



Original Article

Nest environment modulates begging behavior of a generalist brood parasite

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In young birds, the intensity of the begging signal varies according to the chick's internal condition (i.e., hunger or nutritional state) but may be additionally modulated by the external conditions experienced in the nest (e.g., nestmate competition or feeding success). Flexibility of begging in response to nest environment should be especially beneficial for the chicks of generalist brood parasites, which encounter diverse brood conditions depending on the host nest in which they are reared. We investigated variability in the begging behavior of an extreme generalist brood parasite, the shiny cowbird (*Molothrus bonariensis*). We compared visual and vocal begging variables of cowbird young of 5 days of age reared in nests of 2 common hosts, one smaller (house wren, *Troglodytes aedon*) and one larger (chalk-browed mockingbird, *Mimus saturninus*) than the parasite. Cowbird chicks were standardized for short-term hunger prior to recording and were similar in mass/condition in each host, but nevertheless begged more intensely in mockingbird than house wren nests, as indicated by increased stretching of the neck, lower latency to beg, increased time spent begging per bout and greater call rate. These results are consistent with young cowbirds adjusting their begging intensity based on the intrabrood competition of a given host, independent of need, an adaptability that likely contributes to their success as parasites utilizing diverse host species.

Key words: begging, brood parasitism, cowbird, *Molothrus bonariensis*.

INTRODUCTION

Avian begging is a multicomponent display, comprising both visual (posturing and gaping) and vocal (calling) elements, that is used by offspring to elicit food from their parents (Kilner 2002). The begging signal encodes both the short-term need (i.e., hunger) and long-term need (i.e., condition) of a chick such that, as a general rule, begging intensity increases as the nutritional status of the chick decreases (Price et al. 1996; Budden and Wright 2001; Leonard et al. 2003). Parents respond to increases in begging intensity by increasing the rate of provisions brought to the nest (Glassey and Forbes 2002) and/or preferentially feeding 1 chick in a given provisioning visit (Kitamura et al. 2011).

There is some evidence that nestling solicitation can also be modulated by the external cues of the nest environment (Leonard and Horn 1998; Leonard et al. 2000; Rodríguez-Gironés et al. 2002). Thus, begging intensity has been shown to increase as a result of intrabrood competition (Leonard and Horn 1998), varying with either the number of siblings in the nest (Leonard et al. 2000) or the body size asymmetry between nestmates (Price et al.

1996; Cotton et al. 1999). Also, a chick's experience during provisioning visits may influence the begging intensity they display in later feeding events (Lotem 1998). For example, chicks of the house sparrow (*Passer domesticus*) learn to maintain high begging intensities, independent of their hunger level, if trained to receive food only following intensive begging (Kedar et al. 2000), and inversely, reduce their begging intensity for a given hunger level following positive reinforcement for low begging postures (Grodzinski et al. 2008). Given that intense begging carries some direct costs (e.g., higher predation-risk or reduced growth; Haskell 1999; Kilner 2001), such flexibility in response to external conditions allows chicks to display a begging intensity that is optimal to receive food in a given nest environment.

The ability to vary begging behavior in response to nest environment should be especially critical for the nestlings of generalist brood parasitic birds. Generalist parasites lay their eggs in nests of multiple host species, which then rear the young parasite alongside (e.g., *Molothrus* spp., cowbirds), or in place of (e.g., *Cuculus* spp., cuckoos), their own chicks. Nestlings of these parasites may find themselves reared by parents of varying body size and with nestmates of varying number, size, and age, such that unpredictability in the nest environment far exceeds that experienced by

