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Begging and short-term need in cowbird nestlings: how different are brood parasites?

Abstract Because brood parasitic nestlings are usually unrelated to their nestmates and to the provisioning adult, they are free from indirect costs of begging. Consequently, they are predicted to beg more intensely than host nestlings, and some models predict they will beg at an invariantly high level, regardless of short-term need. Previous work has shown intense begging by parasitic cowbirds, but short-term need was not controlled. In this study, we manipulated short-term need and measured begging intensity in two species pairs of host and parasitic nestlings: shiny cowbirds (*Molothrus bonariensis*) parasitizing larger hosts than themselves (rufous-bellied thrushes, *Turdus rufiventris*), and brown-headed cowbirds (*M. ater*) parasitizing smaller hosts than themselves (yellow warblers, *Dendroica petechia*). All four species increased their begging intensity with short-term need, though the change was much less pronounced between food-deprived and control treatments than between control and hand-feeding treatments. Shiny cowbirds begged more intensely than rufous-bellied thrushes following each treatment. In contrast, brown-headed cowbirds did not beg significantly more intensely than yellow warblers under any of the treatments. Intense begging by both species of parasites was as effective as host begging in stimulating the adults to make provisioning visits, but shiny cowbirds were less successful at acquiring food from adult thrushes. A wide array of factors may underlie the apparent differences in the begging behavior and success of brown-headed and shiny cowbirds, including relative size, experience, and local risk of nest predation. Our experiments clearly demonstrate, however, that these two species of parasitic cowbirds adjust their begging intensity based on short-term need.

Keywords Begging · Brood parasite · Cowbird · *Molothrus* · Short-term need

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Introduction

Begging by nestling birds has been used extensively as a model for studying both communication and conflict (Wright and Leonard 2002). However, controversy continues to exist over the question of whether begging by nestling birds functions as a signal to parents of nestling need, or as scramble competition among nestmates, with parents "accepting" the outcome by feeding the winner of the scramble, or as a mix of the two (Kilner and Johnstone 1997; Royle et al. 2002). Models of these scenarios have generally not made testable predictions that would differentiate among them (Parker et al. 2002; Royle et al. 2002). Under any of these paradigms, direct costs of begging have long been thought to be an important component of the system (Zahavi 1977; Macnair and Parker 1979; Grafen 1990; Godfray and Parker 1992). However, the evidence for direct costs is surprisingly weak (Chappell and Bachman 2002; Haskell 2002; but see Rodriguez-Girones et al. 2001), and this is generating new interest in cost-free models of stable signaling (Silk et al. 2000; Lachmann et al. 2001; Johnstone and Godfray 2002).

A non-exclusive alternative to direct costs is the potential for indirect costs of begging to generate stability for either a signaling paradigm or a competition paradigm
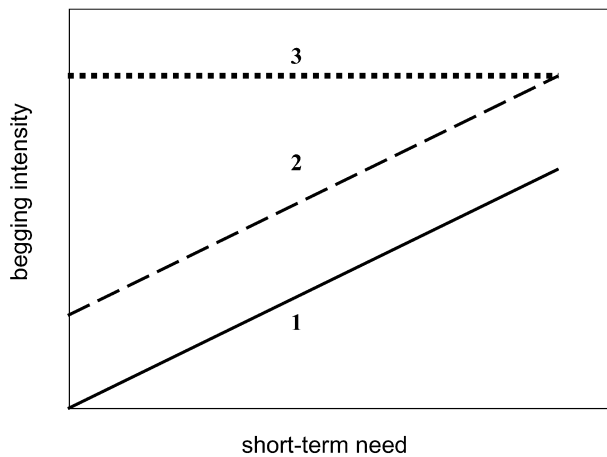
Fig. 1 Begging intensity of parasitic nestlings may show different relationships to short-term need. The *solid line* numbered *1* shows a positive relationship as typically seen in non-parasitic nestlings. *Line number 2* shows the parasitic nestling begging more intensely than a host nestling but still in a manner that increases with short-term need, as predicted by most signaling models. *Line number 3* shows the begging intensity of the brood parasite as constantly elevated and unrelated to need

