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# The exaggerated begging behaviour of an obligate avian brood parasite is shared with a nonparasitic close relative

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Offspring signalling models predict that the begging displays of obligate brood parasites are more intense than nonparasitic species because parasitic young are never reared by their genetic parents and often compete against unrelated host young during development. The brown-headed cowbird, *Molothrus ater*, has been described as having exaggerated begging relative to nonparasitic species, but an effective test of this idea is lacking because previous studies have not controlled for evolutionary history while simultaneously standardizing rearing conditions. We quantified the begging intensity of cowbirds and the closely related, nonparasitic red-winged blackbird, *Agelaius phoeniceus*, when both species experienced identical rearing conditions in two distinct nest environments: reared alone by a small cowbird host, or reared with two host young by a moderate-sized cowbird host. Against theoretical predictions, we found that in both nest environments four components of the cowbird begging display were similar to (or less intense than) blackbird begging displays (i.e. latency to beg, begging score, call rate and call amplitude) when nestlings were tested across a gradient of short-term need. Our results provide the first experimental evidence that a closely related, yet nonparasitic, species shares an exaggerated begging display with a brood-parasitic species when reared under conditions typically experienced by parasitic offspring. We discuss three nonexclusive explanations for our findings: (1) relatedness among cowbird nestmates reduced cowbird begging intensity (kin selection hypothesis), (2) reduced body condition of blackbirds elevated their begging intensity (body condition hypothesis) and (3) intense competition in blackbird nest environments led to increased blackbird begging intensity (competitive environment hypothesis).

Begging is part of a dynamic behavioural interaction in which dependent offspring solicit critical resources from care-giving adults, and adults use begging displays to decide how resources should be distributed to offspring (Kilner & Johnstone 1997; Budden & Wright 2001). For a wide range of animals, begging is the primary means by which offspring acquire food resources (Weygoldt 1980; Budden & Wright 2001; Smiseth et al. 2007; Madden et al. 2009), especially for species with altricial development that are unable to forage independently until after leaving the nest (Kilner & Johnstone 1997; Budden & Wright 2001). Thus, begging serves as a behavioural means for obtaining food resources that are critical to fitness while in the natal environment, making it perhaps the most important behaviour of nest-bound offspring.

Signalling models of offspring begging posit that dependent young honestly signal their need to provisioning adults, who, in turn, use those signals to make decisions about their degree of parental investment (Godfray 1991, 1995). Signalling models assume that the honesty of begging signals is maintained by three costs that rise with a concomitant increase in begging intensity: growth, nest predation and inclusive fitness (Mock & Parker 1997; Johnstone & Godfray 2002). Growth costs are based on reallocating energy from growth and development towards increased energetic expenditure that stems from elevated begging intensity (Chappell & Bachman 2002), whereas nest predation costs are based on a greater likelihood of a nest being detected and depredated due to more intense begging (e.g. louder or more frequent begging vocalizations; Haskell 2002). Inclusive fitness costs are due to decreased reproductive value of close kin that rise with an increase

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in begging intensity (Johnstone & Godfray 2002). Although empirical estimates of begging costs have been elusive (Chappell & Bachman 2002; Haskell 2002; Johnstone & Godfray 2002), such costs are thought to place an upper limit on the intensity of begging displays in dependent young (Mock & Parker 1997; Johnstone & Godfray 2002).

Obligate brood parasites are unique among birds because they are reared by unrelated adults and, in most cases, occur alone in the nest or compete against unrelated young for critical food resources during development (Payne 1977; Rothstein 1990; Davies 2000). Brood-parasitic young are therefore thought to be free of inclusive fitness costs during development, so their begging intensity is more intensive and exaggerated than nonparasitic species, all else being equal (Harper 1986; Motro 1989; Holen et al. 2001). In accordance with this notion, several empirical studies have confirmed that parasitic nestlings beg more intensively than nonparasitic species under similar conditions in a range of brood-parasitic species (e.g. Davies et al. 1998; Kilner et al. 1999; Lichtenstein 2001). In particular, several studies have found that nestlings of the brown-headed cowbird, *Molothrus ater* (hereafter cowbird) show begging displays that are more intense and exaggerated than those of nonparasitic species; cowbirds respond faster, beg longer, call louder and more frequently, and attain a greater begging posture than do nonparasitic young (Briskie et al. 1994; Dearborn 1998; 1999; Glassey & Forbes 2003; Rivers 2007; Pagnucco et al. 2008). Despite these clear differences, only a handful of studies have compared cowbird begging to close relatives to control for differences in evolutionary history (i.e. Briskie et al. 1994; Glassey & Forbes 2003; Rivers 2007), and none has examined parasitic and nonparasitic species in a standardized rearing environment where both species were cared for by heterospecific ‘parents’. Nevertheless, both factors must be controlled for experimentally because rearing environments can greatly affect begging behaviour (e.g. Kedar et al. 2000; Rodríguez-Gironés et al. 2002) and because species-specific parent–offspring signals may lead to differential treatment of host young and parasitic offspring (Glassey & Forbes 2003; Schuetz 2005).

