



Original Article

Host provisioning behavior favors mimetic begging calls in a brood-parasitic cowbird

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The vocalizations of some young brood-parasitic birds closely resemble those of their host's young. Such similarities might arise because hosts bestow the greatest parental care in response to their own species' call type. We used a playback experiment to assess the effectiveness of the nestling call structures of 2 brood parasites, the specialist screaming cowbird (*Molothrus rufoaxillaris*) and the generalist shiny cowbird (*M. bonariensis*), in stimulating parental provisioning in a shared host, the baywing (*Agelaioides badius*). Screaming cowbird begging calls closely resemble those of baywing young and thus should best exploit any bias for species-specific cues. Shiny cowbird calls, in contrast, are unlike baywings but can instead exploit nonspecific sensory biases for long call duration and syllable repetition. We found that playback of screaming cowbird's mimetic calls elicited increases in feeding rates equivalent to those of playback of the host's own young, whereas shiny cowbird calls failed to increase provisioning rates above those of no-broadcast control sessions. These results indicate that baywings discriminate between nestling call structures in favor of their own species calls when adjusting parental investment and support the view that selection for optimal host provisioning can favor vocal mimicry by parasitic offspring.

Key words: begging call, brood parasitism, cowbird, mimicry, *Molothrus*, parental care.

INTRODUCTION

The young of obligate avian brood parasites face the challenge of obtaining adequate parental care from species whose parenting behaviors evolved to nurture their own kind. Parasitic chicks often thus generate begging signals that “tune into” the parent–offspring communication system of their host (Davies 2011). Such tuning is particularly evident in the vocal component of nestling begging displays, which parents use to adjust nest provisioning rates and allocate food within the brood (Kilner et al. 1999; Leonard and Horn 2001). Many parasitic chicks manipulate host parental behavior in their favor by exploiting host's biases for nonspecific acoustic features: for instance, parasites call more loudly or more rapidly to induce host parents to deliver more food than they would to their own young (Dearborn 1998; Lichtenstein and Sealy 1998; Kilner and Davies 1999; Lichtenstein and Dearborn 2004; Gloag and Kacelnik 2013).

Parasitic nestlings could also optimize the provisioning behavior of their adoptive parents by mimicking the acoustic structure

of the begging call itself, that is, by exploiting host-specific vocal cues (Langmore et al. 2008; Anderson et al. 2009). As for non-structural call features, parasites' mimicry of call structure may be a form of tuning to pre-existing parental bias, if hosts tend to provision more in response to familiar call types than foreign ones. Alternatively, vocal mimicry by parasites may reflect coevolution, where host preferences for own call type evolved in response to parasitism as a form of defense. Call structure does appear to play a role in chick rejection decisions by some hosts; Superb fairy wrens (*Malurus cyaneus*) are less likely to abandon Horsfield's bronze-cuckoo (*Chalcites basalus*) chicks, which produce fairy wren-like begging calls, than shining bronze-cuckoo (*Chalcites lucidus*) chicks, which do not (Langmore et al. 2003). Further, Horsfield's bronze cuckoos develop different host-matched calls depending on which host species rears them (Langmore et al. 2008), and fairy wrens use a vocal “password” to recognize their own young from other chicks making structurally equivalent calls, presumably a counter-adaptation made necessary by parasites' vocal mimicry (Colombelli-Négrel et al. 2012). Whether selection is expected to favor call structure mimicry on the basis that it increases parental provisioning, however, remains unclear. The notion that hosts should always prefer their own species' calls seems intuitive; yet,

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the most direct evidence for call structure's role in exploiting host provisioning comes from the shiny cowbird (*Molothrus bonariensis*), an extreme generalist parasite whose calls are not mimetic, but rather function like nonspecific call cues via a syllable repetition that can simulate exaggerated call rate in hosts or non-hosts with simple call types (Gloag and Kacelnik 2013).