(Parker et al. 2002); these indirect costs are manifested as the reduced inclusive fitness from denying food to full- or half-sibs or decreasing the residual reproductive value of parents. Some evidence already exists that supports the role of indirect costs. In a comparative analysis, Briskie et al. (1994) found that begging intensity increased with declining expected relatedness among nestmates. In addition, work with brood parasites has shown that parasitic nestlings beg more intensely than host nestlings (Redondo 1993; Davies et al. 1998; Kilner and Davies 1999; Dearborn and Lichtenstein 2002). Intense begging by parasitic nestlings might reflect lower indirect costs of begging (Rodriguez-Girones et al. 2002), but an alternative is that the intense begging of parasitic nestlings might simply reflect greater need. Only a few studies have experimentally manipulated the short-term need of parasitic and host nestlings or fledglings in order to compare the manner in which their begging intensity varies with need (Kilner and Davies 1999; Lichtenstein 2001a; Redondo and Zuniga 2002; Hauber and Ramsey 2003).

If indirect costs are important in limiting the escalation of begging behavior, we would expect the relationship between begging intensity and short-term need to be different for parasites and hosts. Specifically, most non-parasitic species show a positive relationship between begging intensity and short-term need (Redondo and Castro 1992; Price and Ydenberg 1995; Leonard and Horn 1998). Parasites might show a relationship that is (1) positively related to short-term need in the same manner as for host species, (2) positively related to short-term need but following a different relationship than host species, or (3) elevated and independent of short-term need (see Fig. 1).

We used food-deprivation and hand-feeding experiments to explore the relationship between begging and short-term need in two parasite–host pairs: shiny cow-

birds (*Molothrus bonariensis*) parasitizing rufous-bellied thrushes (*Turdus rufiventris*), and brown-headed cowbirds (*M. ater*) parasitizing yellow warblers (*Dendroica petechia*). Shiny cowbirds and brown-headed cowbirds are host generalists, parasitizing at least 214 and 226 species, respectively (Davies 2000). Rufous-bellied thrushes are larger in adult size than shiny cowbirds (70–80 g vs 50 g; Dunning 1993; Lichtenstein 1998). Yellow warblers are typical hosts of brown-headed cowbirds, having a similar or slightly longer incubation period (Lowther 1993; Lowther et al. 1999) and a much smaller adult body size (9.5 g vs 44 g; Dunning 1993). Both of these hosts are commonly parasitized by these cowbird species across much of their breeding ranges (Lichtenstein 1998; Lowther et al. 1999). Previous studies have shown that shiny cowbirds fare badly at thrush nests (Lichtenstein 2001b), whereas yellow warblers are good hosts for brown-headed cowbirds (Lichtenstein and Sealy 1998). Because of the differential size advantage and differential success at food acquisition, the two species of brood parasites in our study are experiencing different competitive environments.

Methods

Study sites

Fieldwork with shiny cowbirds was conducted at a residential area with parks and gardens near Del Viso (34°29′S, 58°35′W), in the Province of Buenos Aires, Argentina. Data were collected from October 1994 to January 1995. The area was visited by shiny cowbirds that were feeding in nearby agricultural land.

Fieldwork with brown-headed cowbirds was conducted from the beginning of June until early July 1994 on a section of a forested dune ridge that separates Lake Manitoba from Delta Marsh, about 5 km west of Delta (50°11′N, 98°19′W), Manitoba, Canada. The study area was comprised of properties of the Portage Country Club, the University of Manitoba Field Station, and Rural Municipality of Delta.

Experimental methods

We located nests and monitored clutch progress daily until the eggs hatched. We then manipulated brood contents in order to create broods containing one host and one cowbird nestling of the same age (±1 day). The remaining host or cowbird nestlings were cross-fostered to nearby nests containing nestlings of approximately the same age. Nestlings were weighed early in the morning with a 50 g Pesola spring balance each day until they were 12 days old. Tibia, tarsus, gape length and gape width were measured with vernier calipers to the nearest 0.1 mm.

