



Non-mimetic shiny cowbird nestlings escape discrimination by baywings in absence of host nest mates

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Abstract

Nestlings of obligate brood parasites must obtain resources from heterospecific hosts that are attuned to the solicitation behaviours of their own progeny. Failing to match the appropriate stimuli may result in suboptimal provisioning or even the starvation of parasite young. Parasitic nestlings could overcome it by sharing the nest with host young, as long as they are able to compete efficiently for parental feedings. Here, we examined if non-mimetic shiny cowbird (*Molothrus bonariensis*) nestlings reared alone fail to elicit sufficient parental care from the grayish baywing (*Agelaioides badius*), a host that discriminates between their own and parasitic nestlings based on species-specific begging cues. We manipulated baywing broods to assess the ability of shiny cowbird nestlings to elicit parental provisioning and survive without host nest mates. Host provisioning rates and survival did not differ between shiny cowbirds reared alone and host nestlings in singleton broods. Also, growth patterns of experimental nestlings reared alone were similar to those reported for shiny cowbirds reared alongside baywing young. Hence, we did not find support for the hypothesis that non-mimetic nestlings require the assistance of host nest mates to elicit sufficient parental care from its baywing host. Furthermore, we found that shiny cowbirds that were reared alone continued receiving care from baywings after fledging, unlike shiny cowbirds from mixed broods. Our results add evidence to the idea of opposing selective pressures on the evolution of nest mate acceptance in cowbirds and suggest context-dependent host's discrimination abilities that deserve further investigation.

Significance statement

The evolution of nest mate killing versus tolerance strategies is a long-standing question in the study of brood parasitism. Parasitic nestlings may benefit from sharing the nest with host young if they collectively induce more parental provisioning and the parasite can benefit from it. Host nest mates could also confer protection against discrimination when hosts respond preferentially to stimuli of their own kind. We examined this idea in a generalist brood parasite, the shiny cowbird (*Molothrus bonariensis*), and a host able to discriminate species-specific begging cues. The results showed that shiny cowbirds reared alone performed well and circumvent host discrimination also after leaving the nest. Our study supports the existence of trade-offs on the evolution of nest mate killing behaviours and adds evidence that context-dependent host's discrimination abilities similar to those observed towards parasitic eggs can be at play towards parasitic fledglings.

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Introduction

Young of obligate avian brood parasites rely entirely on their heterospecific hosts for parental care. They must then face the challenge of obtaining food from foster parents that are attuned to the solicitation behaviours of their own progeny. Nestlings demand food by using complex begging displays, in which they exhibit visual (gape exhibition, body posture) and vocal (begging calls) traits that can serve as signals for parents to adjust provisioning effort and allocate resources within the brood (Kilner et al. 1999; Leonard and Horn 2001; Glassey and Forbes 2002). Parasitic nestlings are thus expected to ‘tune’ their begging displays into their hosts’ parent-offspring communication systems to avoid host discrimination and obtain appropriate care (Davies and Brooke 1989; Langmore et al. 2003; Madden and Davies 2006).

Nestlings of many parasite species produce begging calls that allow them to effectively manipulate the host’s provisioning behaviour in their benefit. Such manipulation is evident in host-specialist parasites that mimic the begging call structure of host young (Langmore et al. 2008; Colombelli-Négrel et al. 2012; Rojas Ripari et al. 2018). Other parasites do not mimic any particular host, but they can achieve adequate provisioning by flexibly adjusting certain features of their begging calls. For instance, common cuckoo (*Cuculus canorus*) nestlings can learn to modify some parameters of their begging calls in a host-specific manner so that they better stimulate provisioning (Madden and Davies 2006). Likewise, great spotted cuckoo (*Clamator glandarius*) nestlings show plastic begging and can presumably adjust the number of notes in their calls according to their feeding with the rearing host (Roldán et al. 2013). Another mechanism of host manipulation is to exhibit generic begging calls that serve to exploit widespread provisioning rules of parenting birds, such as increasing food delivery in response to longer begging bouts and higher begging rate (Kilner et al. 1999). The long and repetitive begging calls of shiny cowbird (*Molothrus bonariensis*) nestlings appear to serve this function since they induced similar provisioning responses in both a common host species and a species with no history of parasitism (Gloag and Kacelnik 2013). To exhibit this kind of ‘jack-of-all-trades’ begging calls can be adaptive in a wide range of hosts. However, it may also pose a disadvantage when hosts respond preferentially to stimuli provided by their own young. In this case, a mismatch of the appropriate signals can result in suboptimal provisioning, or even the starvation, of parasitic young (Lichtenstein 2001; Langmore et al. 2013; Rivers et al. 2014).