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most nonparasitic nestlings species. Parasitic chicks typically beg more intensely than host young (Redondo 1993; Dearborn and Lichtenstein 2002) or the young of nonparasitic relatives (Harper 1986; Briskie et al. 1994) for the same level of hunger, presumably in part because they are not related to either their caregivers or their nestmates and therefore do not incur costs for begging selfishly. Several studies have found that parasitic species vary their begging intensity with short-term hunger (Lichtenstein 2001; Butchart et al. 2003; Hauber and Ramsey 2003; Lichtenstein and Dearborn 2004; Tanaka and Ueda 2005; Soler et al. 2012), but whether other factors, such as nest environment, also determine a parasite's begging intensity are poorly understood. Rivers (2007) found that for generalist parasitic brown-headed cowbirds (*Molothrus ater*), time spent begging varied between chicks reared in different sized hosts and not with short-term need, suggesting that the level of competition for food between parasite and host nestlings is the key determinant of cowbird's begging intensity. Other studies of generalist parasite begging have identified host-specific flexibility in the structure of begging vocalizations (Madden and Davies 2006; Langmore et al. 2008; Roldán et al. 2013), but it is unclear if the vocal differences in these cases are accompanied by shifts in begging effort.

In this study, we investigated whether nest environment (i.e., host) influences the visual and/or vocal components of begging by the generalist brood parasitic shiny cowbird (*Molothrus bonariensis*). Shiny cowbirds are one of the world's most generalist parasites, using as many as 260 host species across their range (Lowther 2014), and are usually reared together with host young and/or other cowbirds in the same nest (Ortega 1998). We compared begging behavior of shiny cowbirds chicks reared in 2 common hosts that markedly differ in body size and host chick competitiveness: one large (the chalk-browed mockingbird, *Mimus saturninus*, adult body mass: 75 g) and the other small (house wren, *Troglodytes aedon*, adult body mass: 14 g) relative to the cowbird (adult body mass: 45–50 g). Comparisons were made at 5-day posthatch, when cowbirds have similar body weight in each host and followed standardization of short-term hunger. If brood environment modulates begging behavior in shiny cowbirds independent of need, then we expected that cowbird chicks' begging intensity would differ between hosts. Specifically, we predicted that cowbirds would beg more intensely when reared alongside more competitive nestmates (i.e., mockingbirds) than less competitive nestmates (i.e., wrens). We also tested the assumption that cowbirds' feeding success in each host was dependent on their begging intensity.

METHOD

Study site and species

We carried out this study at "Reserva El Destino" (35°08'S, 57°23'W), near the town of Magdalena, Province of Buenos Aires, Argentina, during the breeding seasons (October–January) 2007–2008, 2008–2009, and 2009–2010. The site comprises flat, marshy grasslands with old and second growth stands of vegetation dominated by tala (*Celtis ehrenbergiana*) and coronillo (*Scutia buxifolia*). Shiny cowbirds, house wrens and chalk-browed mockingbirds (hereafter: cowbirds, wrens, and mockingbirds) are common species at the site. Per breeding season, we followed 40–60 wren nesting attempts made in nest-boxes, and 80–100 mockingbird nesting attempts. Nest-boxes were located in tala trees at a height of 1.5–1.8 m. Because they were separated by at least 30 m, we assumed that successive nesting attempts in the same box or territory in a given season were made by the same host pair. Mockingbirds build

open-cup nests, and their preferred nest sites are shrubs or trees with dense foliage (Fiorini et al. 2009). The frequency of cowbird parasitism in mockingbirds at the site is 70–80% (Fiorini et al. 2009), whereas the frequency of parasitism in wrens is up to 60% (Tuero et al. 2007). At this study site, mean egg weight was 4.6, 1.8, and 6.8 g for cowbirds, wrens, and mockingbirds, respectively (Tuero DT, unpublished data). Mean weight at hatching for cowbird chicks is 4.5 g, for wren chicks is 1.5 g, and for mockingbird chicks is 6 g (Fiorini et al. 2009).