In this study, we investigated whether cowbirds have evolved exaggerated begging behaviour that serves as an adaptation for brood parasitism by comparing cowbird begging displays to those of the red-winged blackbird, *Agelaius phoeniceus* (hereafter blackbird), a closely related, nonparasitic species that is closely allied with the *Molothrus* cowbirds within the family Icteridae (Johnson & Lanyon 1999; Price et al. 2009). We used an approach in which both species were reared in heterospecific host nests that represented two common rearing environments for cowbirds in our study system (Rivers et al. 2010a): (1) reared alone by a small cowbird host and (2) reared with two host offspring by a moderate-sized cowbird host. In both host species, we experimentally controlled for nestling age and brood size, as both are known to influence begging behaviour (Budden & Wright 2001). In the middle of their developmental period we assayed nestling begging behaviour across a gradient of short-term need (Clark 2002) under controlled laboratory conditions. We predicted that the intensity of four components of the begging display of cowbird nestlings (i.e. latency to beg, begging score, call rate and call amplitude) would be greater than that of blackbirds for a given level of need and that this pattern would be consistent across the distinctly different rearing environments.

## METHODS

### *Study Locations and Focal Species*

We conducted experiments during the 2004–2007 breeding seasons at Konza Prairie Biological Station, KS, U.S.A., a 3487 ha tallgrass prairie preserve where the cowbird is abundant, occurs in all available habitats and parasitizes more than 20 host species (Rivers et al. 2010a, 2012). The blackbird is also abundant at this location, nesting in lowland habitats and rearing offspring that are similar to cowbirds in size and appearance during the early nestling period (Weatherhead 1989). The blackbird has a socially monogamous breeding system with extrapair fertilizations that often result in a mixture of full and half siblings in broods (Yasukawa & Searcy 1995). Although genetic data are not available from Konza Prairie, we have no reason to expect that the mean relatedness of blackbird nestling at this site would be different from previous studies that have reported a mean of one to two extrapair young per brood (e.g. Westneat 1993; Weatherhead & Boag 1995; Gray 1997). Long-term research on cowbird–host interactions at Konza Prairie has found that the Bell’s vireo, *Vireo bellii* (hereafter vireo), and the dickcissel, *Spiza americana*, are the two primary cowbird host species, harbouring more than 75% of total cowbird offspring found in more than 3000 host nests (Rivers et al. 2010a). However, these two cowbird hosts differ markedly in the rearing environments they provide for parasitic young. Cowbirds are reared alone in parasitized vireo nests because in these nests host young rarely hatch, host nestlings do not survive when competing against cowbirds, and vireos cannot rear more than one cowbird in a single breeding attempt (Parker 1999; Kosciuch & Sandercock 2008). In contrast, cowbirds in dickcissel nests typically compete against slightly smaller host offspring and/or other cowbirds, some of which survive to fledging (Zimmerman 1983). Thus, these two hosts provide two distinct rearing environments that are experienced by cowbird offspring in this host community (Rivers et al. 2010a) and throughout their geographical range (Friedmann 1963; Ortega 1998).

### *Creation of Experimental Broods*

Because of high predation rates we were forced to collect most cowbird and blackbird eggs and place them into incubators (Lyon Electronics, model TX-7) to maximize the number of nestlings for experiments. Nevertheless, we found no difference in the begging behaviour of incubator-hatched and field-hatched individuals for either species (J. W. Rivers, B. D. Peer & S. I. Rothstein, unpublished data), and thus we combined nestlings from both approaches for subsequent analyses. To create vireo broods, we transferred a single cowbird or blackbird into vireo nests that were close to hatching (mean placement = 1.1 days prior to hatch date) to mimic the nest environment experienced by cowbirds in this small host (Parker 1999; Kosciuch & Sandercock 2008); at the same time, any additional nest contents were collected under permit (i.e. 58 vireo eggs, 37 vireo nestlings, 2 cowbird eggs, and 7 cowbird nestlings from 28 nests; nestlings were killed via cervical dislocation and eggs were killed via freezing). For dickcissel broods, we manipulated nests to contain a single focal nestling (cowbird or blackbird) and two dickcissels. We transferred focal nestlings into dickcissel nests on the same day host eggs hatched to ensure that all three nestmates were the same age; any additional nest contents were collected under permit (i.e. 38 dickcissel eggs, 17 dickcissel nestlings, 1 cowbird egg, 1 cowbird nestling from 27 nests; nestlings were killed via cervical dislocation and eggs were killed via freezing). All experimental broods for both hosts were created before noon local time, and a brood size of three was used for the dickcissel because it is a common brood size for parasitized nests in northeast Kansas (Zimmerman 1983; Rivers et al. 2003).