One way in which parasitic nestlings could circumvent the fitness costs of producing inadequate begging signals is by sharing the nest with host young, as long as the former have

better competitive abilities and, thus, can take advantage of the begging displays of host nest mates to elicit parental provisioning (Gloag et al. 2012). This idea first arose from studies showing that nestlings of brown-headed cowbird (*Molothrus ater*) can benefit, in terms of mass gain and physical condition, from being reared alongside host young of smaller body size (Kilner 2003; Kilner et al. 2004). This is because host and cowbird nestlings collectively induce parents to bring extra food that the parasite can later monopolise due to its physical superiority (Kilner et al. 2004). A similar effect was demonstrated for shiny cowbird nestlings parasitising a small-sized host, the house wren (*Troglodytes aedon*) (Gloag et al. 2012). However, the begging assistance hypothesis has not been supported in other studies involving both evictor and non-evictor parasites (Soler 2017). Common cuckoo nestlings experimentally forced to share parental care with host nest mates in nests of rufous bush robins (*Cercotrichas galactotes*), great reed warblers (*Acrocephalus arundinaceus*), and redstarts (*Phoenicurus phoenicurus*) received less food than those reared alone (Martín-Gálvez et al. 2005; Hauber and Moskát 2008; Grim et al. 2009), which had detrimental consequences in terms of nestling growth and survival (Grim et al. 2009). In turn, nestlings of the non-evictor great spotted cuckoo reared alone in nests of its magpie (*Pica pica*) host were provisioned at similar rates and grew equally well than in mixed broods (Soler and de Neve 2013). Therefore, the question of whether parasitic nestlings benefit from the assistance of host nest mates in stimulating parental care remains a contentious issue. Moreover, it is still unclear from those previous studies if the presence of host young can confer protection to non-mimetic parasitic nestlings when hosts are able to discriminate between own and foreign young based on species-specific begging cues. Exploring this possibility is important to better understand the fitness trade-offs of nest mate acceptance for parasitic nestlings and the evolution of alternative mechanisms of host manipulation across parasite species.

Here, we study if having host nest mates is key for non-mimetic shiny cowbird nestlings to obtain parental care from the grayish baywing (*Agelaioides badius*; hereafter baywing), a host species that have evolved discrimination against young unlike their own. Baywings are secondary hosts of shiny cowbird and primary hosts of the closely related screaming cowbird (*Molothrus rufoaxillaris*; De Mársico et al. 2010). Nestlings and fledglings of shiny cowbird differ from those of baywings in visual appearance and vocalisations, as opposed to screaming cowbirds, which mimic the plumage colouration and begging call structure of its host (Fraga 1998; De Mársico et al. 2012; Rojas Ripari et al. 2018). Previous work showed that resembling host young is adaptive because baywings stop caring for shiny cowbirds soon after

they leave the nest, but continue to provide prolonged post-fledging parental care to own and screaming cowbird juveniles (Fraga 1998; De Marsico et al. 2012). In addition, playback experiments demonstrated that baywings increased nest provisioning in response to begging calls of conspecific and screaming cowbird nestlings, but not in response to shiny cowbird begging calls (Ursino et al. 2018). Begging calls of shiny cowbird fledglings also failed to capture the attention of adult baywings when broadcast outside the nest (F. Lama, C.A. Ursino, JCR and MCDM, unpublished data). Yet, despite the observed host discrimination abilities, shiny cowbird nestlings typically grow normally in baywing nests when they are reared in mixed broods (Fraga 1998; De Marsico et al. 2012). This suggests that the presence of host nest mates may be necessary for shiny cowbird nestlings to elicit sufficient parental care to survive to fledging. Doing it so, in turn, opens the possibility to escape host discrimination entirely because shiny cowbird fledglings can sometimes engage individuals other than their foster parents to feed them (De Marsico et al. 2012).

