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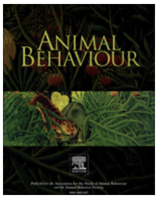

Brown-headed cowbird nestlings influence nestmate begging, but not parental feeding, in hosts of three distinct sizes

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Avian brood parasites typically depress the fitness of their hosts by reducing the number of host offspring produced, yet little is known about how parasitic nestlings influence the behaviour of host parents and host offspring. In this study, we used three hosts of the brown-headed cowbird, *Molothrus ater*, that varied in size (i.e. smaller, similar to and larger than cowbirds of a given age) to determine whether parasitic nestlings altered patterns of food provisioning by host parents and begging by host young under field conditions. Adult provisioning did not change in the presence of a cowbird but instead was influenced by feeding treatment and host size. In parasitized broods where nestlings differed in size (i.e. the small and large hosts), the larger nestling received the majority of food brought to the nest, regardless of whether it was the cowbird or host nestling. In contrast, similar-sized host nestlings received a similar amount of food in parasitized and unparasitized host broods. Relative to unparasitized broods, the presence of a cowbird led to increased begging intensity by the small host, had no clear effect on begging behaviour of the intermediate-sized host, and reduced begging intensity of the large host. Taken together, these results suggest the presence of a cowbird did not lead to changes in provisioning behaviour in parents, and the extent to which cowbirds influenced host begging behaviour depended on the size of the host.

Obligate avian brood parasitism is an uncommon reproductive strategy in which a female parasite lays her eggs in the nests of other species (the 'hosts'), and these hosts provide all care for the parasitic young (Rothstein 1990; Payne 1998; Davies 2000). Numerous studies have shown that brood parasitism can have strong fitness costs for hosts, including costs inflicted by the behaviour of parasitic nestlings. In some brood parasitic species, parasitic nestlings decrease host fitness by direct nestmate killing, by either evicting host offspring from the nest (e.g. *Cuculus* spp.; Wyllie 1981), or through repeated stabbing of host young with specialized bill hooks (e.g. *Indicator* spp.: Friedmann 1955; *Tapera naevia*: Morton & Farabaugh 1979). In other brood parasitic species, parasitic nestlings do not attempt to kill host offspring directly and instead are often raised alongside them in the host nest (e.g. *Vidua* finches, *Molothrus* cowbirds, and *Clamator* cuckoos: Rothstein 1990; Payne 1998; Davies 2000). These parasitic nestlings often engage in intense competition with host young during feeding visits by parents, and this heightened competition for food can lead to reduced growth of host nestlings or even death (Goguen & Mathews 1996; Dearborn et al. 1998; Kus 1999; Lorenzana & Sealy 1999; Redondo & Zuniga 2002). In addition to costs arising from competitive interactions between parasitic and host young, parasitic nestlings may also alter the behaviour of host parents. For some hosts, more intense begging of the parasitic nestling increases feeding levels beyond that of a brood of host young (Grim & Honza 2001; Kilpatrick 2002; Hoover & Reetz 2006). In turn, increased energy expenditure from elevated provisioning rates can reduce annual return rates via a reduction in adult survival (Hoover & Reetz 2006). Thus, parasitic offspring can influence behaviours of adult and nestling hosts, and both must be considered simultaneously to understand fully how brood parasites impact host fitness.

Although the overall fitness costs inflicted by brood parasites are well documented (Rothstein 1990; Lorenzana & Sealy 1999; Hauber 2003), few investigations have quantified how parasitic young influence the behaviour of host parents and offspring, and how the extent of this influence varies relative to the size of the host. Most studies have been limited to investigating a single small host

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(Dearborn et al. 1998; Lichtenstein & Sealy 1998; Hoover & Reetz 2006), a single similar-sized host (Clotfelter 1997; Glassey & Forbes 2003; Lichtenstein 2001a), or have examined hosts of different sizes in different brood parasitic species (e.g. Lichtenstein & Dearborn 2004). Nevertheless, host size is a particularly important factor for nonevicting brood parasites because larger nestlings often dominate smaller nestmates and obtain a disproportionate food share during provisioning events for both brood parasites and nonparasitic species alike (Bengtsson & Ryden 1983; Price & Ydenberg 1995; Lichtenstein & Sealy 1998; Lichtenstein 2001b; Rivers 2007). Thus, size differences between parasitic and host nestlings have important implications for determining the outcome of competitive contests for food and, in turn, the extent to which a brood parasite is harmful to the growth and/or survival of host young.

In this study, we examined how nestlings of the brown-headed cowbird, *Molothrus ater* (hereafter cowbird) influenced the provisioning behaviour of adult hosts and begging of their offspring under field conditions when short-term need was experimentally controlled. The cowbird is an ideal species for this investigation because it is one of the most generalized brood parasites in the world and is raised by hosts whose size range is among the largest observed in any avian brood parasite (Friedmann & Kiff 1985; Lowther 1993; Ortega 1998). Our objectives in this investigation were to quantify (1) parental provisioning behaviours in hosts of three distinct sizes whose young are smaller, similar to and larger than a cowbird of the same age, and (2) behavioural interactions between host and parasitic nestlings. Within each host, we compared broods of two host young to broods with one cowbird and one host nestling from a previously published study (i.e. Rivers 2007). We tested all broods over disparate levels of short-term need (i.e. hunger, sensu Clark 2002) because hunger levels have a clear influence on parental provisioning and competition between nestmates (Budden & Wright 2001). We predicted that parental provisioning to broods containing a cowbird nestling would be greater than that to broods without a cowbird nestling because the exaggerated begging of cowbirds should increase parental feeding. Based on previous work (Lichtenstein 2001b; Rivers 2007), we also predicted that the largest nestlings would get the majority of food in broods with size differences between nestlings, whereas there would be similar levels of food obtained by each nestling in broods where nestlings were similar in size. Finally, we predicted that the more intense begging of the cowbird would lead to increased begging intensity of host nestlings in broods containing a cowbird relative to broods containing two host nestlings.

METHODS

Study Area and Selection of Host Species

This research was conducted during the 2002–2004 breeding seasons at Konza Prairie Biological Station (39°05′N, 96°35′W), in northeast Kansas, U.S.A. Although cowbirds parasitize at least 24 host species at this site (Elliott 1978; Rivers et al., in press), initial field work determined that only three hosts were available in sufficient number to conduct experiments: (1) a small host (field sparrow, *Spizella pusilla*, hereafter sparrow), (2) an intermediate-sized host (red-winged blackbird, *Agelaius phoeniceus*, hereafter blackbird), and (3) a large host (brown thrasher, *Toxostoma rufum*, hereafter thrasher). These species were assumed to represent weak, moderate and strong nestling competitors, respectively, to a cowbird nestling of similar age (see Rivers 2007). Nestlings of these host species are altricial, have similar growth patterns (Starck & Ricklefs 1998), and cover most of the size range of host species against which cowbirds typically compete (Friedmann & Kiff 1985; Lowther 1993; Ortega 1998). Although cowbird eggs often hatch prior to host eggs (Briskie & Sealy 1990), nestling age was standardized in experiments to control for developmental stage. Note, however, that although thrashers typically reject cowbird eggs (Rothstein 1975), they occasionally raise cowbirds at our study site (Elliott 1978; J. W. Rivers, unpublished data) and in other locations throughout the Great Plains (Strausberger & Rothstein 2009).

