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Original Article

Mismatched begging displays between foreign and host offspring reduce brood parasite fitness

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Obligate brood parasites must obtain food from unrelated host parents during the developmental period, and this may be especially difficult when parasitic nestlings are raised alone. Unlike specialist brood parasites, generalist brood parasites use a single begging display for a range of host species. In this study, we 1) tested whether the begging display of the generalist brown-headed cowbird (*Molothrus ater*) was more exaggerated than the closely related, nonparasitic red-winged blackbird (*Agelaius phoeniceus*) and 2) examined how begging displays were linked to food provisioning when both foreign species were raised by the Bell's vireo (*Vireo bellii*), a small cowbird host. We also quantified parental provisioning to unparasitized broods containing 1–4 vireo nestlings to provide a reference provisioning curve to provide context for assessing the feeding rate to foreign offspring. We found blackbirds begged as intensely as (or more intensely than) cowbird nestlings, vireo parents provisioned both species similarly, and the amount of food provisioned to unparasitized broods increased with brood size and maintained per-capita vireo growth. However, feeding of a single foreign nestling was significantly less than that of a modal brood of 4 vireos, indicating parents fed foreign nestlings at submaximal rates. Vireos did not respond to begging of foreign nestlings in the same manner as their own offspring, and this led to significant fitness costs for foreign nestlings. We conclude that a single foreign nestling provided an inadequate stimulus for vireos, probably because of a mismatch between the begging displays of foreign and host offspring.

Key words: ***Agelaius phoeniceus*, begging, Bell's vireo, brood parasitism, brown-headed cowbird, *Molothrus ater*, provisioning behavior, red-winged blackbird, *Vireo bellii*.**

Begging serves as the primary means by which dependent young obtain food from care-giving adults (Weygoldt 1980; Budden and Wright 2001; Smiseth et al. 2007; Madden et al. 2009) and, therefore, serves as one of the of the most important behaviors exhibited by developing offspring (Budden and Wright 2001; Wright and Leonard 2002). According to signaling models of offspring solicitation, dependent young use begging displays to provide information to care-giving adults regarding their resource needs; adults, in turn, use begging displays to make decisions about how much food should be provisioned to each offspring (Godfray 1991, 1995; Mock and Parker 1997; but see Mock et al. 2011). Studies examining the interaction between offspring begging and parental provisioning continue to provide an opportunity for testing ideas about conflict between close relatives and its resolution through behavioral means (Wright and Leonard 2002). Signaling models argue that this conflict is governed by 3 costs that are incurred by begging displays (Godfray 1991, 1995; Wright and Leonard 2002). Growth costs are incurred when offspring spend additional time and energy begging for food that reduces their rate of growth (Chappell and Bachman 2002), whereas predation costs occur when begging increases the likelihood that a predator locates and preys on begging offspring (Haskell 2002). The third type of cost is indirect and is incurred when individuals take a share of resources, typically food, that reduces the fitness of closely related young, provisioning adults, or both (Johnstone and Godfray 2002). Collectively, these costs are thought to place an upper limit on the intensity of begging displays of dependent offspring (Godfray 1991, 1995), although evidence for these costs in nature is rather limited (Chappell and Bachman 2002; Haskell 2002; Johnstone and Godfray 2002; Moreno-Rueda 2007).

Obligate avian brood parasites represent a unique group in which to test hypotheses regarding offspring begging because such species are not cared for by their parents during the developmental period

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(Payne 1977; Rothstein 1990; Davies 2000). Instead, parasitic offspring are raised by unrelated heterospecific hosts. In most cases, parasitic young are raised alone or compete against unrelated host young, freeing them from the constraints of the indirect costs of begging and leading to the expectation that parasitic young should beg more intensively than nonparasitic young, all else being equal (Harper 1986; Motro 1989; Holen et al. 2001). Empirical investigations have confirmed theoretical predictions regarding begging in this group: brood parasites typically exhibit exaggerated begging displays relative to nonparasitic species (e.g., Redondo 1993; Briskie et al. 1994; Davies et al. 1998; Dearborn 1998; Kilner et al. 1999). However, few studies have controlled for evolutionary history by simultaneously quantifying begging displays of parasitic offspring and those of closely related, nonparasitic species (i.e., Briskie et al. 1994; Glassey and Forbes 2003; Madden et al. 2005; Rivers 2007). Furthermore, only 1 study has quantified begging in a parasitic species and nonparasitic close relatives raised in heterospecific nest environments (Madden et al. 2005), and it did not assess how begging was linked to parental provisioning. Nevertheless, studies that control such factors and examine the connection between begging and parental provisioning are crucial for understanding how brood parasites have diverged from nonparasitic species in their begging behavior in the rearing conditions typically experienced by parasitic offspring.

A key challenge for young obligate brood parasites is obtaining adequate food from host parents for growth during the critical developmental period. This is especially true for species that are raised alone and must procure resources without the aid of host offspring, either because of direct killing of host young by parasitic offspring (e.g., via stabbing or nest eviction; Friedmann 1955; Morton and Farabaugh 1979; Honza et al. 2007; Spottiswoode and Koorevaar 2012) or through indirect killing through elevated competition for food (Peer et al. 2013). In response to this challenge, specialized brood parasites that use a single host species may develop begging displays that mimic the begging of host young, as has been demonstrated for *Cuculus* cuckoos in Europe and Asia (Davies et al. 1998; Kilner et al. 1999; Tanaka and Ueda 2005; Tanaka et al. 2005). In contrast to specialists, generalist brood parasites are raised by many hosts and available data suggest that they use a general begging display for obtaining food from foster parents (Rivers 2007; Rivers et al. 2013). The general begging display of generalist brood parasites may incur costs if a parasite's begging display is a poor match to host young and host parents discriminate against mismatched begging displays (Lichtenstein 2001; Schuetz 2005). Reduced feeding by host parents, in turn, can lead to reduced growth and incur fitness costs to parasitic young during development, with the potential for additional fitness consequences after individuals leave the nest (Magrath 1991; Naef-Daenzer et al. 2001).