Field procedures

We artificially parasitized wren and mockingbird nests with 1 cowbird egg collected from the nests of conspecific hosts. Shiny cowbird females typically puncture some host eggs prior to parasitism, leading to a reduction in host's clutch size (Astié and Reboreda 2006; Peer 2006). If necessary, we therefore removed 1–2 host eggs from experimental nests to generate the modal host's clutch size in parasitized nests (4 wren eggs or 5 mockingbird eggs, Tuero et al. 2007; Fiorini et al. 2009). Mockingbird nests are typically parasitized by multiple cowbirds (Gloag et al. 2014), but we standardized experimental nests to contain a single focal cowbird by removing additional parasite eggs. Egg removals were done prior to incubation and the eggs were allocated to other experiments. The synchronization of artificial parasitism with host laying was similarly standardized within hosts to reflect average conditions. Cowbird eggs were added to wren nests 3 days after the onset of incubation, resulting in cowbirds hatching the same day or one day later than wren chicks (incubation periods: 12–13 and 14–15 days, respectively), whereas cowbird eggs were added to mockingbird nests prior to the onset of incubation, resulting in cowbirds hatching the same day or one day later than the first mockingbird chick (mockingbird incubation: 12–13 days). These hatching times reflect approximately 44% and 74% of observed cases of natural parasitism in wren and mockingbird nests, respectively (Fiorini et al. 2009). Because there is some evidence that cowbird eggs laid in mockingbird nests differ in size and pattern to those laid in wrens (de la Colina et al. 2011; Tuero et al. 2012), we also cross-fostered some cowbird eggs ($N = 12$) collected from mockingbird nests into wren nests, so as to assess whether differences in cowbird begging between the hosts could have a genetic component. We could not perform the reciprocal cross due to insufficient cowbird eggs of wren nest origin. Neither host egg removal nor cowbird egg addition caused hosts to desert nests. All experimental manipulations were carried out under permit from the Province of Buenos Aires and complied with Argentinean law.

Following clutch manipulation, we checked nests every other day to confirm the hatching date of cowbird eggs (day 0). All nests that survived until cowbird chicks were 5 days of age were used for the experiment (wren: $N = 13$, mockingbird: $N = 16$, cross-fostered wren: $N = 5$). At this age, we measured cowbird and host chicks' tarsus length using a caliper, and weighed chicks with a digital portable balance (Ohaus LS 200) to the nearest 0.1 g. These measurements were used to estimate body condition of cowbird chicks, by using the residuals from a linear regression of chick tarsus and weight (see Schulte-Hostedde et al. 2005). We then removed cowbird chicks from the nest, fed them by hand until satiation and kept them in a warm, quiet environment for 1 h before returning them to the nest. This food deprivation treatment served to standardize short-term hunger immediately prior to video recordings of begging behavior. We filmed each nest for 2 h using a microcamera (with infrared light for wren nests) suspended above the nest

and connected to a Digital Personal Video Recorder (Handykam: JXD990). At a subset of these nests, we simultaneously recorded audio of the begging calls using a lapel microphone at the lip of the nest cup attached to a digital audio recorder (M-Audio Microtrack; 24-bit, 96 kHz; wren, excluding cross-fostered eggs: $N = 9$, mockingbird: $N = 10$).

Video and audio scoring

We analyzed video recordings to obtain measures of cowbird and host begging. For each feeding visit, we measured 3 begging variables that are indicative of the intensity at which chicks are begging: 1) latency to beg (the time difference between the adult arriving at the nest with food and the onset of begging, in seconds), 2) begging bout duration (the time a chick spent begging during a feeding event, in seconds), and 3) begging posture (the maximum begging posture score during a feeding event). Begging posture scores followed those of Leonard et al. (2003): 0 = no begging, 1 = head up, gaping without neck stretched, 2 = sitting on tarsi and gaping with neck stretched, and 3 = gaping with neck stretched and the body not in contact with the nest cup. We analyzed all feeding visits in each recording (26.9 ± 8.6 feeding visits in wren nests, 17.3 ± 6.5 feeding visits in mockingbird nests, mean \pm standard error [SE]). In order to relate differences in cowbird begging between hosts to feeding outcomes, we also recorded which chick (parasite or host nestling) was fed at each feeding event and estimated the volume of food eaten by cowbird chicks during each feeding visit. We measured food volume as a percentage of bill volume in 10% increments, with bill volume calculated following Greenberg and Droege (1990). Bill volume was calculated with measures taken from 30 adult individual skins of each host species housed at the Museo Argentino de Ciencias Naturales “Bernardino Rivadavia.”

