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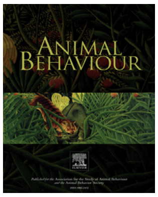

Size matters: shiny cowbirds secure more food than host nestmates thanks to their larger size, not signal exaggeration

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Many hosts of obligate brood parasitic birds invest more in parasitic nestlings than they do in their own young. The shiny cowbird, *Molothrus bonariensis*, a generalist parasite, is fed at a higher proportion than its host nestmates when it is reared in nests of a smaller-bodied host, the house wren, *Troglodytes aedon*. We test two hypotheses that could account for this differential allocation of food by host parents. The signal exaggeration hypothesis states that cowbird chicks have visual and/or acoustic begging signals that elicit preferential feeding. The size-advantage hypothesis states that hosts preferentially feed large chicks and/or that larger chicks outcompete host chicks in a scramble competition for food. To gain insight into the relative importance of size versus species-specific signals on food allocation by house wrens, we performed audio and video recordings in nests with experimental broods of (1) a 2-day-old cowbird chick and a 2-day-old wren chick (different species, different size), (2) a 2-day-old cowbird chick and an 8-day-old wren chick (different species, same size) and (3) a 2-day-old house wren and an 8-day-old house wren (same species, different size). When cowbirds shared the nest with a same-size wren chick, both chicks received food in equal proportion. In contrast, larger chicks (both cowbirds and wrens) paired with small wren nestmates always received a higher food share. Cowbird begging behaviour and call traits differed from house wrens, but these differences did not always coincide with increased food. We conclude that, at least when cowbird nestlings are young (2 days old), their relatively large size accounts for the larger share of food they receive from house wren hosts, rather than some quality of their begging signal.

Interspecific avian brood parasites lay their eggs in nests of other species (hosts), which then incubate the parasite eggs and feed and protect the parasite chicks (Davies, 2000; Ortega, 1998). In many systems, host parents not only willingly care for the imposter chick, but invest more in its care than they would a single chick of their own species (Hauber & Moskát, 2008; Kilner, Noble, & Davies, 1999; Lichtenstein & Sealy, 1998; Redondo, 1993). Indeed, this exaggerated investment can be a necessity from the parasite's perspective – where parasites are larger than their host species, one parasitic nestling may need the same food requirement as a whole brood of host young.

Such parasites have been proposed to succeed in securing this ‘extra’ investment from host parents via two possible means, which are not mutually exclusive. First, visual or acoustic components of the parasite's begging signal may be exaggerated sensory stimuli for host parents, triggering high levels of parental care (Dawkins & Krebs, 1979). For example, in many birds, both call rate and call acoustic features, such as bandwidth, duration and frequency, tend to increase in older and hungrier chicks (Magrath, Haff, Horn, & Leonard, 2010). Parasites can exploit this fact to increase the rate of provisioning to parasitized nests and/or, if sharing the nest with host young, to increase the chance that they are fed once food arrives. Thus, common cuckoos, *Cuculus canorus*, stimulate a high provisioning rate by calling at rates above those typical of a hungry reed warbler, *Acrocephalus scirpaceus*, host nestlings (Davies & Brooke, 1998; Kilner et al., 1999). Other parasitic chicks beg more intensely, louder, longer or more rapidly than host chicks for the same level of hunger, manipulating parental behaviour in their favour (Dearborn, 1998; Dearborn & Lichtenstein, 2002; Soler et al., 1995, 1999), and shiny cowbirds, *Molothrus bonariensis*, achieve the same outcome via a ‘stuttering’ begging call structure, which call for call, elicits a higher provisioning rate than that of some host chicks (Gloag & Kacelnik, 2013). Similarly, the vividly coloured gapes of some cuckoos are proposed to stimulate high provisioning rates in hosts (Alvarez, 2004; Tanaka, Morimoto, Stevens, & Ueda,

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2011). Such exaggerated begging traits of parasites relative to hosts may be specific adaptations to parasitism, or features shared by their nonparasitic relatives. For example, under standardized laboratory conditions, the intense begging of parasitic brown-headed cowbirds, *Molothrus ater*, is similar to that of a close nonparasitic relative, the red-winged blackbird, *Agelaius phoeniceus* (Rivers, Blundell, Loughin, Peer, & Rothstein, 2013).

Second, large body size itself may be key. In this case, wherever parasites share a nest with host young, large size biases the allocation of food between nestmates in the parasite's favour, either because host parents have a preference for feeding large chicks (Soler et al., 1995), or because the chick that receives food on any feeding visit is decided by scramble competition within the brood and large chicks are more competitive (Dearborn, 1998; Lichtenstein & Sealy, 1998). For example, brown-headed cowbird chicks receive more food than the host young of yellow warblers, *Setophaga petechia*, only when they are the larger chick of the clutch (Lichtenstein & Sealy, 1998). A similar trend has been observed across brown-headed cowbird hosts of different sizes, with the parasite receiving more, less or an equal amount of food when it uses hosts that are smaller, larger or of the same body size, respectively (Rivers, Loughin, & Rothstein, 2010).