Despite their importance, we have a limited understanding of how the begging displays of brood parasitic offspring have diverged from nonparasitic close relatives and the extent to which mismatched begging displays incur fitness costs in generalist brood parasites. Nevertheless, both are important for understanding how brood parasitic offspring survive under the care of heterospecific hosts, and how behavioral interactions with host adults during development influence the fitness of developing parasites. Therefore, we initiated a study to 1) test for differences between the begging displays of the parasitic brown-headed cowbird (*Molothrus ater*; hereafter cowbird) and the nonparasitic but closely related red-winged blackbird (*Agelaius phoeniceus*, hereafter blackbird), 2) quantify the relationship between host feeding rates and the begging displays of cowbird and blackbird nestlings, 3) assess whether these 2 foreign species (i.e., cowbirds and blackbirds) were fed at rates similar to a brood of 4 host offspring, and 4) quantify potential fitness costs incurred by foreign nestlings when raised alone in host nests. To do this, we first quantified begging and parental provisioning of foreign nestlings when raised alone in nests of the Bell's vireo (*Vireo bellii*; hereafter vireo), an important cowbird host in our study population (Rivers et al. 2010, 2012). Previously, we found that blackbirds had begging displays as intense as (or more intense than) those of cowbirds when raised under identical natal environments and tested along a gradient of short-term need in a controlled laboratory setting (Rivers et al. 2013). Here, we build on that previous work by quantifying begging displays of and parental provisioning to foreign nestlings when raised alone in vireo nests under field conditions. Based on our previous findings (Rivers et al. 2013), we predicted that begging displays of blackbirds would be as intense as (or more intense than) those of cowbirds for 4 components of the begging display (i.e., latency to beg, time spent begging, begging posture, and begging call rate). We also predicted that the more intense begging of blackbird nestlings would lead to increased provisioning rates relative to cowbirds.

In addition to quantifying the interactions between foreign nestlings and vireo parents, we also quantified offspring begging, parental provisioning, and per-capita offspring growth in unparasitized vireo broods that contained 1–4 vireo nestlings. This provided us with a reference response curve of the relationship between offspring begging and adult provisioning behavior, which could be used to assess whether providing for feeding of experimental broods containing a single foreign nestling was adequate to maintain development. We predicted that the relationship between 2 begging display components that are typically linked to parental provisioning, call rate and gape area displayed (Kilner et al. 1999; Budden and Wright 2001; Kilner 2002), would be similar between broods of foreign nestlings and vireos. Finally, we quantified fitness costs to foreign nestlings when being raised in vireo nests by comparing body condition (i.e., body mass and tarsus length) to conspecifics from reference nests in our study population.

METHODS

Field work took place at the Konza Prairie Biological Station in northeast Kansas (39°05′N, 96°35′W), a 3487 ha comprised largely of tallgrass prairie habitat. The cowbird is abundant at this site and parasitizes nearly 2 dozen passerine hosts in the local community (Rivers et al. 2010, 2012). The blackbird is also abundant at Konza Prairie and has young that are similar in size and visual appearance to cowbird young during much of the nestling period (Weatherhead 1989) although call structure of the 2 species differs (Figure 1). The blackbird has a breeding system that often has extrapair fertilizations resulting in broods of mixed paternity (Yasukawa and Searcy 1995). Blackbird genetic data were unavailable from this site, but we have no reason to expect that the mean relatedness of blackbird nestlings at Konza Prairie would differ from prior studies reporting 1–2 extrapair young per brood on average (e.g., Westneat 1993; Weatherhead and Boag 1995; Gray 1997). The vireo is the most frequently parasitized host at Konza Prairie and >70% of vireo nests examined (n = 689) were parasitized by cowbirds (Rivers et al. 2010). A nest of 4 young is the most common brood size for unparasitized vireo nests (Kosciuch KL, personal communication),