We analyzed audio recordings by uploading the first 60 min of each recording into RavenPro 1.5 (Cornell Lab of Ornithology, NY). Spectrograms were displayed using default settings (filter bandwidth: 248 Hz, frequency grid spacing: 172 Hz, time grid resolution: 2.9 ms). For each bout of cowbird begging, we scored the first 5 clearly defined cowbird calls (those with no overlapping calls) for 3 acoustic variables, ignoring harmonics: 1) maximum frequency (Hz), 2) peak frequency (Hz, the frequency for which amplitude is greatest), and 3) call duration (seconds). We also calculated call rate for each bout by dividing the number of calls in the bout by the duration of the bout (calls per second).

Statistical analyses

We compared begging behavior between cowbirds reared in each host nest (and between wren-reared cowbirds of wren and mockingbird origin) using generalized linear mixed models (GLMM), considering the nonindependence of begging measures within individual chicks (Pinheiro and Bates 2000; Crawley 2007). To analyze begging latency, we used a Gaussian error term, identity link function and the nlme package. To analyze begging posture and duration, we used a Poisson error term, log link function, and the nlme4 package. Because the effects of our food deprivation treatment were expected to diminish over time as cowbirds begged and were fed, we included feeding event as a covariable in models to assess whether behaviors varied over the duration of the recording. Thus in all cases we introduced feeding event plus host (for host-of-rearing comparisons, excluding cross-fostered nests) or egg origin (for host-of-origin comparisons in wren-reared cowbirds) as fixed factors, and chick ID as a random factor. As a further test of

the extent to which results were independent of short-term hunger, we also compared mean values of just the first 5 feeding visits per recording (i.e., immediately following food deprivation) using a Mann–Whitney test.

We compared begging vocalizations and condition of cowbirds reared in each host nest using *t*-tests. To verify that our 2 hosts did vary in nestmate competitiveness, we used a generalized linear model (GLM) with logit link function and binomial error term to analyze the proportion of total provisioning received by cowbird chicks in each host nest, and a binomial test to determine whether the proportion of food received by cowbirds differed to that expected by chance if all chicks in the nest were equally likely to receive food (i.e., expected proportion in wrens = 0.2 because brood size is 5 and expected proportion in mockingbirds = 0.33 because brood size is 3). Finally, to determine whether cowbirds' feeding success was dependent on their begging intensity relative to host nestmates, we also compared begging behavior between parasite and host with a Wilcoxon test.

Analyses were made with Statistica 6.0 (StatSoft Inc 2001). GLMs and binomial test were performed using R software, version 3.2.1 (R Development Core Team 2012). All tests were 2 tailed, and we considered differences significant at $P < 0.05$. We report mean values \pm SE.

RESULTS

Cowbird begging

The visual component of shiny cowbird begging differed depending on the host nest in which they were reared. Cowbird chicks in mockingbird nests had a shorter latency to beg than their counterparts in wren nests (GLMM: $t = -4.02$, $P < 0.01$; Figure 1a). They also used more upright begging postures when sharing the nest with larger mockingbird nestmates than smaller wren nestmates (GLMM: $\zeta = -9.45$, $P < 0.01$; Figure 1b), and spent more time begging during feeding events when reared by mockingbirds than by wrens (GLMM: $\zeta = -2.89$, $P < 0.01$; Figure 1c). Neither latency to beg nor begging posture varied during the 2 h of our recording (GLMM; $t = -1.12$, $P = 0.26$; $\zeta = -0.19$, $P = 0.84$, respectively), though cowbird chicks did increase their begging duration as the recording progressed (GLMM; $\zeta = -9.32$, $P < 0.01$). In all cases, model's interaction terms were not significant. These differences were similarly evident if we considered the first 5 recorded provisioning visits only; cowbird chicks had shorter latency (Mann–Whitney test: $\zeta = -3.57$, $P < 0.01$), more upright begging postures (Mann–Whitney test: $\zeta = -3.97$, $P < 0.01$) and spent more time begging (Mann–Whitney test: $\zeta = -2.09$, $P = 0.03$) when reared by mockingbirds than by wrens. The begging behavior of wren-reared cowbirds was similar irrespective of whether they hatched from eggs originally laid in wren or mockingbird nests (GLMM; latency: $t = -0.09$, $P = 0.93$; begging posture: $\zeta = 0.62$, $P = 0.54$; begging duration: $\zeta = 0.82$, $P = 0.41$; wren laid/wren reared: $N = 13$, mockingbird laid/wren reared: $N = 5$).