Specifically, we assessed the hypothesis that non-mimetic nestlings will fail to elicit sufficient parental care from baywing parents when they are reared in the absence of host nest mates. If this hypothesis is correct, we predict that shiny cowbird nestlings reared alone in the nest should experience lower provisioning and higher mortality rates than host nestlings in singleton broods. We tested this prediction by manipulating baywing broods and quantifying host provisioning response. In addition, to examine if shiny cowbirds went undernourished when reared alone, we compared their mass growth patterns with published data from our study population for cowbird nestlings reared in mixed broods. Finally, we examined post-fledging survival rates of nestlings from experimental broods to determine if host discrimination against non-mimetic shiny cowbird fledglings operates regardless whether they were reared alone.

Materials and methods

Study area and species

The study was conducted in north-eastern Buenos Aires province, Argentina, in two private properties (Estancia La Matilde and Estancia Luis Chico) near the town of Veronica (35° 08' S, 57° 25' W). The study area is part of the Biosphere reserve 'Parque Costero del Sur' (MAB-UNESCO), characterised by the presence of remnants of native woodlands of *Celtis ehrenbergiana* and *Scutia buxifolia* (locally known as 'talares'), surrounded by flooding grasslands and pastures. Baywings and shiny cowbirds are year-round residents in the area. Data were collected during two consecutive breeding

seasons (late November–early February) in 2016–2017 and 2017–2018.

Baywings are secondary cavity-nesters that breed mostly in the domed nests of many furnariid species (*Anumbius annumbi*, *Furnarius rufus*, *Phacellodomus* sp., *Synalaxis* sp.). They are socially monogamous cooperative breeders (Fraga 1991; Ursino et al. 2017) and single-brooders (De Marsico et al. 2010). Breeding pairs can have one to four helpers at the nest that typically join them after hatching and participate in brood provisioning and nest defence (Fraga 1991; Ursino et al. 2011). Baywings' modal clutch size is four eggs, the incubation period lasts 13 days, and chicks remain in the nest for about 12 to 16 days (De Marsico et al. 2010). Fledglings usually stay in the surroundings of the nesting site for at least 2 to 3 weeks and are easy to locate by the alarm calls and defensive behaviours of the attending adults (De Marsico et al. 2012). Cowbird eggs have an incubation period of 12 days, and nestlings are almost completely feathered by day 12 post-hatching.

Field procedures and data collection

We searched exhaustively for baywing nests throughout each breeding season. All nests found were visited regularly until they produced fledglings or failed. In each nest, we marked the eggs individually using Sharpie® markers and assigned them to baywing, screaming cowbird, or shiny cowbird based on diagnostic cues (Fraga 1983).

From 10 to 11 days post-hatching onwards, nest activity was checked from a distance (2–6 m) to avoid inducing premature fledging. On the last visit to the nest, chicks were banded with a numbered metal ring for identification. Host and cowbird young usually leave the nest between days 12 and 16 post-hatching (De Marsico et al. 2010). Nest departure sometimes occurs asynchronously in mixed broods but, to our best knowledge, there is no evidence of conflict over parental care between recently fledged young and those that remained in the nest (Fraga 1986). Once fledging was confirmed, we followed baywing groups every 2–3 days for at least 10 up to 21 days post-fledging, to record fledgling survival and host's behaviour towards shiny cowbird fledglings. As it has been reported for other host-parasite species (e.g. Woodward 1983; Soler et al. 2014a; Kysucan et al. 2019), baywing and shiny cowbird fledglings remain hidden in the vegetation near the nesting site during the first 2–3 days after fledging, and then they progressively increase their movements as their flight abilities improve (De Marsico et al. 2012). Fledglings are easy to locate within the natal territories through their conspicuous begging calls and the noisy alarm calls of the attending adults. We followed shiny cowbird and baywing fledglings from experimental nests (see below) and from 6 non-experimental nests that fledged a shiny cowbird alongside host young. Brood composition ranged from 3 to five nestlings (only one

shiny cowbird per nest). To record the post-fledging survival, we conducted focal observations on each group with shiny cowbird and/or baywing fledglings using 8×42 binoculars. Observations lasted until focal fledglings were seen alive. Previous observations indicate that shiny cowbird fledging mortality due to host discrimination occurs mostly within the first 48–72 h after leaving the nest (Fraga 1998; De Marsico et al. 2012). Fledglings that could not be found despite exhaustive searching were considered dead.