When creating experimental broods, we used only first-hatching ‘core’ blackbirds (sensu Forbes & Glassey 2000) from original blackbird clutches. This is because testosterone, a hormone that can influence begging behaviour (Schwabl & Lipar 2002), varies with egg-laying order in the blackbird but is minimally different among core eggs (Lipar et al. 1999). Moreover, testosterone levels in core blackbird eggs are similar to levels in cowbird eggs (Hauber & Pilz 2003), so the testosterone levels of blackbird and cowbird nestlings used in experiments were expected to have been similar to each other. Despite restricting the experiments to core nestlings, however, our results should be representative of all blackbird young because available evidence indicates there is no difference in begging between core and marginal blackbird nestlings (Griffith 2007). We only used a single blackbird nestling from each original blackbird clutch in our experiments to eliminate the potential for nonindependence in begging behaviour due to relatedness. For cowbirds, we only used a single cowbird nestling from each parasitized host nest to minimize possible relatedness confounds that could stem from relaying by female cowbirds in multiply parasitized nests, which is known to occur at our site (Rivers et al. 2012). As there are currently no procedures that allow rapid, accurate assessment of the gender of hatchling songbirds under field conditions, we were unable to control for nestling sex and instead assumed a 50:50 sex ratio for focal nestlings because primary sex ratios appear to be equal for both cowbirds and blackbirds (Fiala 1981; Kasumovic et al. 2002). During 2004 only, we removed blackbird and cowbird nestlings from nests for about 2 h on the second day after hatching to assess begging behaviour early in the nestling stage under ambient environmental conditions via a mobile testing apparatus that allowed us to measure nestlings in the field. These procedures provided little additional data on offspring begging behaviour and were discontinued in subsequent years. Nevertheless, we found no difference between the begging behaviour of nestlings undergoing this additional procedure and conspecific nestlings tested in other years; thus, we combined nestlings from both groups in subsequent analyses.

### Laboratory Procedures

To assess begging behaviour under standardized environmental conditions, we temporarily removed all nestlings from experimental broods (one nestling in vireo broods and three nestlings in dickcissel broods) to a nearby climate-controlled laboratory on the afternoon of day 5 of the nestling period (where day 0 is the day of hatching). At the time we removed nestlings for laboratory trials, we swapped a nonexperimental nestling into the focal nest to prevent parental abandonment; no nests were abandoned due to this procedure (J. W. Rivers, B. D. Peer & S. I. Rothstein, unpublished data). Thirty minutes after being removed from the nest, we measured each nestling in the laboratory for body mass and right tarsus length and then fed it with up to eight mealworms to standardize hunger level (Leonard & Horn 2001). Although some nestlings continued to beg after ingestion of eight mealworms, feeding more than this amount in pilot trials led to regurgitation of food (see Redondo 1993 for a similar situation in a parasitic cuckoo), so we restricted feeding to a maximum of eight mealworms. In dickcissel nests, we marked host young individually on the bill with a nontoxic marker for identification during quantification of begging behaviours. After feeding, we placed all nestlings into an artificial nest and immediately commenced filming. The artificial nest sat inside an open wooden box whose sides prevented nestlings from seeing the experimenter during the experiment. Ten minutes after the start of filming and every 10 min thereafter for 90 min, we stimulated nestlings to beg by tapping gently four times on the edge of the artificial nest to mimic the auditory and tactile simulation of a parent arriving with food and alighting on the nest; all three species examined readily begged in response to this cue during preliminary trials. Following our previous work in this system (Rivers 2007), we did not feed nestlings during the 90 min trial to allow us to quantify changes in the begging display intensity across a natural continuum of short-term need (Clark 2002). We recorded begging behaviours during trials with a miniature video camera that was mounted to the side of the wooden box and attached to a camcorder, and we recorded begging calls via the sound analysis program SYRINX v2.1h (www.syrinxpc.com) via a lapel microphone placed approximately 10 cm above the centre of the nest that was connected to a laptop computer. We restricted our measurement of call rate to the last stimulation in each trial as calls were most likely to be given at this time because pilot data found that begging calls were not typically given during the first 60 min of experimental trials. We were able to visually distinguish among individual calls when measuring call rate in dickcissel nests as cowbird, blackbird and dickcissel nestlings differ markedly in call structure (J. W. Rivers, unpublished data).