The acoustic components of shiny cowbird begging also showed some variation between hosts, with cowbird chicks reared in mockingbird nests calling at higher rates than those reared in wren nests (Table 1). The acoustic parameters of individual calls (duration, maximum and peak frequency), however, were similar for cowbirds in each host (Table 1).

Feeding success of cowbirds

Cowbirds readily outcompeted wren chicks (i.e., food obtained by cowbird $>$ expected proportion if all chicks fed equally or 0.2, $\chi^2_{21} = 418.05$, $P < 0.001$, Figure 2a), but secured only an equal

share of food against mockingbird chicks (i.e., similar to 0.33, $\chi^2_{17} = 13.30, P = 0.71$, Figure 2a). Cowbird chicks reared in mockingbird nests received a smaller proportion (0.31) of the total food delivered to the nest than those in wren nests (0.50; GLM: Wald = 50.89, degrees of freedom = 36, $P < 0.01$, Figure 2a).

High begging intensity was more critical to feeding outcomes for cowbirds in mockingbird nests than in wren nests. Among mockingbird-reared cowbirds, the intensity of begging posture was higher at those visits in which the cowbird succeeded in securing food than at visits in which they missed out (Wilcoxon test: $\zeta = 1.91, P = 0.05$, Figure 3a). Furthermore, when cowbirds were fed they were begging more intensely than their mockingbird nestmates ($N = 16$ nests; Wilcoxon test: $\zeta = 2.98, P < 0.01$, Figure 3a), whereas when cowbirds were not fed (i.e., mockingbirds were fed) both cowbird and mockingbirds were begging at similar intensities ($N = 16$ nests; Wilcoxon test: $\zeta = 0.98, P = 0.32$, Figure 3a). In contrast, cowbird chicks

reared in wrens nests received food despite begging less intensely than their nestmates (“fed visits”: $N = 13$ nests; Wilcoxon test: $\zeta = 3.18, P < 0.01$, “not fed visits”: $N = 8$ nests; Wilcoxon test: $\zeta = 2.36, P = 0.02$, Figure 3b) and the begging posture intensity of wren-reared cowbirds was similar during visits in which they were fed and visits in which they were not (Wilcoxon test: $\zeta = 0.98, P = 0.33$, Figure 3b).

Ultimately, however, mockingbird-reared cowbirds consumed a greater volume of food per hour than wren-reared cowbirds (t -test: $t_{26} = 4.68, P < 0.001$, Figure 2b). This was because size of prey delivered by mockingbird parents ($1506 \pm 46 \text{ mm}^3, N = 17$ nests) was larger than that delivered by wren parents ($237 \pm 6 \text{ mm}^3, N = 21$ nests; t -test: $t_{36} = 33.45, P < 0.001$).

Cowbird chick condition

At 5 days of age, cowbirds reared in mockingbird nests did not differ significantly in body condition to those reared in wren nests

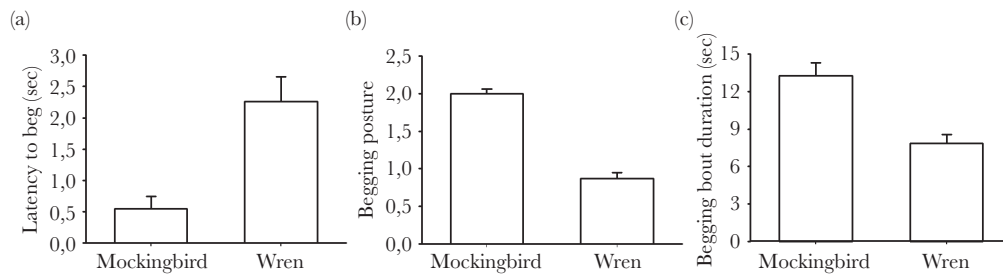


Figure 1 Begging variables scored from videos of shiny cowbirds laid into and reared in mockingbird ($N = 16$) and wren ($N = 13$) nests: (a) latency to beg, (b) begging posture score, and (c) begging bout duration. Values are means \pm SE.