Field Experiments

We created two brood types for each host species, with two nestlings in each brood. The first brood type comprised one cowbird and one host nestling (hereafter a parasitized brood) whereas the second brood type comprised two host nestlings (hereafter an unparasitized brood); thus, there were six host size × brood type combinations. All nestlings were tested from 3–5 days after hatching so that experiments were conducted during the peak of nestling growth for the cowbird and all three hosts (Starck & Ricklefs 1998). Data for parasitized broods were reported in a previous study (Rivers 2007) but were collected at the same time as those for unparasitized broods. Although a brood of one cowbird and one host is common for parasitized small hosts (Carey et al. 1994; Lichtenstein & Sealy 1998), it is not always so for parasitized nests of larger hosts. Nevertheless, because the number of nestmates can influence begging, food acquisition and provisioning (e.g. Leonard et al. 2000), brood size was standardized to two nestlings to ensure that nestmate size was not confounded with brood size.

We created broods of two nestlings by adding and/or removing nestlings from available host nests 1 day prior to videotaping behaviours. A single cowbird was added to most parasitized broods (36 of 46), and a single cowbird nestling was removed from five nests that contained two cowbird nestlings. Most parasitized broods (40 of 46) initially contained more than one host nestling; in those cases, one host nestling was randomly selected to remain in the nest while all other nestlings were cross-fostered to available nests or, if other nests were unavailable, removed under permit. In a similar manner, most unparasitized broods (36 of 41) initially contained more than two host nestlings, and in those cases, two nestlings were randomly selected to remain in the nest while the other nestlings were cross-fostered to available nests or removed under permit. The majority of nestlings within each experimental brood (i.e. 84%, $N = 87$ nests) hatched on the same day, and nestlings in the remaining pairs hatched within 1 day of each other. Logistical constraints made it impossible to control for the nest environment of nestlings prior to experiments; however, nestlings had an average of 19 h (minimum: 11 h) to acclimate to changes in their nest environment. This period was assumed to provide enough time for nestlings to adjust to their new environment since at least one study found that translocated nestlings changed their begging behaviour in response to changes in nestmate size within 2 h (Price et al. 1996).

At the same time we created experimental broods, we placed a plastic sham videocamera close to the nest to allow host adults to acclimate to its presence. On the morning following the placement of the sham camera, we returned to the nest and initiated videotaping between 0600 and 0900 hours Central Daylight Time. Prior to filming, we measured each nestling's mass (±0.1 g) with an electronic balance, after which we replaced the sham videocamera with a miniature videocamera attached remotely by a cable to a Sony camcorder. At the same time, we marked one randomly selected nestling minimally on the bill with a nontoxic black felt marker to distinguish nestlings on videotapes in unparasitized broods and parasitized blackbird broods. Next, two feeding treatments were applied to each nest in one of two sequences as described in Rivers (2007). In the first sequence, both nestlings were fed until satiation with mealworms, after which videotaping immediately commenced and continued for 90 min. After this 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 filmed for 90 min. During deprivation treatments, one to three additional nestlings were swapped into the host nest to prevent abandonment, and focal nestlings were held in a sheltered, secure location where they were kept warm with a hot water bottle during cool weather. The second sequence differed from the first only in that the order of the deprivation and supplementation treatments was reversed. Each nest was randomly assigned to one of the two sequences, a similar number of sequences were used for each host species, and no effect of sequence on begging behaviours was found during preliminary analyses.

Videotape Analysis

A single observer (J. W. R.) scored all videotapes and recorded for each feeding visit (1) the volume of food provisioned, (2) the proportion of food received by each nestling and (3) the taxonomic affiliation (to order) of the prey item(s). In addition, each nestling's (4) latency to beg, (5) time spent begging and (6) maximum begging posture was also scored. Volume of food provisioned was calculated by visually estimating the volume of the food item(s) relative to adult bill volume in 10% increments. When food was given to both nestlings during a single feeding visit (12.5% of 1429 feeding visits), we assigned 50% of the food load to each nestling because the relative proportion of food provisioned to each nestling could not be determined. Bill volume was calculated using the formula of Greenberg & Droege (1990) using measurements of the three host species taken from 30 museum skins of both sexes (sparrows and thrashers) or females (blackbirds) that were collected within 150 km of the study site (see Rivers 2007 for details).

Latency to beg 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 that each nestling spent begging during a provisioning visit until all food had been distributed. Over the same period, we assigned a maximum begging posture score, where $0 =$ not begging, $1 =$ gaping without neck stretched, $2 =$ gaping with neck stretched to three-fourths length and belly in contact with nest cup, and $3 =$ gaping with neck stretched more than three-fourths length and belly not in contact with nest cup. Unfortunately, neither the rate nor the amplitude of begging calls could be quantified because of several factors (e.g. environmental noise, differences in position of cameras among nests).

Statistical Analysis

To assess provisioning behaviour, data were analysed as a split plot design with repeated measures. Each of the six host size × brood type combinations was considered a whole-plot factor assigned to each nest with feeding treatment (i.e. supplementation or deprivation) as the subplot factor assigned within each nest. Within each feeding treatment at each nest, the total amount of food provisioned was summed, and these sums were then standardized according to recording session length and the mass of the brood. A similar approach was used to estimate the amount and proportion of food obtained by 'Nestling 1' (i.e. the cowbird nestling in a parasitized brood, or a randomly selected host nestling in an unparasitized brood) relative to 'Nestling 2' (i.e. the host nestling in a parasitized brood, or the second host nestling in an unparasitized brood). Data were then analysed using a split plot ANOVA model with PROC MIXED in SAS version 9.1 (SAS Institute, Cary, NC, U.S.A.) using the Kenward–Rogers method to calculate degrees of freedom. Type III *F* tests of hypotheses were used for all factors and interactions, and individual *t* tests were used to compare means at selected factor levels. All nonsignificant factors and factor combinations were retained in our models because stepwise removal (or addition) of factors in a model has the potential to be suboptimal, resulting in models that are not as strong as when all factors are considered simultaneously (see Neter et al. 1996).