Here, we use a playback experiment to test the relative effectiveness of the begging calls of 2 brood parasites, the screaming cowbird (*M. rufoaxillaris*) and the shiny cowbird in stimulating parental provisioning in the nest of a shared host, the baywing (*Agelaioides badius*). These parasites differ in their host use and their begging call structure. Shiny cowbirds are generalists using at least 200 other hosts in addition to baywings (Lowther 2000). Regardless of host, shiny cowbird calls are long, polysyllabic, and unlike baywing calls (Gloag and Kacelnik 2013). Screaming cowbirds, in contrast, are specialists on baywings, are visual mimics as fledglings, and produce calls that are structurally similar to baywing calls, consistent with vocal mimicry (De Marsico et al. 2012). If baywings respond most favorably to their species-specific call structure, then screaming cowbirds "mimetic" call should elicit higher provisioning. Alternatively, if nonspecific call features, such as call length or syllable number, are key to stimulating provisioning by baywings, then shiny cowbird calls should elicit higher provisioning rates than screaming cowbird calls.

METHODS

The study was conducted at "Reserva El Destino" (35°80'80"S, 57°82'30"W) located within Parque Costero del Sur Biosphere Reserve (MAB-UNESCO) in the province of Buenos Aires, Argentina, during the breeding seasons (November–February) 2012–2013 and 2013–2014. The study area comprises flooding grasslands with patches of woodland dominated by tala (*Celtis ehrenbergiana*) and coronillo (*Scutia buxifolia*). Baywings, screaming cowbirds and shiny cowbirds are year-round residents in the area. Baywings breed in closed nests built by other species, mainly furnariids, and in secondary cavities located in trees at a height of

1.5–5 m. They are facultative cooperative breeders with one or more helpers often joining the breeding pair after the eggs hatched and assisting them in brood provisioning and nest defense (Fraga 1991; Ursino et al. 2011). Screaming and shiny cowbirds annually parasitize roughly 92–100% and 16–23% of baywing nests, respectively, in the study area (De Marsico et al. 2010).

To assess baywing's response towards "mimetic" and "non-mimetic" parasite begging calls, we compared the provisioning effort of adult baywings at 25 nests in which their broods' begging calls were supplemented by the broadcast of a screaming cowbird ("mimetic"), a shiny cowbird ("non-mimetic"), or an additional baywing nestling (Figure 1). Calls for broadcasts were taken from audio recordings of 8 day-old nestlings made at unparasitized baywing nests (baywing calls, $n = 10$), naturally parasitized baywing nests (screaming cowbird, $n = 10$) or naturally parasitized house wren (*Troglodytes aedon*) nests (shiny cowbird, $n = 10$). Shiny cowbird call structure does not vary between hosts (Tuero et al. 2016). From each recording, we created 10 s broadcasts of 10–15 calls of 1 focal individual with call rate (1.9 calls per second) and RMS (root mean square) amplitude standardized across call samples using Raven Pro 1.5 (Bioacoustics Research Program 2014).

Experimental baywing nests had 4 chicks (i.e. the modal brood size) including, at most, 1 parasitic chick ($n = 6$ unparasitized nests, 12 nests parasitized by screaming, and 7 nests parasitized by shiny cowbird). Because screaming and shiny cowbirds have a shorter incubation period than baywings (incubation periods: 13 days for baywings, and 12 days for shiny and screaming cowbirds), same-age broods with parasites were created by removing any parasite eggs laid prior to incubation and then returning 1 parasite egg to the nest on the second day of incubation. We did not manipulate all nests to be unparasitized in order to minimize impacts on parasite populations and to allow nests to be used for a subsequent experiment. Instead, we accounted for variation in brood composition across baywing nests by using a repeated-measures design in which we presented all call treatments sequentially to each nest, and by including brood composition as a variable in our analysis.