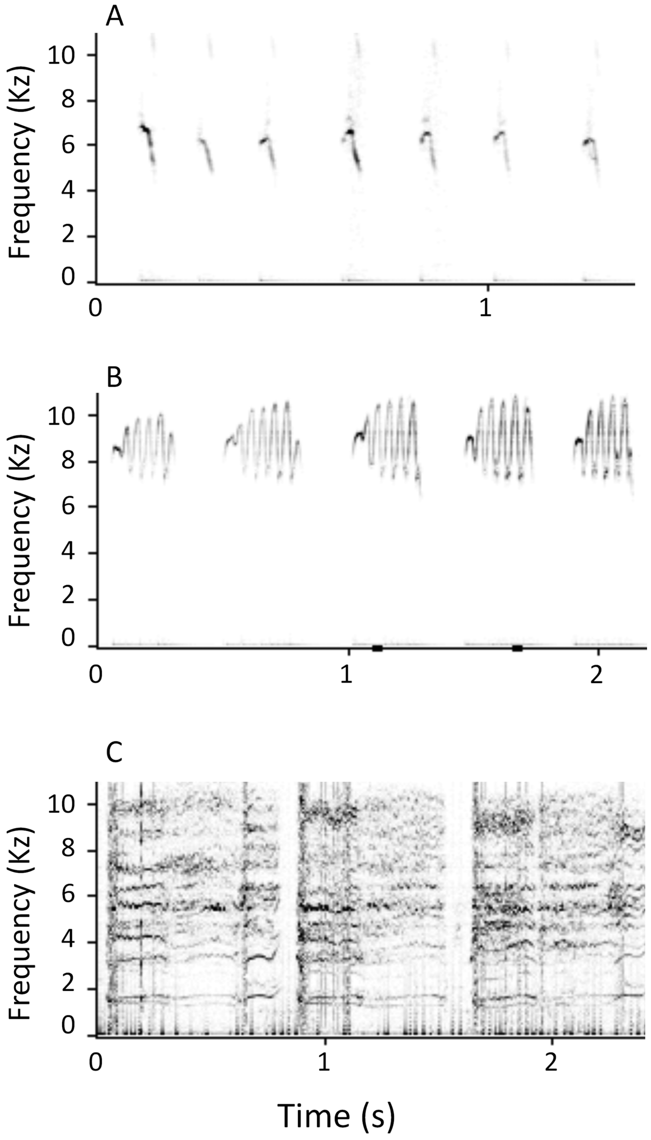

Figure 1

Representative sonograms of begging calls from (A) a single red-winged blackbird, (B) a single brown-headed cowbird, and (C) a brood of 4 Bell's vireos. Note that the scale of the *x* axis varies among the 3 panels.

and vireos in this population have never been documented fledging either >1 cowbird nestling per nest or a mixed brood of cowbird and vireo young (Parker 1999; Kosciuch and Sandercock 2008). Cowbirds parasitize host species across a range of body sizes in this community (Rivers et al. 2010) and across their geographic range (Friedmann 1963; Ortega 1998), with the vireo representing one of the smaller hosts in the host size continuum (Friedmann 1963; Ortega 1998).

The cowbird and blackbird nestlings examined in this study were part of a related investigation that assayed nestling begging displays under standardized laboratory conditions and along a continuum of short-term need (Rivers et al. 2013). The data presented here are separate measurements taken under field conditions prior to laboratory trials, as the objective of this study was to understand begging behavior of foreign and host nestlings during natural feeding events when interacting with vireo parents. Because of this, some aspects of this study are described in greater detail in Rivers et al. (2013). Briefly, we searched for vireo nests, blackbird nests, and host nests likely to contain cowbird offspring during the 2005–2007 breeding seasons. We moved most cowbird and blackbird eggs to commercially manufactured egg incubators (Lyon Electronics, model TX-7) because high nest predation rates markedly reduced sample sizes. However, we found no difference between the begging displays of individuals hatched in incubators and those that hatched from natural nests (Rivers JW et al., unpublished data), so nestlings from both approaches were combined in our analyses. We created experimental broods by manipulating nest contents so they contained either a single cowbird nestling, a single blackbird nestling, or an unparasitized brood containing 1–4 vireo young. All experimental broods were created prior to noon local time, single cowbird or blackbird nestlings were added to vireo nests an average of 1.1 days prior to hatching, and we removed any additional nest contents under permit. Predation events reduced the number of nests available for filming, ultimately resulting in 13 cowbird broods, 10 blackbird broods, and 14 vireo broods (1-vireo broods: n = 4, 2-vireo broods: n = 2, 3-vireo broods: n = 2, and 4-vireo broods: n = 6).

We restricted the blackbird nestlings used in this study to core (i.e., first hatched, sensu Forbes and Glassey 2000) individuals from nests because 1) testosterone (T) levels differ with laying order but are most similar between core eggs (Lipar et al. 1999) and 2) T levels in core blackbird eggs are similar to those in cowbird eggs (Hauber and Pilz 2003). Despite our focus on core blackbird nestlings, our study is representative of both types of blackbird nestlings because core and marginal (i.e., later hatched, sensu Forbes and Glassey 2000) blackbirds do not differ in begging intensity (Griffith 2007). To reduce relatedness confounds, we only used 1 blackbird nestling from its original nest and 1 cowbird nestling from multiply parasitized host nests (see Rivers et al. 2012). We assumed an even sex ratio for foreign nestlings, which appears reasonable because primary sex ratios appear equal for both cowbirds and blackbirds (Fiala 1981; Kasumovic et al. 2002).

Quantification of offspring begging and parental provisioning

Nestling begging and parental provisioning behaviors were quantified under field conditions on nestling day 5 (where day 0 is the day of hatching) without manipulation of short-term need (i.e., hunger; Clark 2002). On the afternoon of nestling day 4, we placed a sham video camera at the nest to allow parents to acclimate to its presence for a minimum of 12 h. On the following morning, we returned to the nest, replaced the sham video camera with a miniature video camera, and filmed continuously for 3 h starting at 07:30–09:30 AM local time if there was no precipitation; videotaping was delayed until 10:45 AM at a single nest because of rain. Immediately prior to filming, all nestlings in broods containing 2–4 vireos were individually marked on the head with a nontoxic black felt marker to distinguish individual nestlings on videos. In addition, each nestling was measured with dial calipers (both ±0.1 mm) for gape width (i.e., the maximum distance between the points of the rictal flanges of the bill) and gape length (i.e., the distance between the tip of the bill to the furthest point on the rictal flange on the right side of the bill from the nestling's perspective). Measures of gape width and gape length were used to calculate the maximum gape area displayed for each nestling when begging, assuming a fully open gape. Each of the upper and lower portions of a nestling's gape display was considered to be an isosceles right triangle, with gape width as the base and gape length as the 2 equal-sized legs of the triangle. The area formula for a right triangle was used to calculate area for one of the triangles and that value was doubled to estimate the total gape area displayed when begging.