Previous research has shown that a nestling's begging behaviour can influence and be influenced by its nestmate(s) (see Forbes 2002). Therefore, we used the difference between the nestlings within a brood (i.e. Nestling 1 value minus Nestling 2 value) to assess the effects of feeding treatments on nestling begging behaviour within the statistical framework described above. Least-squares means analysis was used to calculate means for statistical tests because of unequal sample sizes. Although statistical tests were conducted on the differences between means, raw means are reported in Figs. 4–6 for ease of presentation. Finally, paired *t* tests were used to assess the extent of body mass differences between nestlings within broods. Means and respective 95% CIs are reported unless otherwise noted, and significance levels for all tests were set at $P < 0.05$.

RESULTS

Begging and provisioning were assessed in 24 sparrow broods (13 parasitized, 11 unparasitized), 34 blackbird broods (17 parasitized, 17 unparasitized) and 29 thrasher broods (16 parasitized, 13 unparasitized); some nests were represented by only one feeding treatment because of technical problems with filming. On average, the cowbird nestling in parasitized broods was significantly larger than the host nestling in sparrow broods (mean difference: 5.17 g, 95% CI: 3.69, 6.65 g; $P < 0.001$), was not significantly different in mass than the host nestling in blackbird broods (mean difference: 1.21 g, 95% CI: −0.09, 2.51 g; $P = 0.067$), and was significantly smaller than the host nestmate in thrasher broods (mean difference: −10.27 g, 95% CI: −11.61, −8.93 g; $P < 0.001$). In contrast, there were no significant differences in mass between host nestlings in unparasitized broods for the sparrow (mean difference: 0.31 g, 95% CI: −1.30, 1.92 g; $P = 0.704$), the blackbird (mean difference: 0.20 g, 95% CI: −1.10, 1.50 g; $P = 0.760$), or the thrasher (mean difference: −1.42 g, 95% CI: −2.90, 0.07 g; $P = 0.061$).

Parental Provisioning Behaviour

The mass-corrected volume of food brought to the nest per hour (hereafter provisioning rate) varied significantly relative to the size of the host ($F_{2,75.3} = 39.1$, $P < 0.001$) and feeding treatment ($F_{1,74.3} = 30.2$, $P < 0.001$), with no significant effect of cowbird parasitism ($F_{1,75.3} = 0.1$, $P = 0.796$) or any main effect interactions (host × parasitism: $F_{2,75.3} = 1.6$, $P = 0.202$; host × feeding: $F_{2,74.3} = 0.6$, $P = 0.533$; parasitism × feeding: $F_{1,74.3} = 0.6$, $P = 0.430$; host × parasitism × feeding: $F_{2,74.3} = 0.8$, $P = 0.476$). Among hosts, mean provisioning rate by blackbirds was greater than either that of sparrows or thrashers during both feeding treatments (Fig. 1). Thrashers tended to have a higher rate of food provisioning to parasitized broods than to unparasitized broods for each feeding treatment, whereas the opposite was true for sparrows, although neither reached statistical significance (Fig. 1a, c). The proportion of food provided to the first nestling in each nest varied significantly relative to host size ($F_{2,79.3} = 10.6$, $P < 0.001$), with no significant effect of cowbird parasitism ($F_{1,79.3} = 0.3$, $P = 0.616$), feeding treatment ($F_{1,78.5} = 1.7$, $P = 0.195$), or any main

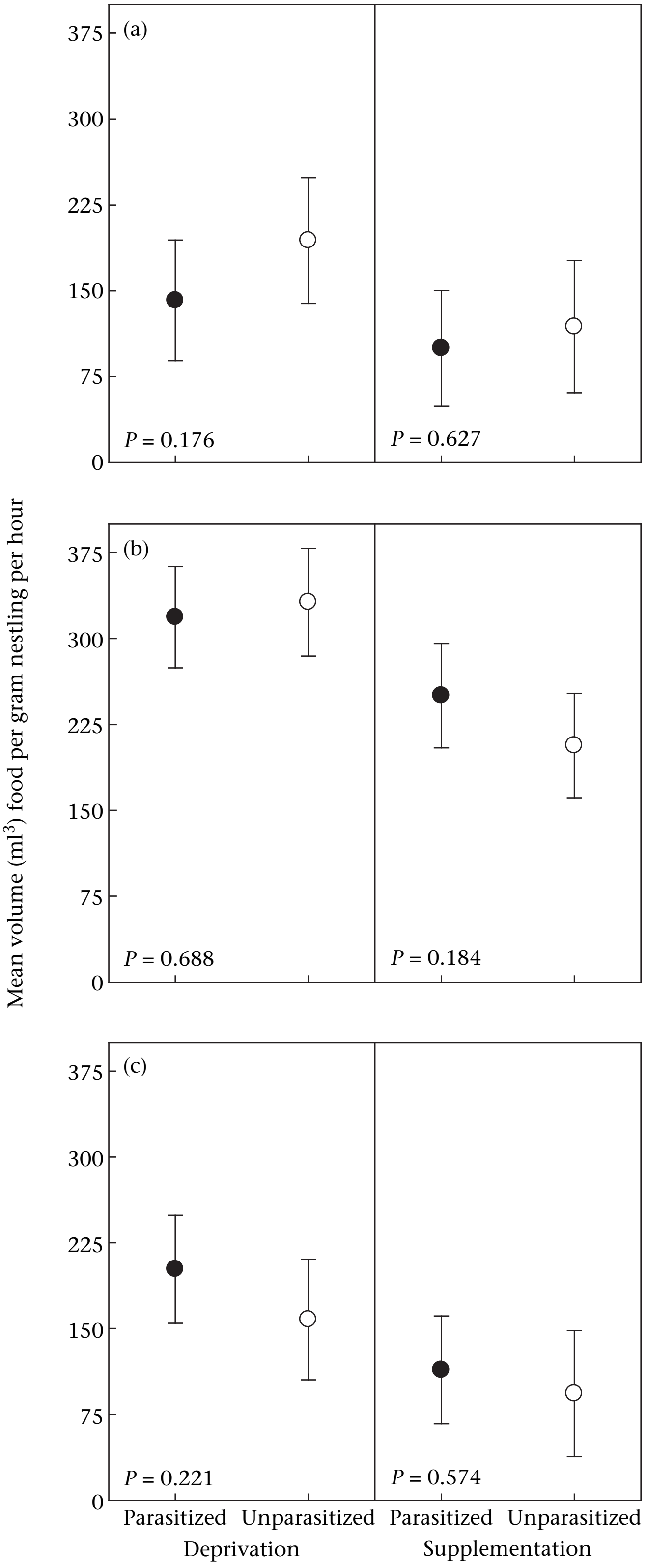

Figure 1. Mean (95% CI) provisioning rate to (a) sparrow, (b) blackbird and (c) thrasher nests over two feeding treatments (deprivation, supplementation) and relative to whether a brood contained a cowbird and a host nestling (parasitized) or two host nestlings (unparasitized). *P* values that test for mean differences between parasitized and unparasitized broods for a given feeding treatment are given below interval estimates. $N = 11–17$ broods.

