Nest mate size, but not short-term need, influences begging behavior of a generalist brood parasite

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Hosts of generalist brood parasites often vary with regards to their life-history traits, and these differences have the potential to influence the competitive environment experienced by brood-parasitic nestlings. Although begging by brood parasites is more exaggerated than their hosts, it is unclear if generalist brood parasites modulate their begging behavior relative to host size. I examined the begging behavior of brown-headed cowbird (*Molothrus ater*) nestlings when competing against nest mates that differ in size and under different levels of short-term need. Cowbird nestlings begged on nearly all feeding visits, responded to adults as fast as (or faster than) their nest mates, and typically begged more intensively than their nest mates. Latency to beg, time spent begging, and maximum begging posture of cowbirds were similar during supplementation and deprivation treatments, indicating begging intensity was not influenced by short-term need. Time spent begging by cowbirds varied among hosts of 3 different sizes when short-term need was standardized, suggesting that nest mate size strongly influenced begging behavior. Cowbirds obtained more food when competing against an intermediate-sized host due to lower provisioning rates of small hosts or because of increased competitive ability of large host nestlings. Overall, cowbirds obtained the greatest volume of food per unit time spent begging when competing against intermediate hosts, but this value approached that of the small host when adjusted for modal brood size. These results demonstrate that cowbirds adjust their begging relative to the size of the hosts against which they compete but not to levels of short-term need. *Key words:* begging behavior, begging intensity, brown-headed cowbird, *Molothrus ater*, nestling competition, short-term need. *[Behav Ecol 18:222–230 (2007)]*

Begging, defined as the calling and movements used by offspring to elicit resources from adults, is a dynamic interaction between dependent offspring and their care-giving parents (Mock and Parker 1997). Begging has important fitness consequences in songbirds because the intensity of begging can influence the amount of food obtained by a nestling which, in turn, influences its rate of mass gain and subsequent probability of survival (Kilner and Johnstone 1997; Budden and Wright 2001; Wright and Leonard 2002). Theoretically, nest mate size can have an important influence on the amount of food a nestling receives and, indirectly, its begging behavior (Johnstone 2004). Although size differences among nest mates may be small in some species (e.g., those in which eggs hatch synchronously), this factor may play an important role in other species such as those that exhibit asynchronous hatching (Stoleson and Beissinger 1995). In asynchronously hatching species, competitive ability appears to be strongly correlated with size because larger nestlings are able to use their size to procure more than their expected share of food from provisioning parents (Ryden and Bengtsson 1980; Bengtsson and Ryden 1983; Teather 1992; Price and Ydenberg 1995; Lotem 1998; Cotton et al. 1999; Glassey and Forbes 2002). Thus, larger nestlings reduce the amount of food smaller nestlings receive through competitive interactions, and smaller nestlings respond to this reduction in food by increasing their begging intensity (Ryden and Bengtsson 1980; Bengtsson and Ryden 1983; Teather 1992; Price and Ydenberg 1995; Lotem 1998; Cotton et al. 1999; Glassey and Forbes 2002).

Obligate avian brood parasitism occurs when a female (the brood parasite) lays her egg into the nest of another species (the host), and the host provides all parental care to the brood parasite's offspring (Rothstein 1990; Davies 2000). Those brood parasites that 1) use many host species to raise their young (i.e., generalist brood parasites) and 2) have offspring that are raised alongside host nestlings provide a natural setting in which to understand how nest mate size influences nestling begging behavior (Dearborn and Lichtenstein 2002). For example, the size range of hosts that typically raise the brown-headed cowbird (*Molothrus ater*, hereafter cowbird) vary from 13–200% of the adult mass of a cowbird (Friedmann and Kiff 1985; Lowther 1993; Hauber 2003), and this variation in host use can occur even at the level of individual females (Woolfenden et al. 2003; Strausberger and Ashley 2005). Thus, nestlings of an individual female cowbird may experience markedly different nest environments, with nest mate size serving as a potentially important influence on the degree of competition experienced by a nestling and, ultimately, its begging behavior.

In addition to the size of nest mates, short-term need (sensu Clark 2002) may also influence the begging behavior of parasitic nestlings in a similar manner to the way in which it influences nonparasitic species (Kilner and Johnstone 1997; Budden and Wright 2001). Despite the finding by Redondo (1993) that the begging intensity of great spotted cuckoo (*Clamator glandarius*) nestlings remained high after supplemental feeding, there is a growing body of evidence that indicates that short-term need influences begging behavior in brood parasites. For example, Lichtenstein and Dearborn (2004) and Hauber and Ramsey (2003) reported that begging intensity in both the brown-headed cowbird and shiny cowbird (*Molothrus bonariensis*) was related to short-term need. In addition, nestlings of the common cuckoo (*Cuculus canorus*)

increased their calling rate with increasing hunger (Butchart et al. 2003) and nestlings of the Horsfield's hawk-cuckoo (*Cuculus fugax*) increased the rate at which they display a wing patch that appears to aid in food solicitation food as the interval between parental feeding visits increased (Tanaka and Ueda 2005). Collectively, these studies suggest that short-term need influences begging in brood-parasitic species in a way similar to nonparasite species. Unlike nonparasitic species, however, brood parasites are influenced only by the direct costs of begging (i.e., predation and growth costs; see Dearborn 1999; Chappell and Bachman 2002; Haskell 2002; Johnstone and Godfray 2002) because they receive parental care from unrelated hosts and compete against unrelated nestlings, except in rare instances of multiple parasitism (e.g., Martinez et al. 1998; Alderson et al. 1999). Brood parasites should therefore beg more intensively than nonparasitic nestlings for the same level of need because they do not incur inclusive fitness costs when acquiring extra food (Godfray 1991, 1995a; Redondo 1993). Indeed, several studies have found that begging by brood parasites is especially intense, and selection appears to have increased the begging intensity of brood parasites relative to nonparasitic species (Briskie et al. 1994; Kilner et al. 1999; Lichtenstein and Dearborn 2004).