The house wren, *Troglodytes aedon* (10–12 g), is a common small host of the generalist shiny cowbird (45 g; Kattan, 1998; Fiorini, Tuero, & Reboreda, 2009, 2012; Tuero, Fiorini, & Reboreda, 2007). Parasitized wren nests typically receive a single cowbird egg, which hatches more or less synchronously with wren young and is reared alongside them for some or all of the nesting period (Fiorini et al., 2009). Previous studies confirm that shiny cowbirds are commonly fed more than their house wren nestmates (Tuero, Gloag, & Reboreda, 2016). Shiny cowbird begging calls are highly effective at soliciting a high provisioning rate to the brood in house wrens (Gloag & Kacelnik, 2013), and cowbirds also benefit from the begging of house wren nestmates in maintaining high brood-level provisioning (Gloag, Tuero, Fiorini, Reboreda, & Kacelnik, 2012). Importantly, however, cowbirds best capitalize on these high provisioning rates because they also receive an outsized share of total feeding events (Gloag et al., 2012; Tuero et al., 2016). Under the size-advantage hypothesis, this skew in food allocation is the result of cowbirds being larger, at the same age, than house wren nestmates. Under the signal exaggeration hypothesis, it is the result of wren parents' response to one or more components of the cowbird's begging signal at the time of food allocation.

Here, we test predictions of these hypotheses by evaluating the begging behaviour and the allocation of food between cowbird and wren chicks in broods manipulated to contain nestlings of either the same or different sizes. In systems with large parasites and small hosts, there is no simple way to tease apart experimentally the effect of chick size from the effect of chick species. At just 2 days posthatch, shiny cowbird nestlings have reached a similar body size and mass as a house wren nestling of around 8 days of age. Pairing together host and parasite chicks of the same size therefore means pairing together chicks of different developmental stage. Nevertheless, comparisons of food allocation and begging behaviour between broods when chicks are either the same or different size and either the same species (both host) or different species (host and parasite) provide valuable insights into whether factors other than size are likely to have a role in host parents' food allocation decisions.

METHODS

Study Area and Brood Manipulation

We monitored house wrens nesting in boxes in stands of tala trees at El Destino Reserve, Magdalena, Buenos Aires Province, Argentina (35°08′S, 57°23′W), during the breeding seasons October–January 2011–2012, 2013–2014 and 2015–2016. House wrens at this site lay four to five eggs per clutch, of which one to two are typically punctured by cowbirds during nest visits by the parasite (Tuero et al., 2007). We manipulated the clutches of 103 experimental nests to ensure standard brood sizes of three house wren chicks and one cowbird chick. This required manipulating the relative timing of incubation, as cowbird incubations are shorter than those of house wrens (12–13 days versus 14–15 days, respectively). We therefore removed one or more wren eggs and any early-laid cowbird eggs prior to the onset of incubation, and then returned one cowbird egg after incubation had begun (or added one collected fresh from another nest). In this way, all experimental nests contained broods with synchronously hatched wren and cowbird chicks. Due to nest predation, not all experimental nests survived to nestling stage and the final sample size for each treatment is shown in Fig. 1.

At hatching, we visited nests daily and marked chick tarsi with waterproof ink for individual identification. Chicks were weighed with a digital portable balance, to the nearest 0.1 g until they were 9–10 days of age, because after that age they can fledge prematurely if they are disturbed. Marking and weighing procedures were conducted at 15 m from the nest and lasted less than 5 min, minimizing the distress of adults and chicks due to the manipulation. The weight of the chick was used to estimate its body size (Lichtenstein & Sealy, 1998). At hatching, wrens typically weigh 1.6 g and cowbirds typically weigh 4.2 g. At fledging, wrens weigh ~11.5 g and cowbirds weigh ~40.3 g (Tuero et al., 2007). Our work adheres to the ASAB/ABS Guidelines for the use of animals in research. The study was conducted with the permission of the Provincial Organism for Sustainable Development (OPDS, Buenos Aires, Argentina; permit no. 202/12-O.P.D.S.) and complies with the current laws of Argentina.