To ensure consistency, only one of us (M.A.B.) scored videotapes for data pertaining to nestling begging and vireo provisioning collected under field conditions. Videotapes were examined on a frame-by-frame basis to obtain data on the components of nestling begging displays during each feeding visit, measured as the period between parent arrival and the time when all food was distributed. Measurements included 1) number of nestlings that gaped in response to parents provisioning food, 2) the per-capita time spent begging, 3) the per-capita maximum begging posture, and 4) the calling rate of the brood. Time spent begging was determined by summing the time spent begging from the arrival of the parent at the nest with food until all food items were provisioned for each separate feeding event. As in Rivers (2007), maximum begging posture was measured on a scale from 0 to 3, where 0 = no beg; 1 = gaping without stretched neck; 2 = gaping, neck stretched 75% or less, and abdomen resting on nest cup; and 3 = gaping, neck stretched >75%, abdomen not touching nest cup. Call rate was quantified from videotapes using the sound-analysis program SYRINX v2.1h (www.syrinxpc.com) by tallying the number of distinct begging calls given during each feeding visit; we were unable to assign individual calling rates in broods containing multiple vireos because of call similarity. In addition to components of offspring begging displays, we also recorded 1) the time it took parents to provision the food item(s) brought to the nest and 2) the volume of the food item(s) delivered by parents, which we measured by visually estimating the total volume of the prey item(s) relative to adult bill volume in 10% increments. Adult bill volume was calculated following the procedures outlined in Rivers (2007), with bill measurements originating from 30 study skins of adult vireos (15 males and 15 females; both sexes provision offspring) collected close to the study site and housed at the University of Kansas Natural History Museum.

Quantification of nestling body condition

Nestling begging behavior can be influenced by long-term need (i.e., body condition; Clark 2002), so we used body mass and right tarsus length data collected by one of us (J.W.R.) to assess whether cowbird and blackbird nestlings in experimental broods differed from those raised in reference broods at our study site. At this location, the vireo and dickcissel (*Spiza americana*) are the 2 most important hosts for cowbirds (Rivers et al. 2010), so we compared size measurements of cowbird nestlings raised in vireo broods in this study with measurements of cowbird nestlings raised in dickcissel nests alongside 2 host young (see Rivers et al. 2013 for details). We compared blackbird body size in vireo broods to the average body size measurements of core blackbird nestlings in unmanipulated blackbird nests containing 4 blackbird offspring (i.e., the modal brood size for unparasitized blackbird nests). We used body size measurements of foreign nestlings that were taken immediately prior to laboratory trials on the afternoon of nestling day 5 to match the developmental stage and time of day that reference broods were measured.

Statistical analysis

We used the PROC MIXED modeling function in SAS/STAT v.9.2 for Windows to construct models for individual nestling begging and parental provisioning behaviors (i.e., latency to beg, time spend begging, maximum posture, call rate, bill loads of food, and time to feed) that included fixed effects for nestling type (2 levels: cowbird and blackbird). We used a similar method when modeling visitation rate and feeding rate by parents, with fixed effects for brood type (6 levels: cowbird, blackbird, 1-vireo brood, 2-vireo brood, 3-vireo brood, and 4-vireo brood); for both approaches, we used the individual nest as a random effect and calculated degrees of freedom (df) via the Kenward–Rogers method. We used the PROC REG modeling function to quantify the relationship between 2 components of nestling begging displays (i.e., number of begging calls and gape area displayed) and adult provisioning rate. We used PROC MIXED to compare cowbird and blackbird nestling measurements from experimental broods with values from reference broods. We report least squares means and associated standard errors, and we set alpha at $P < 0.05$ for all tests.

RESULTS

We detected no differences between cowbirds and blackbirds in the latency to beg ($t_{1,21} = 0.70$, $P = 0.491$; Figure 2A) or the time spent begging ($t_{1,21} = -0.16$, $P = 0.871$; Figure 2B). In contrast, blackbirds exhibited a significantly greater begging posture ($t_{1,21} = -2.4$, $P = 0.026$; Figure 2C) and call rate ($t_{1,21} = -2.72$, $P = 0.014$; Figure 2D) than cowbirds. We detected no difference in the rate at which the 2 species were fed ($t_{1,21} = -1.43$, $P = 0.165$; Figure 3A) or in the time it took for parents to provision all food ($t_{1,21} = -0.29$, $P = 0.773$; Figure 3B). The rate of feeding visits by vireo parents varied significantly relative to brood type ($F_{5,31} = 13.36$, $P < 0.001$) and, for vireo broods, generally increased with the number of nestlings in the brood (Figure 4A). Provisioning rate, measured as the bill loads of food delivered per 10 min, also varied significantly relative to brood type ($F_{5,31} = 9.46$, $P < 0.001$) in a similar fashion as the rate of feeding visits (Figure 4B). Relative to a brood of 4 vireos, the modal size for unparasitized nests in the study population, the visitation rate was significantly lower for both foreign nestlings (Figure 4A) as was the provisioning rate (Figure 4B). Pairwise comparisons of per-capita provisioning rates of unparasitized broods were significantly different between 2-vireo and 4-vireo broods ($t_{10} = -3.34$, $P = 0.032$); all other pairwise comparisons between vireo broods were not significant ($P > 0.135$).