effect interactions (host × parasitism: $F_{2,79.3} = 2.1$, $P = 0.133$; host × feeding: $F_{2,78.6} = 0.9$, $P = 0.414$; parasitism × feeding: $F_{1,78.5} = 0.2$, $P = 0.681$; host × parasitism × feeding: $F_{2,78.6} = 1.3$, $P = 0.289$). We therefore averaged across both feeding treatments to look at the main effects of host size on the proportion of food received by the first nestling in parasitized and unparasitized broods. In parasitized broods, the proportion of food obtained by the cowbird in sparrow broods was significantly greater than unity (i.e. even food distribution), did not differ in blackbird broods, and was significantly less than unity in thrasher broods (Fig. 2). In contrast, the amount of food obtained by the first nestling in unparasitized nests was not significantly different from unity in any of the three hosts (Fig. 2).

The total amount provisioned to Nestling 1 in the brood (i.e. cowbird in a parasitized brood, randomly selected host nestling in an unparasitized brood) differed significantly relative to host size ($F_{2,76.4} = 27.2$, $P < 0.001$) and feeding treatment ($F_{1,72.4} = 26.4$, $P < 0.001$) but not cowbird parasitism ($F_{1,76.4} = 0.0$, $P = 0.976$), with no main effect interactions (host × parasitism: $F_{2,76.4} = 0.4$, $P = 0.643$; host × feeding: $F_{2,72.5} = 1.0$, $P = 0.379$; parasitism × feeding: $F_{1,72.4} = 0.1$, $P = 0.794$; host × parasitism × feeding: $F_{2,72.5} = 0.3$, $P = 0.753$). When examined over each of the feeding treatment × host size combinations, the amount of food received by the cowbird in parasitized broods did not differ from that of Nestling 1 in unparasitized broods, despite size differences between cowbirds and host nestlings in sparrow and thrasher broods. The amount of food received by cowbirds was greatest in blackbird broods, intermediate in thrasher broods and lowest in sparrow broods (Fig. 3).

The primary prey type(s) could be identified to 13 different orders in 871 of 1429 (61%) provisioning visits, with the vast majority (>92%) of identified food items belonging to Orthoptera, Lepidoptera, Araneae and Hemiptera (Table 1). Parents brought back food items from two different orders on approximately 10% (83 of 871) of the provisioning visits from which prey could be identified. With each host nest, broods generally had the same relative composition of identifiable food items regardless of whether they were parasitized. Indeed, the difference in the proportional makeup for a given prey type in parasitized and unparasitized broods in each host (with a minimum of 15 observations per prey type) was less than 10% in all cases but two: relative to unparasitized broods, there was an notable increase in the proportion of Hemiptera in both parasitized sparrow broods (11%) and parasitized blackbird broods (20%, Table 1).

Nestling Begging Behaviour

The mean difference in latency to beg varied significantly relative to host size ($F_{2,89.2} = 5.5$, $P = 0.006$), with a significant host × parasitism interaction ($F_{2,89.2} = 4.4$, $P = 0.015$). However, there was no significant effect of cowbird parasitism ($F_{1,93.9} = 1.9$, $P = 0.171$), feeding treatment ($F_{1,98.5} = 0.5$, $P = 0.495$), or main effects interactions between host × feeding ($F_{2,99.3} = 0.0$, $P = 0.974$), parasitism × feeding ($F_{1,98.5} = 0.3$, $P = 0.569$), or host × parasitism × feeding ($F_{2,99.3} = 0.1$, $P = 0.927$). When averaged across both feeding treatments to examine the main effect of cowbird parasitism, there was little variation in latency to beg between nestlings in both parasitized and unparasitized broods for sparrows and blackbirds and for unparasitized thrasher broods (Fig. 4). However, cowbirds in parasitized thrasher broods had a significantly shorter latency to beg than thrasher nestlings (Fig. 4c), and this difference was probably responsible for the significant host × parasitism interaction.

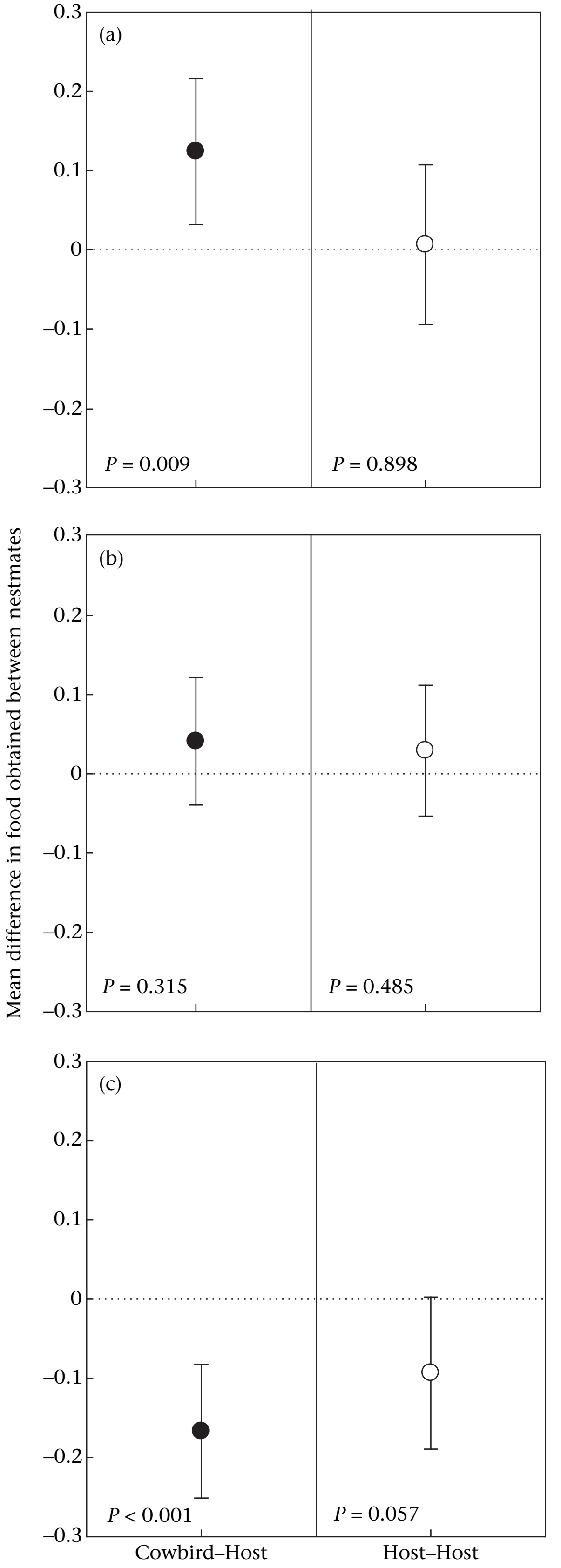

Figure 2. Mean (95% CI) difference in amount of food obtained between nestmates (i.e. first nestling minus second nestling) in the nest of the (a) sparrow, (b) blackbird and (c) thrasher relative to whether a brood contained a cowbird and a host nestling or two host nestlings. *P* values that test the null hypothesis of even food distribution between nestmates (dashed horizontal line) are given below interval estimates. $N = 11–17$ broods.

