Nest identity was first included as a random effect, but the among-nest variance estimate was nearly zero (estimate = 3.18×10^{-15} ,

$SD = 5.64 \times 10^{-8}$); thus, we excluded this term from the model. Dropping the random factor did not affect any other parameter estimate and improved model fitting as checked by simulating residuals using the package *DHARMA* (Hartig 2019).

For all response variables, the significance of fixed effects was tested using LR tests between the full model and the model without the corresponding parameter. Non-significant effects were then excluded from the final models. Then, post hoc pairwise comparisons among playback treatments and calculation of 95% confidence intervals for contrast estimates were done using the *emmeans* package (Lenth 2019). All statistical analyses were performed in R 4.0.2 (R Core Team 2019). For all statistical tests, significance was set at $P < 0.05$.

Results

Baywings responded to broadcasts of screaming cowbird, conspecific and shiny cowbird begging calls at 100%, 69% and 23% of the experimental nests, respectively. Overall, playback treatment had a significant effect on the four response variables, and host response was independent of treatment order and brood composition for all these variables (Table 1 and see video in SI 2).

Regarding the latency to respond, baywings approached the loudspeaker at a 79% lower rate when presented with non-mimetic shiny cowbird calls relative to control baywing calls (hazard ratio: 0.21, 95% CI: 0.09–0.87, $P = 0.021$), whereas broadcast of screaming cowbird calls induced a nearly fourfold increase in that rate relative to control calls (hazard ratio: 3.69, 95% CI: 1.22 – 11.15, $P = 0.006$; Fig. 2). The frequency of approaches to the loudspeaker decreased in response to shiny cowbird calls compared with baywing calls and increased in response to screaming cowbird calls compared with the other call types (Table 2; Fig. 3a). Screaming cowbird calls attracted more individuals than baywing and shiny cowbird calls, and there was also a tendency for baywing calls to increase recruitment compared to shiny cowbird calls; however, post hoc comparisons showed no significant differences between the latter call types (Table 2; Fig. 3b). Finally, response duration did not differ between baywing and screaming cowbird calls but was significantly shorter in response to shiny cowbird calls (Table 2, Fig. 3c).

Discussion

This study presents the first evidence on the ability of adult baywings to discriminate between begging calls of own-species' and foreign fledglings, in the absence of any

Table 1 Significance of the explanatory variables on host response to playbacks of fledgling begging calls. Response variables were the latency for the first adult baywing to approach the loudspeaker within a radius of 50 cm (“latency”), the number of times an adult baywing approached the loudspeaker at less than 50 cm (“frequency”), the maximum number of baywings approaching the speaker simultaneously (within a radius of 50 cm) relative to the total number of attending adults (“recruitment”) and the total time spent by at least one adult baywing at less than 50 cm from the loudspeaker during 3-min playback sessions (“duration”). Statistical models included playback treatment, treatment order and brood composition as fixed effects and nest identity as a random effect (see Methods for details on variable definitions and model specifications). Significance of fixed effects was tested using likelihood ratio tests between the full model and the model without the corresponding parameter. Columns show the test statistic, degrees of freedom and p-value for each model comparison. Sample size is 13 baywing nests (five nests with host chicks only, five with host chicks plus a screaming cowbird and three with host chicks plus a shiny cowbird). Alpha level was 0.05 for all tests

Response variable	Explanatory variable	χ^2	df	P
Latency	Playback Treatment	25.40	2	<0.0001
	Treatment Order	0.12	1	0.73
	Brood Composition	2.93	2	0.23
Frequency	Playback Treatment	40.43	2	0.0001
	Treatment Order	0.004	1	0.95
	Brood Composition	2.26	2	0.32
Recruitment	Playback Treatment	24.34	2	0.0001
	Treatment Order	0.01	1	0.92
	Brood Composition	1.18	2	0.55
Duration	Playback Treatment	10.38	2	0.006
	Treatment Order	1.67	2	0.20
	Brood Composition	3.01	2	0.22

functionally relevant cue that could be associated with seeing a host or parasitic fledgling. Our playback experiment showed that baywings were overall less responsive to non-mimetic begging calls of shiny cowbird fledglings than to