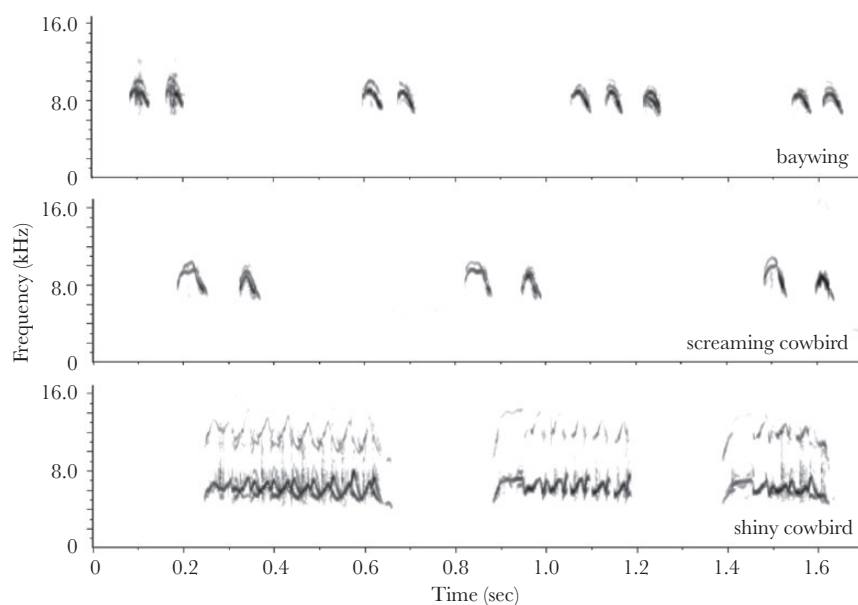


Figure 1

Representative spectrograms of the begging calls used in the playback experiment corresponding to 8 days-old nestlings of (a) baywing, (b) screaming cowbird, and (c) shiny cowbird. Call rate and RMS amplitude were standardized within and among call treatments.

When chicks were 5–6 days post hatch, the nests were fitted with a keychain microspeaker (2 cm³, Purelygadgets Ltd) embedded in the material of the nest wall, connected to an MP3 player. In addition, an infrared microcamera (Handykam, UK) was placed inside the nest and connected to a digital video recorder (PV-500 Lite, LawMate Int., TW) to watch and record the experiment in real time from a hide 5–8 m away from the nest. We placed the equipment as quickly as possible to minimize disturbance and to allow baywings to become familiar with the experimental setting. Baywings resumed their normal behavior shortly after our manipulations. The experiment was conducted on the next morning (7 am to 12 pm). Each nest received four 40-min playback sessions: 1) screaming cowbird calls (specialist brood parasite), 2) shiny cowbird calls (generalist brood parasite), 3) baywing calls (host), and 4) no broadcast (control). Every session was preceded by a 20-min interval of no broadcast and the order of treatments was rotated among nests. During each session, we broadcast the playback treatment each time an adult entered the nest and until it left or began to brood or preen the chicks. Playback volume was set to match the natural amplitude of chicks' begging calls in baywing nests and kept constant throughout the experiment. The number of feeding visits by baywings during each playback session was recorded in real time and double-checked from video recordings. Whenever possible, we also calculated the amount of food delivered per visit by visually estimating prey size relative to host bill width (%BW). All data on food provisioning was scored by 1 researcher (C.A.U.). Baywing group size per nest was 2 (no helpers) or 3 breeding pair plus 1 helper (mean no. helpers \pm variance = 0.5 ± 0.3). We never observed changes in baywing group size (e.g. recruitment of extra helpers) during experimental broadcasts.

The effect of playback treatments on the number of feeding visits by baywing adults was analyzed using generalized linear mixed models (GLMMs) with log link function and Poisson error structure. Models were fitted using the `glmer` function included in `lme4` package in R 3.1.2 (R Core Team 2014; Bates et al. 2015). Explanatory variables were playback treatment, treatment order, and clutch composition (presence/absence of parasites), with nest identity included as a random effect. We first fitted the full model and then removed nonsignificant terms at $P < 0.05$ to obtain a minimal model. We conducted a goodness of fit F-test of the minimal model against the null model, which included an intercept only and a variance parameter for the random effect (i.e. nest identity). To test if baywing parents adjust their provisioning effort via the amount of food delivered per visit we compared the median prey size among playback treatments using the nonparametric Friedman test.

Ethical considerations

The study was conducted under license from the local authority on protected areas (Provincial Organism for Sustainable Development, Buenos Aires, Argentina) and complies with the current laws of Argentina. No animal was harmed during experimental manipulations and we minimized disturbances at nests as much as possible to reduce the risk of abandonment or predation. We continued to monitor all experimental baywing nests until chicks fledged or the nest was depredated. No nest was abandoned as a result of the playback experiment and predation rates of experimental nests were similar to unmanipulated nests.

