Original article

Donald C. Dearborn

Begging behavior and food acquisition by brown-headed cowbird nestlings

Abstract Understanding the selective forces that limit the exaggeration of begging signals is a critical issue in understanding the evolution of begging behavior. I studied the begging behavior of nestlings of the brown-headed cowbird (*Molothrus ater*), a brood parasite. In the nests of indigo buntings (*Passerina cyanea*), brown-headed cowbird nestlings received approximately twice as much food per hour than their host nestmates. I tested three hypotheses for the mechanism by which cowbirds acquired more food than their bunting nestmates: the size advantage hypothesis, the signal exaggeration hypothesis, and the novel begging behavior hypothesis. I found support for the hypotheses that cowbirds acquire more food as a result of their larger body size, and due to the exaggeration of begging signals that are not dependent on body size. I did not find support for the role of novel begging behaviors in cowbird food acquisition. These results suggest that food acquisition by host chicks in unparasitized nests could be increased by the exaggeration of begging signals. Recent work suggests that such exaggeration may be limited by the risk of nest predation, but further studies are needed.

Key words Begging behavior · Brood parasitism · *Molothrus ater* · Nestling behavior · *Passerina cyanea*

Introduction

The evolution of begging behavior has received substantial theoretical and empirical attention recently (re-viewed in Kilner and Johnstone 1997) because of its relevance to both communication theory and parent-offspring conflict. Common to both of these lines of inquiry is the importance of understanding the selective forces that limit begging signals. Many studies have shown that a nestling that produces a more exaggerated begging signal is more likely to receive food (e.g., Smith and Montgomerie 1991; Teather 1992; Price and Ydenberg 1995). If food acquisition affects fitness, selection should favor nestlings that produce exaggerated signals. However, there may be selective forces that limit the runaway exaggeration of signals, such as energetic constraints, risk of nest predation, or the inclusive fitness costs of either denying food to related nestmates or raising the cost of reproduction for the parents (MacNair and Parker 1979; Harper 1986; Motro 1989; Godfray 1995). Researchers have only recently begun to empirically address the question of how natural selection may limit the exaggeration of begging behavior (Haskell 1994; McCarty 1996).

Brood parasites offer an important opportunity to study the selective forces that shape begging behavior. The begging behavior of brood parasites can evolve unconstrained by inclusive fitness effects because brood-parasitic nestlings typically find themselves in a nest with, and being provisioned by, non-kin individuals. This unusual genetic environment could favor the evolution of exaggerated begging behavior (Dawkins 1989, pp. 131–133; Motro 1989) or novel begging behaviors.

Brown-headed cowbirds (*Molothrus ater*) are generalist brood parasites known to successfully parasitize 144 host species (Friedmann and Kiff 1985; Lowther 1993). The majority of these hosts are much smaller in adult body size than are brown-headed cowbirds, and cowbird nestlings attain a much greater body mass before fledging than do typical host chicks. Thus, it is possible that cowbird nestlings take advantage of their larger body size in obtaining food. By studying the role of body size, exaggerated begging signals, and novel begging behaviors in cowbird food acquisition, the mechanisms by

D.C. Dearborn (✉)
Division of Biological Sciences, 105 Tucker Hall,
University of Missouri, Columbia, MO 65211, USA
e-mail: ddearborn@biosci.mbp.missouri.edu, Fax: (614) 292-2030

Present address:
Department of Zoology, 1735 Neil Avenue,
The Ohio State University, Columbus, OH 43210, USA

which brood parasitic nestlings obtain food can be determined. This information can be used to gain insight into the evolutionary forces that shape begging behavior in general by considering why nestlings of nonparasitic species do not use these same mechanisms.

In this paper, I examine begging behavior and food acquisition by brown-headed cowbird nestlings in the nests of indigo buntings (*Passerina cyanea*), a typical, small-bodied host, and in the nests of northern cardinals (*Cardinalis cardinalis*), a species similar in size to brown-headed cowbirds. First, I quantify the distribution of food items among chicks in parasitized nests to determine whether cowbird nestlings receive greater amounts of food than do host nestlings. Second, I address three nonexclusive hypotheses for the mechanism by which cowbird nestlings acquire more food than do the nestlings of smaller hosts: (1) cowbirds are fed more due to direct or indirect effects of their larger body size (size advantage hypothesis), (2) cowbirds are fed more because they produce exaggerated versions of cues that are normally used by host parents in assessing the needs of host nestlings (cues that are not dependent on body size) (signal exaggeration hypothesis), and (3) cowbirds are fed more because they exhibit novel begging behaviors (novel begging behavior hypothesis).

I test five predictions of the size advantage hypothesis. First, in unparasitized indigo bunting nests the largest host chick should be fed more than the smallest host chick. Second, cowbirds should receive more food than their host nestmates in nests of the indigo bunting (a small host) but not in nests of the northern cardinal (a large host). Third, because the height that a chick reaches while begging may influence its probability of food acquisition (Smith and Montgomerie 1991; Teather 1992; Leonard and Horn 1996), and height is limited by a chick's size, cowbirds may be fed more because their larger size allows them to reach higher. Fourth, if a large bunting chick is transferred into an unparasitized nest of smaller bunting chicks, the large transferred chick should receive more food than each of the smaller chicks. Fifth, some studies have found that parents preferentially feed a certain location in the nest and that chicks compete for food by jockeying for this favored position (Kilner 1995). If this occurs in bunting nests, cowbirds may receive more food than buntings because their large size gives them an advantage in jockeying for the favored position.

I test four predictions of the signal exaggeration hypothesis. First, cowbirds may beg on a greater proportion of feeding trips or for more seconds per hour than buntings. Second, on any given trip, the allocation of food may be influenced by the order in which chicks start to beg when the parent arrives (Smith and Montgomerie 1991; Teather 1992; Leonard and Horn 1996). Thus, in addition to begging on more trips or for more total time, cowbirds may start begging earlier than host chicks on the occasions when they do beg. Third, parents may continue to assess nestling need after the delivery of a particular food item. If a chick continues to beg long

after the parent has given food to a different chick, the parent could incorporate that information into its decision about whom to feed on the subsequent trip. Fourth, chicks that direct their begging at the parent may be more likely to be fed, perhaps because they present a stronger stimulus or easier target than a chick that is facing away from the parent. If orienting toward the parent is related to development (e.g., the visual ability to locate and track the parent; Lee 1995), cowbirds may orient sooner or better than buntings.

I test two predictions of the novel begging behavior hypothesis. First, cowbirds should perform begging behaviors that are not performed by bunting chicks. Second, if a novel behavior is performed only on some occasions, cowbirds should be more likely to receive food on feeding trips when they perform the novel behavior.

Methods

Study species and field methods

I studied nestling behavior in parasitized and unparasitized nests of indigo buntings nesting in old-field and forest-edge habitat in central Missouri in 1995 and 1996. Indigo buntings are frequently used cowbird hosts and are typical hosts in terms of body size and taxonomy (Friedmann and Kiff 1985). At my study areas, buntings typically built nests 1–2 m high in shrubs. Modal brood size in parasitized and unparasitized nests was three, and within a nest, cowbird and bunting eggs almost always hatched on the same day. All parasitized nests used in this study were singly parasitized. Unparasitized nests were studied only during the portion of the breeding season when other nests were being parasitized by cowbirds.

I monitored nests and weighed chicks daily. In 1996, I recorded whether each chick begged during the course of handling and being weighed. On the morning of day 6 of the nestling period, I made 2-h video recordings of nestling behavior. Cameras were set up at a distance of 1.5–3 m from the nest, pointing down at approximately at 30° angle. Recordings were started between 0600 and 0730 hours CST. Chicks were individually marked on the top of the head with a black nontoxic marker. These marks were not visible to the parent when a chick's head was tilted back during begging. I made video recordings at 20 unparasitized and 9 parasitized 6-day-old indigo bunting nests.