Experimental Procedure

We recorded video and audio at nests during one morning to determine parental food allocation and chick begging characteristics. On the experimental morning, we manipulated the nest by temporarily changing the brood composition to leave only a pair of chicks in the nest according to one of three treatments (Fig. 1): (1) large cowbird–small wren treatment: a cowbird and a wren chick, both 2 days old, with the cowbird being the larger chick; (2) large cowbird–large wren treatment: a cowbird and a wren chick of similar size (t test: $t_{36} = 1.3$, $P = 0.2$) but with the cowbird being the younger chick; (3) large wren–small wren treatment: two wren chicks with different body weight due to their different ages.

The cowbirds of the large cowbird–small wren treatment and the large cowbird–large wren treatment did not differ in their body weight from the largest wren of the large wren–small wren treatment (ANOVA: $F_{2,50} = 2.98$, $P = 0.06$). There were also no differences between the body weight of the small wrens used in each treatment with small wrens (t test: $t_{28} = 1.11$, $P = 0.28$). If the larger chick in the brood always received a greater share of provisions, irrespective of species (cowbird or house wren), then cowbird's success in food allocation is consistent with chick size being a key factor determining food allocation. If cowbirds always received a greater share of food, irrespective of wren nestmate size, then their success in food allocation is consistent with the signal exaggeration hypothesis. In the latter case, we would also expect to find that cowbird begging signals exaggerate features most likely to affect food allocation decisions by parents (e.g. begging intensity, begging duration or call features; Dearborn & Lichtenstein, 2002; Gloag et al., 2013) relative to host nestmates, regardless of host nestmate size.

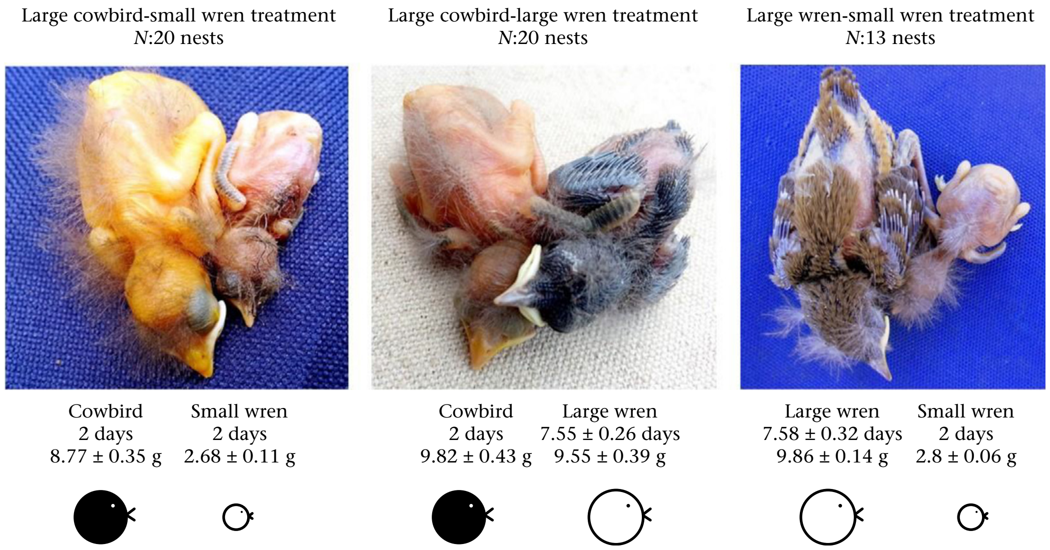

Figure 1. The treatments used in the experimental broods, showing the types of chicks per treatment and their age and mean ± SE weight.

Video recordings were performed during the morning; between 0700 and 1200 hours. Short-term need (i.e. hunger level) is expected to affect the begging behaviour of both host and parasite young (Hauber & Ramsey, 2003; Lichtenstein & Dearborn, 2004). Therefore, to standardize this variable, when we removed the chicks from their respective nests, we fed them by hand until satiation with a mixture of minced beef and eggs (Lichtenstein & Dearborn, 2004) and then kept them quiet for 40 min before returning them to the nest to start the experiment. We used chicks from different nests to make the experimental pairs, and all chicks were used once. To avoid disturbing adult wrens and chicks during the time that experimental chicks were out of the nest, we concealed the chicks 20 m from the nest in a small container (10 cm diameter) lined with nest-like material. Moreover, during this period, the nonexperimental chicks remained in their nests, being feeding normally by their parents. The chicks were filmed for 3 h using microcameras suspended above the nest, connected to a video recorder (Lawmate PVR500 ECO) and a power resource at the base of the tree. At a subset of nests (large cowbird—small wren: 11 nests; large cowbird—large wren: 6 nests; large wren—small wren: 9 nests), we simultaneously made audio recordings of chick begging, using a lapel microphone at the lip of the nest cup attached to a digital audio recorder at the base of the tree (Zoom H4N; 24-bit, 96 kHz). We attached microcameras and microphones as quickly as possible (5—10 min) to minimize disturbance at the nest. We began video analyses from the point that wrens first resumed feeding visits (normally after an initial 2—3 visits were made without food). There were no cases of nest abandonment associated with our manipulations and chicks maintained good health after the experiment. Video recordings were observed with VLC 2.1.5 Rincewind program and audio recordings were displayed as spectrograms through the Raven Pro 1.5 software (Bioacoustics Research Program, 2014).