Table 1 Begging call variables and test statistics of shiny cowbird chicks reared in mockingbird ($N = 10$) and wren ($N = 9$) nests

Host-of-rearing	Calls rate (number of calls/s)	Call duration (s)	Maximum frequency (Hz)	Peak frequency (Hz)
Cowbird in mockingbird	1.99 ± 0.09	0.13 ± 0.02	7246 ± 297	6246 ± 202
Cowbird in wren	1.33 ± 0.14	0.10 ± 0.01	6915 ± 401	5775 ± 338
t -test	$t_{17} = 4.05, P < 0.01$	$t_{17} = 1.05, P = 0.31$	$t_{17} = 0.67, P = 0.51$	$t_{17} = 1.23, P = 0.24$

Values are means \pm SE.

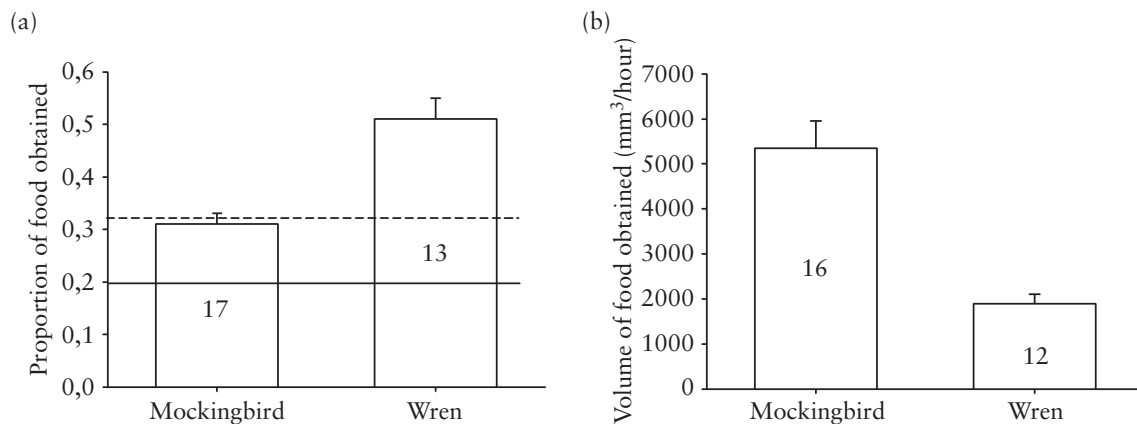


Figure 2 (a) Proportion of food deliveries and (b) amount of food obtained by shiny cowbird chicks laid into and reared in mockingbird and wren nests. The dotted line indicates the expected proportion of food obtained by cowbirds in mockingbird nests if all chicks in the brood are fed equally often. The straight line is the expected proportion of food obtained by cowbirds in wren nests if all chicks in the brood are fed equally often. Values inside the bars correspond to sample sizes. Values are means \pm SE.