To evaluate the role of cowbird body size in food acquisition, I also made video recordings at 6-day-old northern cardinal nests. Northern cardinals are also frequent cowbird hosts and are in the same subfamily as indigo buntings. However, northern cardinals are substantially larger than indigo buntings and slightly larger than brown-headed cowbirds (mean of male and female adult body mass: 14.5 g for indigo buntings, 44.6 for northern cardinals, and 43.9 g for brown-headed cowbirds; Dunning 1993). The nestling period of all three species is 9–10 days. I made video recordings at six unparasitized and three parasitized 6-day-old northern cardinal nests.

To further differentiate effects of body size and cowbird-specific behavior, I performed a nestling transfer experiment. I made video recordings at five unparasitized 2-day-old indigo bunting nests at which I exchanged on of the nestlings with a 6-day-old indigo bunting nestling. The mean mass of the transferred 6-day-old indigo bunting chicks was not different from that of 2-day-old cowbird chicks (7.24 ± 0.29 SE g, $n = 5$, for 6-day-old transferred buntings; 7.99 ± 0.38 g, $n = 14$, for 2-day-old cowbirds; $t = 1.13$, $df = 17$, $P = 0.274$). By placing a 6-day-old indigo bunting chick into a 2-day-old unparasitized bunting nest, I created a "brood parasite" that had the size advantage of a cowbird nestling but lacked any cowbird-specific behaviors. To conduct this

experiment, I removed one randomly-selected chick from an un-parasitized 2-day-old indigo bunting nest and replaced it with a 6-day-old indigo bunting chick from a different nest. I weighed and exchanged the nestlings at 0600 hours, waited 1.5 h for the parents and nestlings to adjust their behavior, and then began a 2-h video recording at 0730 hours. Several studies have made video recordings following the exchanges of nestlings among nests. Although most of these (Gottlander 1987; Smith and Montgomerie 1991; Kilner 1995; Price and Ydenberg 1995) have begun filming nestling behavior immediately after transferring nestlings, at least one study suggests that it may take 30 min following brood manipulation before parents resume normal feeding behavior (Bengtsson and Rydén 1983). Because chicks have been shown to adjust their begging in response to both hunger (Gottlander 1987; Smith and Montgomerie 1991; Kilner 1995; Price and Ydenberg 1995) and the behavior of their nestmates (Smith and Montgomerie 1991), I wanted to ensure that, when I began video recording, there had been enough time for both parents and nestlings to adjust their behavior in response to the presence of the large transferred nestling.

Following the video recording at transfer experiment nests, I weighed the chicks again and returned the transferred chicks to their original nests. Given that the remainder of my data pertain to 6-day-old nests, it would have been ideal to perform a similar manipulation in 6-day-old nests. However, 6-day-old cowbird nestlings are larger than adult indigo buntings; hence there are no indigo bunting chicks large enough to mimic the body size of a cowbird in a 6-day-old nest.

Video transcription

Based on video recordings from indigo bunting, northern cardinal, and transfer experiment nests, I quantified food acquisition by scoring the number and size of items fed to each chick in a nest. I scored the size of items by comparing the volume of the item to the volume of the parent's bill, using four size classes: 0.25, 1, 1.75, and 2.5 bill-equivalents. The feeding rate for a given chick was expressed as total bill-equivalents of food received per hour. I compared the food acquisition of cowbirds and their indigo bunting nestmates using a two-way factorial ANOVA with chick species as a fixed factor and nest as a random factor. This allowed the use of data from all chicks but controlled for differences among parents in their provisioning rates.

To test the three hypotheses about the mechanism by which cowbirds acquire food, I scored chicks for a variety of begging behaviors that theoretical or empirical considerations suggested might be related to the probability of food acquisition. On each feeding trip made by a parent, I ranked the nestlings on the order in which they began to beg and the order in which they stopped begging. When the parent was in the "aiming phase" (just prior to reaching forward to deliver food), I ranked the chicks on the height that they reached while begging. In the case of ties, chicks were assigned the mean of the ranks that they would have received had they not been tied (e.g., if the first and second chicks were tied, they would each receive a rank of 1.5). On each feeding trip, I assigned ranks only to chicks that begged on that particular trip. Because brood size and number of chicks begging per trip varied, I used standardized ranks in all analyses [standardized rank $= (\text{rank} - 1)/$ (number of chicks begging $- 1$)]. Standardized ranks range from 0 to 1.

On each feeding trip, I recorded the quadrant of the nest rim at which the parent arrived and the sector of the nest (front, center, back, left, right) occupied by each chick. I also recorded the total time that each chick begged and whether each chick oriented toward the parent when begging. Finally, I recorded the size of the food item and which chick received it. In indigo bunting nests, parents brought a single item on 98.9% of trips (531 of 537). On the six trips in which parents brought multiple items, I used the height rank data for the feeding of the first chick only. However, I included all food items when quantifying the amount of food acquired by nestlings.

Statistical tests of the size advantage hypothesis

To test the first prediction of that size advantage hypothesis, that large buntings should be fed more than their smaller bunting nestmates, I used a paired t-test to compare the rate of food acquisition (bill-equivalents per hour) of the heaviest and the lightest bunting chick in each unparasitized 6-day-old nest.

The second prediction of the size advantage hypothesis is that cowbirds should not receive more food than host chicks in nests of the northern cardinal, a large host species. I compared cowbirds to their cardinal nestmates using a two-way factorial ANOVA as described earlier for bunting nests.

The third prediction is that cowbirds may be fed more because their larger size enables them to reach higher while begging. In testing this prediction and several others to follow, I first tested whether the particular behavior was correlated with food acquisition in unparasitized bunting nests. If so, I then examined parasitized nests to test whether cowbirds consistently received greater scores on that behavior than did their bunting nestmates. In unparasitized nests, I compared the mean height rank of fed chicks to the mean height rank of unfed chicks (but excluding chicks when they did not beg at all) using a Wilcoxon paired rank sum test in which each nest contributed a single pair of data points (sensu Smith and Montgomerie 1991). For each nest, I subtracted the mean rank of unfed chicks from the mean rank of fed chicks and used the Wilcoxon test to test the null hypothesis that the median of the difference scores from all unparasitized nests was zero (Zar 1996). I then used data from parasitized nests to compare the mean height rank of cowbirds to the mean height rank of their bunting nestmates. I used a Wilcoxon paired rank sum test for this analysis also.

The fourth prediction involves food acquisition by chicks in the nestling transfer experiment. In 2-day-old bunting nests in which I performed nestling transfers, the 6-day-old transferred chicks should receive more food (bill-equivalents per hour) than normal 2-day-old host chicks but the same amount of food 2-day-old cowbird chicks. I compared transferred chicks to their host nestmates using a 2-way factorial ANOVA with chick type as a fixed factor and nest as a random factor. I compared 2-day-old cowbird chicks to their 2-day-old bunting nestmates in the same manner. I compared transferred chicks and 2-day-old cowbird chicks using an independent samples t-test.

The final prediction of the size advantage hypothesis is that cowbirds' larger size may enable them to jockey for a location that is preferentially fed by the adults. First, I tested the critical assumption that parents are consistent in their arrival locations. Because it is important only that each set of parents is consistent, I performed a separate chi-square test for each nest, testing the null hypothesis that parents arrive at each quadrant of the nest rim with equal frequency. I used the sequential Bonferroni method to adjust alpha for a family-wide alpha of 0.05 (Rice 1989). I then tested whether parents at unparasitized nests preferentially feed a given location. I used a chi-square contingency table to test the null hypothesis that the number of times a spot is fed or not fed does not vary with location (front, center, back, left, right). Because brood size ranged from one to four, not all locations in the nest could be simultaneously occupied. Thus, I only included a location as "not fed" on a particular trip if it was occupied by a begging chick. I analyzed each nest separately, employing a sequential Bonferroni adjustment of alpha (Rice 1989). I then performed a heterogeneity analysis (Zar 1996) to determine if I could pool data across nests. Because the null hypothesis of homogeneity was not rejected (heterogeneity $\chi^2 = 41.914$, $df = 44$, $0.75 > P > 0.50$), I pooled data from all nests and analyzed them together using a chi-square test. For the pooled data, I rejected the null hypothesis that all locations are fed equally (see Results). As a follow-up analysis to determine the source of the significant χ^2 (Zar 1996), I discarded the data from the two locations that showed the greatest departure from expected values (center and back) and tested for a difference among the remaining three locations. Because I did not detect a difference between these locations (front, left, right; $\chi^2 = 0.229$, $df = 2$, $P = 0.892$), I pooled them to test them against the center and back locations. Next, I examined parasitized bunting nests to

determine if cowbirds occupied the favored central position more than did their bunting nestmates. I used a paired *t*-test to compare the proportion of trips on which the cowbird was in the center location to the proportion of trips on which a bunting was in the center (adjusted for the number of buntings in the nest). Finally, for both parasitized and unparasitized nests, I quantified the proportion of trips on which each sector of the nest was occupied.