Immediately after each trial was completed, we measured begging call amplitude (dB) of the cowbird or blackbird nestling in the nest with a hand-held digital sound meter (RadioShack model no. 33-2055) placed 30 cm away from the nestling; in dickcissel broods, we removed host nestmates from the artificial nest prior to measuring amplitude to maximize clarity of cowbird or blackbird begging calls. A series of begging calls were typically given by nestlings in response to this stimulation, and we recorded the loudest begging call in the series as the maximum begging call amplitude. In four instances (three cowbirds, one blackbird), a nestling produced audible begging calls that were below the detection threshold of the sound meter (i.e. 50 dB); we recorded a value of 50 dB in those cases. We ended trials after begging call amplitude was recorded. Next, we fed the nestling(s) to satiation with mealworms and then returned them to their nest in the field.

A single observer (J.W.R.) quantified all begging behaviours from video recordings to eliminate interobserver variation and for comparison with concurrent research projects (see Rivers 2008). To quantify begging, we only considered begging that occurred in the 15 s following each of the nine stimulations because under natural conditions most food items are provisioned within this period in three cowbird hosts (Rivers 2007). Begging behaviour was measured on a frame-by-frame basis to quantify each nestling's latency to beg and begging score for each of the nine stimulations that occurred during each 90 min laboratory trial. We defined latency to beg as the elapsed time between the onset of the tapping that was used to stimulate begging and the initiation of begging behaviour by a nestling. For every 1 s of the 15 s stimulation period we calculated begging score by determining the maximum begging posture on a scale of 0–3 following our previous work in this system (Rivers 2007), where 0 = no beg, 1 = gaping without stretched neck, 2 = gaping, neck stretched up to 75%, and abdomen resting on nest cup, and 3 = gaping, neck stretched >75%, abdomen not touching nest cup; begging scores could therefore range from 0 to 45.

### Quantification of Body Condition

Nestling begging behaviour can be influenced by both short-term (i.e. hunger) and long-term need (i.e. body condition; Clark 2002), and this experiment was designed specifically to assess the influence of short-term need on begging behaviour during laboratory trials. To quantify the potential influence of long-term need on begging behaviour, a single observer (J.W.R.) measured body size (i.e. body mass, right tarsus length) of all nestlings in experimental broods immediately prior to laboratory experiments for comparison with nestlings reared in reference broods. Because cowbirds are generalist brood parasites, they lack a single host reference brood against which measurements of experimental nestlings can be compared. Therefore, we compared experimental cowbird body mass on posthatch day 5 to a reference value for cowbird body mass that was averaged over 18 hosts from Kilpatrick (2002; tarsus data were unavailable). For blackbirds, we compared nestlings in our experimental broods to reference broods at Konza Prairie that consisted of four blackbird nestlings (the modal brood size at this location) reared in a blackbird nest. A single observer (J.W.R.) measured reference blackbird broods for body size (i.e. mass, right tarsus length) on the afternoon of day 5 of the nestling stage to match the time of measurement of blackbird nestlings in experimental broods. We restricted our comparisons to core blackbird nestlings in reference blackbird broods because experiments were restricted to core blackbird nestlings as described above. Because there were typically two to three core nestlings in each blackbird reference brood, we calculated average body size measurements over all core nestlings within each brood to eliminate the potential for nonindependence in body size due to relatedness.

### *Statistical Analysis*

Nestling begging can be influenced by nestmates (Forbes 2002). Therefore, we summed the begging scores of host young in dickcissel broods for each stimulation for use as a covariate. We found no evidence for a significant brood type*host begging score interaction in our initial analysis, indicating dickcissel begging behaviour was similar in cowbird and blackbird broods, so we dropped this interaction term from our final models. We used the PROC MIXED modelling function in SAS/STAT v.9.2 for Windows (SAS Institute, Cary, NC, U.S.A.) to assess latency to beg and begging score during laboratory trials, and calculated degrees of freedom with the Kenward–Rogers method. We modelled host species (vireo and dickcissel) separately, and we constructed models that included fixed effects for brood type (two levels: cowbird, blackbird), individual nest as a random effect, and stimulation (nine levels: 1…9) as the repeated measure. We used the correlation structure for each repeated measure response variable that generated the lowest Akaike Information Criterion values corrected for small sample size (AICc) relative to other candidate correlation structures. We used *t* tests to compare single measures of begging responses between brood types (i.e. call rate, maximum call amplitude) and to compare body size measurements between nestlings from experimental and reference broods. We report means (least squares means for repeated measures analysis) and associated standard errors (SEs), and set alpha at $P < 0.05$ for all tests.

## RESULTS

We created 43 vireo broods ($n = 24$ cowbird, $n = 19$ blackbird) and 61 dickcissel broods ($n = 28$ cowbird, $n = 33$ blackbird), of which 47% were depredated before experiments could be conducted. This reduced the number of nests available for experiments to 28 for the vireo ($n = 15$ cowbird broods, $n = 13$ blackbird broods) and 27 for the dickcissel ($n = 14$ cowbird broods, $n = 13$ blackbird broods).