Statistical Analysis

Food allocation

For each adult feeding visit, we determined the chick that was fed. To determine whether the proportion of food obtained for the two chicks in each treatment differed from a ratio of 50:50, we performed generalized linear models (GLM) with logit link function and binomial error term.

Begging behaviour and begging signals

To determine whether the begging behaviour differed between chicks in each treatment, we analysed two variables: (1) begging intensity: measured as the maximum begging posture scored during the feeding event, following the scale of Tuero et al. (2016) (and modified from Leonard, Horn, & Parks, 2003), where 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 and (2) begging duration: from the time the nestling started to beg until food was given (seconds). We analysed begging intensity using a generalized linear mixed model (GLMM) with zero-inflated Poisson error distribution and log link function. For begging duration, we performed a GLMM with negative binomial error distribution and log link function. In both analyses, chick type was introduced as the predictor variable, and nest and adult visit were introduced as random factors. For both analyses we estimated that overdispersion was close to 1, indicating that the models fitted their distribution.

To determine whether the acoustic structure of the begging calls differed between chicks in each treatment, we analysed variables of begging calls visualized from sonograms. We used Raven Pro 1.5 to visualize calls (filter bandwidth of 248 Hz, a frequency grid spacing of 172 Hz and a time grid resolution of 2.9 ms). Bouts of calls were identified by the presence of contact calls of adults followed by calls of nestlings on spectrograms. These sequences were verified by comparing real-time sonograms with the video of each nest. We analysed the first three bouts (for each type of nestling) where only one of the nestlings begged (in order to avoid superposition of begging). For each bout, we scored the first five clearly defined calls (i.e. those without overlapping calls), omitting harmonics, for the following variables: (1) F_{Min}: minimum frequency (Hz); (2) F_{Max}: maximum frequency (Hz); (3) bandwidth: frequency bandwidth (Hz); (4) F_{Peak}: peak frequency (Hz); (5) call duration (seconds) and (6) call rate: call rate per bout, calculated by dividing the number of calls in the bout by the duration of the bout. Then, to determine whether these acoustic characteristics differed between chick types within each treatment, we performed a GLMM including the variable chick type as the predictor variable with nest and bout included as random factors. Variables were analysed using a normal error distribution and identity link function. Normality and homoscedasticity were tested for these variables. We performed univariate analysis for the acoustic variables because the aim was to identify the variable(s) that might explain the food allocation between chicks.

Statistical analyses were carried out using R software, v.2.15.3 (R Development Core Team, 2013), and we used the ‘lme4’ and ‘glmmADMB’ R packages (Skaug, Fournier, Nielsen, Magnusson, & Bolker, 2013). All tests were two tailed, values are reported as means ± SE and we considered significant differences at $P < 0.05$.

RESULTS

When cowbirds were paired with same-age but smaller wren nestmates, as is typical under natural parasitism, the cowbird received food on a majority of the feeding visits ($Z = 9.01$, $N = 20$, $P < 0.001$; Fig. 2a, Supplementary Video S1). Cowbirds in this treatment begged more intensely and for longer than their small house wren nestmates (Fig. 2b and c, Table 1), but the calls of each species did not differ in rate or structure (F_{Min}, F_{Max}, bandwidth, F_{Peak}, call rate, call duration) (Tables 2, 3, 4). In contrast, cowbirds paired with wrens of similar size to themselves received an equal share of total feeds ($Z = 0.90$, $N = 19$, $P = 0.37$; Fig. 2a, Supplementary Video S1), despite the cowbird's more intense and longer begging behaviour (Fig. 2b and c, Table 1) and exaggerations by cowbirds of some call structure features (F_{Min}, F_{Max} and F_{Peak}; Tables 2, 3, 4).

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When two house wrens shared a nest, the larger house wren secured more feeds than its smaller nestmate ($Z = 6.93$, $N = 13$, $P < 0.001$; Fig. 2a, Supplementary Video S1). Large wrens differed from small wrens in the same nest with respect to call structure (F_{Max}, F_{Min}, bandwidth, F_{Peak} and call duration; Tables 2, 3, 4) and begging intensity (Fig. 2b, Table 1), but not call rate (Table 1 and 2) or begging duration per bout (Fig. 2c, Tables 1, 4). Moreover, large wrens paired with small wrens enjoyed a similar advantage in the proportion of feeds as did cowbirds paired with small wrens, consistent with size (rather than species) being the key factor determining food allocation in our experimental nests ($Z = -1.64$, $N = 33$, $P = 0.10$; Fig. 2a).