Statistical tests of the signal exaggeration hypothesis

The first prediction of the signal exaggeration hypothesis is that cowbirds should beg more often than their indigo bunting nestmates. In parasitized bunting nests, I measured the proportion of feeding trips on which each chick begged. I compared cowbirds and the mean of their bunting nestmates using a *t*-test with the prediction that cowbirds would beg on more trips. Next, I examined the total number of seconds that chicks spent begging per hour. I compared cowbirds and their bunting nestmates using a two-way factorial ANOVA with chick species as a fixed factor and nest as a random factor.

The second prediction of the signal exaggeration hypothesis is that cowbirds may be fed more because they start begging sooner than their bunting nestmates. I used a Wilcoxon paired rank sum test to compare the start rank of fed and unfed chicks in unparasitized bunting nests. Next, I compared the mean start rank of cowbirds and the mean of their bunting nestmates. In this second analysis, I used a paired *t*-test instead of a Wilcoxon test because the difference scores were normally distributed. If cowbirds beg sooner than do host chicks, it may be because they are less particular about the stimuli that elicit begging. To test this, I compared cowbirds and their bunting nestmates on the proportion of days that a chick begged from me while I was weighing it. I tested the null hypothesis that cowbirds did not differ from the mean of their bunting nestmates in the proportion of days that a chick begged while being weighed. Difference scores were normally distributed and were analyzed with a paired *t*-test. As before, for rank scores (e.g., order in which chicks start to beg) I did not assign a rank to chicks on trips in which they did not beg.

The third prediction is that cowbirds may be fed more because they stop begging later than their bunting nestmates. In unparasitized bunting nests, I used a Wilcoxon paired rank sum test to compare fed and unfed chicks on the rank order in which they stopped begging on the previous trip. Next, I compared the mean finish rank order of cowbirds and their bunting nestmates. For this analysis I used a paired *t*-test because the difference scores were normally distributed. It is possible that the motivation of a hungry chick carries over from one trip to the next such that a chick that stops begging last on one trip starts begging first or reaches the highest on the subsequent trip. If parents allocate food based on start order or height, a correlation of these behaviors with the order in which chicks stopped begging on the previous trip could give the impression that parents incorporate information from one trip into their decisions about food allocation on the next trip. To test for a correlation of stop rank and start or height rank, I performed two types of Spearman rank correlations for indigo buntings in unparasitized nests: the first compared the standardized rank scores for the cessation of begging on one trip and the start of begging on the subsequent trip, and the second compared the standardized rank scores for the cessation of begging on one trip and the height of begging on the subsequent trip. To avoid spurious correlations that might result from differences among nestlings in average ranks, I performed separate analyses for each chick for which I had at least ten data points (i.e., individuals who begged on at least ten pairs of sequential feeding trips). For all results with positive correlation coefficients, I used Fisher's method (Sokal and Rohlf 1995) to combine *P*-values for an overall test. I repeated this process for all results with negative correlation coefficients.

The final prediction of the signal exaggeration hypothesis is that cowbirds may be fed more because they are more likely to orient their begging towards the provisioning adult. For unparasitized bunting nests, I used a paired *t*-test to compare fed and unfed chicks on the proportion of trips during which they oriented while begging. I then compared cowbirds and their bunting nestmates in the same fashion. For both comparisons, I used *t*-tests because the difference scores were normally distributed.

Statistical tests of the novel begging behavior hypothesis

The first prediction of this hypothesis is that cowbirds perform novel begging behaviors. When transcribing tapes, I recorded any cowbird behaviors that were not exhibited by buntings.

The second prediction of this hypothesis is that the performance of novel begging behavior increases the probability of food acquisition: For each parasitized nest, I used a chi-square contingency table to test whether cowbirds were more likely to be fed on trips during which they exhibited a novel behavior while begging. After I analyzed each nest separately, I performed a heterogeneity analysis (Zar 1996) to determine whether I could pool data across nests. Because the null hypothesis of homogeneity was not rejected (heterogeneity $\chi^2 = 0.098$, $df = 1$, $P > 0.75$), I pooled data from all nests and analyzed them together using a chi-square test. Because I did not detect an effect of novel begging behavior (wing-fluttering while begging) on the probability of food acquisition and because sample sizes were small, I performed a post-hoc power analysis using G · Power (Buchner et al. 1996). I calculated an effect size for the chi-square contingency table by using the row and column probabilities (i.e., the overall probability of being fed and the overall frequency of wing-fluttering) from the videotape data. Under the null hypothesis these two factors are independent; under the alternate hypothesis, I specified that wing fluttering would cause a 50% increase in the probability of the cowbird being fed. This gives an estimated effect size of $w = 0.218$, a value slightly smaller than the medium effect size of Cohen (1988) of $w = 0.30$.

I used SAS (SAS Institute 1989) for all statistical analyses. Critical assumptions were met for all statistical tests. All tests are two-tailed. For single degree of freedom chi-square tests, I used Yates' continuity correction as recommended by Zar (1996). To conduct an overall test of hypotheses based on multiple statistical analyses (i.e., the size advantage and signal exaggeration hypotheses), I used Fisher's method to combine *P*-values from multiple tests (Sokal and Rohlf 1995). In these analyses, I used only those statistical tests that were directly informative about the hypothesis of interest. For example, one aspect of the signal exaggeration hypothesis predicts that orienting while begging may affect food acquisition in unparasitized nests and that cowbirds may orient more often than their bunting nestmates. In the combined Fisher analysis, I included the *P*-value for the second part of this prediction but not the first part.

Results

Cowbirds received significantly more food than their indigo bunting nestmates (6.01 ± 0.25 SE bill-equivalents per hour for cowbirds, 2.81 ± 0.20 for buntings; ANOVA: $F_{1,6} = 16.59$, $P = 0.006$; Fig. 1). I tested three hypothesized mechanisms underlying cowbirds' food acquisition. For each of the three hypotheses, the predictions and evidence are summarized in Table 1.