Experiments were conducted on shiny cowbirds and rufous-bellied thrushes on day 7–8 of the nestling period, and on the brown-headed cowbirds and yellow warblers on day 3–4 of the nestling period. Four additional yellow warbler nests were tested when the nestlings were 7–8 days old. We were not able to experiment with older yellow warblers due to the high predation rate in the study area.

We filmed 9 rufous-bellied thrush nests and 15 yellow warbler nests. We were unable to complete the 10 h of experimental treatment in one rufous-bellied thrush nest and four 3- to 4-day-old yellow warbler nests as a result of predation occurring during the filming session or heavy rain interrupting the experimental treatment.

The experimental procedure consisted of the following three treatments: hand-feeding, food-deprivation, and a control. The experimental treatments were done twice (once for each nestling) and the control treatment was done once. Only one nestling was tested at any one time; for example, the thrush did not receive any treatment during the treatment in which the cowbird was hand-fed, and vice versa.

1. For the hand-feeding treatment we temporarily removed one of the nestlings from the nest and kept it in a cushioned, formed, artificial nest. This nest was located within meters of the original nest so the parents would not return to the nest until the manipulation ended. We stimulated the nestling to beg with noises that imitated the parents' feeding calls and fed it to satiation using forceps. The food consisted of small pellets made from a mixture of raw minced-meat and egg. The feeding process did not last more than 2 min, after which we returned the nestling to the nest and began filming.
2. The food-deprivation treatment began with removing a nestling from the nest for 1 h. The nestling was kept in a cushioned, formed, artificial nest inside a box. We replaced the nestling with a similar sized nestling during its absence. The filming session started as soon as we replaced the original nestling in the nest.
3. The control treatment involved filming for 2 h, without manipulating the nestling's hunger level. The parasitic and host nestlings were tested simultaneously.

The order of treatments was randomized during the day, although no nestling was assigned an experimental treatment twice in a row (e.g. after the treatment in which the cowbird was hand-fed, we either tested the thrush nestling or conducted a control period). Nests were filmed for 2 h after the manipulations.

Parents resumed feeding promptly after we left the nests. In the three cases in which parents did not go back to the nest in the first 30 min after the manipulation (two rufous-bellied thrush nests and one yellow warbler nest), we removed the video camera and stopped testing the nests.

Video analysis

Begging intensity was ranked using the criteria of Redondo and Castro (1992): 0: did not beg; 1: gaped, tarsi flexed; 2: neck stretched, tarsi flexed; 3: tarsi extended; 4: tarsi extended plus wing flapping. This scale has been used in previous studies of cowbirds (see Lichtenstein and Sealy 1998; Lichtenstein 2001b) and is similar to scores of begging intensity used in studies of other species (e.g., Redondo and Castro 1992; Leonard et al. 2003). We will concentrate only on the postural elements of begging for the analysis, due to the difficulty of measuring individual vocalizations when two nestlings are sharing a nest in the field. Latency to start begging was measured in ranks (see Lichtenstein 2001b).

We considered three features of the begging display: (1) begging intensity when the adults arrive at the nest and before they deliver the food, (2) latency to the start of begging, and (3) begging intensity after the adults have finished delivering food, but are still at the nest.

We limited the data analysis to the first hour after the experimental manipulation in order to insure that the effects that we recorded were a result of our experimental manipulations and not due to natural variations in hunger level.

The proportion of feeds received is a measure of the amount of food that the nestlings received during the 10 h of filming. It was calculated as the number of successful feeds given to a nestling over the total number of feeds given to the brood during the 10 h filmed.

Data analysis

The provisioning rate of the adults and the begging of each nestling was measured for 1 h following a period of hand-feeding, food deprivation, and control (i.e. natural rate of food delivery by the adults). Preliminary tests revealed no change in begging intensity in a nestling within an observation period. Thus, across all feeding visits within the hour following a treatment, we computed an average score for a nestling's begging intensity when the adult arrived with food, the nestling's start rank, and its intensity of begging after food was delivered. These three variables were used as dependent variables in a repeated measures MANOVA. In this MANOVA, treatment (hand-fed, food-deprived, control) was the within-subjects factor. There were two between-subjects factors: species (parasite vs host), and nest (to account for any non-independence between the behavior of the parasite and its host nestmate). Two such analyses were performed, one for the brown-headed cowbird/ yellow warbler nests and one for the shiny cowbird/thrush nests. Significant omnibus multivariate tests were followed by univariate tests on each of the three dependent variables, using a Bonferroni-adjusted alpha of $0.05/3=0.0167$. Planned comparisons, using the simple contrasts procedure in SPSS, were used to compare the begging behavior of a given species across the three treatments.