### *Cowbird and Blackbird Begging in Experimental Broods*

In vireo broods, we found no difference in latency to beg between cowbirds and blackbirds ($F_{1,44.9} = 0.54$, $P = 0.468$; Fig. 1a). However, we did detect a significant change in latency to beg during trials ($F_{8,43.9} = 3.07$, $P = 0.008$), but no brood type*time interaction ($F_{8,43.9} = 1.00$, $P = 0.453$). Although the mean call rate during the last stimulation was higher for blackbirds (19.4 ± 3.07 calls/15 s), this difference was not significant (cowbird = 12.1 ± 2.87 calls/15 s; $t_{26} = -1.7$, $P = 0.094$). We detected no difference in begging score between cowbirds and blackbirds ($F_{1,26.2} = 0.02$, $P = 0.897$; Fig. 1b). However, there was a significant time effect ($F_{8,50.5} = 19.54$, $P < 0.001$), but no brood type*time interaction ($F_{8,50.5} = 0.39$, $P = 0.919$). Finally, we found that blackbirds had a significantly louder maximum call amplitude (72.8 ± 1.11 dB) relative to cowbirds (62.8 ± 2.56 dB; $t_{10} = -3.6$, $P = 0.005$).

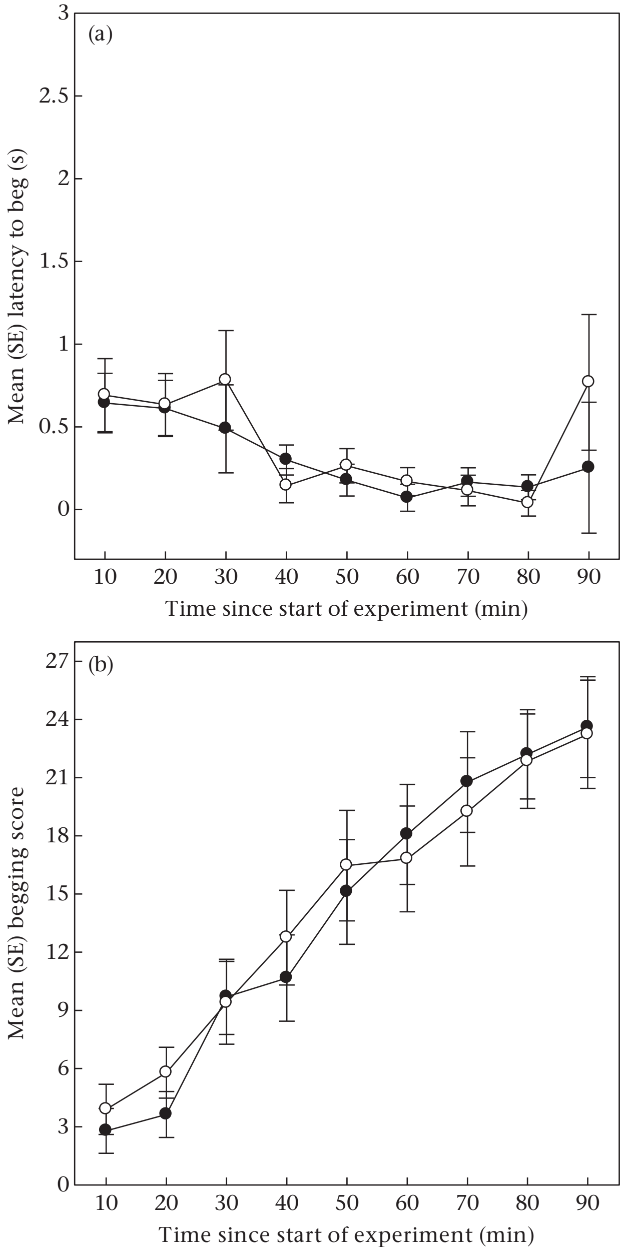

**Figure 1.** Components of the nestling begging display of the brood parasitic brown-headed cowbird (filled circles) and the closely related, nonparasitic red-winged blackbird (open circles) when individuals of each species were reared alone in Bell's vireo nests and tested under laboratory conditions. (a) Mean ± SE latency to beg (s). (b) Mean ± SE begging score, a composite of the time begging and the maximum posture (see text). $N = 15$ cowbirds, $N = 13$ blackbirds for both measures.