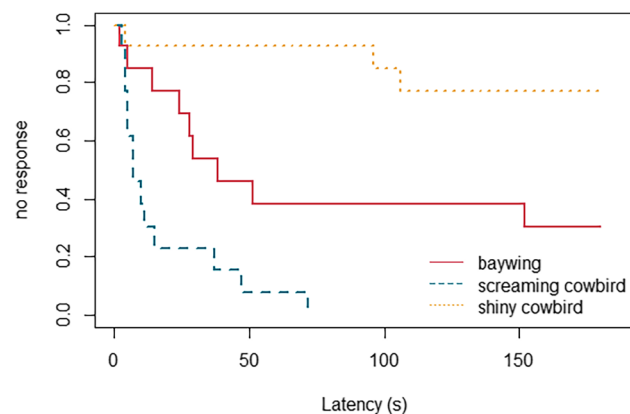


Fig. 2 Kaplan–Meier curves for latency (in seconds) in response to the playback treatments. The curves indicate the proportion of nests in which there was no response to each call type as a function of time since the treatment began ($n = 13$ nests)

conspecific and screaming cowbird calls. These results suggest that baywings cue in on species-specific acoustic signals, in addition to visual traits, to discriminate between their own and foreign fledglings, thus supporting the idea that vocal resemblance with host young in screaming cowbird fledglings plays a role in overcoming host discrimination. This conclusion is strengthened if we consider that shiny cowbird calls have been shown to stimulate efficiently parental provisioning in both host and non-host species (Gloag and Kacelnik 2013), yet they were ineffective at attracting the attention of baywing hosts. The lower responsiveness to shiny cowbird calls is in agreement with previous work showing that baywings delivered food at lower rates when broods were supplemented with begging calls of shiny cowbird nestlings *versus* begging calls of host and screaming cowbird nestlings (Ursino et al. 2018).

The present study also revealed that baywings were more attracted to begging calls of screaming cowbirds than conspecific fledglings. Such a differential response was not observed in earlier studies that compared host response to begging calls of 8-day-old baywing and screaming cowbird nestlings (Ursino et al. 2018; Rojas Ripari 2019b). Altogether, these results might indicate that screaming cowbirds have not only evolved vocal mimicry of baywing young, but also develop acoustic traits that intensify host species stimulation by the time they leave the nest. The exaggeration of begging signals is a feature common to several brood-parasitic species and is thought to be adaptive for eliciting adequate levels of provisioning and/or competing with host nestlings (Kilner and Davies 1999; Gloag and Kacelnik 2013; Tuero et al. 2016; Jamie et al. 2020). Screaming cowbirds typically fledge alongside baywing nestmates with which they must compete for parental care over a prolonged post-fledging period (Fraga 1998; De Mársico et al. 2010). It therefore seems plausible that the acoustic structure of their begging calls reflects the dual function of signalling recognition cues to hosts and exaggerating the stimulus to compete for parental attention after fledging.

Tanaka and Ueda (2005) made a distinction between manipulative signals of parasitic young that amplify components already present in host’s begging displays (i.e. supernormal stimulus) and those that are not part of the host’s parent–offspring communication but exploit the host’s pre-existing sensory biases (Tanaka and Ueda 2005). Which of these mechanisms is at play in screaming cowbirds is yet to be determined. More detailed analyses of begging call structure combined with playback experiments would help to dissect the acoustic traits involved in offspring recognition by baywing hosts and their exploitation by parasitic fledglings.

Begging call similarity between brood parasites and their hosts has been reported from many systems, but relatively few studies have assessed it quantitatively, and even fewer have examined its function (reviewed in Jamie and Kilner

Table 2 Post hoc pairwise comparisons among playback treatments following model analyses (see [Methods](#) for model specifications). Response variables were the number of times an adult baywing approached the loudspeaker at less than 50 cm (“frequency”), maximum number of baywings approaching the speaker simultaneously (within a radius of 50 cm) relative to the total number of attending adults (“recruitment”) and the total time spent by at least one adult baywing at less than 50 cm from the loudspeaker during 3-min play-