We performed a post hoc power analysis for the key test of a species difference in the behavioral analysis of brown-headed cowbird nestlings and yellow warbler nestlings. We conducted this analysis for the multivariate test (i.e. on all three behavioral measures simultaneously) of the between-subjects factor, "species," which compared brown-headed cowbirds and yellow warblers. We used an alpha of 0.05, the actual sample size ($n=11$ warbler nests) and df from the F-test at warbler nests. Instead of the observed effect size at warbler nests (which only leads to an estimate of observed power—generally proportional to P; Steidl and Thomas 2001), we used the effect size seen in the analysis of thrush nests, where there was a significant difference in behavior of host and parasitic nestlings. Thus, this power analysis asked: what was our power at warbler nests to detect an actual effect that was equal to the one seen at thrush nests? Second, we used similar methods to calculate power for an effect size that was half as large as that seen at thrush nests. Finally, we asked how large an effect would have been detectable with a power of 0.8. Effect size at thrush nests was measured as partial eta-squared reported by SPSS, and post hoc calculation of power was made with G Power (Buchner et al. 1996).

Ethical note

We adhered to the legal requirements of Argentina and Canada and complied with the required permits. No chicks died and no nests were deserted as a result of the manipulations. In one case where the host parents did not return to the nest to feed the chicks for 1 h after we had placed the video camera we removed the equipment and decided not to use that nest. The duration of food deprivation experiments used in the experiments may occur periodically under natural circumstances, and deprivations of similar (Price and Ydenberg 1995; Leonard and Horn 1998; Clotfelter et al. 2003) or greater (Smith and Montgomerie 1991; Teather 1992) length have been used experimentally in other studies of passerine nestlings.