RESULTS

Baywings' provisioning behavior differed among playback treatments (Table 1, Figure 2). Baywings increased the number of

feeding visits in response to conspecific and screaming cowbird (i.e. "mimetic") calls, but not in response to shiny cowbird (i.e. "non-mimetic") calls, compared to no-broadcast sessions (Table 1, Figure 2). The number of feeding visits did not differ between screaming cowbird and baywing call treatments (estimate \pm SE: 0.11 ± 0.08 , $P = 0.18$), but it was higher in response to screaming cowbird than shiny cowbird calls (estimate \pm SE: 0.26 ± 0.09 , $P = 0.002$). Baywing calls tended to elicit more feeding visits than shiny cowbird calls, but not significantly so (estimate \pm SE: -0.15 ± 0.09 , $P = 0.087$). Treatment order and clutch composition had no significant effect on the number of feeding visits (Table 1). A goodness of fit F-test indicates that the minimal model with playback treatment as an explanatory variable and nest identity as a random effect fitted the data significantly better than the null model ($P < 0.001$). Prey size delivered to the brood did not differ among treatments (Friedman test: $X^2_3 = 3.07$, $P = 0.38$) as baywings usually brought a single, relatively large prey item, such as a locust, caterpillar, or moth, per feeding trip.

DISCUSSION

Baywing hosts provisioned their nests more in response to the begging calls of the specialist screaming cowbird, whose calls match those of baywings' own chicks, than in response to the non-mimetic calls of the generalist shiny cowbird. This was despite the fact that shiny cowbird calls are longer in duration, and that increased call duration is a cue commonly used by passerines to signal nestling hunger and so provoke increased provisioning (Leonard and Horn 2001; Magrath et al. 2010). Baywings' greater responsiveness to baywing-like call types reveals that chick begging call structure, independent of call amplitude or rate, can play an important role in determining host provisioning decisions to parasitized broods, and that mimetic begging signals can benefit parasites by increasing host provisioning.

Vocal similarity in screaming cowbird chicks may have evolved either to tune into baywing's pre-existing sensory biases (i.e. those that exist independent of baywings status as a host, Davies 2011) or as a coevolved counter-defense to baywing's discrimination against foreign call types. In either case, screaming cowbirds may further benefit from their host-like call type at the fledgling stage. Baywings do not reject nestling parasites in mixed broods, but screaming cowbirds enjoy higher survival as fledglings than shiny cowbirds do, presumably due to differences in host care during this critical phase (Fraga 1998; De Mársico et al. 2012). Although the exact cues used

Table 1
Results of GLMM analysis with log link function and Poisson error structure ($n = 25$)

Parameter	Estimate \pm SE	<i>P</i>	95% CI	
Intercept	2.15 \pm 0.12	<0.001*	1.92–2.38	
Playback treatment	baywing	0.23 \pm 0.09	0.009*	0.06–0.41
	screaming	0.35 \pm 0.09	<0.001*	0.17–0.52
	shiny	0.08 \pm 0.09	0.37	-0.10–0.27
Playback order	-0.02 \pm 0.03	0.46	-0.08–0.03	
Clutch composition	-0.02 \pm 0.11	0.85	-0.25–0.21	

Response variable was the number of feeding visits by baywings and explanatory variables were playback treatment (i.e. call type), treatment order and clutch composition, with nest identity included as a random effect. No-broadcast treatment (control) was taken as the reference level.

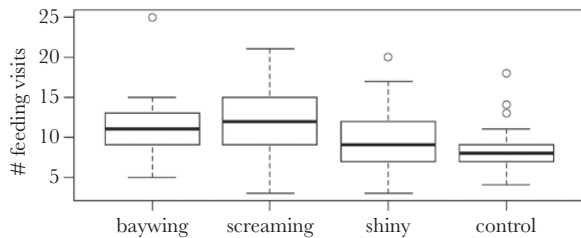


Figure 2

Boxplots of the number of feeding visits at experimental baywing nests during each playback treatment.

by baywing parents to discriminate between own and foreign fledglings remain uncertain, begging calls can be important drivers of host parent attention after fledging (Lama et al., unpublished data) and it seems probable that the vocal preferences observed in this study continue to shape provisioning decisions once chicks have left the nest.