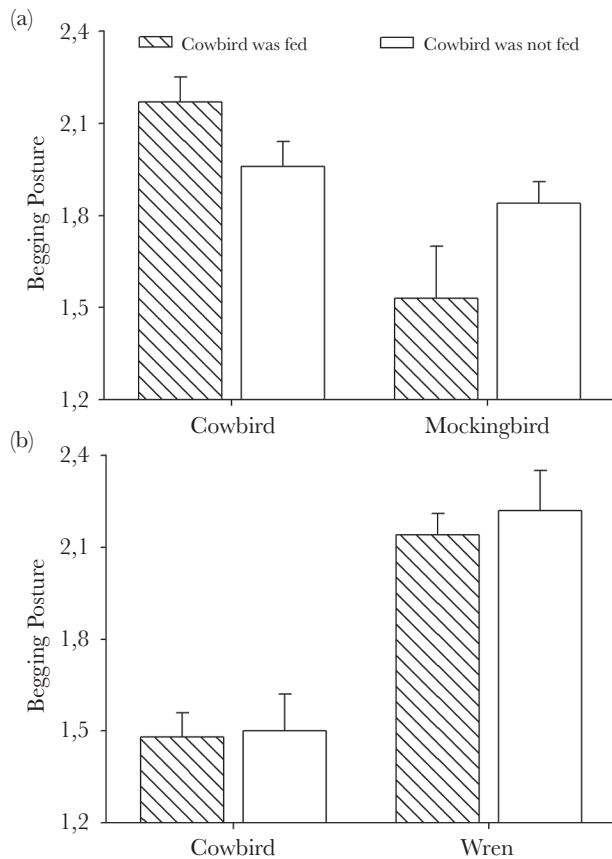


Figure 3

Cowbird and host begging posture scores in mockingbird nests (a) and wren nests (b) during feeding visits when begging cowbird chicks were and were not successful in securing food. Values are means \pm SE.

(residual scores: 0.50 ± 0.49 , $n = 13$ and 0.79 ± 0.64 , $n = 13$, respectively; t -test: $t_{25} = 1.63$, $P = 0.11$; tarsus length: in mockingbird nests: 16.3 ± 0.5 mm, $N = 13$, in wren nests: 17.1 ± 0.4 mm, $N = 13$) nor did they differ in body mass (in mockingbird nests: 19 ± 1 g, $N = 14$, in wren nests: 19.8 ± 0.6 g, $N = 13$; t -test: $t_{25} = -0.02$, $P = 0.98$). Also, no size differences were observed between wren-reared cowbirds hatched from eggs laid in wren nests and wren-reared cowbirds that hatched from eggs laid in mockingbird nests (t -test: tarsus length, $t_{16} = 0.43$, $P = 0.67$, mockingbird laid: 16.8 ± 0.6 mm, $N = 5$, wren laid: 17.1 ± 0.4 mm, $N = 13$; body mass: $t_{16} = -0.13$, $P = 0.89$, mockingbird laid: 19.4 ± 1.2 g, $N = 5$, wren laid: 19.8 ± 0.6 g, $N = 13$). We detected no correlation between chick condition at day 5 and latency to beg (Spearman correlation: $\zeta = 0.25$, $P = 0.80$, $\rho = 0.05$, $N = 27$), begging posture (Spearman correlation: $\zeta = 1.05$, $P = 0.29$, $\rho = 0.21$, $N = 26$), begging bout duration (Spearman correlation: $\zeta = 0.94$, $P = 0.35$, $\rho = 0.19$, $N = 27$), or begging call rate (Spearman correlation: $\zeta = -0.11$, $P = 0.91$, $\rho = -0.02$, $N = 18$).

DISCUSSION

We found that shiny cowbird chicks differed in their begging behavior depending on the host in which they were reared, despite being similar in their condition and degree of short-term hunger. Five-day-old cowbirds reared in a large host nest (the chalk-browed mockingbird) showed an increased stretching of the neck, lower latency to beg, increased time spent begging per bout, and greater

call rate than those reared in a small host (the house wren), all variables which indicate an increased begging effort by cowbirds in large hosts. Such differences in cowbird begging suggest young birds learn to modulate their begging behaviors to their advantage, as proposed by Kedar et al. (2000). The ability of cowbird young to vary their begging investment according to the brood environment likely contributes to their success as generalist parasites utilizing a large and diverse catalogue of host species.