The 2-day-old cowbirds of this experiment had simple, single-syllable call structures similar to those of house wrens of all ages (Fig. 3). The number of feeding events per hour did not differ among the three treatments ($F_{2,3381} = 1.82$, $P = 0.17$; large cowbird–small wren: 9.9 ± 0.7; large cowbird–large wren: 12.7 ± 1.3; large wren–small wren: 10.3 ± 1.5).

DISCUSSION

Faced with a parasitized brood, house wrens feed the shiny cowbird in their nest more than they feed their own chicks (Tuero et al., 2016; this study). Here we show that young cowbirds experimentally paired with size-matched (i.e. older) house wren chicks fail to secure a higher share of feeds, and that larger, older house wrens paired with small wrens enjoy a similar skew in food allocation to that of cowbirds paired with small wrens. Together these findings suggest that in this host, the large size of cowbird chicks relative to host young is sufficient to explain the disproportionately high share of food they receive under natural parasitism conditions. Exaggerated begging stimuli might also play some role in favouring shiny cowbird chicks. Indeed, begging intensity, begging duration and several aspects of begging call structure that may be correlated with chick need (Magrath et al., 2010) were higher in cowbirds relative to house wren nestmates, regardless of relative size. However, cowbirds paired with same-sized house wrens received an equal food allocation (and similar food allocation to large wrens paired with small wrens) despite the cowbird's begging differences, indicating that begging must play a far smaller role in food allocation decisions than does relative chick size.

Is the willingness of house wrens to preferentially feed a large parasite shared by other cowbird hosts? Previous studies on shiny and brown-headed cowbirds have found that parasitic chicks receive a greater proportion of feeding events than smaller or similar size host nestlings with which they share the nest (Dearborn, 1998; Lichtenstein & Dearborn, 2004; Lichtenstein & Sealy, 1998; Rivers, 2007; Tuero et al., 2016). Signal exaggeration via chick begging posture was suggested to explain this preference in indigo bunting, *Passerina cyanea* (Dearborn, 1998). Other studies have found that parasitic chick success is due to cowbirds physically outcompeting the smaller chicks of their hosts (Lichtenstein & Dearborn, 2004). Lichtenstein and Sealy (1998) studied the food allocation in nests of a small host (*Dendroica petechia*) parasitized by the brown-headed cowbird – a system similar to our shiny

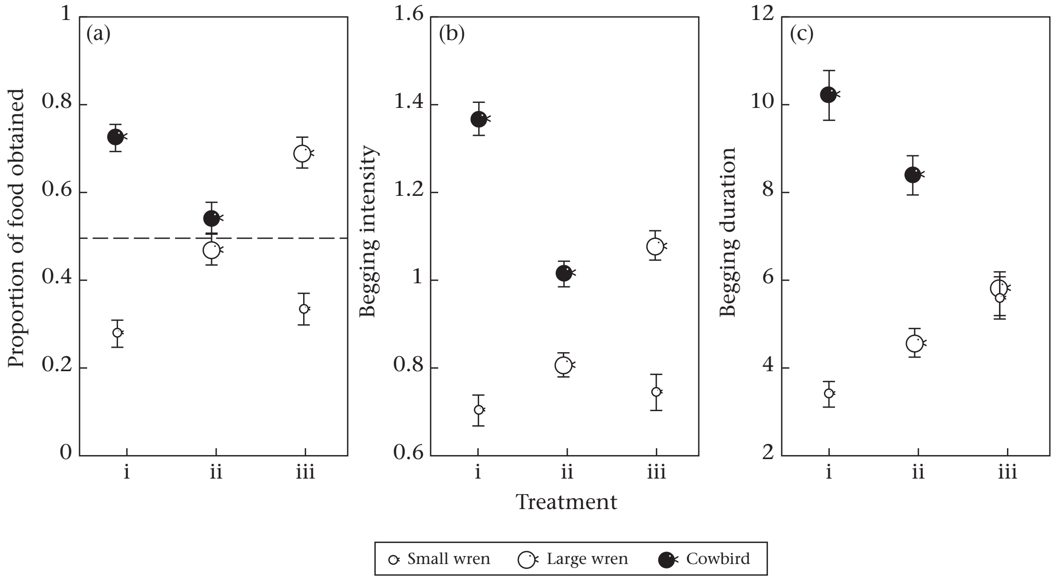

Figure 2. Mean ± SE (a) proportion of food obtained, (b) begging intensity and (c) begging duration of chicks in each treatment: (i) large cowbird–small wren; (ii) large cowbird–large wren; (iii) large wren–small wren.