We detected no relationship between the call rate of foreign nestlings during feeding visits and adult provisioning rate ($R^2 = 0.01$, $P = 0.729$); in contrast, there was a strong, significant relationship between these measures for vireo broods ($R^2 = 0.64$, $P < 0.001$; Figure 5A). Likewise, we detected no relationship between the gape area display rate of foreign nestlings and adult provisioning rate ($R^2 = 0.04$, $P = 0.357$), whereas we observed a strong, significant relationship between the gape area display rate and adult provisioning rate for vireo broods ($R^2 = 0.78$, $P < 0.001$; Figure 5B). We found that call rate and gape area display rate were strongly correlated for vireo nestlings ($r_{\text{Pearson}} = 0.94$, $P < 0.001$) but not for foreign nestlings ($r_{\text{Pearson}} = 0.33$, $P = 0.127$), thereby preventing us from isolating the relative importance of each factor as a predictor of feeding rate to vireo broods.

Finally, we found that neither mean tarsus length ($F_{3,10} = 0.42$, $P = 0.742$) nor body mass ($F_{3,10} = 0.83$, $P = 0.505$) differed among vireo broods of different sizes. Cowbirds raised alone in vireo nests were significantly smaller than cowbirds that were raised alongside 2 host nestlings in dickcissel nests for body mass (vireo nests: 15.2 [±0.57] g, dickcissel nests: 18.7 [±0.54] g; $t_{1,25} = -4.41$, $P < 0.001$) and for right tarsus length (vireo nests: 17.9 [±0.39] mm, dickcissel nests: 19.9 [±0.38] mm; $t_{1,25} = -3.60$, $P = 0.001$). Similarly, blackbirds raised alone in vireo nests were significantly smaller

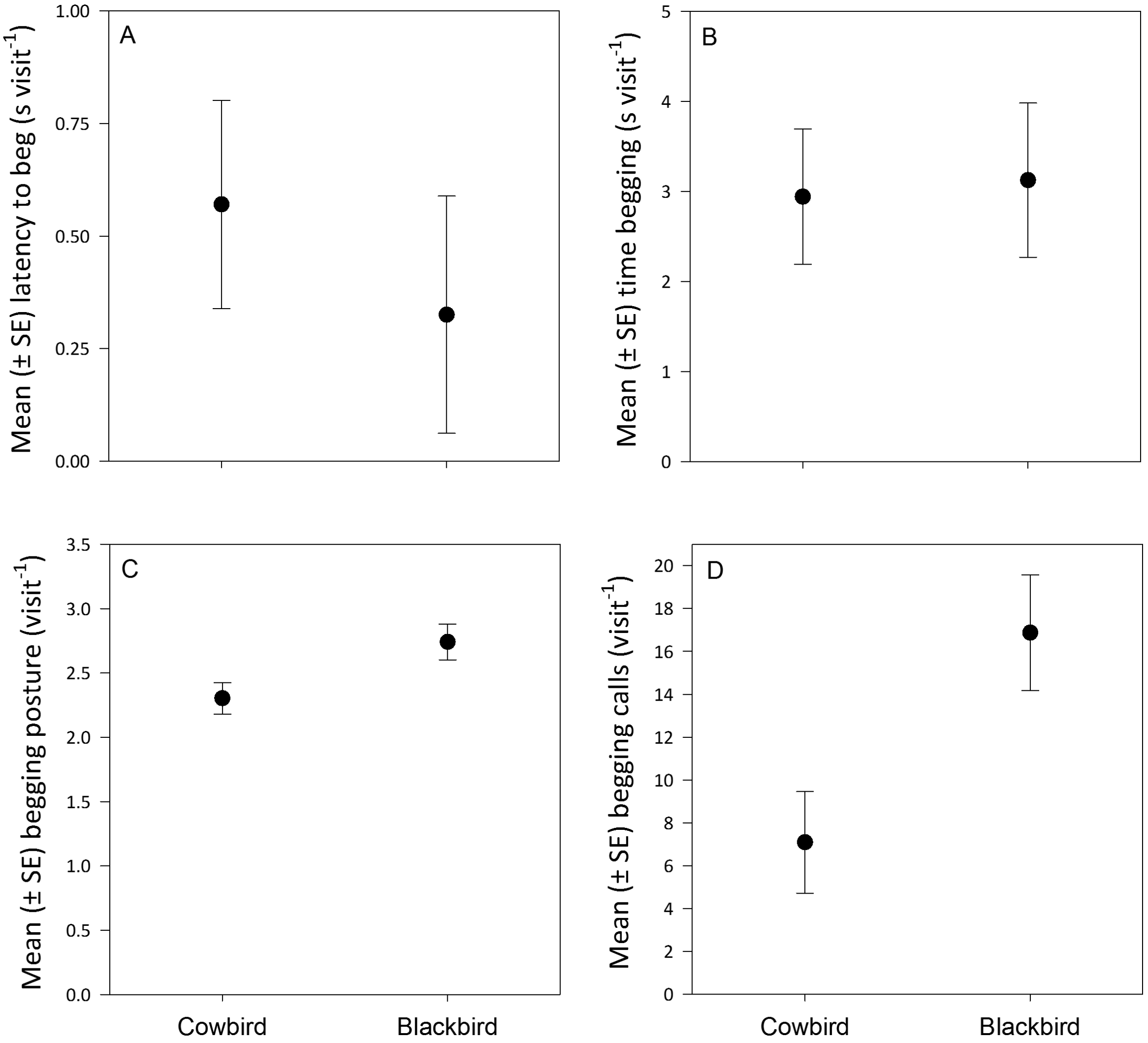

Figure 2

Four components of the begging display of the brood parasitic brown-headed cowbird and the closely related, nonparasitic red-winged blackbird when both species were provisioned by Bell's vireos under ambient conditions. (A) Latency to beg, (B) time spent begging, (C) begging posture, and (D) number of begging calls.