In this study, I assessed the influence of short-term need on the brood-parasitic brown-headed cowbird when competing against host nestlings of different sizes. Because begging intensity has been demonstrated to influence short-term need (Budden and Wright 2001; Lichtenstein and Dearborn 2004), I hypothesized that short-term need would influence the begging behavior of cowbird nestlings in a manner similar to that of nonparasitic species. Following Lichtenstein and Dearborn (2004), I predicted that cowbird begging intensity would be negatively correlated with the degree of short-term need, that is, cowbirds would beg at a higher intensity when deprived of food than when supplemented with food. Because theory predicts that begging is costly and that individuals should reduce begging intensity to minimize these costs (Godfray, 1991, 1995a,b), I also hypothesized that cowbirds would vary their begging behavior when raised with hosts of different competitive abilities. Specifically, I predicted that 1) the proportion of food visits where cowbirds begged would be positively correlated with nest mate size, 2) the latency to beg in cowbirds would be negatively correlated with nest mate size, and 3) cowbird begging intensity would be positively correlated with nest mate size because the long-term need of cowbirds varies among hosts, because cowbirds base their begging behavior on nest mate size, or both. In addition to cowbird begging, I also quantified the volume of food provisioned to nests by adults and the relative share that cowbirds received to assess the influence of nest mate size on the amount of food obtained by cowbirds. I predicted that the amount of food provisioned to nests would be positively correlated with nest mate size, whereas the proportion of food obtained by cowbirds would be negatively correlated with nest mate size (Kilner 2003; Kilner et al. 2004). Collectively, these experiments provide information that is currently lacking on the extent to which nest mate size and short-term need interact to influence the begging behavior of a generalist brood parasite.

METHODS

Study area and selection of host species

Experiments were conducted during the 2002–2003 breeding seasons at Konza Prairie Biological Station (39°05′N, 96°35′W), a 3487-ha tallgrass prairie preserve located in the Flint Hills region of northeast Kansas. Cowbirds are the second most abundant songbird recorded on Konza Prairie and use at least 20 species of songbird hosts on this site (Elliott 1978; Parker 1999; Jensen and Cully 2005; Rivers JW and Jensen WI, unpublished data). However, cowbird hosts vary markedly in the degree to which their nests are amenable to experimentation. Therefore, to determine which hosts would be used in this study, I first categorized the host community at Konza Prairie into 3 broad classes: 1) hosts that had nestlings smaller than a cowbird for a given age, 2) hosts that had nestlings of approximately the same size of a cowbird for a given age, 3) hosts that had nestlings larger than a cowbird for a given age. I assumed that these categories would represent weak, moderate, and strong nestling competitors, respectively, to a cowbird nestling of similar age following previous authors that have used nestling size as a proxy for competitive ability (e.g., Price and Ydenberg 1995; Lotem 1998; Cotton et al. 1999).

Next, I assessed the degree to which the nests of host species on the study site were amenable for experimentation. Of several small hosts available, the field sparrow (*Spizella pusilla*, hereafter sparrow) was the only abundant species for which a reasonable number of nests could be found during preliminary fieldwork. Of the two similar-sized species available (dickcissel [*Spiza americana*] and red-winged blackbird [*Agelaius phoeniceus*], hereafter blackbird), only the closely related blackbird was suitable for experiments because dickcissels were intolerant of videocameras at their nests and would not resume normal provisioning behaviors during preliminary experiments. Of the two large hosts on the study site (eastern meadowlark [*Sturnella magna*] and brown thrasher [*Toxostoma rufum*, hereafter thrasher]), I could only find a reasonable number of nests of the thrasher during preliminary fieldwork. Therefore, I was restricted to assessing cowbird begging in the nests of a single small host (sparrow), a single similar-sized host (blackbird), and a single large host (thrasher). Importantly, nestlings of all 3 species have similar growth patterns and modes of development (Starck and Ricklefs 1998) and cover most of the size range of species against which cowbirds typically compete (Friedmann and Kiff 1985; Lowther 1993). Therefore, these host species were assumed to provide a reasonable approximate for the range of host sizes that raise cowbirds on the study site.

One key assumption of this research is that, in unparasitized nests, hosts' adults are more likely to provision a nestling that is fastest to respond or reaches higher than its nest mates. In a closely related study, it was found that parents were significantly more likely to feed nestlings that 1) responded fastest to the arrival of parents at the nest and 2) reached highest (Rivers JW, unpublished data). Thus, the assumption that these 3 hosts use similar provisioning rules and preferentially feed the fastest responding and/or highest reaching nestling is upheld and should allow for direct comparisons of cowbird begging and host provisioning across the 3 host species.

Although thrashers are infrequent cowbird hosts because they typically reject cowbird eggs (Rothstein 1975), their inclusion is warranted in this investigation because 1) my goal was to isolate host size as a focal variable on cowbird begging and is not concerned with an evolutionary response of hosts to cowbirds and 2) there is no evidence that the nestling behavior of any accepter host has been shaped by cowbird parasitism. In addition, it should also be noted that because of their short incubation period (Briskie and Sealy 1990), cowbirds often hatch before their nest mates, particularly in the nests of large hosts with longer incubation periods (Hauber 2003). However, marked differences in developmental stage can be present between individuals that differ in age by only 1–2 days (Khayutin 1985), and this can strongly influence the ability of young to solicit and compete for food (Hauber 2003, Kilner et al. 2004). Thus, age was standardized in experiments to

reduce any variation in developmental stage that might influence the begging behaviors or competitive ability of nestlings (see below).

Field experiments

All nestlings were tested from 3 to 5 days after hatching; thus, experiments were conducted during the peak of nestling growth for the cowbird and all 3 hosts. On the afternoon, prior to filming, I created broods of 2 nestlings (one cowbird, one host) that hatched within ±1 day of each other, with the majority of nestling pairs (i.e., 80% of 46 nests) hatching on the same day. Any additional nestlings were cross-fostered to nearby host nests containing similar-aged young. At the same time, I placed a sham camera near the host nest to allow adults to acclimate to its presence. Logistical constraints made it impossible to control the prior experience of cowbird and host nestlings prior to testing. However, experimental broods were created the day prior to filming so that nestlings had at least 12 h to acclimate to changes in their nest environment. This period was assumed to have provided enough time for cowbirds to adjust their behavior relative to changes in their competitive environment because at least one previous study has demonstrated nestlings modify their begging behaviors in new competitive environments within 2 h of placement (Price et al. 1996).