Table 1
Estimates ± SE, *Z* values and significance (*P*) of the response variable begging intensity and begging duration based on generalized linear mixed models (GLMM)

Treatment	Predictor variable	Begging intensity			Begging duration		
		Estimate ± SE	*Z*	*P*	Estimate ± SE	*Z*	*P*
Large cowbird–small wren	Intercept (small wren)	-0.41±0.003	-4.77	<0.001	0.99±0.004	7.49	<0.001
N=1000 visits; *N*=20 nests	Cowbird	0.71±0.003	6.26	**<0.001**	1.22±0.005	7.63	**<0.001**
Large cowbird–large wren	Intercept (large wren)	-0.25±0.002	-3.32	<0.01	1.41±0.003	11.61	<0.001
N=1570 visits; *N*=20 nests	Cowbird	0.26±0.002	2.55	**<0.05**	0.68±0.004	4.46	**<0.001**
Large wren–small wren	Intercept (small wren)	-0.29±0.003	-3.07	<0.001	1.58±0.006	9.39	<0.001
N=814 visits; *N*=13 nests	Large wren	0.31±0.004	2.34	**<0.05**	0.05±0.006	0.26	**0.8**

Significant P values are shown in bold.

Table 2
Mean ± SE of each acoustic variable obtained from sonograms of the begging of each chick in the three brood treatments (large cowbird–small wren; large cowbird–large wren; large wren–small wren)

Predictor variable	Treatment					
	Large cowbird	Small wren	Large cowbird	Large wren	Large wren	Small wren
	(*N*=20 bouts)	(*N*=9 bouts)	(*N*=9 bouts)	(*N*=12 bouts)	(*N*=21 bouts)	(*N*=19 bouts)
F_{Min} (kHz)	4118±141	4588±95	**6134±504**	**6484±388**	**6546±216**	**5868±210**
F_{Max} (kHz)	6901±216	7131±150	**10597±925**	**10108±590**	**11038±344**	**9780±392**
Bandwidth (kHz)	2783±222	2542±142	4462±518	3624±322	**4745±254**	**3912±238**
F_{Peak} (kHz)	5587±173	5929±84	**8258±638**	**8425±478**	**8542±161**	**7534±242**
Call duration (s)	0.06±0.003	0.06±0.004	0.05±0.004	0.05±0.005	**0.07±0.01**	**0.05±0.01**
Call rate (calls/s)	0.99±0.09	0.67±0.10	1.80±0.18	2.32±0.29	2.23±0.34	2.73±0.18

F_{Min}: minimum frequency (Hz); F_{Max}: maximum frequency (Hz); bandwidth: frequency bandwidth (Hz); F_{Peak}: peak frequency (Hz); call duration (seconds); call rate: call rate per bout, calculated by dividing the number of calls in the bout by the duration of the bout. Significant comparsions are shown in bold.

Table 3
Means ± SE, *Z* values and significance (*P*) of acoustic response variables based on generalized linear mixed models (GLMM)

Variable	Treatment		Estimate ± SE	*Z*	*P*
F_{Min}	Large cowbird–small wren	Intercept (small wren)	4266±32.8	20.21	<0.001
		Cowbird	-82.2±24.9	-0.52	**0.60**
	Large cowbird–large wren	Intercept (large wren)	6476±115	12.29	<0.001
		Cowbird	-774±44.1	-3.84	**<0.001**
	Large wren–small wren	Intercept (small wren)	5945±35.1	26.75	<0.001
		Large wren	471±22.1	3.37	**<0.001**
F_{Max}	Large cowbird–small wren	Intercept (small wren)	6990±61.5	21.14	<0.001
		Cowbird	-135±37.7	-0.66	**0.51**
	Large cowbird–large wren	Intercept (large wren)	10455±212.1	10.76	<0.001
		Cowbird	-777±44,3	-3.83	**<0.001**
	Large wren–small wren	Intercept (small wren)	9741±55.3	27.79	<0.001
		Large wren	1113±22.3	7.88	**<0.001**
Bandwidth	Large cowbird–small wren	Intercept (small wren)	2812±56.8	9.20	<0.001
		Cowbird	-144±29.3	-0.91	**0.36**
	Large cowbird–large wren	Intercept (large wren)	3956±113.5	7.60	<0.001
		Cowbird	104±46.3	0.49	**0.62**
	Large wren–small wren	Intercept (small wren)	3693±47.4	12.23	<0.001
		Large wren	1018± 22.1	7.29	**<0.001**
F_{Peak}	Large cowbird–small wren	Intercept (small wren)	5702±47.2	22.42	<0.001
		Cowbird	-153±24.7	-1.16	**0.25**
	Large cowbird–large wren	Intercept (large wren)	8660±157.8	11.98	<0.001
		Cowbird	-1009±44.3	-4.98	**<0.001**
	Large wren–small wren	Intercept (small wren)	7552±28.9	41.17	<0.001
		Large wren	900±21.8	6.51	**<0.001**
Call duration	Large cowbird–small wren	Intercept (small wren)	0.061±0.001	10.61	<0.001
		Cowbird	-0.0014±0.0010	-0.25	**0.80**
	Large cowbird–large wren	Intercept (large wren)	0.048±0.001	7.06	<0.001
		Cowbird	0.003±0.001	0.51	**0.61**
	Large wren- small wren	Intercept (small wren)	0.054±0.002	4.49	<0.001
		Large wren	0.0090±0.0007	2.05	**0.04**
Call rate	Large cowbird–small wren	Intercept (small wren)	0.81±0.02	7.02	<0.001
		Cowbird	0.15±0.01	1.95	**0.051**
	Large cowbird–large wren	Intercept (large wren)	2.22±0.07	6.70	<0.001
		Cowbird	-0.30±0.04	-1.49	**0.14**
	Large wren- small wren	Intercept (small wren)	2.57±0.05	7.71	<0.001
		Large wren	-0.32±0.05	-1.05	**0.29**