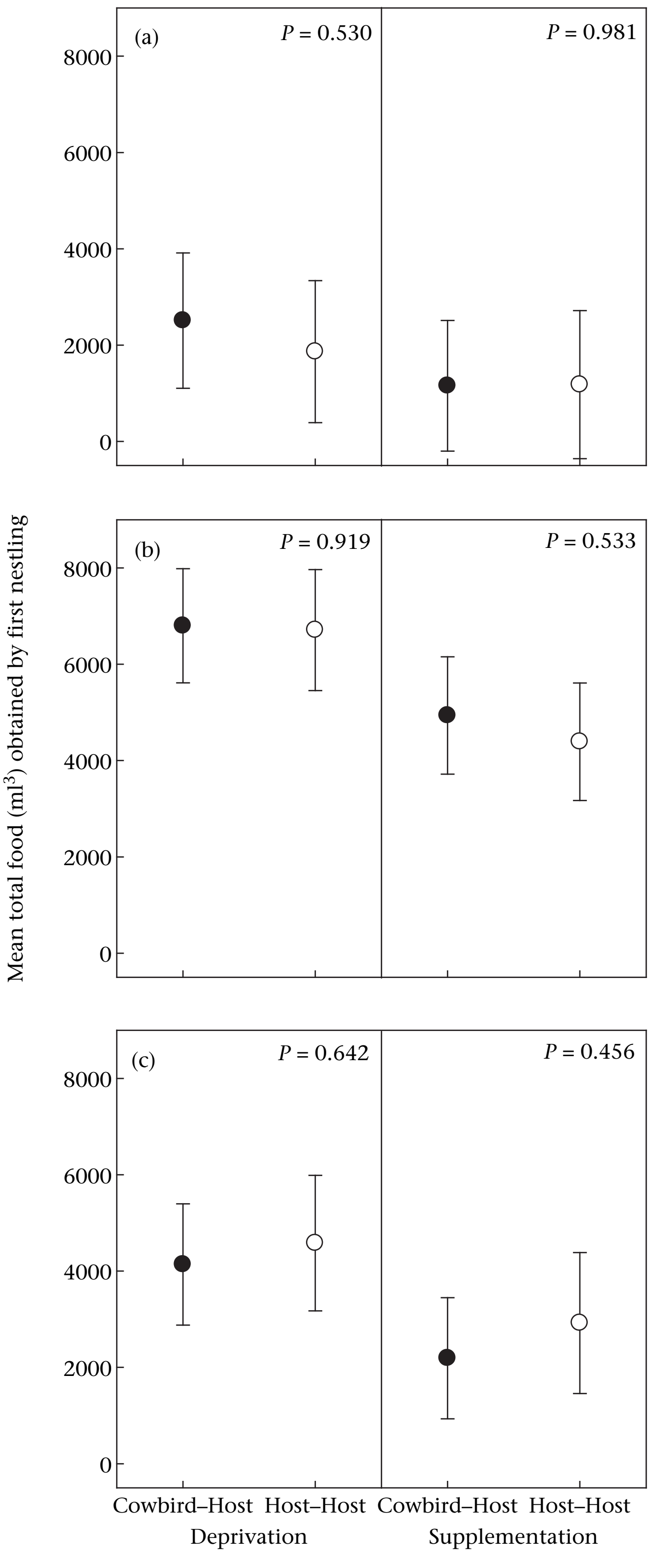

Figure 3. Mean (95% CI) total food obtained (ml^3) by first nestlings in nests of the (a) sparrow, (b) blackbird and (c) thrasher over two feeding treatments (deprivation, supplementation) and relative to whether a brood contained a cowbird and a host nestling or two host nestlings. *P* values that test for mean differences between values for parasitized and unparasitized broods for a given feeding treatment are given above interval estimates. $N = 11–17$ broods.

Table 1
Relative percentage and total number (in parentheses) of identifiable prey types in parasitized and unparasitized broods of three host species

Prey type*	Field sparrow		Red-winged blackbird		Brown thrasher	
	Parasitized	Unparasitized	Parasitized	Unparasitized	Parasitized	Unparasitized
Orthoptera	27.9% (36)	26.9% (25)	34.1% (75)	40.8% (86)	31.0% (54)	40.9% (52)
Lepidoptera	48.1% (62)	57.0% (53)	10.5% (23)	10.9% (23)	19.5% (34)	25.2% (32)
Araneae	8.5% (11)	7.5% (7)	33.2% (73)	26.5% (56)	8.1% (14)	7.9% (10)
Hemiptera	13.2% (17)	2.2% (2)	20.5% (45)	19.9% (42)	24.7% (43)	4.7% (6)
Coleoptera	1.6% (2)	3.2% (3)	0.5% (1)	1.0% (2)	10.3% (18)	6.3% (8)
Diptera	0% (0)	1.1% (1)	0.5% (1)	1.0% (2)	1.2% (2)	8.7% (11)
Hymenoptera	0.8% (1)	2.2% (2)	0% (0)	0% (0)	3.5% (6)	3.2% (4)

Note that totals for a given host and brood type may not sum to 100% because of rounding errors.

* Nine prey items in six additional orders (Haplotaxida, Geophilomorpha, Scorpiones, Blattodea, Odonata and Squamata) were observed but are not included in this table because they were extremely rare (<1% of all identified prey items).

The mean difference in time spent begging varied significantly relative to host size ($F_{2,88.7} = 12.1$, $P < 0.001$) and cowbird parasitism ($F_{1,90.2} = 25.6$, $P < 0.001$) but not feeding treatment ($F_{1,84.9} = 1.1$, $P = 0.290$). There were significant main effect interactions for host × parasitism ($F_{2,88.7} = 5.2$, $P = 0.007$) and host × feeding treatment ($F_{2,85.3} = 4.5$, $P = 0.014$), but not for parasitism × feeding ($F_{1,84.9} = 0.2$, $P = 0.667$) or host × parasitism × feeding ($F_{2,85.3} = 0.6$, $P = 0.537$). When averaged across both feeding treatments to examine the main effect of cowbird parasitism, there was no difference in time spent begging between nestlings in unparasitized nests and between nestlings in parasitized sparrow nests. In contrast, cowbirds begged significantly longer than either blackbird or thrasher nestlings, with the magnitude of the difference being greater in thrasher nests (Fig. 5).