Results

Provisioning response of adults

At thrush nests, adult thrushes made more frequent provisioning trips in response to the food-deprivation treatment than the hand-feeding treatment (two-factor ANOVA, main effect of treatment: $F_{1,14}=21.11$, $P=0.004$; 4.81 ± 0.64SE overall mean trips per h for hand-feeding
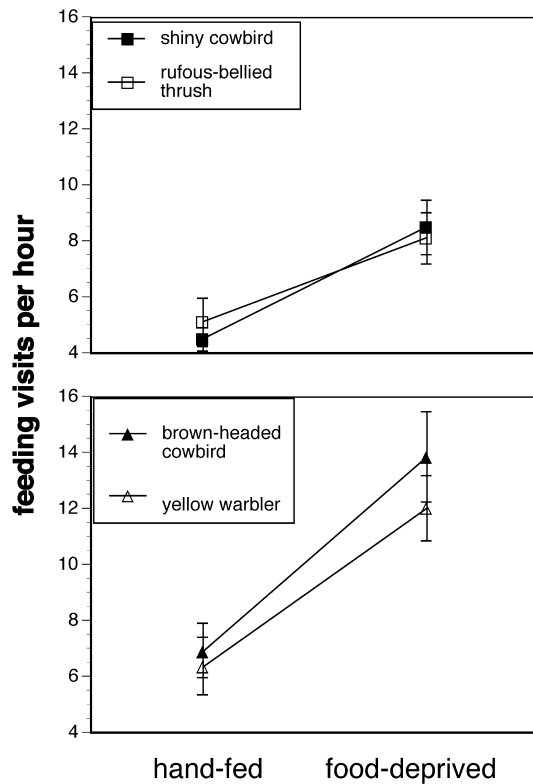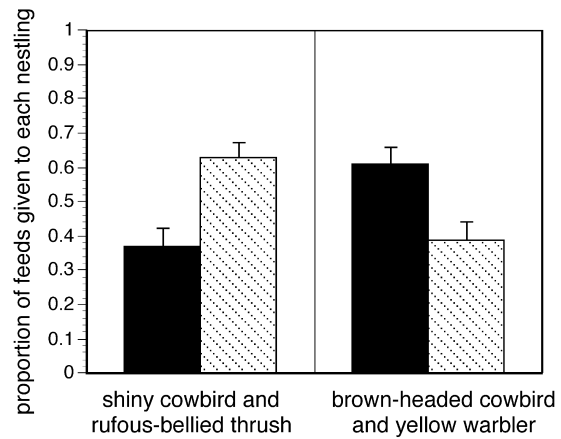
Fig. 2 Host adults made significantly more feeding visits to nests containing a food-deprived nestling than to nests containing a hand-fed nestling. *Symbol* indicates which nestling was manipulated during the treatment, but all nests contained one host nestling and one cowbird nestling, and *Y-axis value* represents food delivery to the entire brood. The food-deprived parasitic nestling was equally effective as the food-deprived host nestling at stimulating an increase in adult visitation rate, both at rufous-bellied thrush nests and yellow warbler nests
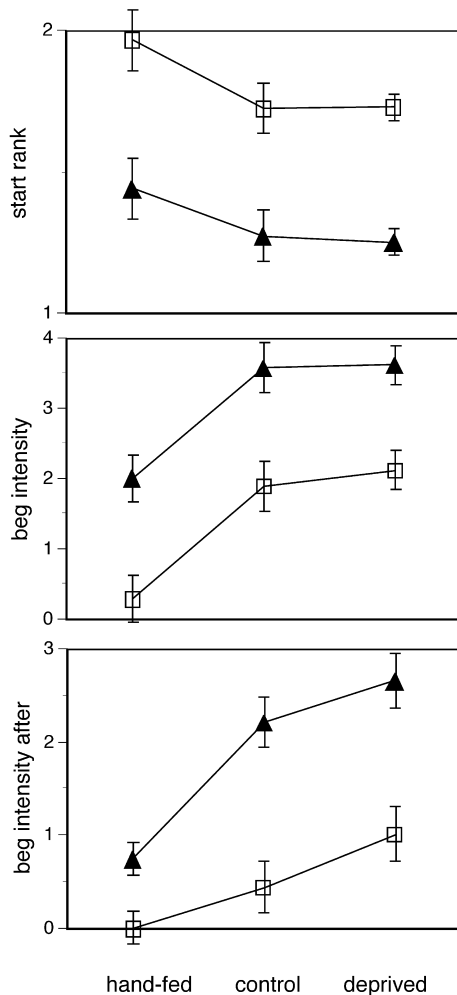

Fig. 3 Within a given nest, delivered food was not equally distributed between the cowbird nestling (*solid bars*) and the host nestling (*hatched bars*). Shiny cowbirds received less food than rufous-bellied thrushes, whereas brown-headed cowbirds received more food than yellow warblers