Large cowbird–small wren treatment: *N* = 29 observations; large cowbird–large wren treatment: *N* = 21 observations; large wren–small wren treatment: *N*=40 observations. Abbreviations as in Table 2. Significant P values are shown in bold.

Table 4
A summary of the visual and acoustic begging traits of each chick type per treatment, in relation to their success in monopolizing food over their nestmate

Treatment	Prop. of food	Visual variables		Acoustic variables					
		Begging intensity	Begging duration	F_{Max} bout	F_{Min} bout	Bandwidth	F_{Peak} bout	Call duration	Call rate
Large cowbird–small wren	$\neq$	$\neq$	$\neq$	$=^*$	$=^*$	$=^*$	$=^*$	$=^*$	$=^*$
Large cowbird–large wren	$=$	$\neq^*$	$\neq^*$	$\neq^*$	$\neq^*$	$=$	$\neq^*$	$=$	$=$
Large wren–small wren	$\neq$	$\neq$	$=^*$	$\neq$	$\neq$	$\neq$	$\neq$	$\neq$	$=^*$

An equal sign (=) indicates that there was no significant difference in this variable between the two chick types. An unequal sign (≠) indicates a significant difference in this variable between the two chick types. An asterisk indicates nonconcordance between the proportion of food obtained for the chicks and the visual or acoustic variables (i.e. exaggeration in a begging variable did not equate to a higher proportion of feeds). Abbreviations as in Table 2.

cowbird and house wren system – and also concluded that the cowbird's success arose simply from its larger size. They suggested that large size allowed cowbirds to push away other nestlings and position it closer to the nest entrance where it then monopolized feeding events (Lichtenstein & Sealy, 1998). Although we did not measure chick position relative to the entrance in our study, a similar mechanism of competition might apply in the shiny cowbird–house wren system.

In our large cowbird–large wren treatment, both chicks received similar amounts of food, but cowbird chicks in this treatment were 2 days old and blind, while wrens were 8 days old with eyes open. Could food allocation in this case, therefore, be the result of wren chicks outmanoeuvring cowbirds, rather than a size-based provisioning behaviour of parents? From our observations of videoed chick behaviour, this explanation is unlikely. During provisioning visits in which both chicks begged simultaneously, we never observed the older wren chick intercepting food that parents were trying to give to the cowbird (see Supplemental Video S1).

In this study, we focused on cowbirds in the early nesting phase (2 days of age). At this age, the begging call of cowbirds is a simple repeated monosyllabic call, as is the call of house wrens at all ages (Gloag & Kacelnik, 2013). The acoustic characteristics of cowbird begging calls change, however, with age (De Mársico, Gantchoff, & Reboreda, 2012; Gloag & Kacelnik, 2013). At later nestling ages (6–8 days of age), shiny cowbirds' individual calls become multisyllabic and begin to resemble several wren chick calls repeated rapidly end to end (Gloag & Kacelnik, 2013). It is possible that at these older nestling ages, an ‘exaggerated stimulus’ effect is acting together with large size to increase a cowbird's share of total food and/or increase the total number of feeding visits to the nest. At these ages, the type of experimental pairing with same-age chicks undertaken in this study is impossible, because cowbirds at 6–8 days have grown larger even than adult house wrens. For the same reason though, it may be that by this time, the needs of the cowbird chick are so great that it can no longer rely on simple monopolization of feeds to meet its needs, but must also increase the overall number of feeds to the nest (Gloag et al., 2012; Gloag & Kacelnik, 2013).