On the morning, after the placement of the sham camera, I returned to the nest and initiated filming between 06:00–08:00 Central Daylight Time (except in one instance where filming started at 08:30 due to equipment problems). Prior to filming, an electronic balance was used to measure nestling masses, after which the sham camera was replaced by a miniature videocamera attached to a Sony camcorder, filming at 30 frames per second and capable of recording sound, by ~33 m of cable. In nests containing cowbird and blackbird nestlings, one randomly selected nestling was minimally marked on the bill with a nontoxic black felt marker to distinguish between cowbird and blackbird nestlings on videotapes.

Two feeding treatments were applied to each nest in one of two sequences; prior to both treatments baseline begging and provisioning behaviors were videotaped for 90 min. Because baseline behaviors were collected for purposes other than this study and because of the potential for a time confound (i.e., baseline behaviors were only recorded in the early morning), they are not considered further. In the first sequence, the recording of baseline data was followed by a supplementation treatment in which both nestlings were fed until satiation with commercially purchased mealworms and then videotaped for 90 min. After the supplementation treatment, a deprivation treatment was applied in which both nestlings were removed from the nest, held without food for 90 min, and then returned to the nest and videotaped for 90 min. During deprivation treatments, 1–3 additional nestlings were swapped into the host nest to prevent abandonment. All focal nestlings were held in a sheltered, secure location, and a hot water bottle was used to keep nestlings warm during cool weather. The second sequence differed from the first only in that the order of the deprivation and supplementation treatments were reversed. Each nest was randomly assigned one of the 2 sequences, a similar number of sequences were used for each host species, and no effect of sequence on begging behaviors was found during preliminary analyses (Rivers JW, unpublished data).

Although a brood of one cowbird and one host is typical of small, parasitized hosts (e.g., Lichtenstein and Sealy 1998), larger hosts parasitized by cowbirds often contain 2–3 host nestlings (Hauber 2003; Kilner 2003). However, because the number of nest mates influences begging and food acquisition in some species (e.g., Leonard et al. 2000), brood size was standardized to 2 nestlings (i.e., 1 cowbird, 1 host) to insure that nest mate size was not confounded with the number of nest mates. To determine how cowbird begging was influenced by a modal brood size in similar-sized and larger hosts, additional experiments were conducted during 2005 in which cowbirds competed against same-aged, modal-sized broods of blackbirds (i.e., 2 blackbird nestlings) and thrashers (i.e., 3 thrasher nestlings). These experiments were conducted in the same manner and only differed from those described above in that cowbirds competed against additional nest mates (i.e., 1 cowbird competed against 2 host nestlings in a blackbird nest or against 3 host nestlings in a thrasher nest). All experiments were conducted under state, federal, and institutional permits as well as under the guidelines for the ethical treatment of animals as outlined by the joint guidelines of the Animal Behavior Society and the Association for the Study of Animal Behavior. No nestlings were known to die from the experiments described here.

Videotape analysis

After field experiments were completed, I analyzed videotapes frame-by-frame to obtain data on nestling begging and adult provisioning behaviors during food visits. The majority of food visits were short in duration (i.e., ≤120 s), and in these cases, the time spent begging by each nestling was quantified over the entire food visit. If food visits extended beyond 120 s and nestlings continued to beg while parents remained at the nest (e.g., to sanitize nest) after all food was provisioned, I collected begging data for only the first 120 s. I selected this period because all food items were provisioned within 120 s of a parent arriving at the nest in 99% of 269 food visits combined from all hosts (Rivers JW, unpublished data).

For each food visit, I recorded each nestling's 1) latency to beg, 2) time spent begging, and 3) maximum begging posture; I also recorded, 4) the volume of food provisioned to the nest and (5) which nestling(s) was fed. Latency was measured as the elapsed time between a parent's arrival at a nest to the time when begging was initiated by each nestling. Time spent begging was quantified by summing the time spent begging during a given food visit. Over the same period, a maximum begging posture score was assigned following previous authors (e.g., Redondo 1993; Leonard et al. 2003), where 0 = not begging, 1 = gaping without neck stretched, 2 = gaping with neck stretched to three-fourth of the length and belly in contact with nest cup, and 3 = gaping with neck stretched more than three-fourth of the length and belly not in contact with nest cup. I was unable to measure the amplitude of begging calls or calling rate due to several factors (i.e., environmental noise, differences in position of cameras among nests, and indistinguishable calls of nestlings of different species on videotapes).

Volume of food provisioned was calculated for each visit by visually estimating the volume of food items relative to adult bill volume, in 10% increments; thus, accuracy of food items was ±5%. I did not include food item's wings or appendages in my estimate of its volume. In the majority of food visits (>91%), adults fed a single nestling. In the limited occasions when food was given to both nestlings, I did not record the proportion of food provisioned to each nestling during videotape transcription and instead assumed that 50% of the food load was given to each nestling. Bill volume was calculated using the formula for bill volume proposed by Greenberg and Droege (1990): $1/3\pi L \times W \times D$, where L is distance from the most proximal edge of the commissure to the bill tip measured on the right side of the bill, W is the distance between most proximal points of the commissure, and D is the vertical distance from the top of the maxilla to the bottom of the lower mandible

measured at the base of the bill. Bill measurements of the 3 host species examined here were taken from 30 museum skins of adult individuals that were collected near the study site and housed at the University of Kansas Natural History Museum. Measurements were taken from an equal number of both sexes for the sparrow and thrasher but were restricted to female blackbirds because <1% of recorded provisioning events to blackbird nests were made by males (Rivers JW, unpublished data).