Experimental procedure

To test the performance of shiny cowbird nestlings in the absence of host nest mates, we conducted an experiment with two treatments, each consisting in singleton broods of either shiny cowbird (experimental group) or baywing (control group) nestlings. A total of 23 and 17 nests were randomly assigned to each treatment, respectively. Given that parasitism rates of baywing nests by shiny cowbirds are naturally low ($\sim 2\%$ during this study), experimental nests were artificially parasitised with a single fresh shiny cowbird egg collected from nearby, multiply parasitised nests of two common hosts (*Mimus saturninus* and *Turdus rufiventris*). Shiny cowbird eggs were added during the host's egg-laying period or shortly after the onset of incubation; hence, they always hatched a day before or on the same day that host eggs (De Marsico et al. 2010). In order to secure that only a single (cowbird or host) egg hatched, the other host eggs were replaced with unviable eggs—obtained from nearby abandoned nests—at the end of the laying period. Once the experimental clutch was set up, nests were checked every 4 days until the estimated hatching date. From the nests originally assigned to the experimental and control groups, we obtained 9 broods with a single shiny cowbird and 9 with a single baywing nestling. These nests were visited regularly until the age of 9–10 days post-hatching to record nestling mass using Pesola spring scales (± 0.5 g). In each visit, we also recorded the number of adult baywings present at the nest as an estimator of cooperative group size (Ursino et al. 2011).

To quantify host provisioning, we video recorded experimental nests using a full HD Sony camcorder (Handycam HDR-CX110) attached to tree branches at a distance of 50–150 cm from the nest entrance. We placed the camera on the day previous to filming to allow adult baywings to habituate to its presence, though they are quite tolerant to video recording devices during the nestling stage (e.g. Ursino et al. 2018). Whenever possible, nests were filmed twice because host response towards non-mimetic nestlings could vary with nestling age, as differences in appearance and vocalisations from baywing young become more apparent (Fraga 1998). At each nest, the first recording session was conducted between days 3 and 5 post-hatching, whereas the second one was conducted 4 days later (i.e. when chicks were between 7 and 9 days of age). Video recordings were conducted between 7:00–12:00

and 15:30–19:30 and lasted 1.5 to 4 h, after which the camera was removed. Videos were analysed in slow motion or frame by frame using VLC 2.6.6 media player to score the number of visits in which baywings delivered food. It was not possible to record data blind because our study involved focal animals in the field.

Data analyses

To compare the effect of shiny cowbird and host nestlings on nest provisioning rates, we performed a generalised linear mixed model (GLMM) with Poisson distribution and log link function. The model was fitted by a Laplace approximation using *glmmTMB* library (Brooks et al. 2017) in R 3.4.2 (R Core Team 2017) with the number of feeding visits per hour as the response variable. Log-transformed video duration was included as a variable offset to account for differences in recording span across nests. Explanatory variables were nestling species (shiny cowbird vs. host), nestling age, treatment:age interaction, cooperative group size, and time of video recording (morning vs. afternoon). Nest identity was included as a random effect.

We examined if mass growth patterns of shiny cowbird nestlings differed between those reared alone or in mixed broods using published data as reference values of mass growth in the presence of baywing nest mates (De Marsico et al. 2010). Briefly, those mixed broods ($n = 10$) were obtained by parasitising baywing nests with a single shiny cowbird egg or newly hatched nestling obtained from nearby mockingbird (*M. saturninus*) or southern house wren (*Troglodytes aedon*) nests. Nest monitoring and collection of growth data in that study followed the same procedures as described here for experimental nests (see De Marsico et al. 2010 for further details). We fitted the three-parameter Richards model (Richards 1959) to the combined data set of nestling mass using the parameterisation proposed by Tjorve and Tjorve (2010) and Svagelj et al. (2019) (see also Vrana et al. 2019) to test for differences in asymptotic mass, maximum relative growth rate, and age of maximum growth:

$$W_{(x)} = A \times \left((d-1) e^{\frac{(-K \times (x-c))}{d^{1-d}}} \right)^{\frac{1}{1-d}}$$

where W is the value of mass growth, A is the upper asymptote for body mass (in grams), K is the maximum relative growth rate (in day^{-1}), c is the age at the inflexion point (in days), d is a shape parameter so that $d^{1/d}$ is the relative mass value at maximum growth, and x the age of the nestling (in days). The model was fitted by maximum likelihood using *nlme* library (Pinheiro et al. 2018) in R 3.4.2 (R Core Team 2017) with nestling identity as a random effect to account for repeated measures on each individual. Brood status (single or mixed) was included as a predictor for parameters A , K , and c , and significance was tested using a chi-squared likelihood ratio

test (LR) against the null model containing only intercept and random effects. In addition, we estimated mass growth parameters for baywing nestlings in mixed broods by fitting the equation above to provide a comparison of the relative size of host and cowbird nestling in mixed broods. Mass of baywing nestlings was averaged per brood and estimates of asymptotic mass were then compared between shiny cowbird and host nestlings using paired *t* tests.

Results

Nestling provisioning and survival in singleton broods

Shiny cowbird nestlings reared alone elicited similar provisioning rates from their foster parents than baywing nestlings in singleton broods. There was no significant interaction effect of brood treatment and nestling age on nest provisioning (Table 1). Both shiny cowbird and host nestlings were fed more often as they grew older, but the number of feeding visits was unaffected by nestling species (Table 1, Fig. 1). Provisioning rate was unrelated to time of video recording, but it showed a non-significant tendency to increase with cooperative group size (Table 1).

We did not find differences in nestling survival between shiny cowbird and control broods. In each treatment, 8 out of 9 nestlings (89%) fledged successfully. Nestling deaths were attributable to nest depredation.

Mass growth of shiny cowbird nestlings with and without host nest mates

Cowbird nestlings were always the heaviest in mixed broods, attaining a mass at fledging that was nearly 10% higher, on average, than that of host nestling (43.9 ± 2.7 (SE) and $39.9 \pm$

Table 1 Results of the GLMM analysis of the effect of brood treatment

(shiny cowbird vs. host nestling) on provisioning rates by baywings. Nestling age, cooperative group size (i.e. parents plus helpers at the nest), time of video recording (morning vs. afternoon), and an interaction effect of brood treatment and nestling age were included as covariates. Nestling identity was included as a random effect (see the 'Materials and methods' section for model details)

Model parameter	Estimate \pm SE	Wald <i>z</i>	<i>P</i>
Brood treatment	0.37 \pm 0.31	1.223	0.22
Age	0.13 \pm 0.04	3.777	0.0001
Group size	0.09 \pm 0.05	1.875	0.06
Time of video recording	-0.09 \pm 0.11	0.110	0.41
Brood treatment:age	0.07 \pm 0.05	-1.382	0.17

Significance level at $P < 0.05$

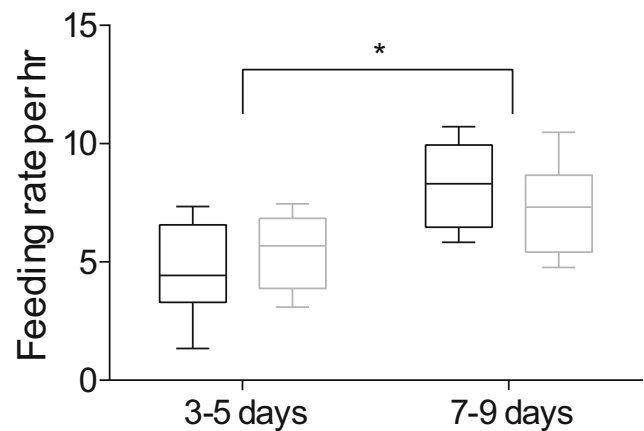


Fig. 1 Boxplot of feeding rates of experimental nestlings by baywing parents in singleton broods (black, baywing; grey, shiny cowbird), separated by age class (3–5 and 7–9 days of age). Asterisks indicate significant differences ($P < 0.05$). The boxes show median and interquartile range while whiskers go down to the smallest value and up to the largest. Sample sizes were 9 nests of each treatment for the age of 3–5 days, and 8 and 9 nests, respectively, for shiny cowbird and baywing treatments at the age of 7–9 days