Finally, the mean difference in maximum begging posture varied significantly relative to cowbird parasitism ($F_{1,91.8} = 4.4$, $P = 0.038$) but not host size ($F_{2,90.3} = 1.9$, $P = 0.152$) or feeding treatment ($F_{1,89.0} = 0.0$, $P = 0.892$). There was a significant interaction for host × parasitism ($F_{2,90.3} = 8.7$, $P < 0.001$) but not for host × feeding treatment ($F_{2,89.5} = 0.8$, $P = 0.441$), parasitism × feeding ($F_{1,89.0} = 1.7$, $P = 0.202$) or host × parasitism × feeding ($F_{2,89.5} = 0.68$, $P = 0.443$). When averaged across both feeding treatments to examine the main effect of cowbird parasitism, the only significant difference between nestlings occurred in parasitized thrasher nests, where the begging intensity of cowbird nestlings was significantly greater than that of thrashers (Fig. 6).

DISCUSSION

Cowbird Influence on Host Provisioning Behaviour

Our study found that provisioning rates differed significantly between hosts and between feeding treatments within each host, but were not influenced by the presence of a cowbird in the brood. Parental provisioning among hosts was therefore not based on whether a brood contained a cowbird nestling but was instead adjusted relative to the physical size of nestlings in the brood. Two other studies of small cowbird hosts found that the presence of a cowbird led to greater nest visitation rates relative to unparasitized broods (Dearborn et al. 1998; Hoover & Reetz 2006). Although these studies suggest that an increase in nest visitation may lead to more food being delivered to the brood, both of these studies assessed only the number of provisioning visits and not the volume of food brought to the nest, and one study did not adjust for overall brood mass (Dearborn et al. 1998). If we assume, however, that nest visitation rates are positively correlated with food delivery to the nest, our results contrast markedly with those of Hoover & Reetz (2006), who found that parasitized broods had higher visitation rates even when brood mass was controlled for. Note, however, that visitation rates of unparasitized broods in that study were compared to broods that contained one to three cowbird nestlings (Hoover & Reetz 2006). If the number of cowbird nestlings in a nest has a nonlinear effect on adult provisioning rate, nest visitation rates to multiply parasitized nests may be higher than those to singly parasitized nests. Such a situation might arise because cowbirds often beg in response to the begging of their nestmates (Rivers 2009), and a cowbird sharing the nest with another cowbird may lead to begging beyond that observed for host nestlings, which could increase host provisioning. Whether or not such a scenario occurs under natural conditions is unknown; however, the results of our study suggest that provisioning rates of parasitized broods containing a single cowbird nestling and those of unparasitized broods are similar when brood mass is controlled for.

In parasitized sparrow and thrasher broods, parents fed significantly more than half of the food to the largest nestling, regardless of whether it was a cowbird or a host. However, those same two hosts fed approximately half of the food to each nestling in unparasitized broods. In addition, there was an even distribution of food in both parasitized and unparasitized blackbird broods, where cowbird and host nestlings were similar in size. These results suggest that size discrepancies between cowbird and host nestlings in sparrow and thrasher broods influenced whether the larger nestling received more food than its nestmate, and accord well with other studies of open-cup nesters that have found that the largest nestling in the brood receives the most food (see Budden & Wright 2001). These results also provide further evidence against the idea that the cowbird provides a ‘supernormal’ stimulus to its hosts through intense begging (Dawkins & Krebs 1979), which leads to elevated provisioning levels, an explanation that has already been shown to be unsupported in at least two other small cowbird hosts (Dearborn 1998; Lichtenstein & Sealy 1998).

Cowbird Influence on Nestling Begging Behaviour

Previous analysis of cowbird–host begging in the host nests examined here found that cowbirds begged more intensively than hosts and that cowbird begging intensity was greatest in sparrow and thrasher broods (Rivers 2007). In the small host, the sparrow nestling in a parasitized brood spent more time begging and attained a greater maximum begging posture than did a similar-sized sparrow nestling in an unparasitized brood (Figs 5, 6). In contrast, the opposite occurred in the significantly large host: time spent begging and maximum begging posture of a thrasher nestling in a parasitized brood were reduced relative to those of a similar-sized thrasher in an unparasitized brood. For the blackbird, both begging metrics were similar for host nestlings that competed against either a cowbird or blackbird nestling. Collectively, these findings suggest that the presence of a cowbird in the brood leads