than reference blackbirds for body mass (vireo nests: 16.6 [±0.69] g, blackbird nests: 22.9 [±0.72] g; $t_{1,17} = -6.33$, $P < 0.001$) and for right tarsus length (vireo nests: 19.2 [±0.27] mm, blackbird nests: 21.7 [±0.29] mm; $t_{1,17} = -6.52$, $P < 0.001$).

DISCUSSION

Against theoretical predictions, we found that the begging displays of brood parasitic cowbirds were not more intense than the blackbird, a nonparasitic but closely related species. Indeed, measurements of begging posture and call rate measure were more intense in blackbirds than in cowbirds. These results, which were based on feeding events conducted under natural feeding conditions, corroborate results from laboratory-based assessments of cowbird and blackbird begging displays (Rivers et al. 2013). Elsewhere we describe 3 potential explanations for why components of cowbird begging displays were similar to (or less intense than) those of blackbird begging displays; they include 1) a reduction in cowbird begging intensity due to being raised alongside kin, 2) poor body condition of blackbirds that increased the intensity of blackbird begging displays, and 3) intense competition for food in blackbird nests that has selected for especially intense begging (see Rivers et al. 2013 for further discussion). Despite these differences in begging displays, however, vireo parents did not differ in their treatment of cowbirds and blackbirds in their nests: both nest visitation rate and the amount of food brought to the nest were nearly identical for cowbirds and blackbirds. This was despite the 2 species having begging calls that are acoustically distinct from one another (Figure 1).

We found that vireo parents increased the amount of food they provisioned to unparasitized nests as brood size increased in a manner that maintained per-capita feeding rates. Importantly, this adjustment did not lead to fitness costs for host nestlings in broods of different sizes: vireo nestlings raised alone were of similar body mass and tarsus length as brood-averaged values for brood containing 2, 3, or 4 vireos. Thus, vireo parents adjusted their feeding rate in a way that did not lead to differences in individual nestling growth, regardless of how many host offspring were in the brood. In contrast, vireo parents provisioned foreign nestlings at a rate that was significantly less than their feeding rate for a typical brood.

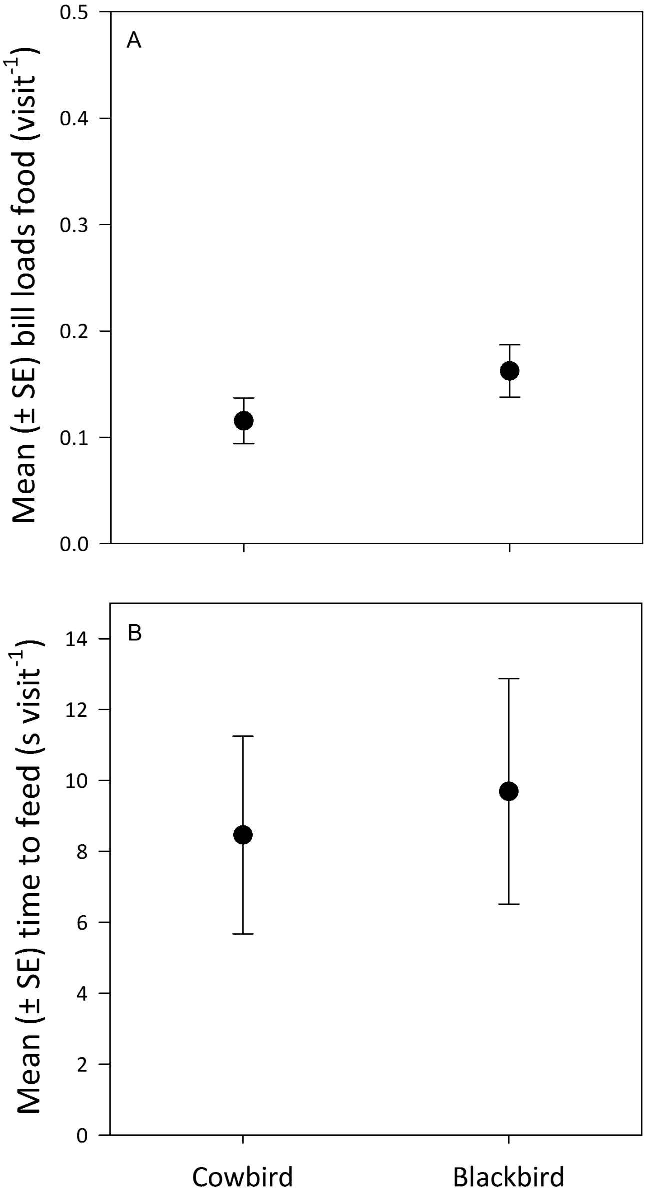

Figure 3
(A) Feeding rate of brown-headed cowbird and red-winged blackbird nestlings fed by Bell's vireos during ambient provisioning conditions and (B) the time it took for parents to provision food to cowbirds and blackbird nestlings.