Nestling behavior

At rufous-bellied thrush nests there was a significant effect of treatment on the suite of begging response variables (Wilks' lambda=0.101, Rao's $F_{6,9}$=13.42, P<0.0001), and univariate follow-up tests showed significant treatment effects on all three begging variables for host and parasite (all Bonferroni-adjusted $P\leq0.006$). Within-subjects contrasts detected significant changes in all three begging variables between hand-fed and control treatments (all $P\leq0.017$), but begging after food delivery was the only behavior that increased between control and food-deprived treatments (P=0.044). Across treatments the shiny cowbirds begged more strongly than the thrushes (Wilks' lambda=0.265, Rao's $F_{3,12}$=11.08, P<0.001), with univariate differences in all three variables: they started begging sooner ($F_{1,14}$=25.00, Bonferroni-adjusted P<0.001) and begged more intensely both before ($F_{1,14}$=20.82, Bonferroni-adjusted P<0.001) and after ($F_{1,14}$=29.19, Bonferroni-adjusted P<0.001) food delivery in comparison to thrushes under similar treatments (Fig. 4). There was not a significant interaction between treatment and type of nestling (Wilks' lambda =0.390, Rao's $F_{6,9}$=2.34, P=0.121), meaning that shiny cowbirds and thrushes responded similarly to the treatments despite the fact that cowbirds had more intense begging overall. There was not significant variation in begging behavior among nests (P=0.14).
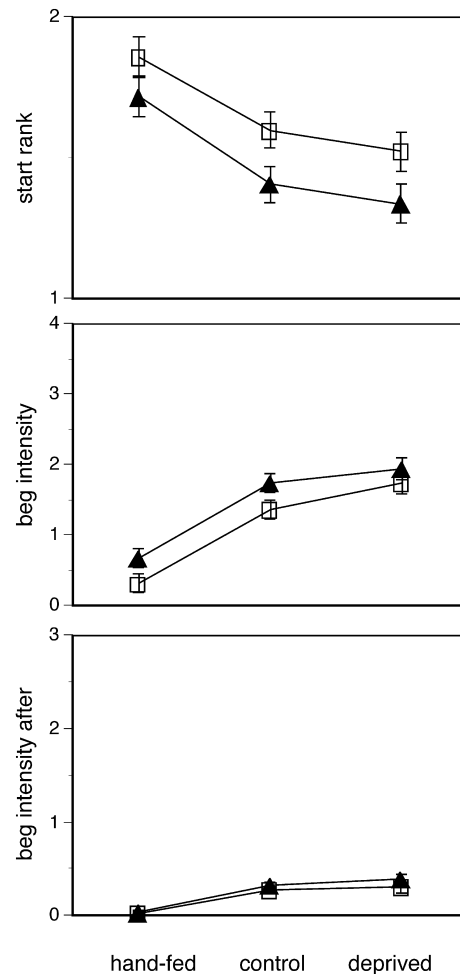
At yellow warbler nests there was also a significant effect of treatment on the suite of begging response variables (Wilks' lambda =0.014, Rao's $F_{6,5}$=57.53, P<0.001), and univariate follow-up tests showed significant treatment effects on all three begging variables (all Bonferroni-adjusted $P\leq0.001$). Within-subjects contrasts detected significant changes in all three begging variables between hand-fed and control treatments (all P<0.0001), but begging behavior did not change significantly between control and food-deprived treatments (all P>0.05).

treatment and 8.31±0.95 for food-deprivation treatment), and the provisioning rate did not vary with which species of nestling (thrush or shiny cowbird) was the subject of the treatment ($F_{1,14}$=0.02, P=0.89; Fig. 2).

The same pattern was seen at yellow warbler nests, where adult warblers made more frequent provisioning trips in response to the food-deprivation treatment than the hand-feeding treatment (two-factor ANOVA, main effect of treatment: $F_{1,20}$=31.97, P<0.0001; 6.64±1.01 overall mean trips per h for hand-feeding treatment and 12.91±1.39 for food-deprivation treatment), and the provisioning rate did not vary with which species of nestling (warbler or brown-headed cowbird) was the subject of the treatment ($F_{1,20}$=0.79, P=0.38; Fig. 2).

Across all treatments, shiny cowbirds received a smaller proportion of feeds than did their thrush nestmates (0.37±0.05 vs 0.63±0.04; sign test, n=8 nests, P=0.008), whereas brown-headed cowbirds received a greater proportion of feeds than did their warbler nestmates (0.61±0.05 vs 0.39±0.05; sign test, n=11 nests, P=0.04; Fig. 3).

Fig. 4 Marginal means (±SE) for begging behavior of shiny cowbirds (*filled triangles*) and rufous-bellied thrushes (*open squares*) following periods of hand-feeding, control (fed at natural rates by adult birds), and food deprivation

Fig. 5 Marginal means (±SE) for begging behavior of brown-headed cowbirds (*filled triangles*) and yellow warblers (*open squares*) following periods of hand-feeding, control (fed at natural rates by adult birds), and food deprivation

Accounting for treatment effects, there was no significant difference in the begging behavior of yellow warblers and brown-headed cowbirds (Wilks' lambda =0.665, Rao's $F_{3,8}$=1.34, P=0.327; Fig. 5). There was not a significant interaction between treatment and type of nestling (Wilks' lambda =0.359, Rao's $F_{6,5}$=1.49, P=0.339), indicating that brown-headed cowbirds and yellow warblers responded similarly to the treatments. Significant variation in begging behavior did exist among nests (Wilks' lambda =0.007, Rao's $F_{30,24}$=3.50, P=0.001).