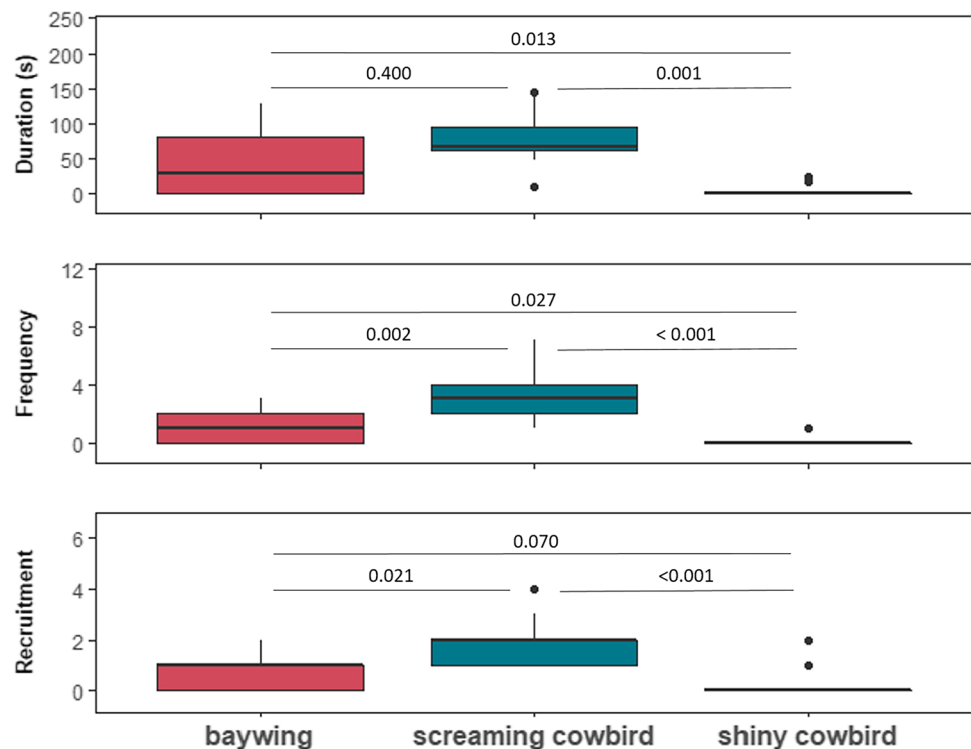
back sessions (“duration”). Values are contrast estimates (on log scale) with the corresponding standard errors, 95% confidence intervals and significance. Sample size is 13 nests (five nests with host chicks only, five with host chicks plus a screaming cowbird and three with host chicks plus a shiny cowbird). Baywings at each nest were presented sequentially with the three playback treatments (treatment order was rotated among nests)

Response variable	Pairwise comparison	Estimate \pm SE	95% CI	<i>P</i>
Frequency	screaming cowbird vs. baywing	1.006 \pm 0.302	0.309, 1.702	0.002
	shiny cowbird vs. baywing	-1.609 \pm 0.632	-3.070, -0.149	0.027
	screaming cowbird vs. shiny cowbird	2.361 \pm 0.468	1.264, 3.457	<0.001
Recruitment	screaming cowbird vs. baywing	1.393 \pm 0.524	0.165, 2.620	0.021
	shiny cowbird vs. baywing	-1.421 \pm 0.645	-2.932, 0.089	0.070
	screaming cowbird vs. shiny cowbird	2.814 \pm 0.654	1.281, 4.301	<0.001
Duration	screaming cowbird vs. baywing	0.300 \pm 0.228	-0.860, 0.260	0.400
	shiny cowbird vs. baywing	-1.109 \pm 0.367	-2.012, -0.206	0.013
	screaming vs. shiny cowbird	1.409 \pm 0.354	0.539, 2.278	0.001

2017). In this regard, this study adds new insights into the acoustic discrimination abilities of baywings and provides evidence in line with the hypothesis that screaming cowbirds have evolved vocal mimicry as a counter-defence against host rejection. These findings expand existing knowledge about begging call mimicry in brood-parasitic nestlings (Langmore et al. 2003, 2008; Jamie and Kilner 2017; Noh et al. 2018) by showing that similar coevolutionary interactions between parasites and hosts could occur at the

fledgling stage. Like Horsfield’s bronze-cuckoo nestlings, screaming cowbirds follow an innate “program” of vocal development that produces begging calls structurally and functionally equivalent to those of baywing nestlings (Rojas Ripari et al. 2019b). However, unlike bronze-cuckoos (Langmore et al. 2008), screaming cowbirds show little plasticity in vocal development, still expressing the innate baywing-like call structure when cross-fostered to nests of another species (Rojas Ripari et al. 2019b). This