Size advantage hypothesis

Prediction 1

Within unparasitized bunting nests, the heaviest chick was not fed more than the lightest chick (paired *t*-test: $t = -0.310$, $P = 0.765$, $n = 9$ nests).
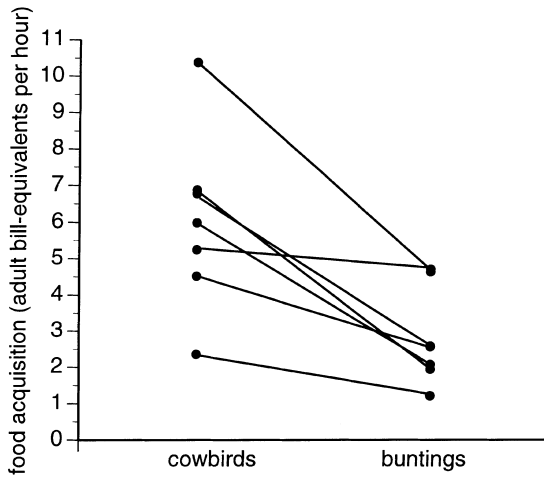
Fig. 1 Food acquisition by cowbirds and their indigo bunting nestmates. *Lines* connect the value for each cowbird with the mean value for its bunting nestmates. Cowbirds received significantly more food than buntings in parasitized nests (ANOVA: $F_{1,6} = 16.59$, $P = 0.006$)

Prediction 2

Although cowbirds in bunting nests received more food than host chicks, cowbirds in cardinal nests did not differ from host chicks in food acquisition (3.58 ± 1.06 cardinal-bill-equivalents for cowbirds, 3.10 ± 0.97 for cardinals; ANOVA: $F_{1,2} = 0.23$, $P = 0.675$).
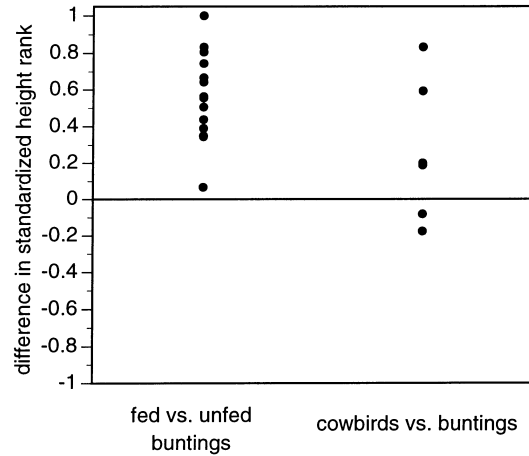

Fig. 2 Comparisons of the rank order of nestling height during begging in 6-day-old indigo bunting nests. Standardized ranks range from 0 to 1 and account for variation in brood size. The *left side* compares the begging height rank of fed and unfed bunting nestlings in unparasitized nests. The *right side* compares the begging height rank of cowbirds and their bunting nestmates. Fed buntings differed from unfed buntings (Wilcoxon paired rank sum test: $S = 76.5$, $P = 0.0001$, $n = 17$ nests), but cowbirds did not differ from their bunting nestmates ($S = 7.5$, $P = 0.156$, $n = 6$ nests)

Prediction 3

In unparasitized bunting nests, chicks that reached higher were more likely to be fed (median difference in ranks $= 0.563$; Wilcoxon paired rank sum test: $S = 76.5$, $P = 0.0001$, $n = 17$ nests; Fig. 2). However,

Table 1 Summary of predictions and evidence for the three hypotheses to explain the mechanism by which brown-headed cowbird nestlings acquire more food than their indigo bunting nestmates. Evidence is categorized as *Yes*** if the *P*-value from the relevant test was less than 0.01, *Yes** if $P < 0.05$, *trend* if $P < 0.1$, and *No* if $P > 0.1$

Size advantage hypothesis (overall $P = 0.00325$)	Evidence
1. In unparasitized indigo bunting nests, larger chicks should be fed more than small chicks.	No
2. Cowbirds should receive more food than host chicks in indigo bunting nests but not in northern cardinal nests.	Yes**
3. In unparasitized bunting nests, chicks that reach higher should be more likely to receive food.	Yes**
Cowbirds should reach higher than bunting nestmates.	No
4. In 2-day-old bunting nests, experimentally transferred bunting chicks should receive more food than host chicks and the same amount as cowbird chicks.	Yes**
5. If parents preferentially feed a location within the nest, cowbirds should occupy that location more frequently than host chicks.	Yes*
	Trend
Signal exaggeration hypothesis (overall $P < 0.00001$)	Evidence
1. Cowbirds should beg on a greater proportion of feeding trips and for more seconds per hour than do their bunting nestmates.	Yes*
	Yes**
2. In unparasitized nests, chicks that begin to beg sooner should be more likely to receive food.	Yes**
Cowbird should begin begging sooner than bunting nestmates.	Yes**
Mechanism: cowbirds beg in response to wider range of stimuli.	Yes**
3. In unparasitized nests, chicks that stop begging last should be more likely to receive food on subsequent trip.	Yes*
Cowbirds should stop begging later than do their bunting nestmates.	Yes**
4. In unparasitized nests, chicks that orient to parent when begging should be more likely to receive food.	Yes**
Cowbirds should orient more often than do their bunting nestmates.	No
Novel begging behavior hypothesis	Evidence
1. Cowbirds should exhibit behavior(s) not seen in host chicks.	Yes
2. If this behavior is performed only on some occasions, cowbirds should be more likely to receive food on trips when they perform this behavior.	No

in parasitized bunting nests, cowbirds did not reach higher than their nestmates (median difference in ranks = 0.194; Wilcoxon paired rank sum test: $S = 7.5$, $P = 0.156$, $n = 6$; Fig. 2).

Prediction 4

In transfer experiment nests, transferred bunting chicks were fed significantly more than 2-day-old host chicks (6.04 ± 0.18 for transferred chicks, 1.50 ± 0.13 for host chicks; ANOVA: $F_{1,4} = 62.78$, $P = 0.001$), and transferred bunting chicks did not differ from 2-day-old cowbirds in food acquisition (6.04 ± 0.18 for transferred chicks, 4.19 ± 1.06 for cowbirds; t-test: $t_7 = -1.75$, $P = 0.124$). There was a tendency for cowbirds to be fed more than their 2-day-old host nestmates (4.19 ± 1.06 for cowbirds, 1.42 ± 0.29 for host chicks; ANOVA: $F_{1,3} = 6.00$, $P = 0.091$).

Prediction 5

At 25 of 26 nests, parents arrived consistently at certain quadrants of the nest rim (for 25 of 26 nests, $\chi^2 \geq 14.67$, $df = 3$, family-wide $P < 0.05$). Parents arrived at the most frequently used arrival location on a median of 95.9% of trips and at the second most frequently used arrival location on a median of 4.1% of trips. In separate analyses of each nest, there was only one nest with a significant relationship between location and frequency of feeding. However, nests were not heterogeneous (heterogeneity $\chi^2 = 41.914$, $df = 44$, $0.75 > P > 0.50$),
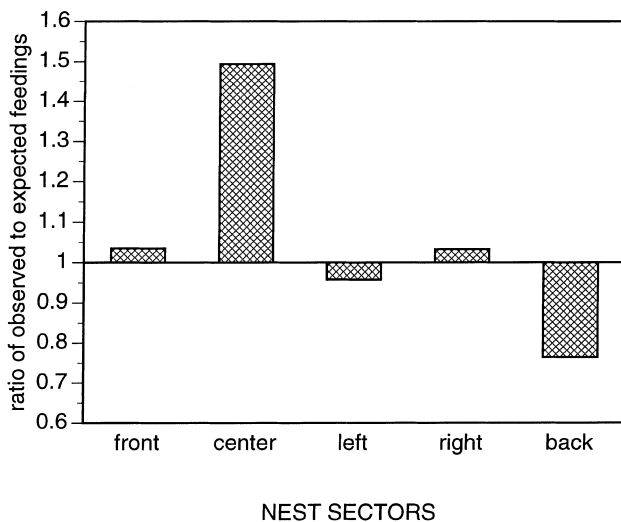

Fig. 3 Ratio of observed to expected number of feedings to each of five sectors within 6-day-old unparasitized indigo bunting nests. Expected number of feedings was calculated based on number of feeding trips made and number of trips on which each location was occupied by a begging chick. The center location was fed more often than expected, and the back location was fed less often than expected ($\chi^2 = 9.976$, $df = 4$, $P = 0.041$)

so I pooled data across nests for an overall test. This test was significant ($\chi^2 = 9.976$, $df = 4$, $P = 0.041$). The locations "back" and "center" showed the largest departure from expected values (Fig. 3). Follow-up analyses found no difference between feeding frequencies at the other three locations ($\chi^2 = 0.229$, $df = 2$, $P = 0.892$) but a strong effect when comparing back versus center versus the remaining locations pooled ($\chi^2 = 9.746$, $df = 2$, $P = 0.008$). This confirms that the significance of the original overall chi-square analysis was due to the high frequency with which the center location was fed and the low frequency with which the back location was fed. In parasitized nests, there was a trend for cowbirds to occupy the center position more often than the mean of their bunting nestmates (mean difference = 0.276; paired t-test: $t = 2.09$, $P = 0.0812$, $n = 7$ nests). However, the central position was not always occupied: in parasitized nests, the center position was occupied on only 35.3% of feeding trips.