2.5 g, respectively; $n = 10$ broods, $t = 3.05$, $P = 0.003$). Shiny cowbird nestlings reared alone differed slightly in mass growth pattern from those reared alongside baywing nest mates (LR test: $\chi^2 = 9.94$, $P = 0.02$; Fig. 2). The visual inspection of growth curves shows a small difference during the first phase of nestling growth, with shiny cowbirds in singleton broods performing better than in mixed broods. This difference was compensated by the age of 5 days, when mass gain became similar for cowbird nestlings in both brood types (Fig. 2). Consistent with this, shiny cowbirds in mixed broods

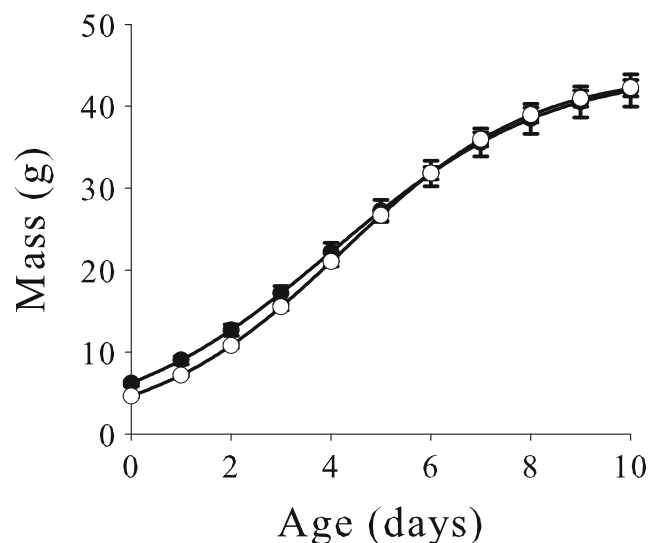


Fig. 2 Mass growth curves of shiny cowbird nestlings reared alone ($n = 9$, full circles) or in mixed broods with baywing nestlings ($n = 10$, empty circles) fitted by maximum likelihood to the Richard's three-parameter model (see the 'Materials and methods' section). Dots indicate mean (\pm SE) nestling mass derived from the adjusted growth curves of each data set

Table 2 Estimates (\pm SE) for mass growth parameters of shiny cowbird nestlings reared alone ($n = 9$; this study) or in mixed broods with 1 to 5 host nest mates ($n = 10$; data from De Mársico et al. 2010). Values were obtained by fitting mass growth data to the Richard's three-parameter

model (see the 'Materials and methods' section for details). The shape parameter d was kept constant across brood treatments and estimated as 2.06 ± 0.27 . Significantly different parameters at $P < 0.05$ are in italic

Growth parameter	Singleton	Mixed brood	<i>P</i>
Asymptotic mass (g)	44.6 \pm 2.4	43.9 \pm 2.7	0.81
Maximum relative growth rate (days ⁻¹)	<i>0.11 \pm 0.01</i>	<i>0.12 \pm 0.01</i>	<i>0.04</i>
Age at inflexion point (days)	4.1 \pm 0.2	4.2 \pm 0.2	0.43

showed on average a higher maximum growth rate, but we did not detect differences in asymptotic mass and age of maximum growth (Table 2; Fig. 2).

Nestling and post-fledging survival of experimental broods

We did not find differences in post-fledging survival between shiny cowbird and host nestlings from singleton broods. All shiny cowbird nestlings that fledged successfully from our experimental nests were found alive and in the company of baywing hosts after 1 week since nest departure ($n = 8$). Of these, three were still alive 2 weeks after leaving the nest. Meanwhile, five out of eight baywing fledglings from control broods were alive a week after leaving the nest, and three of them survived for at least another week.

By contrast, none of the six shiny cowbird fledglings reared in mixed broods could be located a week after fledging, despite intensive searching. Their host and screaming cowbird nest mates were seen after fledging in the vicinity of the nesting sites escorted by adult baywings.