In dickcissel broods, we found no difference in latency to beg between cowbirds and blackbirds ($F_{1,13.1} = 0.00$, $P = 1.000$; Fig. 2a), although latency to beg changed significantly during trials ($F_{8,28.1} = 3.52$, $P = 0.006$) with no brood type*time interaction ($F_{8,26.4} = 0.51$, $P = 0.835$). Six of the 14 cowbird nestlings did not call during the last stimulation, whereas all 13 blackbird nestlings

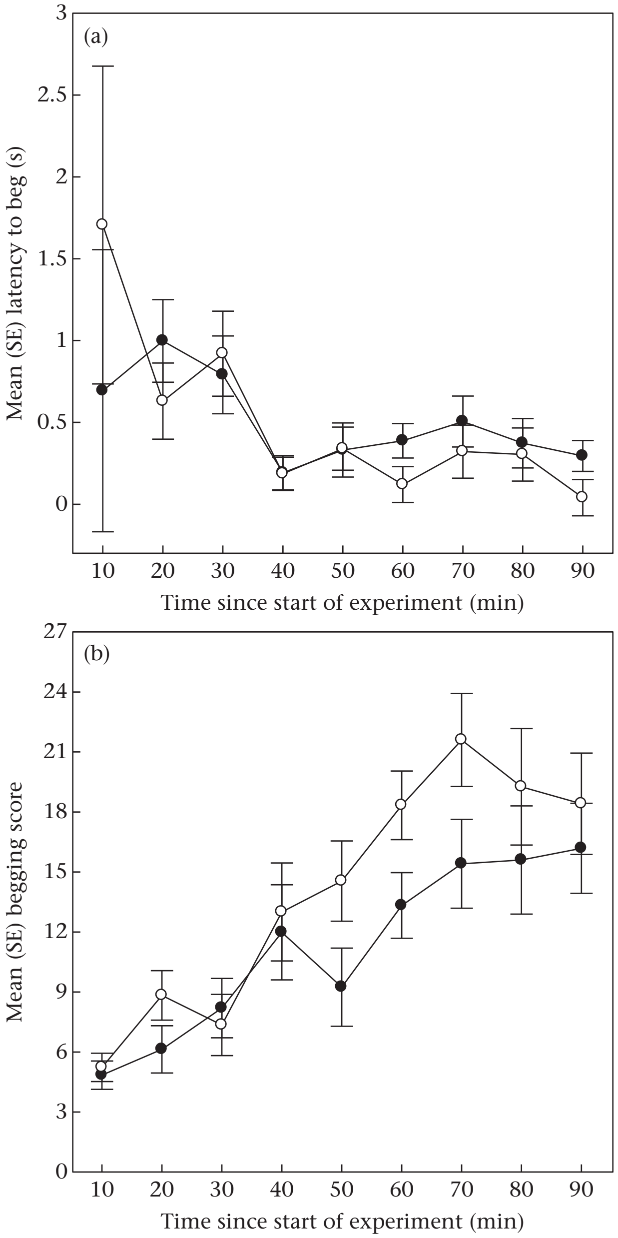

**Figure 2.** Components of the nestling begging display of the brood parasitic brown-headed cowbird (filled circles) and the closely related, nonparasitic red-winged blackbird (open circles) when individuals of each species were reared in dickcissel nests alongside two same-aged host offspring and tested under laboratory conditions. (a) Mean ± SE latency to beg (s). (b) Mean ± SE begging score, a composite of the time begging and the maximum posture (see text). $N = 14$ cowbirds, $N = 13$ blackbirds for both measures.

called. Mean call rate during the last stimulation was significantly greater for blackbirds (20.7 ± 3.29 calls/15 s) than cowbirds (6.9 ± 2.40 calls/15 s; $t_{25} = -3.4$, $P = 0.002$). We found no difference in begging scores of cowbird and blackbird nestlings ($F_{1,29.0} = 2.85$, $P = 0.102$; Fig. 2b), although begging scores changed significantly over the course of trials in both species ($F_{8,52.8} = 8.84$, $P < 0.001$) with no brood type*time interaction ($F_{8,48.5} = 1.39$, $P = 0.223$). Maximum call amplitude for nestlings which called was significantly greater for blackbirds (70.1 ± 2.46 dB) relative to cowbirds (57.5 ± 1.95 dB; $t_{19} = -4.4$, $P < 0.001$). The summed begging score of dickcissel nestmates, used as a covariate in our analysis, did not differ between nests containing cowbirds or blackbirds for either latency to beg (brood type*covariate interaction: $P = 0.807$) or begging score (brood type*covariate interaction: $P = 0.820$). The mean begging score of dickcissel nestmates was also consistently lower than those of cowbirds and blackbirds throughout trials (J. W. Rivers, B. D. Peer & S. I. Rothstein, unpublished data), indicating that both cowbird and blackbird nestlings showed more intense begging behaviour than dickcissel nestlings (J. W. Rivers, B. D. Peer & S. I. Rothstein, unpublished data). Note that cowbird begging call length (0.186 ± 0.027 s) was significantly longer than that of blackbirds (0.047 ± 0.004; $t_{9.5} = 5.1$, $P = 0.006$), and thus, greater call rate by blackbirds did not necessarily result in greater time spent calling in either brood type.