The effect size for the difference in overall host and cowbird nestling behavior at thrush nests was partial eta-squared =0.735. The power to detect an effect of this magnitude at yellow warbler nests was very high, $1-\beta$ =0.960; the power to detect an effect that was half this magnitude (i.e. partial eta-squared =0.3675) was low, only $1-\beta$=0.359. We had power of $1-\beta$=0.80 to detect an effect size of partial eta-squared =0.62 at warbler nests, an effect size that is 84.3% the magnitude of the effect detected at thrush nests. Thus, at warbler nests we had good

power to detect an effect that was at least 85% the size of the effect seen in the thrush nests.

Discussion

As expected and as seen in previous studies (Redondo and Castro 1992; Price and Ydenberg 1995; Cotton et al. 1996; Leonard and Horn 1998), both non-parasitic species altered their begging behavior in response to experimental manipulation of short-term need. Surprisingly, these behavioral changes were mirrored by the cowbird nestlings under reciprocal experimental conditions: in both the shiny cowbird/thrush system and the brown-headed cowbird/warbler system, the effect of treatment on begging behavior was the same for parasites as it was for hosts, meaning that parasitic cowbirds do alter their begging based on short-term need. This evidence parallels what has been seen in the screaming cowbird (Lichtenstein 2001a), a host specialist that parasitizes bay-winged cowbirds. However, it contrasts with scenario 3 in Fig. 1, in

which brood parasites would beg at a constant elevated level that is not related to short-term need, a type of invariantly pronounced begging that has been shown in parasitic great-spotted cuckoos parasitizing magpies (Redondo 1993). Interestingly, the most pronounced behavioral change in our experiment was between the hand-feeding treatment and the control treatment; the begging of food-deprived nestlings (whether host or parasite) was rarely more pronounced than that of nestlings under control conditions of natural feeding rates. One interpretation of this is that these birds are begging near their maximal limit—or are food-deprived—under natural conditions. Alternately, a 1-h period of food deprivation may not have impacted short-term need very much compared to control treatments, though this seems somewhat unlikely.

Across all three levels of short-term need, shiny cowbirds begged more strongly than did their thrush nestmates. In contrast, there was not a significant difference between the begging of brown-headed cowbirds and yellow warblers, although the non-significant trend was for cowbirds to start begging sooner and beg more intensely before and after food delivery under each of the three treatments (Fig. 5). Thus, shiny cowbirds appear to follow pattern 2 in Fig. 1, whereas brown-headed cowbirds may fall under either pattern 2 or 1. We will briefly explore some of the factors that might account for this apparent difference in begging behavior of the two cowbird species. First, brown-headed cowbirds might beg more strongly than hosts and we lack the power to detect the difference, as suggested by the visual inspection of the marginal means. We had excellent power to detect an effect as large as that seen in the shiny cowbird/thrush comparison and good power to detect somewhat smaller effects, but our power was low for detecting an effect half as large as that seen in the thrush nests. Second, shiny cowbirds may have learned to beg more strongly than hosts because of the competitive environment in their nests, as shiny cowbirds lack the size advantage that brown-headed cowbirds have over their hosts, and as rufous-bellied thrushes tended to beg more strongly than yellow-warblers. We know that ontogeny plays an important role in the development of begging strategies (Kedar et al. 2000; Rodriguez-Girones et al. 2002). Chicks that have to compete strongly to obtain food develop the strategy of begging at higher intensities, even if they are in the same condition, and some aspects of common cuckoo begging vary depending upon host species with which they are reared (Butchart et al. 2003). Third, shiny cowbirds may have a greater long-term need, meaning that they require a greater total investment to reach fledging size (Price et al. 1996). This might be due to a shiny cowbird nestling's history of being underfed when being reared by rufous-bellied thrushes (Lichtenstein 2001b); nestlings of small size or poor condition have greater long-term need than their bigger nestmates (Litovich and Power 1992; Price et al. 1996; Cotton et al. 1999). Fourth, because shiny cowbird nestlings are smaller than thrush nestlings, they might need to beg