Overall, the tests of the five predictions provided strong support for the size advantage hypothesis (Fisher's combined analysis: $\chi^2 = 23.09$, $df = 8$, $P = 0.003$).

Signal exaggeration hypothesis

Prediction 1

In parasitized nests, cowbirds begged on a greater proportion of trips than did their bunting nestmates (paired t-test: $t = -2.64$, $P = 0.034$, $n = 8$ nests). Cowbirds also spent more time per hour begging than did their bunting nestmates (ANOVA; $F_{1,6} = 38.40$, $P = 0.0007$).

Prediction 2

In unparasitized nests, chicks that started to beg sooner were more likely to be fed (median difference in ranks = 0.238; Wilcoxon paired rank sum test: $S = 75.5$, $P = 0.0001$, $n = 17$ nests; Fig. 4). In parasitized nests, cowbirds started begging much sooner than buntings (mean difference in ranks = 0.708; paired t-test: $t = 7.56$, $P = 0.0006$, $n = 6$ nests; Fig. 4). Cowbirds begged while being weighed on 71.4% of days, whereas buntings in parasitized nests begged while being weighed on only 10.0% of days (paired t-test: $t = 4.19$, $P = 0.0042$, $n = 6$ nests).

Prediction 3

In unparasitized bunting nests, chicks that stopped begging later were more likely to be fed on the subsequent trip (median difference in ranks = 0.07; Wilcoxon paired rank sum test: $S = 36$, $P = 0.042$, $n = 17$ nests; Fig. 5). In parasitized nests, cowbirds stopped begging later than did their bunting nestmates (mean

difference in ranks = 0.26; paired *t*-test: $t = 5.07$, $P = 0.004$, $n = 6$ nests; Fig. 5). The Spearman correlation coefficients for stop order on one trip and start order on the next trip ranged from $r = -0.283$ to $r = 0.705$, based on data from 20 chicks. Fisher's overall test for significance of the 6 negative correlations was not significant ($\chi^2 = 6.218$, $df = 12$, $P = 0.904$), nor was it significant for the 14 positive correlations
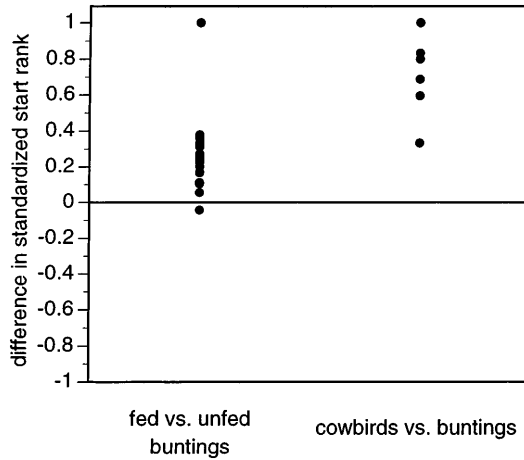

Fig. 4 Comparisons of begging start rank in 6-day-old nests. Standardized ranks range from 0 to 1 and account for variation in brood size. The *left side* compares the start rank of fed and unfed bunting nestlings in unparasitized nests. The *right side* compares the start rank of cowbirds and their bunting nestmates. Fed buntings differed from unfed buntings (Wilcoxon paired rank sum test: $S = 75.5$, $P = 0.0001$, $n = 17$ nests), and cowbirds differed from their bunting nestmates (paired *t*-test: $t = 7.56$, $P = 0.0006$, $n = 6$ nests)
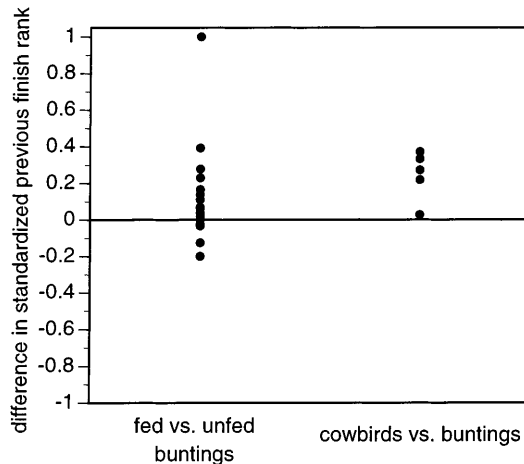

Fig. 5 Comparisons of begging finish rank in 6-day-old nests. Standardized ranks range from 0 to 1 and account for variation in brood size. The *left side* portrays the begging finish rank during the previous feeding trip for fed and unfed bunting nestlings in unparasitized nests. The *right side* compares the begging finish rank for cowbirds and their bunting nestmates. Fed buntings differed from unfed buntings (Wilcoxon paired rank sum test: $S = 36.0$, $P = 0.042$, $n = 17$ nests), and cowbirds differed from their bunting nestmates (paired *t*-test: $t = 5.07$, $P = 0.004$, $n = 6$ nests)
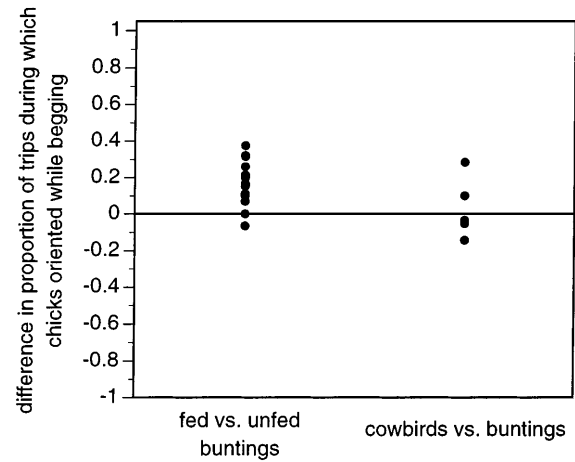

Fig. 6 Comparisons of the proportion of feeding trips during which 6-day-old chicks oriented to the parent while begging. The *left side* portrays the difference between fed and unfed bunting nestlings in unparasitized nests. The *right side* portrays the difference between cowbird nestlings and their bunting nestmates. Fed buntings differed from unfed buntings (paired *t*-test: $t = 5.24$, $P = 0.0001$, $n = 16$ nests), but cowbirds did not differ from their bunting nestmates ($t = 0.69$, $P = 0.521$, $n = 6$ nests)

($\chi^2 = 36.906$, $df = 28$, $P = 0.121$). The Spearman correlation coefficients for stop order on one trip and height on the next trip ranged from $r = -0.757$ to $r = 0.765$, based on data from 18 chicks. Fisher's overall test for significance of the 7 negative correlations was not significant $\chi^2 = 11.113$, $df = 14$, $P = 0.677$), but it was significant for the 11 positive correlations ($\chi^2 = 40.102$, $df = 22$, $P = 0.011$).

Prediction 4

In unparasitized bunting nests, chicks that oriented were more likely to be fed (mean difference between fed and unfed chicks in the proportion of trips when chicks oriented while begging = 0.163; paired *t*-test: $t = 5.24$, $P = 0.0001$, $n = 16$ nests; Fig. 6). However, cowbirds did not differ from their bunting nestmates in the proportion of begging trips during which chicks oriented while begging (mean difference in proportions = 0.043; paired *t*-test: $t = 0.689$, $P = 0.521$, $n = 6$ nests; Fig. 6).

Overall, the tests of the four predictions provided support for the signal exaggeration hypothesis (Fisher's combined analysis: $\chi^2 = 59.42$, $df = 10$, $P < 0.00001$).

Novel begging behavior hypothesis

Prediction 1

Three of nine (33.3%) 6-day-old cowbirds in indigo bunting nests occasionally fluttered their wings while begging (on 15.7%, 17.1%, and 23.3% of feeding trips). No buntings ever fluttered their wings while begging.