Discussion

Contrary to our prediction, shiny cowbird nestlings reared alone elicited similar provisioning levels from baywings and survived equally well as host nestlings in singleton broods. Furthermore, shiny cowbirds in singleton broods performed slightly better during the first days after hatching and had a higher maximum growth rate than those in mixed broods, though they finally reached a similar asymptotic mass. These results indicate that shiny cowbirds reared alone grew normally and fledged in good physical condition from experimental nests. Therefore, we did not find support for the hypothesis that non-mimetic nestlings require the assistance of host nest mates to elicit adequate parental care from its baywing host. Similar results were reported for great spotted cuckoo nestlings reared alone or in mixed broods in magpie nests, where the absence of host nest mates had no negative effects on the probability of nest abandonment and on cuckoo's growth rates (Soler and de Neve 2013).

A possible explanation is that shiny cowbird nestlings were able to compensate the lack of species-specific begging signals by exaggerating other features of their begging displays (Kilner et al. 1999; Tanaka and Ueda 2005; Tuero et al. 2016). It has been shown that cowbird nestlings can adjust their begging behaviour according to their perceived level of within-brood competition, suggesting that they are able to learn the begging intensity at which they are more likely to be fed (Rivers 2007; Tuero et al. 2016). Likewise, shiny cowbird nestlings could flexibly adjust their begging intensity in the absence of host nest mates based on their feeding experience, increasing its begging effort if hosts are less responsive to parasite's begging signals than to those of their own species. On the other hand, our results could reflect a constraint in host discrimination abilities during the nestling stage. Nestling discrimination can be a costly antiparasitic defence for baywings because the risk of incurring in recognition errors is likely to be high under the dim light conditions of their nests (Fraga 1998; De Mársico et al. 2012). Hence, hosts may simply accept and feed any nestling in their nests until fledging, when they can better distinguish between own and alien young. Such 'rule of thumb' would help explain the success of shiny cowbird nestlings in eliciting provisioning from baywings, despite the observed host preferences for species-specific begging cues (Ursino et al. 2018). Additional studies that compare the begging effort of shiny cowbird and baywing nestlings in singleton and mixed broods will be useful to disentangle between these alternative explanations.

We also found that baywings continued providing parental care to shiny cowbird fledglings that were reared alone in the nest. Indeed, the post-fledging survival rate was similar to that of host nestlings from singleton broods. By contrast, shiny cowbirds fledged from mixed broods vanished soon after leaving the nest, as reported in previous studies (Fraga 1998; De Mársico et al. 2012). Although our sample sizes are small, the results were consistent for all cowbird fledglings that could be monitored for at least 10 days after nest departure. Interestingly, the observed differences in post-fledging survival between shiny cowbirds reared alone and in mixed broods (De Mársico et al. 2012; this study) suggest that fledgling discrimination by baywings is not 'all-or-nothing'. Rather, host response towards non-mimetic fledglings appears to

depend on whether they have fledged alongside host young or not. This is in agreement with previous studies involving radio-tracking of great spotted cuckoo fledglings from ‘only cuckoo’ and mixed broods, the former of which were more likely to be fed by magpies during the first weeks after leaving the nest (Soler et al. 2014a). Curiously, however, Soler et al. (2014a) did not detect differences in post-fledging survival between cuckoos from both brood types. They demonstrated that this could be because cuckoo fledglings that went undernourished left their foster parents and joined other cuckoo fledglings to look for new caregivers (Soler et al. 2014a). Cuckoo fledglings translocated away from their natal area were able to obtain feedings from adult magpies that were already caring for parasitic young, suggesting that looking for non-parental feedings is a co-evolved strategy to overcome host discrimination (Soler et al. 2014b). Feeding of shiny cowbird fledglings by individuals other than their foster parents sometimes occurs, but available data suggest that death is the most likely outcome of baywing discrimination against shiny cowbird fledglings from mixed broods (Fraga 1998; De Mársico et al. 2012; this study). The more recent origin of brood parasitic cowbirds, together with the generalist host-use strategy of shiny cowbirds, may explain why they do not exhibit that putative post-fledging adaptation.