more strongly to "make up" for their different appearance to the adults (Redondo 1993). Fifth, ecological differences between the two cowbird species may create different trade-offs between food acquisition and predation risk. Because predation rates are higher in the Delta Marsh population of yellow warblers (54.6% of nests are depredated; Hebert and Sealy 1993) than in the Del Viso population of rufous-bellied thrushes (34.3%; Lichtenstein 1998), escalation of begging could be more limited by the risk of nest predation for brown-headed cowbirds than it is for shiny cowbirds (as predicted by general models of Godfray 1995; Haskell 2002). Sixth, brown-headed cowbirds and shiny cowbirds might differ in the frequency with which they are naturally reared with kin due to multiple parasitism of nests by a single female. Genetic studies of brown-headed cowbirds have revealed varying levels of repeated parasitism by single females (Alderson et al. 1999; Hahn et al. 1999; Strausberger and Ashley 2003), and comparable genetic data are lacking for shiny cowbirds. But if shiny cowbirds are never reared with full- or half-sibs, they would be expected to beg more strongly (Briskie et al. 1994). A final possibility is that brown-headed cowbirds do not out-beg their host nestmates because we measured their behavior at a younger age than we did for shiny cowbird/thrush nests (Stamps et al. 1989). This explanation is unlikely because a small sample of experiments with 7- to 8-day-old nestlings of brown-headed cowbirds and yellow warblers showed results similar to those found at the younger age.

The effectiveness of begging by cowbirds and hosts was not entirely equal. In general, shiny cowbird nestlings were not as effective at obtaining food from adult thrushes as were thrush nestlings (Lichtenstein 2001b). In contrast, brown-headed cowbird nestlings were more effective than host nestlings at obtaining feeds from host adults, as has been seen in previous studies with yellow warblers (Lichtenstein and Sealy 1998) and indigo buntings (Dearborn 1998). Thus, the more intense begging of shiny cowbirds (compared to hosts) might be explained by their low success rate rather than by a lack of indirect costs of begging.

Despite the fact that shiny cowbirds were not as effective as host nestlings at acquiring food when adults arrived at the nest, both species of parasite seemed effective at stimulating the adults to make provisioning trips (Fig. 2). At thrush nests and warbler nests, adults made more trips during food-deprivation treatments than during hand-feeding treatments, and the provisioning rate did not depend on which species of nestling (host or parasite) was the subject of the manipulation. In other words, the rate of provisioning by the adult seemed to be determined by the amount of begging regardless of the species that was begging, but the subsequent allocation of food was not equal between species. Thus, thrushes might represent an interesting twist on a model recently proposed by Kilner (2003), who suggested that the presence of host nestlings might actually benefit non-evicting parasitic nestlings by providing a stronger stimulus to parents but then being poor competitors for food when it arrives. This might

conceivably be the case at warbler nests, where brown-headed cowbirds and yellow warblers were equally effective at stimulating adults to bring food but cowbirds were then preferentially fed over warbler nestlings. In thrush nests, host and parasite were also equally effective at stimulating feeding visits, but the thrush nestling received most of the resulting food. Thus, a thrush nestling might actually benefit from the presence of a hungry shiny cowbird nestmate, although removal of a host egg by a female cowbird would probably cause a greater loss of inclusive fitness than any gains from the begging efforts of the parasitic nestling.

Overall, we have shown that two species of parasitic cowbird do modify their begging behavior in response to experimental manipulation of short-term need, in contrast to work with cuckoos that show constant elevated begging by the parasite. Shiny cowbirds, but not brown-headed cowbirds, begged more intensely than host nestmates across all experimental treatments. Additional experiments with other populations (that differ in predation risk or frequency of multiple parasitism), with parasites of varied ages, or with naive parasites reared in the absence of host nestlings (see, e.g., Hauber 2003), would help assess the generality of the relationships between host begging and cowbird begging that were observed here.

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