Could the observed differences in provisioning rates we observed arise from host's particular discrimination against shiny cowbird calls, rather than an active preference for baywing (and thus screaming cowbird) calls? In this scenario, baywings have evolved to recognize and ignore the distinctive tremulous call of shiny cowbirds, but otherwise respond similarly to a wide variety of nestling call types. This possibility can be ruled out only by assessing baywings' relative provisioning responses to other non-mimetic begging calls; however, it is difficult to explain the remarkable vocal resemblance between nestlings of the phylogenetically distant screaming cowbird and baywing unless these hosts have recognition mechanisms that involve innate or learned preference for own-species calls (Fraga 1998; De Marsico et al. 2012). Also left open in our experiment is the possibility that the observed increases in nest provisioning were due to broadcasts influencing the behavior of the brood, rather than adult baywings directly. Previous studies in cowbirds have shown that parasitic chicks can influence the begging intensity of host nestmates and vice versa, which in turn may influence nest provisioning rates and food allocation (Dearborn 1998; Pagnucco et al. 2008; Rivers 2009; Tuero et al. 2016 but see Grayson et al. 2013). Both direct and indirect mechanisms for increased provisioning could drive selection for mimicry: that is, mimicry in order to influence parents provisioning and mimicry in order to "win" in the scramble competition for food in the nest among siblings. In the baywing-cowbird case, direct effects on adult responses seem most likely. Our sample included nests with varying brood composition and we standardized call rate and amplitude within and among playback treatments. Therefore, to explain the results on the basis of changes in brood-level begging signals, it would be necessary that both host and parasite chicks similarly adjust their begging effort in response to baywing-like versus non-mimetic shiny cowbird calls within the brood, and that such changes be consistent across experimental broods of varying parasitism status.

The distinctive tremulous begging call of the shiny cowbird is a highly effective stimulus of provisioning by one of its common hosts, the house wren (Gloag and Kacelnik 2013). Shiny cowbird calls also provoked the same effect on a naive species (the great tit, *Parus major*) with which it shares no coevolutionary history, suggesting that it is able to tune into relatively widespread sensory biases among passerines for call duration and/or syllable number per unit time (Gloag and Kacelnik 2013). Baywings must, therefore,

be using different rules to these hosts to determine provisioning effort to their broods. In their case, a species-specific cue (structure) trumps the nonspecific cue of call duration. Herein lies the dilemma for generalist parasites, which cannot respond optimally to every host: faced with host discrimination they must either evolve mimicry, becoming locked into an evolutionary path of host specialism, show phenotypic plasticity and adjust the signals to host preferences through a learning process, or suffer reduced reproductive success in that host. The severity of this reduced success will vary. Shiny cowbird nestlings are still fed in baywing nests, at least when reared alongside host chicks. Indeed, despite "bad" vocal tuning, shiny cowbird chicks growth rate in baywing's nests is not detectably worse than it is in other hosts (De Marsico and Rebores 2008; De Marsico et al. 2010). Provided that they can compete adequately for food within the brood, shiny cowbirds can exploit the vocal signals of host nestmates to provoke parental care (Kilner et al. 2004; Gloag et al. 2012). Alternatively, shiny cowbird chicks may compensate for their mismatched begging calls by begging louder or faster than their nestmates. It would be interesting to compare provisioning rates to shiny cowbird chicks reared with and without host nestmates to further assess the importance of begging signals in eliciting parental care from baywings. Specialist parasites of course experience the flip-side of this trade-off. They enjoy better provisioning rates in the host that they mimic, but may have less potential to switch hosts. Parental preferences such as this, whether they exist prior to parasitism pressure or evolve in response to it, could therefore drive specialization in host use, and ultimately speciation, by locking parasites into particular evolutionary trajectories.

In summary, this study shows that begging call structure can play a role in eliciting host parental behavior and that generalist and specialist brood parasites differ in their effectiveness to manipulate host provisioning through their begging calls. Further knowledge of host's responses towards both structural and nonstructural begging features will inform our understanding of the evolution of begging displays in brood parasites and the outcomes of coevolutionary interactions between parasites and hosts at the nestling stage.

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Author Contributions: C.A.U. performed the experiment, analyzed the data, and drafted the manuscript. R.G. recorded shiny cowbird begging calls and edited the call sequences for the playback experiment. J.C.R. supervised the project. M.C.D.M. designed the experiment. All co-authors contributed substantially to interpreting the data and writing the paper, and all approved the submission.

Conflict of Interest: The authors have no competing interests

Data accessibility: Analyses reported in this article can be reproduced using the data provided by Ursino et al. (2017).

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