Statistical analysis

Previous research shows that a nestling's begging behavior can be influenced by its nest mates (e.g., Smith and Montgomerie 1991). Therefore, instead of using raw values for begging metrics (i.e., latency to beg, time spent begging, and maximum begging posture), I took the difference between the cowbird and host nestlings (i.e., cowbird value—host value) for each metric to assess the effects of feeding treatments on the begging behavior of cowbirds. Adopting this approach allowed for a standardization of cowbird begging behavior across hosts of different sizes while upholding the assumptions of the statistical tests used. Nevertheless, data for cowbird and host begging values are presented as raw values in Figures 1–3 for ease of presentation. Paired t-tests (i.e., cowbird metric—host metric) were used to assess differences between cowbird and host nestlings with regards to nestling mass. In addition, I used Fisher's least significant difference (LSD) comparisons in the PROC MIXED procedure in SAS version 9.1 to assess the influence of feeding treatment and feeding treatment order on 1) latency to beg, 2) time spent begging, and 3) maximum begging posture of cowbirds. Because my initial analysis found no significant differences in cowbird begging behavior between feeding treatments within each host (see Results), I combined data from both feeding treatments for each nest and calculated a single mean value for cowbird begging metrics and adult provisioning behaviors. I then used a single-factor ANOVA to examine the influence of host size on cowbird begging metrics and adult provisioning behaviors. Least-squares means analysis (SAS version 9.1) was used to calculate means for statistical tests because of unequal sample sizes, and Fisher's LSD was used to test for all pairwise comparisons when the full ANOVA model was significant. Means and standard errors are reported unless otherwise noted, and significance levels for all tests were set at $P < 0.05$ unless otherwise indicated.

RESULTS

Compared with the host nestlings with which they were paired, cowbirds had significantly more mass than sparrows (cowbird mass: 10.7 ± 0.63 g, sparrow mass: 5.6 ± 0.23 g; $n = 13$, $P < 0.001$), similar mass as blackbirds (cowbird mass: 13.0 ± 0.67 g, blackbird mass: 11.8 ± 0.59 g; $n = 15$, $P = 0.184$), and significantly less than thrashers (cowbird mass: 13.8 ± 0.67 g, thrasher mass: 24.0 ± 1.00 g; $n = 16$, $P < 0.001$). Cowbirds in blackbird and thrasher nests were typically a day older than cowbirds tested in sparrow nests, which led to differences in cowbird mass among hosts.