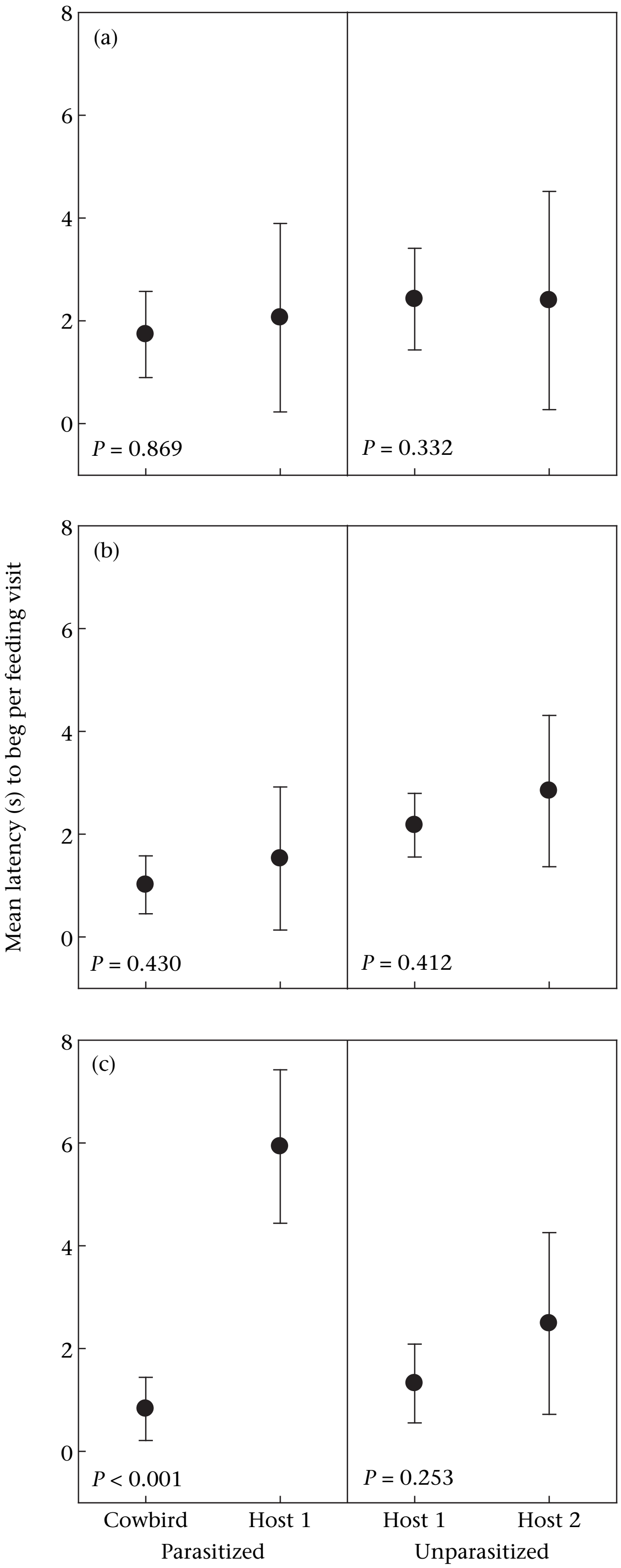

Figure 4. Mean (95% CI) latency to beg (s) per feeding visit in (a) sparrow, (b) blackbird and (c) thrasher broods that contained a cowbird and a host nestling (parasitized) or two host nestlings (unparasitized). *P* values that test for mean differences between nestmates within each brood type (parasitized or unparasitized) for each host are given below interval estimates. *N* = 11–17 broods.

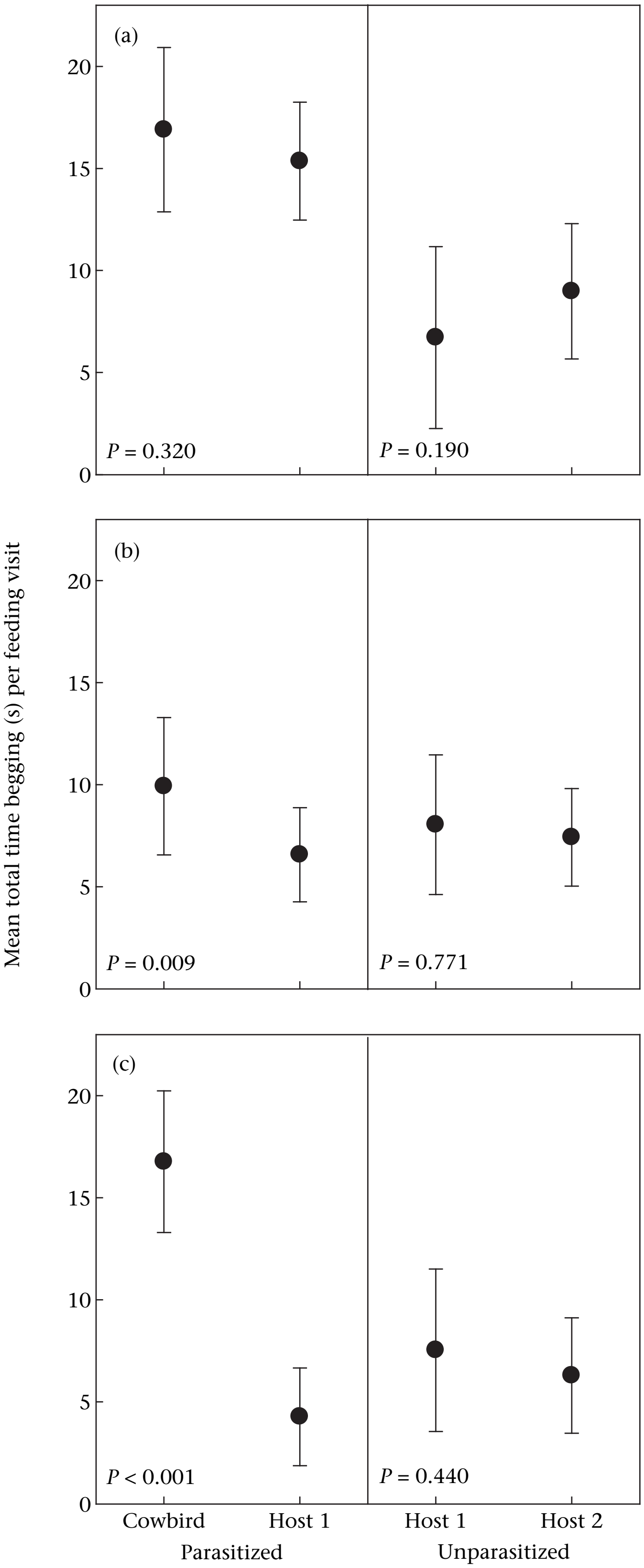

Figure 5. Mean (95% CI) time spent begging (s) per feeding visit in (a) sparrow, (b) blackbird and (c) thrasher broods that contained a cowbird and a host nestling (parasitized) or two host nestlings (unparasitized). *P* values that test for mean differences between nestmates within each brood type (parasitized or unparasitized) for each host are given below interval estimates. *N* = 11–17 broods.