Fig. 3 Box plots showing the response of adult baywings to playback of begging calls of baywing (control), screaming cowbird (mimetic) and shiny cowbird (non-mimetic) fledglings. Calls were broadcast from a loudspeaker placed near baywing nests having 9–11-day-old nestlings. Response variables were: a) duration measured as the total time spent by at least one baywing at less than 50 cm from the loudspeaker, b) frequency measured as number of times at least one baywing approached the loudspeaker and c) recruitment as number of responding adults relative to total group size. Sample size was 39 measures in 13 nests for all response variables. Boxes indicate the inter quartile range (IQR), the line within each box indicates the median, and whiskers depict 1.5*IQR. Dots outside the box represent outliers



mode of development is consistent with the expectation of a genetically fixed begging call structure in host-specialist brood parasites, for which relying on environmental cues to adjust their begging calls might be redundant or even maladaptive (Jamie and Kilner 2017). It is worthwhile to recall that our playback experiment used begging calls from hand-reared host and parasitic fledglings; therefore, the results further corroborate that having social experience with baywings during the transition to the juvenile stage is not necessary for the acquisition and expression of host-specific acoustic signals in screaming cowbirds.

Mimicry in response to host discrimination seems the most plausible explanation for both vocal and visual resemblance of host young by screaming cowbird fledglings (Fraga 1988; De Mársico et al. 2012). However, we cannot fully rule out the alternative hypothesis that the observed vocal similarity is the result of parasites “tuning” into host’s pre-existing sensory biases. Under such a scenario, screaming cowbirds would have evolved begging calls that matched innate preferences of baywing hosts. Such “tuning” would be adaptive since it can serve parasitic fledglings to attract parental care, but it cannot be regarded as mimicry in the sense of a coevolved adaptation against a host’s anti-parasitic defence (Grim 2005, 2013). This idea opens an intriguing possibility, namely that selection has been acting on host young to match the begging signals of their parasites rather than the other way around (Hauber and Kilner 2007). Phylogenetic comparative analysis of begging calls would be useful to disentangle if vocal similarity between screaming cowbirds and baywings represents true mimicry, sensory exploitation or both (Rothstein 1990; Grim 2005; Anderson et al. 2009).

The results presented here supports the existence of a general ability in baywings to discriminate between baywing-like and non-mimetic fledgling begging calls in the absence of any visual stimuli. Although this study was conducted during the late nestling stage, the robust differential response observed during playbacks points towards a role of acoustic signals in fledgling recognition by baywings. Indeed, the statistical analysis indicates that variation in host response between playback treatments was large and consistent enough to produce significant results despite the low sample size. Our data also showed that current brood composition did not affect host response to playbacks, as it has been found previously in [playback experiments](#) using nestling calls (Ursino et al. 2018; Rojas Ripari et al. 2019b). Although this lack of effect should be taken cautiously given the low statistical power, the observed pattern points towards the existence of host’s innate or learned templates for fledgling recognition. Nevertheless, previous work involving cross-fostering of shiny cowbird nestlings to baywing nests rather suggests that the host’s discrimination abilities are context dependent

and based on simultaneous comparison between its own and foreign young (Soler 2014; Rojas Ripari et al. 2019a). This apparent discrepancy highlights the fact that fledgling discrimination by baywings is likely a complex process involving at least two sensory modalities. Clearly, more research is needed to fully understand how baywing hosts integrate visual and vocal cues in fledgling recognition and the cognitive mechanisms underlying their rejection decisions.

In conclusion, this study provides evidence for the first time about the function of begging call similarity between host and brood-parasitic fledglings as an adaptation to escape host discrimination. Future studies that further examine the function of begging call similarity in other host–parasite systems will help to better understand how widespread vocal mimicry is among brood parasites, and, more generally, increase our knowledge about the role of acoustic signals in host manipulation by parasitic young.

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Data availability Lama F, Ursino CA, Reboreda JC, De Mársico MC (2022) Acoustic discrimination by hosts favours vocal trickery in fledglings of the brood-parasitic screaming cowbird. Dryad, Dataset, <https://doi.org/10.5061/dryad.wpzgmsbkh>

Declarations

Ethical approval Experimental manipulations were conducted under a permit from the local authority (Organismo Provincial para el Desarrollo Sostenible, OPDS, Res. 202/12). All applicable national institutional guidelines for the use of animals were followed. We did not detect any negative effect of playback treatments on nesting success. Six of the 13 experimental nests were visited on the days following the playback experiment, and in all cases, we could corroborate nest success through direct observations of banded fledglings out of the nest. Baywings tolerated the experimental set-up well and they typically resumed their normal parental activity as soon as we placed the equipment and moved away from the nest. There was no case of brood abandonment or undernourishment following the experiment.

Competing interests All authors declare that they have no affiliations with or involvement in any organization or entity with any financial interest or non-financial interest in the subject matter or materials discussed in this manuscript.

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