Cowbird nestlings begged on nearly all food visits by adults. In sparrow nests, the mean proportion of visits during which cowbirds begged averaged 98% (±2.1, $n = 13$) for both feeding treatments across all nests. Cowbirds begged on an average of 93% (±1.8, $n = 17$) of food visits in blackbird nests and on an average of 97% (±1.9, $n = 16$) of food visits in thrasher nests. Within each host, there was no influence of feeding treatment on latency to beg (all $P > 0.237$, Figure 1), time spent begging (all $P > 0.463$, Figure 2) or maximum begging posture by cowbirds (all $P > 0.175$, Figure 3). As these metrics
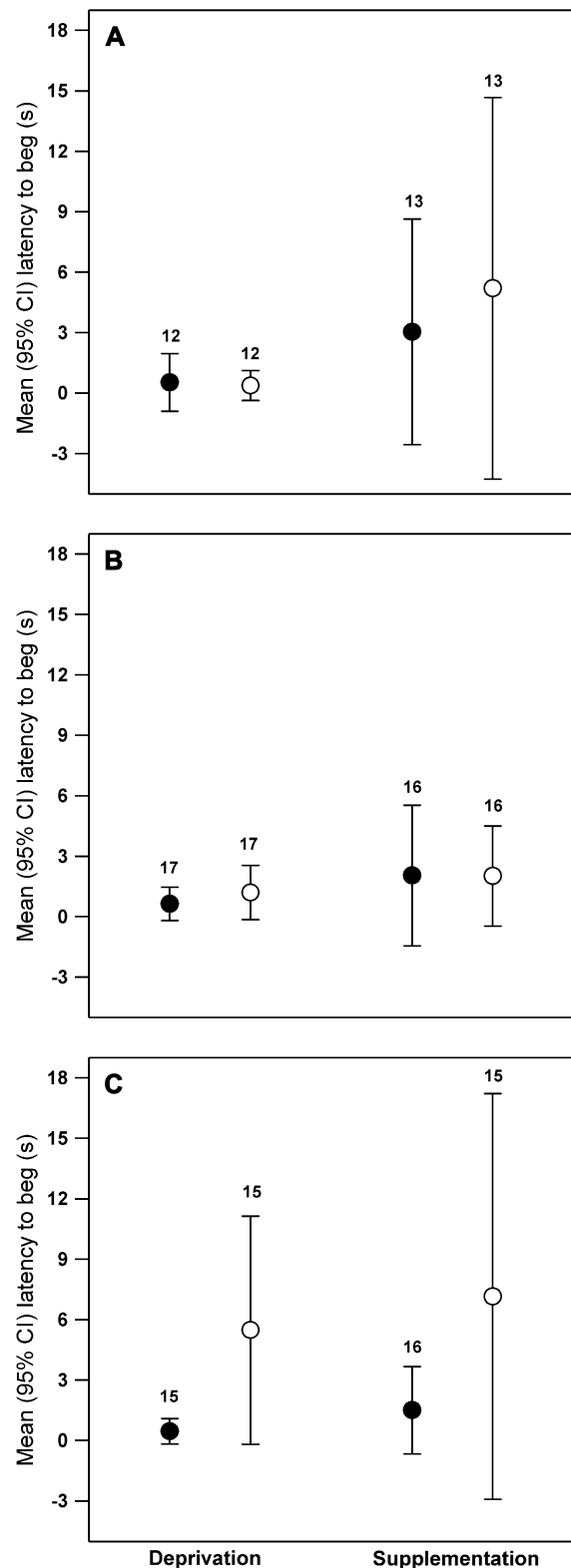
Figure 1
Mean (95% confidence interval) latency to beg for cowbird (solid circles) and host nestlings (open circles) in nests of (A) small, (B) intermediate, and (C) large hosts. Within each host, no significant differences in the latency to beg by cowbirds were found between feeding treatments. Sample sizes are noted above point estimates.
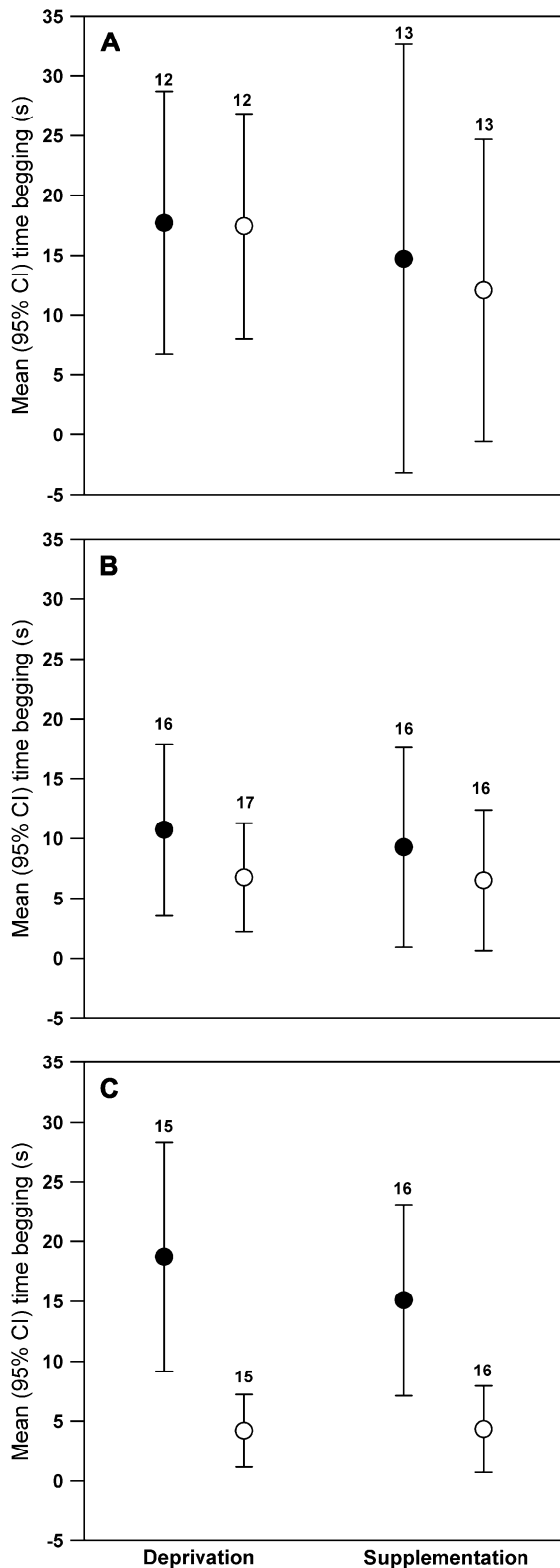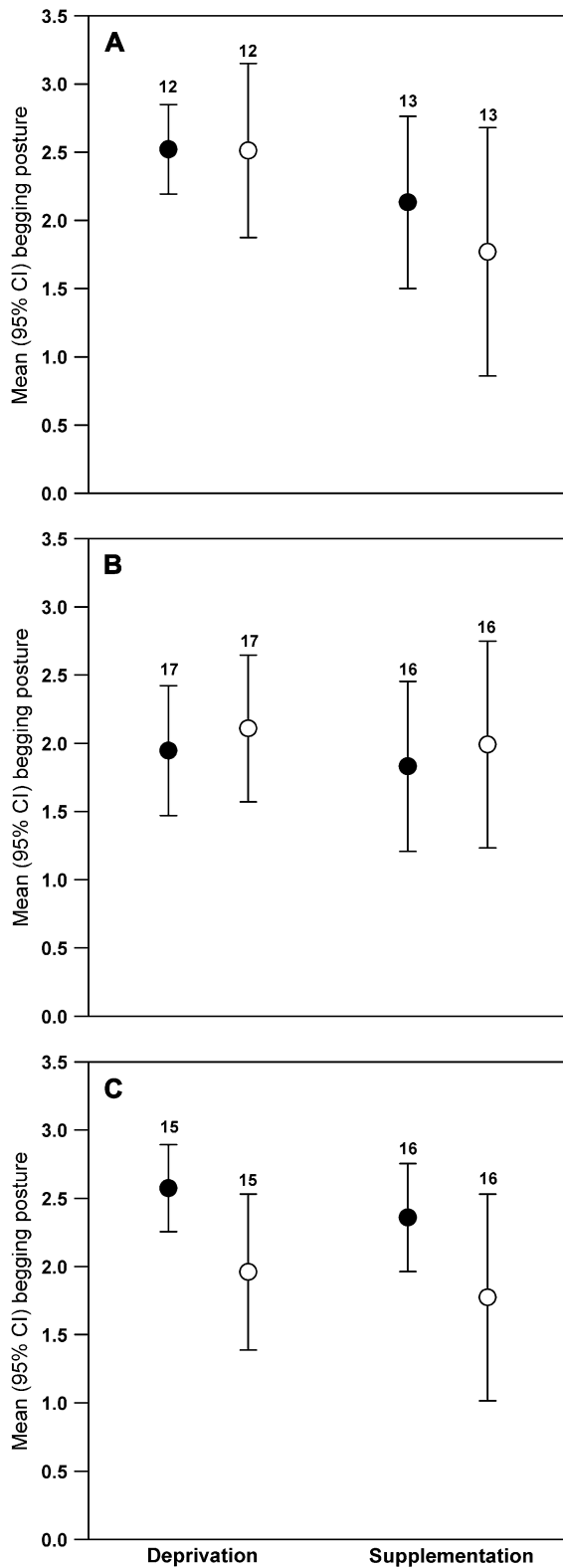
Figure 2
Mean (95% confidence interval) time spent begging for cowbird (solid circles) and host nestlings (open circles) in nests of (A) small, (B) intermediate, and (C) large hosts. Within each host, no significant differences in the time spent begging by cowbirds were found between feeding treatments. Sample sizes are noted above point estimates.

did not vary with feeding treatment within each host and because there was no effect of the order in which feeding treatments were presented, both feeding treatments were combined for further analyses of cowbird begging and host provisioning.