Some host-specific traits in parasitic birds have a genetic origin, arising due to host-specific maternal lineages (e.g., egg color, Gibbs et al. 2000). This is unlikely to explain the differences in cowbird begging behavior we observed because while generalist cowbirds may exhibit nonrandom laying behavior (Mahler et al. 2007), they do not show strict host fidelity at the individual level (Gloag et al. 2014), and because chick behaviors are unlikely to be inherited only from mothers. We also failed to detect differences in chick size or behavior between cowbirds from naturally parasitized wren nests and those laid in mockingbird nests but cross-fostered into wrens.

The flexibility in cowbird begging intensity that we observed is consistent with the idea that begging involves direct costs (Briskie et al. 1999; Haskell 1999), that these costs increase as begging intensity increases (Dearborn 1999; Haff and Magrath 2011), and that chicks begging intensity is therefore proportionate to that needed to secure food during intrabrood competition (Leonard et al. 2003; Neuenschwander et al. 2003; Rivers 2007). Thus, shiny cowbird chicks reared alongside larger and/or more competitive mockingbird young were most likely to receive food when begging with more upright postures than their nestmates. In contrast, cowbirds reared by wrens readily outcompeted the host's young and were fed despite begging at lower postures than their wren nestmates. That is, cowbirds "scaled back" their begging effort in house wren nests, relative to when reared by mockingbirds. In addition to it being easier to out-jostle smaller-bodied hosts, cowbirds' begging intensity may be further relaxed in wrens because the polysyllabic nature of the cowbirds' call structure already serves to simulate a high provisioning rate relative to house wren calls (Gloag and Kacelnik 2013) and because cowbirds ability to monopolize food means they benefit from the begging signals of their smaller hosts (Fiorini et al. 2009; Gloag et al. 2012). The energetic cost incurred by cowbirds for high begging intensity is difficult to quantify. Interestingly, however, we found that although mockingbird-reared cowbirds received more total food than wren-reared cowbirds (owing to the larger host capturing larger prey items), this extra food was not reflected in a higher body mass or condition for cowbirds in mockingbird nests. One explanation, consistent with a metabolic cost of begging, is that mockingbird-reared cowbirds expend the energy difference on the higher begging effort required to win each food item, ultimately equating their condition with their wren-reared counterparts (Kilner 2001; Rodríguez-Gironés et al. 2001).

Rivers (2007) assessed the begging behavior of brown-headed cowbirds in hosts of different sizes and similarly found that begging varied according to host size (and thus competitiveness of host young), independent of short-term need and condition. It is worth noting though that in both shiny and brown-headed cowbirds, begging differences between hosts may reflect not only responses to differences in nestmate competitiveness or parental feeding rates but also a learning process (Lotem 1998; Kedar et al. 2000; Rodríguez-Gironés et al. 2002). Kedar et al. (2000) trained house sparrow chicks to beg at different intensities while receiving the same amount of food and found that chicks learnt the begging intensity at which they were most likely to receive food. Similarly,

shiny cowbird chicks could learn which begging intensity is more effective to receive food in a given host based on their previous feeding experiences. In this case, host-specific variation in cowbird begging behavior could occur even in the absence of differences in nestmate competition, provided hosts differ in other key ways such as their provisioning rules or responsiveness to parasite's begging signals. Further work is needed to assess whether cowbirds regularly utilize learning when modulating their begging behavior and its importance to cowbird begging flexibility.

Cowbirds' begging behavior has long been proposed as one of their key adaptations to the brood parasitic lifestyle (Gochfeld 1979). This is particularly true for the generalist cowbirds. These cowbirds lack host mimicry or other host-specific variation in the structural aspects of their begging signals (Broughton et al. 1987; Glog and Kacelnik 2013; this study), unlike other well-studied generalist parasites (Madden and Davies 2006; Langmore et al. 2008), yet can nevertheless efficiently secure food in a wide range of host species. Our results add to growing evidence that the success of cowbird begging lies beyond a tendency to simply beg louder and longer than nonparasitic young (Kilner et al. 2004; Rivers 2007; Glog and Kacelnik 2013). We propose that flexibility in begging behavior in response to nest environment, while potentially widespread among avian taxa, is put to particularly good use by generalist cowbirds, where it forms an important element of their begging strategy.

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