What are the selective pressures acting on the begging signals of shiny cowbirds? Shiny cowbirds use a large range of host sizes, ranging from much smaller to much larger than themselves (10–80 g) (Fiorini, De Mársico, Ursino, & Reboreda, 2019). They are also true generalists – that is, individual females will often use more than one host in their lifetime, although they may have preferences for certain host types (de la Colina, Hauber, Strausberger, Reboreda, & Mahler, 2016; Gloag, Fiorini, Reboreda, & Kacelnik, 2014; Mahler, Confalonieri, Lovette, & Reboreda, 2007). The extent to which this type of generalism constraints coevolution with hosts is an open question. Traits that increase the rate of provisioning to the nest are presumably favoured in both large and small hosts. In contrast, traits that affect relative food allocation are most likely to be strong in large hosts but weaker in small hosts, where size alone is often enough to secure a large share of food. Likewise, some types of ‘exaggerated stimulus’ will be general across hosts (e.g. call rate, high begging intensity) but others may not be (e.g. species-specific aspects of begging calls such as call structure or gape colour). One possibility is that parasites might also be selected to be ‘flexible’ in traits that affect success in different hosts. That is, cowbirds may beg differently in large and small hosts as a result of behavioural plasticity or learning. Indeed, Tuero et al. (2016) found that shiny cowbird chicks beg more intensely in nests of a large host (chalk-browed mockingbird, *Mimus saturninus*) than in wren nests, consistent with parasites adjusting their begging based on the intrabrood competition of a given host. Evidence in other altricial birds showed that begging might be affected by the asymmetry in the body sizes (Cotton, Wright, & Kacelnik, 1999) or the begging intensity (Smith & Montgomerie, 1991) of nestmates.

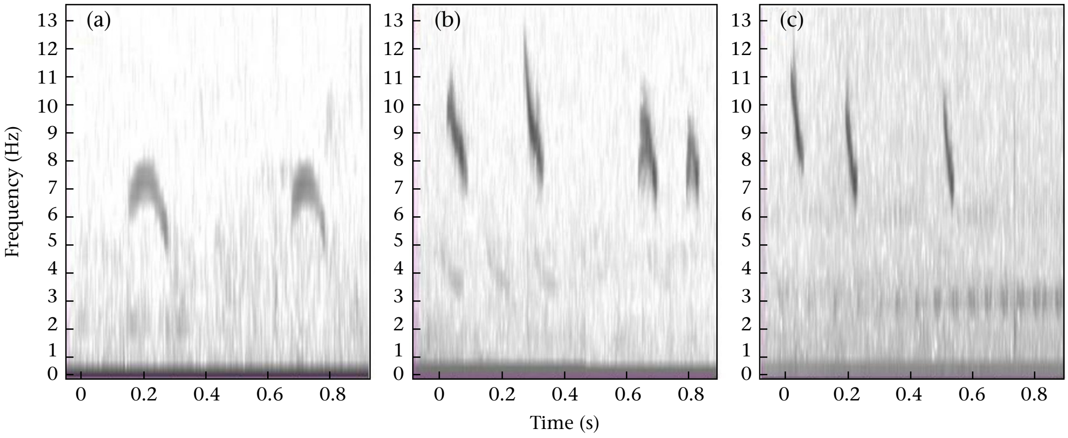

Figure 3. Spectrograms showing the begging calls of (a) a 2-day-old cowbird, (b) a 2-day-old house wren and (c) an 8-day-old house wren.

The idea that brood-parasitic birds manipulate their hosts via special aspects of their begging signals has had long-standing appeal since Dawkins & Krebs (1979) first proposed the analogy of a cuckoo's supernormal begging stimuli affecting hosts in the same way as a drug affects the nervous system. The picture that has emerged from research on diverse brood parasite systems, however, is that manipulation of this kind is not ubiquitous, and may be just one weapon in the diverse arsenal of parasites. Rather, most parasitic species use multiple strategies to secure host care, which may differ between hosts or between stages of the nestling cycle (Davies, Kilner, & Noble, 1998; Gloag & Kacelnik, 2013, Kilner, Madden, & Hauber, 2004; Langmore, Maurer, & Kilner, 2008; Lichtenstein & Dearborn, 2004; Roldán, Soler, Márquez, & Soler, 2013; Tuero et al., 2016; Ursino, Gloag, Reboreda, & De Mársico, 2018). Our study contributes to this view, showing that newly hatched shiny cowbirds in nests of house wren hosts enjoy a high feeding rate thanks mostly to their larger size.

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