Because the great majority of host visits resulted in a single nestling being fed (see Methods), mean provisioning rates were best calculated over a period of time as opposed to a per-visit basis. Host provisioning rates varied significantly among hosts ($F_{2,43} = 29.08$, $P < 0.001$; Figure 4A). Sparrows provisioned an average of 334.6 ± 89.6 mm^3 of food per 10 min ($n = 13$), blackbirds an average of 1217.6 ± 78.4 mm^3 of food per 10 min ($n = 17$), and thrashers an average of 1012.9 ± 80.8 mm^3 of food per 10 min ($n = 16$). Notably, the provisioning rates of blackbirds and thrashers were not significantly different from one another (see Figure 4A). The proportion of food received by cowbird nestlings varied significantly among hosts ($F_{2,43} = 12.69$, $P < 0.001$; Figure 4B) and was inversely correlated with the host size. Cowbirds received an average of $62 \pm 4.4\%$ ($n = 13$) of the food brought to sparrow nests, which was significantly greater than an even share between nestlings ($P = 0.023$). Cowbirds received $55\% \pm 3.9$ ($n = 17$) of the food in blackbird nests which was not different from an even share ($P = 0.234$). In contrast, cowbirds received only $33\% \pm 4.0$ ($n = 16$) of the food at thrasher nests, a value significantly less than even ($P < 0.001$).

When combined over both feeding treatments, variation in time spent begging by cowbirds among hosts was marginally significant ($F_{2,43} = 3.17$, $P = 0.052$; Figure 5A). Time spent begging by cowbirds in blackbird nests was significantly lower (9.9 ± 2.0 s, $n = 17$) than in thrasher nests (16.6 ± 2.1 s, $n = 16$, $P = 0.025$) but only marginally lower than in sparrow nests (15.8 ± 2.3 s, $n = 13$, $P = 0.060$). When both the amount of food provisioned to nests and the proportion of that food received by cowbirds is considered, the mean amount of food cowbirds obtained varied significantly among host nests ($F_{2,43} = 22.06$, $P < 0.001$; Figure 5B). Cowbirds received the most food from blackbirds (651.4 ± 46.4 mm^3 food per 10 min, $n = 16$), the least from sparrows (201.2 ± 53.0 mm^3 food per 10 min, $n = 13$), and an intermediate level from thrashers (349.5 ± 47.8 mm^3 food per 10 min, $n = 16$). Finally, to assess the benefits of begging (i.e., food gained) relative to a proxy for the costs of begging (i.e., time spent begging) among hosts, I calculated a mean payoff for each cowbird nestling. To calculate the mean payoff for each nest, I first summed the volume of food gained over both feeding treatments and divided it by the seconds spent begging over the same period. I then calculated the average mean payoff over all nests within each host. Using this metric, the mean payoff varied significantly among hosts ($F_{2,43} = 29.01$, $P < 0.001$; Figure 5C), with the relative payoff to cowbirds in blackbird nests (98.4 ± 8.0 mm^3 food per second begging, $n = 17$) being 4× to 5× greater than in either sparrow (20.9 ± 9.1 mm^3 food per second begging, $n = 13$) or thrasher nests (23.0 ± 8.2 mm^3 food per second begging, $n = 16$). Of note, the relative payoff between sparrows and thrashers was very similar and not statistically different ($P = 0.869$, Figure 5C).

Additional experiments conducted with modal brood sizes found that when competing against blackbird nestlings, the proportion of food received by cowbirds was close to their expected share ($26 \pm 12.2\%$, $n = 2$), and cowbirds were fed at a similar rate (572.3 ± 318.1 mm^3 per 10 min, $n = 2$) as when they competed against a single blackbird (compare with Figure 5B). However, the mean payoff to cowbirds was lower in modal broods (39.0 ± 30.5 mm^3 food per second begging, $n = 2$; compare with Figure 5C) because cowbirds spent more time begging in modal blackbird nests. When competing against modal thrasher broods, cowbirds received less than