Prediction 2

The cowbird that wing-fluttered most frequently was the sole occupant of its nest and was therefore fed on each trip. Of the other two cowbirds, one was fed on 2 of 3 (66.7%) fluttering trips and 8 of 16 (50.0%) non-fluttering trips, and the other was fed on 3 of 6 (50.0%) fluttering trips and 13 of 29 (44.8%) non-fluttering trips. For each of these cowbirds there was no significant association between wing fluttering and the probability of being fed (for each nest, $\chi^2_{Yates} = 0$, $df = 1$, $P = 1$). Data from these two nests were not heterogeneous (heterogeneity $\chi^2 = 0.098$, $df = 1$, $P > 0.75$) and were therefore pooled for combined analysis. This analysis detected no association between fluttering and the likelihood of being fed ($\chi^2_{Yates} = 0.015$, $P = 0.903$). Power to detect a 50% increase in the probability of being fed when fluttering (compared to when not fluttering) was fairly low ($1 - \beta = 0.158$ and $1 - \beta = 0.252$ for the two cowbirds individually, and $1 - \beta = 0.361$ for the combined analysis).

Discussion

Food acquisition by cowbird nestlings

Cowbird nestlings received more than twice as much food per hour as their indigo bunting nestmates. Soler et al. (1995) found a similar discrepancy in the amount of food acquired by nestlings of the brood-parasitic great spotted cuckoo (*Clamator glandarius*) and their magpie (*Pica pica*) nestmates. Such an inequality in food distribution allows for the comparison of begging behaviors between a brood parasitic species and a non-parasitic species.

The first hypothesis explaining the inequitable allocation of food, that cowbirds receive more food as a direct or indirect result of their larger size, was generally supported. In unparasitized bunting nests, larger bunting chicks did not receive more food than did smaller chicks. However, indigo buntings hatch relatively synchronously, and the size difference among chicks in a nest is fairly small (mean difference between heaviest and lightest 6-day-old bunting nestmates = 1.19 ± 0.12 g, $n = 32$). If size directly or indirectly affects food acquisition, it is possible that the size difference between bunting nestmates is too small to be important, whereas the size discrepancy between a cowbird and its bunting nestmates (difference in 6-day-old mass = 13.51 ± 0.86 g, $n = 8$) is large enough to affect food distribution.

Cowbirds received more food than their nestmates in nests of the indigo bunting, a small host. They did not receive more food than did host chicks in nests of the northern cardinal, a large host. The cowbirds' failure to receive more food than did host chicks in cardinal nests may be because cowbirds lack a size advantage in this situation. However, this difference in relative food acquisition of cowbirds in the two hosts' nests may also be due to differences between the hosts that are not related to body size. For example, adult buntings and adult cardinals might differ in the hierarchy of cues that they use to assess nestling need.

In unparasitized nests, chicks that reached higher when begging were more likely to receive food. The height that a bunting chick reaches up when begging probably depends in part on motivation (i.e., hunger), as has been demonstrated experimentally in other species (Smith and Montgomerie 1991; Kacelnik et al. 1995), but body size determines an upper limit for the height that a chick can reach. Although cowbird nestlings are larger than their indigo bunting nestmates, I did not detect a corresponding difference in height reached while begging.

The results of the nestling transfer experiment support the size advantage hypothesis. In 2-day-old bunting nests, the 6-day-old transferred chicks received more food than their 2-day-old host nestmates, and they did not receive a significantly different amount of food than did 2-day-old cowbirds. In addition to being larger than the 2-day-old host chicks, the transferred chicks were more developed and they oriented more frequently while begging – none of the 2-day-old bunting chicks ever oriented to the feeding adult, whereas the transferred chicks oriented on an average of 37.6% of feeding trips. Thus, the transferred chicks may have received more food than their nestmates due to a combination of their larger size and their advanced developmental stage.

The final evidence for the size advantage hypothesis relates to the parents' location bias in food distribution. Indigo bunting parents preferentially fed the center location in unparasitized nests, and cowbird nestlings tended to occupy this position more often than bunting nestlings in unparasitized nests. Jockeying for position and other types of physical competition among nestmates have recently been hypothesized to be an important step in the evolution of begging behavior from an original non-signaling condition (Rodriguez-Girones et al. 1996). One important component of this argument is that parents may be "forced" to accept the outcome of these contests (Kacelnik et al. 1995). This lack of choice on the part of the provisioning adult is most plausible if parents are physically prevented from feeding any chick other than the winner of the contest. Such an outcome is conceivable in the case of cavity- or box-nesting birds, in which chicks may compete to occupy the sector of the nest closest to the entrance hole, and indeed most studies that have supported the importance of jockeying for position have been of box-nesting birds (Kilner 1995; but see McRae et al. 1993). For indigo buntings in the current study, the importance of the link between nestling location and food acquisition is called into question by the low frequency with which the central position was occupied. Although this position was occupied more often in parasitized nests than in unparasitized nests, it was still vacant on 65% of feeding trips. This is not consistent with the hypothesis that nestlings are com-

peting to occupy this location. Hence, this piece of support for the size advantage hypothesis is weak.

The second hypothesis, that cowbirds receive more food due to the production of exaggerated signals that are not related to body size, was strongly supported. First, cowbirds begged on a greater proportion of trips and for more seconds per hour than did their bunting nestmates. Because a chick must beg (open its mouth to gape) in order to be fed, cowbirds are making themselves available as potential food recipients more often than are buntings.

In unparasitized nests, chicks that started begging sooner were much more likely to be fed; in parasitized nests, cowbirds almost always began begging before their bunting nestmates. Thus, in addition to begging on more trips, cowbirds start to beg sooner than their nestmates on the feeding trips in which both types of nestmates beg at all. This appears to be because cowbirds are more flexible in the stimuli to which they respond with begging. Cowbirds begged while being weighed much more frequently than did their bunting nestmates, and cowbirds seemed to beg from a broader range of stimuli while in the nest as well. On a typical feeding trip at a bunting nest, the parent would land in the vegetation near the nest prior to hopping or flying a very short distance to the nest rim. The landing of the parent would usually vibrate the nest and/or the surrounding vegetation. The cowbird chicks generally began begging at this initial stimulus, while the bunting chicks usually did not beg until the parent had landed on the rim of the nest. Thus, when the parent arrived at the nest, the cowbird was already begging but the bunting chicks were not. One consequence of this rapid response by cowbirds was that cowbirds sometimes begged in response to vegetation movement caused by wind or rain. This behavior may have energetic or predation-risk costs. However, given the wide range of host species' nests in which a cowbird chick could find itself (144 "good" hosts; Friedmann and Kiff 1985), it is conceivable that begging in response to a wide range of stimuli is adaptive. This indiscriminant begging by parasitic nestlings has been noted previously in both the brown-headed cowbird (Friedmann 1929) and the shiny cowbird (*Molothrus bonariensis*; Gochfeld 1979), another generalist brood parasite.

In addition to starting to beg sooner than their bunting nestmates, cowbirds generally stopped begging later. In unparasitized nests, chicks that stopped begging later on a given trip were more likely to be fed on the subsequent trip. This could be because parents continue to assess nestling need after they have distributed a food item, and this post-feeding assessment influences food distribution on the next trip. Previous studies of begging behavior have not tested for this "carryover" of information from one trip to the next. However, in order for parents to distribute food in relation to information received on a previous trip, parents would need to either be able to identify and remember individual chicks or, if chicks do not change positions frequently, be able to

remember information about begging and associate it with a particular location within the nest. An alternate explanation is that chicks that are highly motivated (i.e., hungry) continue begging if not fed, and then, on the following trip, produce stronger begging signals that result in food acquisition. I tested this explanation with the correlation analyses: for some chicks, begging late on one trip was indeed correlated with begging early or reaching high on the next trip. However, many correlation coefficients were negative and the overall tests were equivocal. These two alternative explanations (carryover of information by parents or continued motivation by nestlings) could best be tested in a species in which adult males provision offspring frequently (unlike indigo buntings at my sites, where only 5% of feeding trips are made by males). This would provide the opportunity to compare nestling behavior and parental food allocation when sequential feeding trips are made by different adults.