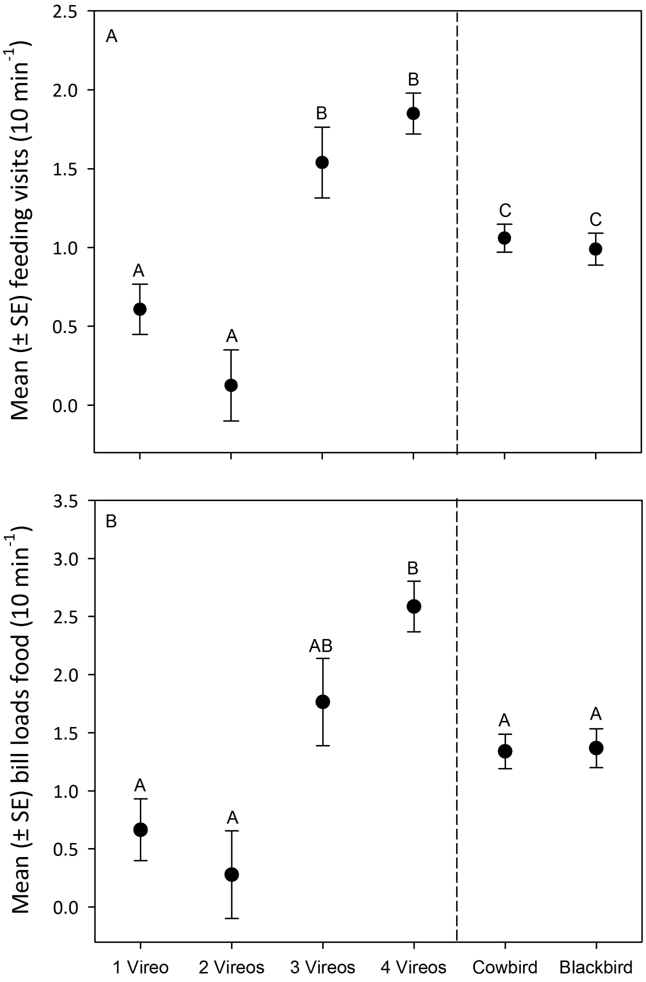

Figure 4
(A) The number of feeding visits and (B) feeding rate of nestlings by vireo parents to vireo broods containing 1–4 host offspring or foreign broods containing either a single cowbirds or blackbird. Point estimates with the same letter were not significantly different at the $P = 0.05$ level.

This led to significant fitness costs for foreign young, as cowbirds raised alone in vireo nests were 19% lighter and 10% smaller than conspecifics raised alongside 2 host young in Dickcissel nests, and blackbirds were 28% lighter and 12% smaller than blackbirds raised in blackbird broods. This indicates the vireo, despite being one of the most important hosts in the community based on overall parasitism frequency (Rivers et al. 2010), serves as a suboptimal host for the cowbird. Such a reduction in growth has been observed for other brood parasites when raised by hosts of different sizes (e.g., Wiley 1986; Kleven et al. 1999) and, when considered with our results, provides clear evidence that the quality of different hosts within a community can vary substantially.

Why did vireo parents provide suboptimal parental care to foreign nestlings? One explanation is that suboptimal care may have stemmed from a mismatch between the begging displays of foreign and host offspring. In vireo broods, we found a strong and significant relationship between the amount of food parents brought to the nest and the calling rate of the brood; however, this was not the case with foreign nestling broods. Nevertheless, the mean calling rate for a single foreign nestling equaled and, in several instances, exceeded the mean calling rate of a brood of 4 vireo nestlings (Rivers et al., unpublished data). This indicates that it was not call rate per se that reduced feeding to foreign nestlings but some other factor that may have been linked to calling behavior. During data collection, we noted that vireo begging calls sounded markedly different from those of foreign nestlings, being of lower frequency and having less frequency modulation that either cowbirds or blackbirds (Figure 1). Thus, it may be that call structure divergence reduced feeding rates because parent vireos were "tuned" to the begging calls of their own young and away from divergent calls of parasitic offspring because of coevolved parent–offspring communication signals (Glassey and Forbes 2003; Schuetz 2005). Even if this explanation holds, it is worth noting that we did not observe any cowbirds starving to death in our experimental broods (n = 13), nor were any such observations