Figure 3
Mean (95% confidence interval) maximum begging posture for cowbird (solid circles) and host nestlings (open circles) in nests of (A) small, (B) intermediate, and (C) large hosts. Within each host, no significant differences in the latency to beg by cowbirds were found between feeding treatments. Sample sizes are noted above point estimates.
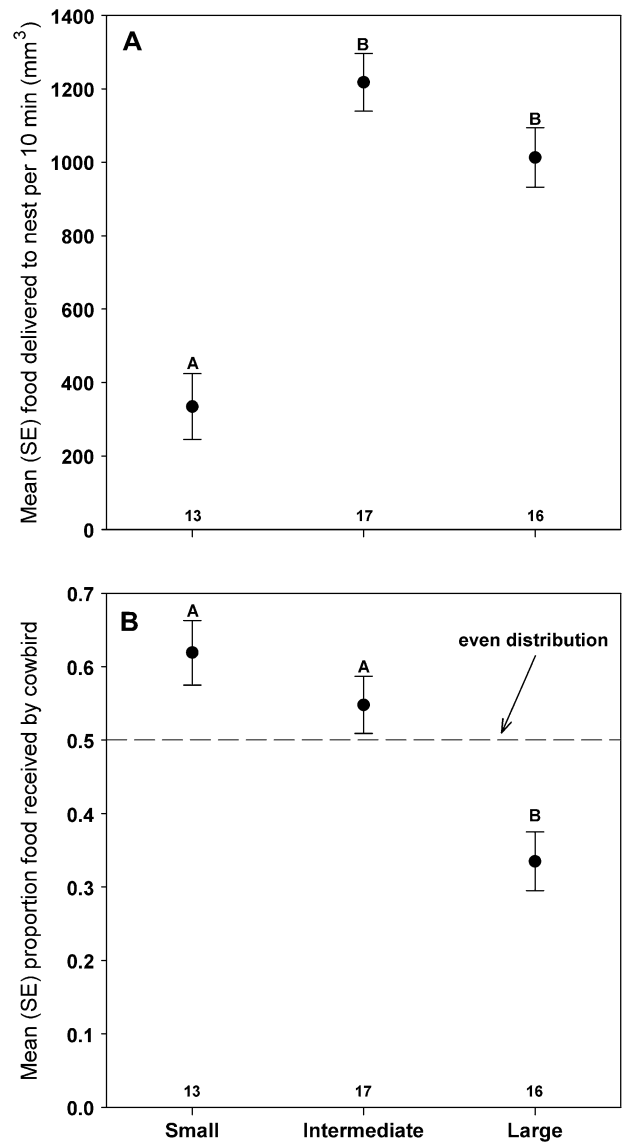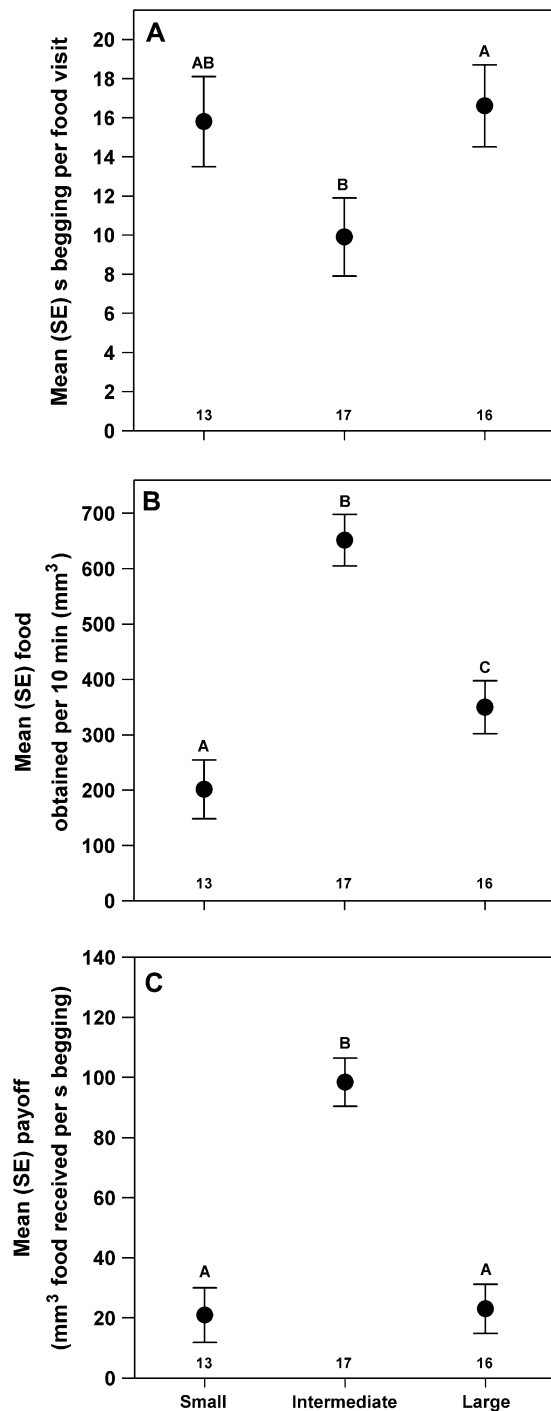

Figure 4
Mean (standard error) for (A) host provisioning rates and (B) proportion of food received by cowbirds over both feeding treatments combined in small, intermediate, and large hosts. Point estimates with the same letter were not significantly different at the $P = 0.05$ level as determined by Fisher's LSD. Sample sizes are noted below point estimates.

their expected share of the food coming to the nest (16.1 $\pm$ 10.7%, $n = 2$ nests) and were fed at a lower rate (230.7 $\pm$ 141.4 mm^3 per 10 min, $n = 2$). This led to a much lower mean payoff (8.0 $\pm$ 4.8 mm^3 food per second begging, $n = 2$) relative to cowbirds competing against a single thrasher chick (compare with Figure 5C).

DISCUSSION

In this study, the mean intensity of begging by cowbirds was similar during deprivation and supplementation treatments within each of the 3 hosts examined. The finding of no effect of feeding treatment differs with the study of Lichtenstein and Dearborn (2004) which reported that cowbirds significantly increased their maximum begging posture in response to feeding treatments when competing against a small host, the yellow

Figure 5
Mean (standard error) for (A) time spent begging per food visit (B) volume of food obtained per 10 min, and (C) mean payoff for cowbirds over both feeding treatments combined in small, intermediate, and large hosts. Point estimates with the same letter were not significantly different at the $P = 0.05$ level as determined by Fisher's LSD. Sample sizes are noted below point estimates.

warbler (*Dendroica petechia*). Why cowbird begging intensity changed little with regard to short-term need is not clear but one explanation may be the length of the deprivation period in this study was insufficient to modify the short-term need of cowbirds relative to supplementation treatments. The deprivation period in this study was chosen based on the work of pre-

vious authors that used 90–110 min experimental periods to assess the influence of food deprivation on begging behavior (e.g., Kilner et al. 1999; Maurer et al. 2003). Notably, the deprivation period in this study was 50% longer than that used in a previous study of cowbird begging (i.e., Lichtenstein and Sealy 1998) that found an effect of short-term need on the maximum begging posture of cowbirds (Lichtenstein and Sealy 1998). Based on previous work, therefore, it would appear that the deprivation periods used in this study were reasonable for detecting an effect of deprivation on begging behavior, and this methodological difference is unlikely to explain the pattern observed in this study.