Taken together, the results of this study suggest context-dependent fledgling discrimination, as it happens in the great spotted cuckoo-magpie system (Soler et al. 2014a, 2014b). The observed differences in host response towards shiny cowbirds in singleton versus mixed broods do not support recognition mechanisms based on innate or learned host’s internal templates (Rothstein 1975; Hauber and Sherman 2001; Moskát et al. 2010; Manna et al. 2017). Instead, this pattern points to flexible recognition mechanisms based on the comparison between own and parasitic young. Discordancy would be the simplest recognition mechanism, well known to operate in host rejection of parasitic eggs, which consists in recognising as foreign the offspring with more dissimilar phenotypes to the other in the clutch (see Manna et al. 2017 for a recent review). Such mechanism would be advantageous for baywings because they typically fledged mixed broods where parasitic offspring is outnumbered by their own (De Mársico et al. 2010). An alternative, non-mutually exclusive mechanism that could explain the results is online self-referencing (Bán et al. 2013), by which hosts discriminate against parasitic young only when they can simultaneously view their own (Bán et al. 2013; Yang et al. 2014). Future experiments that manipulate brood composition to vary the relative proportion of mimetic and non-mimetic young would be helpful to dissect the cognitive basis of fledgling recognition by baywings.

The better performance of shiny cowbirds when they were reared alone in baywing nests adds evidence to the idea of opposing selective pressures driving the evolution of nest mate killing versus nest mate acceptance strategies (Gloag

et al. 2012; Soler and de Neve 2013; Moskát et al. 2017). The trade-off hypothesis states that the extent of virulence of parasitic nestlings reflects a balance between the costs and benefits of eliminating host nest mates (Kilner 2005). Two major costs of nest mate killing behaviour are the increased risk of nest abandonment and the loss of assistance in stimulating parental care, but none of them appear to be at play for shiny cowbirds parasitising baywing hosts (see also Soler and de Neve 2013). Perhaps the explanation for the seemingly maladaptive strategy of accepting host nest mates when they would do better alone relies on the fact that shiny cowbirds are extremely generalist in host use (270 species reported as victims so far, Lowther 2018). That is, despite they might benefit from eliminating host nest mates under certain conditions, the costs of losing assistance in stimulating parental care in other host species may pose trade-offs that ultimately favours acceptance over nest mate killing behaviours (Kilner et al. 2004; Gloag et al. 2012). On the other hand, nest mate acceptance can be favoured when hosts are brood-reducers and feed preferentially the largest nestling in the brood, as it is the case of baywing parents. Under this scenario, if parasitic nestlings enjoy a size advantage and are thus able to outcompete host nestlings, nest mate acceptance would be a successful and less costly strategy (Soler and de Neve 2013; Moskát et al. 2017; Soler 2017). The larger size of cowbird nestlings relative to baywings’, which becomes more pronounced from day 5 of age onwards, may also explain why they were able to compensate initial differences in mass growth curves compared with cowbird nestlings in singleton broods. Another factor that may influence nest mate acceptance is the occurrence of repeated parasitism, that is, the laying of multiple eggs in a single nest by the same parasitic female (Soler and de Neve 2013). Repeated parasitism can weaken the selection for increased virulence because there is a risk of eliminating close kin. However, although repeated parasitism by shiny cowbird females sometimes occurs (de la Colina et al. 2016; but see Gloag et al. 2014), whether it plays a role or not in shaping nestling virulence needs further investigation. Considering its narrow chances of success in baywing nests, it remains intriguing why shiny cowbird females do not entirely avoid parasitising this host in the first place. Increasing our knowledge about the factors driving nest finding and host selection by cowbird females and the ecology of host-parasite interactions during the post-fledging stage may help better understand why shiny cowbird parasitism persists on baywings, even when host defences almost certainly result in parasite’s death.

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Data availability All data generated or analysed during this study are included in this published article (and its [supplementary information files](#)).

Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

Ethical approval All applicable international, national, and/or institutional guidelines for the care and use of animals were followed. As the experimental protocols involving the handling of birds were of minimal impact, the University of Buenos Aires committee for animal care and use did not intervene. Manipulations of baywing nests were done under permit issued by the local authority (OPDS; 303/16). Whenever possible, baywing eggs that were removed were transferred to non-experimental nests in order to minimise host reproductive losses at manipulated broods. No cowbird or host nestling was harmed or died as a result of our manipulations (see below) and we did not detect differences in predation rates between experimental and non-experimental nests.

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