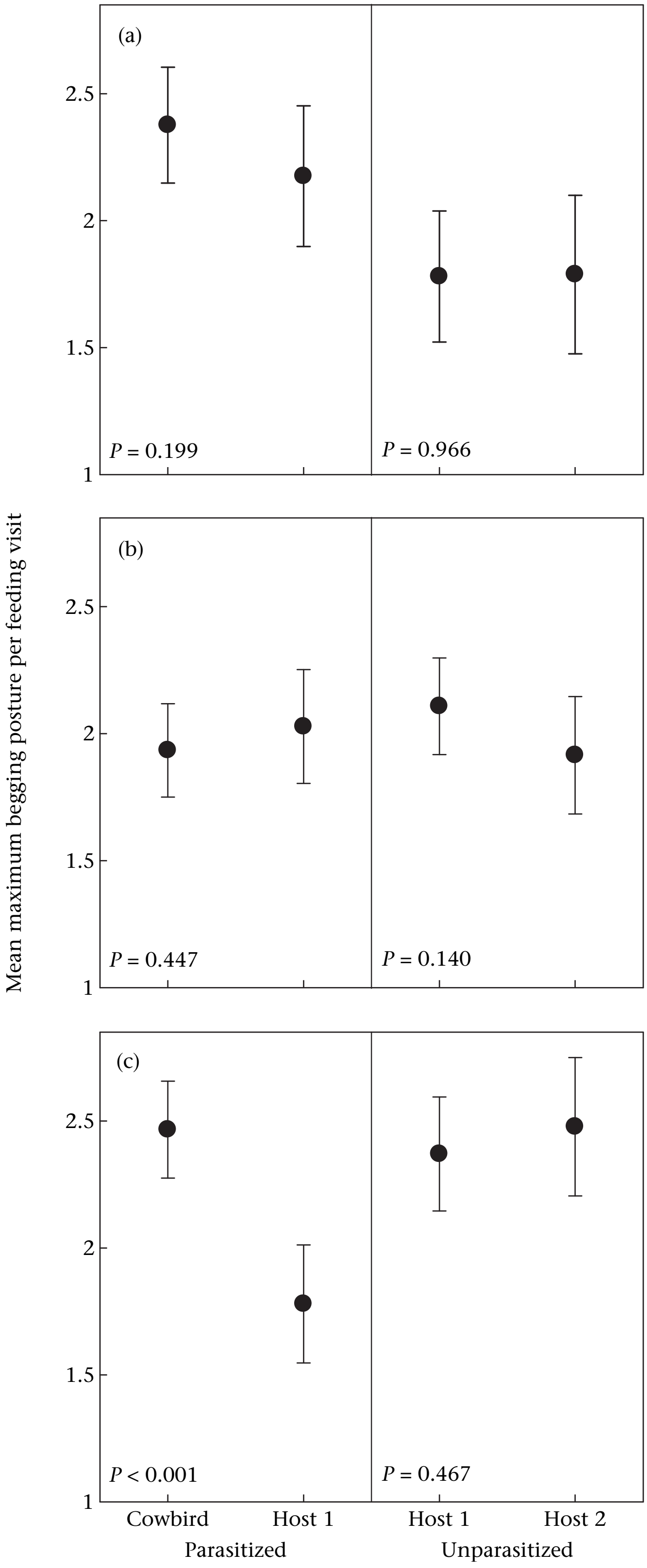

Figure 6. Mean (95% CI) maximum begging posture per feeding visit in (a) sparrow, (b) blackbird and (c) thrasher broods that contained a cowbird and a host nestling (parasitized) or two host nestlings (unparasitized). *P* values that test for mean differences between nestmates within each brood type (parasitized or unparasitized) for each host are given below interval estimates. *N* = 11–17 broods.

to greater begging effort for the small host, less for the large host, and no clear change in begging effort by the intermediate-sized host. This finding complements recent work with song sparrow, *Melospiza melodia*, nestlings, in which host begging call rate and structure changed markedly when hosts shared the nest with a cowbird (Pagnucco et al. 2008). Although we were unable to assess begging calls in our study, it is possible that the change in begging call rate and structure in the song sparrow may not be present in all cowbird hosts, particularly larger hosts like the thrasher, which reduce their begging when competing against a cowbird. Additional work on this topic is clearly warranted.

Why did the presence of a cowbird lead to variation in host begging behaviour in our study? One likely explanation is that the larger nestling in a brood (whether cowbird or host) received the majority of the food provisioned, and the smaller nestling, which received less food than it needed, responded by increasing its begging intensity. This suggests that the size difference between cowbird and host nestlings is the primary factor responsible for differences in the amount of food that nestlings receive, and that elevated begging intensity by a cowbird does not necessarily lead to more food being obtained if that individual competes against larger host nestmates (see Price & Ydenberg 1995). As previous work on this topic has been focused on small and intermediate-sized cowbird hosts (Dearborn et al. 1998; Lichtenstein & Sealy 1998; Glassey & Forbes 2003), our results suggest that the impact of a cowbird nestling on the behaviour of its broodmates varies relative to host size, and that this factor should be considered when assessing the impact of cowbird begging on host fitness. Given that elevated begging should increase host provisioning and that larger nestlings can outcompete cowbirds for food, it may even be that having a cowbird in a brood may provide benefits to large host nestlings if cowbirds stimulate host parents to increase their provisioning rates. A similar pattern has been described in the eastern phoebe, *Sayornis phoebe*, except that in that system the smaller host nestlings appear to stimulate host provisioning, which benefited the larger cowbird nestling (Kilner et al. 2004). However, as the laying of a cowbird egg in a host nest typically leads to a reduction in host fitness via egg removal, any benefits to an individual nestling of being reared with a cowbird must be contrasted against the costs of fewer siblings being produced in parasitized nests.

Our results with the cowbird provide an interesting contrast with recent work on the common cuckoo, *Cuculus canorus* (hereafter cuckoo), an evicting brood parasite that is typically raised alone (Davies 2000; but see Rutila et al. 2002). Cuckoo nestlings, despite being two to four times larger than host young for a given age, have reduced growth and lower fledgling rates when they are forced to share a nest with host young, even when the costs of evicting host young are experimentally removed (Martin-Galvez et al. 2005; Hauber & Moskat 2008; Grim et al. 2009). Given its larger size, it seems surprising that the cuckoo is not able to dominate smaller host nestmates when competing for food in a manner like the cowbird (Lichtenstein & Sealy 1998; Dearborn 1998; Rivers 2007). Instead of competition between nestmates, it may be that provisioning rules of parents are responsible for the reduced food intake of cuckoos reared with host nestlings, as at least one study has suggested that parents may favour their own offspring over cuckoo nestlings during feeding events (Martin-Galvez et al. 2005). Such a pattern of discrimination has been described for one large host of the shiny cowbird, *M. bonariensis*, but not for any hosts of the brown-headed cowbird examined to date (Dearborn 1998; Lichtenstein & Sealy 1998; Rivers 2007). Future research efforts should therefore focus on documenting why evicting cuckoos and the cowbirds differ in their ability to obtain food from host parents when they share the nest with host young.

In the present study, we found that having a cowbird in the brood can lead to clear changes in the behaviour of host nestlings, but not of parents, and that this effect depends on the size of the host nestling relative to the cowbird. Note, however, that these changes did not appear to be in response to the cowbird per se but instead were in response to asymmetries imposed by the cowbird in the hosts we studied. In other words, this finding appears to be the result of a common adjustment by host nestlings to the size of nestmates and not an evolved response to cowbird parasitism. Furthermore, we experimentally matched cowbirds and hosts of equal ages, thus removing the biologically important effect of early hatching by cowbird nestlings. Because cowbird incubation periods tend to be short relative to hosts (Briskie & Sealy 1990), our results may not be representative of how a cowbird would fare in host species with long incubation periods under natural conditions where hatching asynchronies occur. For example, cowbird nestlings might do better in thrasher nests than indicated by the results of our present study because cowbirds normally hatch several days before thrasher young, which may explain why cowbirds can successfully fledge from thrasher nests (Elliott 1978; Haas & Haas 1998; Cavitt & Haas 2000). Nevertheless, behavioural changes caused by cowbirds are likely to be costly to many cowbird hosts and this suggests that cowbird parasitism may have additional, subtle effects on host fitness that are additive to the costs that are typically considered for parasitized broods, such as host egg removal.

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