Finally, I found that buntings in unparasitized nests were more likely to receive food on trips when they oriented toward the parent (i.e., turned to face the parent) while begging. If a chick did not orient, it generally begged in the direction that it was facing before the parent arrived or it faced straight upwards while begging. Cowbirds did not orient more often than did indigo buntings in parasitized nests. Recent work on nestling development in red-winged blackbirds (*Agelaius phoeniceus*) suggests that day 6 is the approximate age at which those nestlings gain the ability to accommodate and focus past the tips of their own bills (A. Clark, unpublished work). If cowbird nestlings develop faster than host nestlings, the difference between cowbirds and hosts in orientation behavior might be more pronounced on day 5 of the nestling period than on day 6, the day studied here.

The third hypothesis, that cowbirds receive food as a result of novel behavior, was not supported. Three of nine cowbirds sometimes exhibited wing fluttering while begging This behavior was observed occasionally in a cowbird nestling handreared by Nice (1939) and in cowbird fledglings studied by Woodward (1983). Nestlings of the red-winged blackbird, a non-parasitic species that is closely related to cowbirds, performed wing flapping on 6 of 371 (1.6%) feeding trips (Lee 1995). The wing fluttering movement seemed to make the cowbird nestlings in my study more visible compared to their nestmates. Wing fluttering had no detectable effect on the probability of food acquisition, but power to detect such an effect was fairly low.

There are two potentially important determinants of food acquisition that I could not address in this study. I could not assess the effect of nestling vocalizations on food acquisition because I could not consistently assign begging calls to individual chicks during transcription of the videotapes. Several studies have demonstrated the importance of begging vocalizations in determining the rate of food delivery or food distribution (Bengtsson and Rydén 1983; Stamps et al. 1985; Price and Ydenberg

1995; Weary and Fraser 1995), and such vocal signals may be important in the species that I studied. I also could not measure gape size from the videotapes. Cowbird gapes are substantially larger than indigo bunting gapes (Payne 1991; Lowther 1993; D.C. Dearborn, personal observations) and could serve as a stronger stimulus to the parent (Clark 1995).

I found support for two of the three hypothesized mechanisms for cowbirds' high rate of food acquisition. Cowbirds acquire more food than buntings apparently in part because their larger size provides a stronger stimulus or perhaps facilitates the use of certain competitive mechanisms such as jockeying for the central position. Cowbirds also receive more food because they are more effective at displaying several important cues that are independent of body size, including begging on more trips, starting begging sooner, and stopping begging later. Novel behaviors do not seem to be responsible for food acquisition by cowbirds. Instead, cowbirds consistently outperformed buntings on several aspects of "normal" begging behavior. These results are similar to those found for great spotted cuckoo nestlings, which appear to acquire large amounts of food due to a combination of their larger body size (Soler et al. 1995) and exaggerated begging behavior (Redondo 1993).

Limits on begging by non-parasitic nestlings

If parasitic nestlings can increase their food acquisition by producing exaggerated begging signals, why have non-parasitic chicks not evolved exaggerated signals in order to increase their own food acquisition? Direct energetic cost is one possible constraint. Cowbirds begged for more seconds per hour and on a greater proportion of trips than did their bunting nestmates. However, recent work has shown that the energetic cost of begging is relatively low in Passeriform nestlings (McCarty 1996, 1997; but see Verhulst and Wiersma 1997; Weathers et al. 1997). McCarty (1996) estimated the incremental cost of begging (cost per gram of nestling per second of begging) for nestling tree swallows (*Tachycineta bicolor*) to be 0.008 J g^{-1} s^{-1}. The nestlings that he measured were approximately halfway through the nestling period and are thus developmentally comparable to 6-day-old indigo bunting nestlings. For the parasitized indigo bunting nests at which I made videotapes, the mean mass of 6-day-old bunting nestlings was 9.3 g (D.C. Dearborn, unpublished work), and cowbirds spent an additional 62 s per hour begging relative to buntings. Thus, the mean cost of a 6-day-old bunting chick increasing the amount of time spent begging to match that of a cowbird could be estimated as

$$(0.008\,\mathrm{J\,g^{-1}\,s^{-1}})(9.3\,\mathrm{g})(62\,\mathrm{s\,h^{-1}}) = 4.6\,\mathrm{J\,h^{-1}}.$$

Based on published energetic data, I can convert this energetic cost into an equivalent amount of food. A lepidopteran larva approximately 15 mm long is typical of the food items that I observed indigo bunting adults feeding 6-day-old nestlings. Using equations developed by Sage (1982), the approximate dry mass of a 15 mm caterpillar is 0.009832 g. The gross energetic content of insects is approximately 24,680 J g^{-1} (Bryant and Bryant 1988; Karasov 1990), and the efficiency with which altricial nestlings assimilate insect food is approximately 69.2% (based on 10 studies reviewed in Bryant and Bryant 1988). Thus, the energy that a 6-day-old bunting chick gains from a typical food item is roughly $(0.009832\,\mathrm{g})\,(24{,}680\,\mathrm{J\,g^{-1}})(0.692) = 168\,\mathrm{J}$. If energy limitation were preventing a bunting chick from begging at the rate of a cowbird chick, a bunting would need to be fed only one additional food item every 36 h (168 J/ 4.6 J h^{-1} = 36.5 h) in order to overcome that limitation. These calculations obviously require numerous assumptions, and my intention is not to pinpoint the exact cost of increased begging by indigo buntings. However, this estimate of the cost of begging suggests that direct energetic limitation may not be sufficient to limit the exaggeration of begging by non-parasitic nestlings such as indigo buntings.

A second factor that could restrict begging by non-parasitic chicks is the potential for inclusive fitness losses due to energetic effects on related individuals. If the overall rate of food delivery to the nest is fixed, any increase in food acquisition by one chick will be at the expense of a nestmate. If nestmates are full sibs, a chick should not relinquish a food item unless its nestmate will receive more than twice the benefit of being fed that particular item. In indigo buntings, extra-pair fertilizations are common (up to 35% of nestlings are sired by extra-pair males; Westneat 1990), and the average relatedness of nestmates is less than 0.5. Thus, while inclusive fitness considerations have the potential to limit the exaggeration of begging, this limit is higher for indigo buntings than for species in which all nestmates are full sibs (Briskie et al. 1994).

If the overall rate of food delivery is not fixed, food acquisition by one chick could be increased at the expense of the adult rather than at the expense of the other nestlings. Many studies have experimentally demonstrated that adult birds are capable of greatly increasing the rate at which they provision nestlings (e.g., Sasvari 1986; Hegner and Wingfield 1987; Cucco and Malacarne 1995), and adult indigo buntings at parasitized nests provisioned at higher rates than those at unparasitized nests at my study sites (Dearborn et al. 1998). Such an increase in the rate of food delivery can decrease the adult's future reproductive success by decreasing survival, decreasing energy available for subsequent broods, or increasing the time until the next reproductive effort (Stearns 1992). The extent to which the begging of a particular nestling is constrained by a reduction in the provisioning adults' future reproductive success depends on the relatedness between chicks in the current brood and chicks in the future brood. This relatedness would be reduced by the prevalence of extra-pair fertilizations in either the current or future brood.

The risk of nest predation is a third factor that could limit begging by nonparasitic nestlings. In this study, begging by both hosts and cowbirds typically involved extensive vocalizations by the nestlings. Nestling vocalizations can affect the risk of nest predation (Haskell 1994), and parasitized and unparasitized indigo bunting nests differ in predation risk due at least in part to the production of louder and more frequent begging calls at parasitized nests (Dearborn 1997; Dearborn in press). If nest predation typically results in the loss of the entire brood, cowbirds and hosts may differ in the fitness loss they suffer from a predation event: cowbirds lose their own genes, whereas a host chick loses its genes plus those that it shares with its full- or half-sib nestmates. Thus, the cost of nest predation may be higher for nonparasitic chicks than it is for cowbirds. If the risk of nest predation places an evolutionary limit on begging behavior, this limit should be higher for cowbirds than for nonparasitic chicks (Harper 1986; Motro 1989). Note, however, that this limit might only apply to vocal aspects of begging. It is possible that vocalizations could be limited by predation risk, but non-vocal aspects of begging may be limited by the factors discussed above.