An alternative explanation to the pattern of invariant begging relative to short-term need might be due to interspecific differences in the begging signal used by host nestlings to elicit feeding. Experiments with common cuckoos parasitizing reed warblers (*Acrocephalus scirpaceus*) showed that nestling cuckoos call at a rate that mimics the calling rate of a modal reed warbler brood (Kilner et al. 1999), and young cuckoos can increase the amount of food provisioned because their calling rate matches the signal that parents associate with a hungry brood. Common cuckoos can apparently exploit the provisioning rules of adult reed warblers because this cuckoo gens has coevolved with reed warblers over a long evolutionary history (Davies and Brooke 1988; Kilner et al. 1999; Davies 2000). Because cowbirds use a wide range of taxonomically distinct hosts (Friedmann and Kiff 1985), they may have evolved a generalized begging signal that is a poor match for the begging signals of some of their hosts. Such mismatches in the begging signal could lead to less food being received by a cowbird nestling which, in turn, could lead to increased begging intensity. Experiments that assess how cowbird begging is modulated in response to different host provisioning rules will help elucidate how generalist brood parasites communicate their need to hosts that may not be "tuned in" to the signaling channels used by nestling brood parasites.

Finally, an additional, nonmutually exclusive explanation to this pattern is that the condition of cowbird nestlings (sensu Clark 2002) tested in this study was low and led to increased begging intensity during all feeding treatments. To examine this possibility, I compared the mass of cowbirds tested in this study to the day-specific cowbird mass taken from the growth equation in Kilpatrick (2002) and averaged over the 19 hosts for which cowbird growth data are available (see Kilpatrick 2002 for details). I assumed that the resulting growth curve would represent the typical condition of a cowbird nestling and that nestling masses that fell below the curve would be indicative of nestlings in poorer than average condition, whereas nestling masses that fell above the curve would be indicative of nestlings in better than average condition. I found that the average day-specific masses of nestlings used in this experiment were greater than predicted by the growth curve (an average of 0.63, 4.54, and 0.99 g heavier in sparrow, blackbird, and thrasher nests, respectively). Thus, the unusually high begging intensity of cowbirds in my study was not due to their condition, and it remains unclear which factors led to elevated begging by cowbirds during both deprivation and supplementation treatments. Nevertheless, this result provides an interesting counter to the growing body of evidence that has found that the begging intensity of brood parasites varies relative to short-term need (e.g., Butchart et al. 2003; Lichtenstein and Dearborn 2004; Tanaka and Ueda 2005) and indicates that begging behavior of brood parasites is not influenced by short-term need under some conditions (see Redondo 1993).

In this study, the time spent begging by cowbirds varied among hosts even when the level of short-term need was

controlled and when cowbird nestlings appeared to be in good condition. This finding raises the question of which cues cowbirds use to assess the level of competition in a nest. One possible cue is the physical size of nest mates, which could be assessed when cowbirds come into contact with nest mates within the nest. An alternative, indirect cue used by nestlings might be the relative proportion of begging scrambles a cowbird wins in competition with nest mates, a factor which could influence nestling condition. As mentioned above, additional analyses showed that at the time of experiments, cowbirds appeared to be in better condition relative to cowbirds in a typical host nest. However, the extent to which cowbird nestling condition may have changed from the time broods were created (i.e., the afternoon prior to filming) to the time when experiments were conducted (i.e., the morning of filming) is not clear because nestling mass was not measured at the time broods were created. Therefore, although my data cannot determine whether nest mate size alone was used by cowbirds to modulate their begging among different sized hosts, these results indicate that nest mate size did play a role in influencing the patterns of begging observed in this study.

Among the 3 hosts I examined, cowbirds begged the least and received the most food when competing against a single blackbird nestling, leading to the greatest mean payoff. Relative to blackbirds, a smaller mean payoff was found for sparrows and thrashers, although the magnitude of the payoff was very similar in these 2 species. This finding indicates that when competing against a single nestling, cowbirds face several limiting factors with regards to the amount of food they receive in host nests and that these factors vary with the size of hosts. In sparrow nests, the biggest challenge faced by a cowbird is the amount of food brought to the nest by adults. In contrast, when competing against a thrasher, the greatest challenge faced by a cowbird is acquiring food during begging scrambles. Nevertheless, when the mean payoff to a cowbird is assessed over modal brood sizes for all hosts, it becomes evident that the mean payoff for cowbirds competing against a single sparrow nestling is similar to that when competing against a modal brood of blackbird nestlings, and both of those mean payoffs are higher than when competing against a modal brood thrasher nestlings (see Kilner 2003). This finding may help explain why cowbirds typically parasitize smaller hosts (Friedmann and Kiff 1985) and why cowbirds are more likely to fledge when raised by hosts of intermediate size (Kilner 2003). In addition, these results indicate an interaction between the size of host nest mates and the number of competitors, factors that need to be examined in future investigations that assess the success of generalist brood parasites (but see Kilner et al. 2004).

Current theoretical models of begging by brood parasites make no explicit predictions as to whether begging intensity should vary relative to proximate factors such as short-term need or the size of nest mates (Lichtenstein and Dearborn 2004). Theoretical models do, however, predict that brood parasites should beg more intensively than species that raise their own young for a given level of need (Godfray 1991), and this pattern has been found for cowbirds in previous empirical investigations (Briskie et al. 1994; Dearborn and Lichtenstein 2002). In addition to begging more intensively than hosts in this study, cowbird begging was largely invariant over disparate levels of short-term need, a result that has been found for at least one other brood parasite (i.e., great spotted cuckoo [*C. glandarius*], Redondo 1993). Although some theoretical models predict invariant begging for brood parasites (Lichtenstein and Dearborn 2004), experimental data are accumulating that indicate several brood-parasitic species have begging behaviors that vary due to short-term need (Butchart et al. 2003; Hauber and Ramsey 2003; Lichtenstein and Dearborn 2004)

and the size of nest mates (this study). Given that the begging behavior of several brood parasites does vary in relation to proximate factors, future studies should focus on documenting the extent to which begging is costly to generalist brood parasites when raised by different hosts. In addition, it is still unclear whether the modulation of begging behavior by cowbirds relative to nest mate size is a clear adaptation for brood parasitism as at least one nonparasitic member of the Icteridae is known to alter its begging behavior relative to nest mate size (Price and Ydenberg 1995; Price et al. 1996). Experiments that test both cowbirds and closely related, nonparasitic species in a range of nest environments will not only address this question but should also provide insights into the evolution of adaptations by brood-parasitic nestlings and have the potential for understanding how nestling begging behavior has evolved in species which raise their own young (Soler M and Soler JJ 1999).

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