### *Condition of Cowbird and Blackbird Nestlings in Experimental Broods*

Cowbird body mass in vireo broods (15.7 ± 0.72 g) did not differ from cowbird body mass averaged across 18 reference host species (15.0 ± 0.57 g; $t_{31} = 0.8$, $P = 0.417$), whereas cowbird body mass was significantly greater in dickcissel broods than in reference host broods (18.7 ± 0.39 g; $t_{30} = 5.0$ and $P < 0.001$). In contrast, blackbird body mass (vireo broods: 16.4 ± 0.58 g; reference broods: 22.9 ± 0.67 g; $t_{20} = 7.2$, $P < 0.001$) and right tarsus length (vireo broods: 18.9 ± 0.31 mm; reference broods: 21.7 ± 0.16 mm; $t_{17.6} = 8.2$, $P < 0.001$) were significantly lower in experimental vireo broods than in reference broods. Similarly, blackbird body mass (dickcissel broods: 20.5 ± 0.68 g; reference broods: 22.9 ± 0.67 g; $t_{20} = 2.4$, $P = 0.026$) and right tarsus length (dickcissel broods: 20.6 ± 0.32 mm; reference broods: 21.7 ± 0.16 mm; $t_{17.4} = 3.0$, $P = 0.008$) were significantly lower in experimental dickcissel broods than in reference broods.

## DISCUSSION

Against predictions from theoretical models of offspring signalling (Harper 1986; Motro 1989; Godfray 1991, 1995; Mock & Parker 1997; Holen et al. 2001), we found that brood-parasitic cowbirds did not show more intense begging behaviour than closely related, nonparasitic blackbirds when both species were reared in identical rearing environments and tested under standardized laboratory conditions. Indeed, for some components of the begging display, blackbird begging was more intense than that of cowbirds. Our results are especially noteworthy because (1) we compared the begging behaviour of cowbirds and blackbirds that were reared in identical heterospecific host nest environments, (2) we found a similar pattern of begging between blackbirds and cowbirds across a gradient of short-term need, and (3) we uncovered repeatable results in markedly distinct host rearing environments. As such, our study provides the most rigorous examination to date to assess whether brood-parasitic offspring beg more intensively than closely related, nonparasitic species under identical rearing conditions. In light of our unexpected findings that exaggerated begging was shared between parasitic cowbirds and nonparasitic blackbirds, three nonexclusive explanations are plausible and can reconcile our empirical results with theoretical models of offspring signalling.

The first explanation posits that cowbird begging intensity was reduced because cowbirds are often reared with siblings in host nests at our study site (kin selection hypothesis). Konza Prairie is located near the centre of cowbird abundance within recent historical times (Lowther 1993) and long-term monitoring has revealed that the cowbird is the second-most abundant passerine species at this site (Rivers et al. 2010b). This results in high parasitism rates of host nests, and an extensive study of 1425 parasitized nests at Konza Prairie found that most cowbird offspring shared their nest with other cowbirds (i.e. 76% of cowbirds were found in host nests with at least one conspecific; Rivers et al. 2010a). Furthermore, a detailed genetic analysis of multiple parasitism at this site revealed a high level of relatedness between cowbird nestmates in multiply parasitized nests: the likelihood that an individual cowbird in a multiply parasitized nest shared its nest with a full sibling was 40.4% (95% CI: 28.4–52.4%; Rivers et al. 2012). Note, however, that this value is a minimum estimate of cowbird nestmate relatedness as that study was unable to differentiate between half siblings in broods (Rivers et al. 2012). Because theoretical models predict relatedness can constrain the intensity of begging displays (Harper 1986; Motro 1989; Godfray 1991, 1995; Holen et al. 2001; Johnstone & Godfray 2002), inclusive fitness costs may have been reduced fitness of cowbirds that begged at a high intensity, thereby decreasing the survival prospects of their siblings in multiply parasitized host nests.