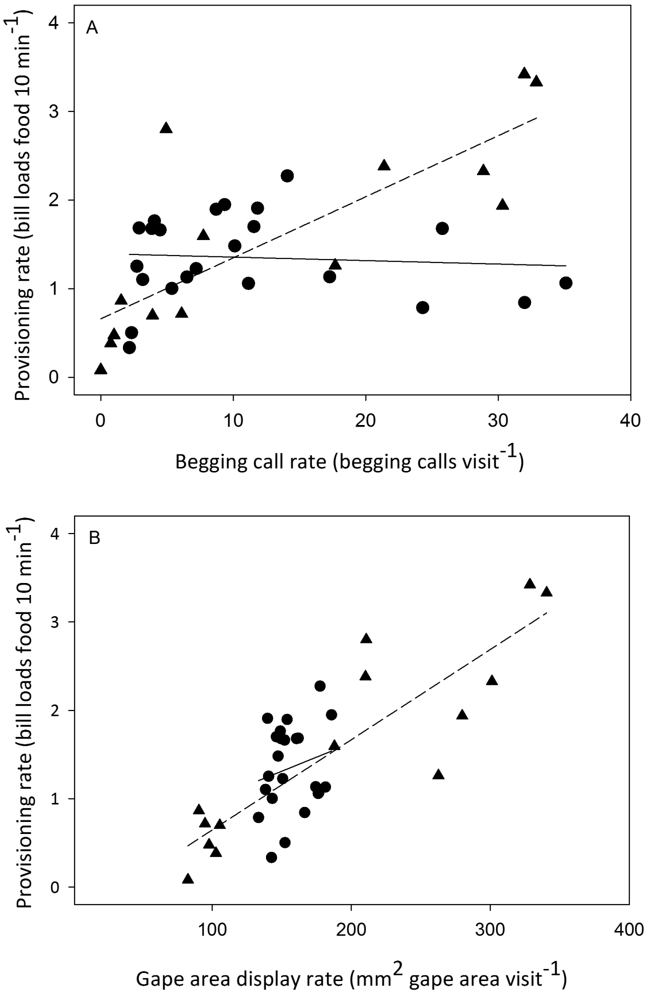

Figure 5
The relationship between the provisioning rate of vireo parents to the (A) brood begging call rate and (B) gape area display rate for foreign nestlings (circles, solid line) and vireo nestlings (triangles, dashed line).

made in a large sample ($n = 436$) of parasitized vireo nests located at our study site (Kosciuch KL, Parker TH, personal communication). In contrast, at least 2 out of the 13 blackbird nestlings we placed in vireo nests died in the nest from apparent starvation prior to fledging, a significant result ($\chi^2 = 69.4$, df = 1, $P < 0.001$). Therefore, despite having mismatched begging displays in vireo nests, cowbirds were still able to obtain adequate food for development and fledge from vireo nests, whereas this was not the case for all blackbirds. This supports the notion that the physiological needs for a developing cowbird can be met despite a mismatched begging display. It also suggests that cowbirds may be more efficient at extracting nutrients from food items and/or differ in how they allocate energy to growth or metabolism, a topic that should be investigated in future studies.

In addition to call structure, foreign nestlings also differed in their appearance from vireo young in this study: the gapes displayed by foreign nestlings are red and bordered by white rictal flanges, whereas vireo gapes are orange and are bordered by yellow rictal flanges (Rivers JW, personal observation). Thus, the mismatch in mouth coloration between the 2 groups may have also contributed to the reduced provisioning rates of vireos to foreign nestlings (see Kilner et al. 2004). A third way in which foreign nestlings mismatched begging displays of vireo nestling was in the extent of the gape area they displayed to parents during feeding events. Parent birds use this component of the begging display to make decisions about provisioning rates to their brood (Budden and Wright 2001; Kilner 2002). This was true vireos provisioning their own young in this study, as we found a very strong relationship between adult provisioning rate and gape area display rate (Figure 5B). Based on our results, we hypothesize that the lone gape of foreign nestlings was insufficient to stimulate vireo parents to feed at a rate that provided optimal growth for foreign nestlings and that the other components of foreign nestling begging displays were inadequate to compensate for a gape of insufficient size.

The possibility of having a poorly matched begging display is an issue faced by all brood parasites, especially those species that are regularly raised alone (Friedmann 1955; Morton and Farabaugh 1979; Honza et al. 2007; Spottiswoode and Koorevaar 2012). In addition to overcoming differences in visual components of the begging display (e.g., gape size and coloration), brood parasites may also need to compensate for divergent acoustic components of the begging display (e.g., begging calls; Kilner 2002). Specialized adaptations that compensate for deficient components of parasitic begging displays in the Cuculinae are thought to have arisen through long coevolutionary histories between cuckoos and their hosts. For example, the nestling common cuckoo (*Cuculus canorus*) evicts host young from reed warbler (*Acrocephalus scirpaceus*) nests and gives begging calls at a rate that match the output of a brood of 4 warbler nestlings (Davies et al. 1998). Having an enhanced vocal component of the begging display allows cuckoo nestlings to maintain adequate provisioning in this host despite displaying a visually deficient gape (Kilner et al. 1999). Another species that has resolved the issue of a single gape comes from the related Horsfield's hawk-cuckoo (*Cuculus fugax*), which also evicts host young and is raised alone. Instead of having enhanced begging calls, which may increase predation risk, the hawk-cuckoo has evolved fleshy patches on its wings that match its mouth coloration, and these wing patches are moved back and forth when host parents provision food (Tanaka and Ueda 2005). Experiments have demonstrated that wing patches serve to increase parental provisioning to the nest, and observations that host parents try to provision food to the wing patches indicate they are perceived as additional gapes (Tanaka et al. 2005). In marked contrast to these specialized cuckoos, most parasitic cowbirds currently lack adaptations that allow them to fine-tune their begging displays to individual hosts, which may be because they have exhibited brood parasitism for markedly less time than the Cuculinae (cowbirds: 2.8–3.8 million years, Cuculinae: 6.3–8.4 million years; Rothstein et al. 2002). Alternatively, it may be that a single begging display allows them to use a wide range of host species (Friedmann 1963; Ortega 1998) yet incurs fitness costs when they are raised alone (Kilner et al. 2004), conditions that occur with some regularity (Peer et al. 2013). Such costs have strong potential to influence postfledging survival (Magrath 1991; Naef-Daenzer et al. 2001) and may even have consequences that extend into adulthood to impact fitness (e.g., Birkhead et al. 1999; Dufty et al. 2002; Monaghan 2008). Very little is known about how costs incurred by brood parasites during the nestling stage influence components of fitness in subsequent life stages, so additional research on this topic is warranted and should provide a broader understanding of the extent to which early environmental conditions have consequences for obligate brood parasites across the entire life cycle.

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