In conclusion, I found that cowbird nestlings received more food than did nestlings of a smaller host species. This inequality in food acquisition appears to be due to a combination of cowbirds' size advantage and the exaggeration of begging signals. Cowbird food acquisition was not related to the performance of any novel begging behaviors. The production of exaggerated signals by cowbirds suggests a limitation on begging by nonparasitic chicks, but the mechanisms of this limitation require further investigation.

References

Bengtsson H, Rydén O (1983) Parental feeding rate in relation to begging behavior in asynchronously hatched broods of the great tit *Parus major*. Behav Ecol Sociobiol 12:243–251

Briskie JV, Naugler CT, Leech SM (1994) Begging intensity of nestling birds varies with sibling relatedness. Proc R Soc Lond B 258:73–78

Bryant DM, Bryant VMT (1988) Assimilation efficiency and growth of nestling insectivores. Ibis 130:268–274

Buchner A, Faul F, Erdfelder E (1996) G · Power: a priori, post hoc, and compromise power analyses for the Macintosh. University of Trier, Trier

Clark AB (1995) Gapes of sexually dimorphic blackbird nestlings do not show sexually dimorphic growth. Auk 112:364–374

Cohen J (1988) Statistical power analysis for the behavioral sciences. Lawrence Erlbaum, Hillsdale

Cucco M, Malacarne G (1995) Increase of parental effort in experimentally enlarged broods of pallid swifts. Can J Zool 73:1387–1395

Dawkins R (1989) The selfish gene. Oxford University Press, Oxford

Dearborn DC (1997) Nestling behavior of a brood parasite: food acquisition and predation risk by brown-headed cowbirds. PhD thesis University of Missouri, Columbia

Dearborn DC (in press) Brown-headed cowbird nestling vocalizations and the risk of nest predation. Auk

Dearborn DC, Anders AD, Thompson FR, Faaborg J (1998) Effects of cowbird parasitism on parental provisioning and nestling food acquisition and growth. Condor

Dunning JB (1993) CRC Handbook of avian body masses. CRC, Boca Raton

Friedmann H (1929) The cowbirds: a study in the biology of social parasitism. Thomas, Springfield

Friedmann H, Kiff LF (1985) The parasitic cowbirds and their hosts. Proc West Found Vert Zool 2:225–304

Gochfeld M (1979) Begging by nestling shiny cowbirds: adaptive or maladaptive? Living Bird 17:41–50

Godfray HCJ (1995) Signalling of need between parents and young: parent-offspring conflict and sibling rivalry. Am Nat 146:1–24

Gottlander K (1987) Parental feeding behaviour and sibling competition in the pied flycatcher *Ficedula hypoleuca*. Orn Scand 18:269–276

Harper AB (1986) The evolution of begging: sibling competition and parent-offspring conflict. Am Nat 128:99–114

Haskell D (1994) Experimental evidence that nestling begging behavior incurs a cost due to nest predation. Proc R Soc Lond B 257:161–164

Hegner R, Wingfield JC (1987) Effects of brood-size manipulations on parental investment, breeding success, and reproductive endocrinology of house sparrows. Auk 104:470–480

Kacelnik A, Cotton PA, Stirling L, Wright J (1995) Food allocation among nestling starlings: sibling competition and the scope of parental choice. Proc R Soc Lond B 259:259–263

Karasov WH (1990) Digestion in birds: chemical and physiological determinants and ecological implications. In: Morrison ML, Ralph CJ, Verner J, Jehl JR Jr (eds) Studies in avian biology no 13. Avian foraging: theory, methodology, and applications. Cooper Ornithological Society, Los Angeles, pp 391–415

Kilner R (1995) When do canary parents respond to nestling signals of need? Proc R Soc Lond B 260:343–348

Kilner R, Johnstone RA (1997) Begging the question: are offspring solicitation behaviors signals of need? Trends Ecol Evol 12:11–15

Lee W-H (1995) The ontogeny and developmental constraints of begging in red-winged blackbirds. M A thesis, State University of New York, Binghamton

Leonard M, Horn A (1996) Provisioning rules in tree swallows. Behav Ecol Sociobiol 38:341–347

Lowther PE (1993) Brown-headed cowbird (*Molothrus ater*). In: Poole A, Gill F (eds) The birds of North America, no 47. Academy of Natural Sciences, Philadelphia

MacNair MR, Parker GA (1979) Models of parent-offspring conflict. III. Intra-brood conflict. Anim Behav 27:1202–1209

McCarty JP (1996) The energetic cost of begging in nestling passerines. Auk 113:178–188

McCarty JP (1997) The role of energetic costs in the evolution of begging behavior of nestling passerines. Auk 114:135–137

McRae SB, Weatherhead PJ, Montgomerie R (1993) American robin nestlings compete by jockeying for position. Behav Ecol Sociobiol 33:101–106

Motro U (1989) Should a parasite expose itself? Some theoretical aspects of begging and vigilance behavior. J Theor Biol 140:279–287

Nice MM (1939) Observations on the behavior of a young cowbird. Wilson Bull 51:233–239

Payne RB (1991) Indigo Bunting. In: Poole A, Stettenheim P, Gill F (eds) Birds of North America, no 4. American Ornithologists' Union, Philadelphia

Price K, Ydenberg R (1995) Begging and provisioning in broods of asynchronously-hatched yellow-headed blackbird nestlings. Behav Ecol Sociobiol 37:201–208

Redondo T (1993) Exploitation of host mechanisms for parental care by avian brood parasites. Etología 3:235–297

Rice WR (1989) Analyzing tables of statistical tests. Evolution 43:223–225

Rodríguez-Gironés MA, Cotton PA, Kacelnik A (1996) The evolution of begging: signaling and sibling competition. Proc Natl Acad Sci 93:14637–14641

Sage RD (1982) Wet and dry-weight estimates of insects and spiders based on length. Am Midl Nat 108:407–411

Sasvari L (1986) Reproductive effort of widowed birds. J Anim Ecol 55:553–564

SAS Institute (1989) SAS/STAT user's guide, version 6. SAS Institute, Cary

Smith HG, Montgomerie R (1991) Nestling American robins compete with siblings by begging. Behav Ecol Sociobiol 29:307–312

Sokal RR, Rohlf FJ (1995) Biometry, 3rd edn. Freeman, San Francisco

Soler M, Martinez JG, Soler JJ, Møller AP (1995) Preferential allocation of food by magpies *Pica pica* to great spotted cuckoo *Clamator glandarius* chicks. Behav Ecol Sociobiol 37:7–13

Stamps J, Clark A, Arrowood P, Kus B (1985) Parent-offspring conflict in budgerigars. Behaviour 94:1–40

Stearns SC (1992) The evolution of life histories. Oxford University Press, Oxford

Teather KL (1992) An experimental study of competition for food between male and female nestlings of the red-winged blackbird. Behav Ecol Sociobiol 31:81–87

Verhulst S, Wiersma P (1997) Is begging cheap? Auk 114:134

Weary DM, Fraser D (1995) Calling by domestic piglets: reliable signals of need? Anim Behav 50:1047–1055

Weathers WW, Hodum PJ, Anderson DJ (1997) Is the energy cost of begging by nestling Passerines surprisingly low? Auk 114:133

Westneat DF (1990) Genetic parentage in the indigo bunting: a study using DNA fingerprinting. Behav Ecol Sociobiol 27:67–76

Woodward PW (1983) Behavioral ecology of fledgling brown-headed cowbirds and their hosts. Condor 85:151–163

Zar JH (1996) Biostatistical analysis. Prentice-Hall, Englewood Cliffs