A reduction in cowbird display intensity would be expected to reduce competition for food among cowbird siblings that are reared together and, in turn, increase fitness gains via kin selection (Hamilton 1964; West et al. 2002). Such a reduction might also reduce fitness when cowbirds compete against unrelated host young, although this possibility appears unlikely for cowbirds at Konza Prairie for several reasons. First, cowbird eggs typically hatch before host eggs (Briskie & Sealy 1990), and cowbird nestlings are typically larger than most hosts in the Konza Prairie community (Rivers et al. 2010a). Second, cowbird hosts bias food distribution towards the largest nestling, regardless of whether it is a cowbird, so the highest-reaching nestling has priority access to food (Dearborn 1998; Lichtenstein & Sealy 1998; Rivers 2007). Finally, the begging intensity of cowbird nestlings is maintained at an intensity that is greater than that of non-blackbird hosts at Konza Prairie (Rivers 2007; this study). Taken together, these factors lead to cowbirds being larger and begging more intensively than non-blackbird host nestmates, allowing them to obtain a disproportionate share of the food disbursed by host parents (Dearborn 1998; Lichtenstein & Sealy 1998; Kilner et al. 2004; Rivers 2007). Although reduced begging could potentially reduce fitness of cowbirds when they compete against unrelated cowbird (Goguen et al. 2011), this also appears unlikely because (1) host young typically fare worst in multiply parasitized nests because they are smaller and/or hatch later than cowbird nestlings (Briskie & Sealy 1990; Dearborn 1998; Lichtenstein & Sealy 1998; Kilner et al. 2004; Rivers 2007), (2) most hosts at Konza Prairie can rear multiple cowbirds during a nesting attempt (Lowther 1993; Ortega 1998; Rivers et al. 2010a), and (3) the majority of cowbird hosts receive three or fewer cowbird eggs, which is within the range that most hosts can rear (Friedmann 1963; Ortega 1998; Rivers et al. 2010a). Therefore, cowbirds can obtain adequate food despite having reduced begging intensity because most hosts can rear multiple cowbirds and because host young often lose out to cowbirds during begging scrambles in multiply parasitized nests.

An alternative and nonmutually exclusive explanation for our results is that being reared by heterospecific hosts reduced the body condition (Clark 2002) of blackbird nestlings and increased their begging intensity (body condition hypothesis). This explanation appears plausible because body condition is known to influence begging intensity (Clark 2002) and blackbirds in experimental broods were significantly lighter and smaller than blackbirds in reference broods. If a reduction in body condition did lead to increased begging intensity by blackbirds, it suggests that one or more components of the begging display was deficient in blackbirds, but not in cowbirds, for obtaining enough food for proper growth and development in heterospecific host nests. Which component(s) of the begging signal may be inadequate is unclear, but call structure is a likely candidate because it differs markedly between cowbirds and blackbirds. This is in contrast to begging movements and gape appearance, both of which are very similar, at least to human observers. An additional factor that could also lead to reduced body condition in blackbirds is that cowbirds may be more efficient than blackbirds at extracting nutrients from food items, or differ in how they allocate retained energy to growth or metabolism (Karasov & Martinez del Rio 2007).

A third nonexclusive explanation for our results is that the intensely competitive rearing environment experienced by blackbirds in natal nests has led to the development of an especially intense begging display for blackbird offspring (competitive environment hypothesis). The blackbird is a species that experiences obligate brood reduction, and broods are structured with first-hatched core nestlings and later-hatched marginal nestlings, with marginal offspring surviving only in years of abundant food resources (Forbes et al. 1997; Forbes 2010). This results in a rearing environment in which blackbird nestlings compete intensely for food against nestmates that are as large as (or larger than) themselves, leading to an elevation in the intensity of begging behaviour. A similar scenario of obligate brood reduction and intense competition for food among nestmates occurs in the yellow-headed blackbird, *Xanthocephalus xanthocephalus*, with similar consequences for offspring survival and begging intensity (Price & Ydenberg 1995; Price et al. 1996; Forbes et al. 2002). Because brood reduction and highly competitive rearing environments are characteristic of several other closely related allies of the parasitic cowbirds (Howe 1978; Teather & Weatherhead 1989; Mermoz & Ornelas 2004; Fernandez et al. 2007; Ruiz et al. 2008), it is interesting to speculate that these factors may have influenced the evolution of brood parasitism in this lineage.

As noted above, the three hypotheses put forward to explain shared begging intensity between parasitic cowbirds and nonparasitic blackbirds are not mutually exclusive, so it may be that the patterns in this study arose due to factors that have led to both a reduction in cowbird begging intensity and an elevation of begging intensity in blackbirds. Regardless of the underlying causes, ours is the first study to provide strong empirical evidence that the begging intensity of a nonparasitic species can equal or exceed that of a closely related parasitic species when both species are reared in identical heterospecific rearing environments. Given our findings, we encourage additional studies that quantify the begging behaviour of parasitic cowbirds and their nonparasitic icterid relatives to assess how begging intensity varies among these two groups. Studies are also warranted that test whether parasitic cowbirds are more efficient at extracting nutrients from food items or differ in how they allocate energy to growth or metabolism, as such investigations may uncover heretofore unknown adaptations of the offspring signalling and digestive systems of brood parasitic young.

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