Nestling competition, rather than supernormal stimulus, explains the success of parasitic brown-headed cowbird chicks in yellow warbler nests

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Interspecific parasitic chicks are usually fed more than the smaller host young with whom they share the nest. This could be due to parasitic chicks having evolved exaggerated features that are preferred by the adults to the features present in their own young (the supernormal stimulus hypothesis). Alternatively, the success of parasitic chicks could be due to them being better competitors. We tested these hypotheses by studying the interaction between brown-headed cowbird chicks, *Molothrus ater*, and a common small host, the yellow warbler, *Dendroica petechia*. Parasitic chicks begged more intensively than the host's young and received most of the feeds. The relative height reached by the begging chicks of both species was the most important variable in determining their feeding success. Being larger and begging intensively, brown-headed cowbirds were better able to reach higher than the host's young, but at equal heights parasitic chicks were no better than the host's young at gaining feeds. It is suggested that the success of the brown-headed cowbirds when parasitizing yellow warblers is due to them physically out-competing the smaller young of their hosts, and not to them evoking a stronger response from the hosts by being a supernormal stimulus.

Keywords: cowbird; begging; supernormal stimulus; brood parasitism

1. INTRODUCTION

Interspecific brood parasites lay their eggs in the nests of other species, thereby leaving the care of their young to the hosts. Available evidence suggests that in the cases in which the parasitic chicks are larger than the host's young, they are usually fed more than the host's young with whom they share the nest (Briskie & Sealy 1987; Redondo 1993). As we would expect hosts to prefer feeding their own offspring to parasitic chicks, the success of parasitic chicks is intriguing.

Recent advances in the field of biological signalling (Godfray 1991, 1995) suggest that provided that begging is costly, an evolutionarily stable strategy (ESS) can exist between the parents and the young so that parents can accurately assess the condition of the young from their begging intensity and feed them accordingly. Empirical studies support the prediction that nestlings vary their begging behaviour in relation to their hunger level (e.g. Redondo & Castro 1992; Cotton *et al.* 1996), and some experimental work suggests that parents choose to feed more needy chicks (Kilner 1995). If parents exert some control over food provisioning and decide whom to feed on the basis of the chicks' signals, they can be manipulated

by brood parasites. Parasites may act as a supernormal stimulus by providing stimuli that hosts would be unable to resist (Dawkins & Krebs 1979). This is supported by studies on great spotted cuckoos (*Clamator glandarius*), which were favoured by magpies (*Pica pica*) over their own chicks (Redondo 1993; Soler *et al.* 1995a).

Alternatively, the distribution of food might be determined by sibling competition. Parents may follow a 'laissez-faire' strategy and feed the chick that is better able to compete (for example, by getting closer to the feeding parent), independently of the chick's identity (Rydén & Bengtsson 1980; Teather 1992; McRae *et al.* 1993; Kacelnik *et al.* 1995). Thus, bigger chicks should be better able to compete for favourable positions than their smaller siblings, and as a result be fed more often. The success of the parasitic chicks will be related only to their size advantage, which will enable them to get closer to the feeding parent and to monopolize most of the feeds.

Here we study whether the success of parasitic brown-headed cowbird chicks (*Molothrus ater*) in parasitizing yellow warblers (*Dendroica petechia*) is due to their better competitive ability, or to their ability to lure the warbler parents by their signals into choosing to feed them. For this purpose we consider that a parasitic chick possesses supernormal stimulus properties to the host if it presents exaggerated traits (e.g. gape size or colour, palatal papillae, vocalizations) that evoke a stronger response from the host than does the stimulus presented by its

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offspring. We do not consider as a supernormal stimulus the components of chick begging behaviour such as jostling, posturing, or relative height reached while begging, that could give the parasitic chicks a physical competitive advantage over the host's young. Thus, chick size *per se* will only be regarded as having supernormal stimulus properties if bigger chicks were preferred when they were positioned at the same distance from the feeding parent as the host's chicks. According to our definition, a parasitic chick would act as a supernormal stimulus if it were preferentially fed, even when placed further away from the parent (i.e. placed relatively lower).

2. METHODS

(a) *Study site*

The research was conducted from the beginning of June until early July 1994 on a section of a forested dune ridge that separates Lake Manitoba from the 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 the Rural Municipality of Delta.

(b) *Daily procedure*

Yellow warblers are small (10 g), frequently parasitized hosts whose fledgling success is significantly reduced by the presence of parasitic nestlings (Weatherhead 1989). We located yellow warbler nests and followed their progress daily until the chicks hatched. We then manipulated brood contents in order to create broods containing one yellow warbler and one brown-headed cowbird chick of about the same age (± 2 d). This age range and brood composition frequently occurs in nature. The remaining host or parasitic chicks were cross-fostered to nearby nests containing chicks of approximately the same age. Brown-headed cowbird chicks originated from eggs procured from yellow warbler nests that hatched either in naturally parasitized nests, or in an incubator. Artificially incubating eggs enabled us to reduce losses due to predation at this stage. Chicks were weighed each morning with a 50 g Pesola spring balance until they were eight days old. Tibia, tarsus, gape length, and gape width were measured to the nearest 0.1 mm with vernier callipers.

(c) *Filming*

Fifteen nests were filmed using a Sony Hi8 video recorder, when nestlings were 3–5 days old, in the middle of the period of rapid growth. The high predation in the area did not allow a sufficient sample size of older chicks. In 9 of the 15 nests filmed, both chicks were of the same age. In the remaining six nests, the brown-headed cowbird was one or two days older than the yellow warbler chick. One day before the start of filming, a fake video camera, mounted on a tripod, was placed 2 m away from the nest; it was gradually moved closer until it was 60 cm away from the nest. The following day, we replaced the artificial camera with a real camera. The camera was positioned in the same location every day. There was no need to mark the chicks for individual recognition as the chicks within each brood had species-specific distinguishable features (e.g. gape colour). Parents appeared to be undisturbed by the presence of the camera and resumed feeding within a few minutes of our departure from the nest area. Nests were filmed for 10 h on one day. This period was divided into five blocks of 2 h, each of which corresponded to a different treatment. The treatments included

Table 1. *Mean $\pm$ s.e. of yellow warbler and brown-headed cowbird body measurements the day that they were filmed (3–5 days old)*

(Data come from 15 nests containing one yellow warbler and one brown-headed cowbird chick each.)

measure	yellow warbler	brown-headed cowbird	z^1	p^1
gape length (mm)	9.0 $\pm$ 0.3	11.6 $\pm$ 0.2	−3.55	0.0004
gape width (mm)	8.7 $\pm$ 0.2	12.8 $\pm$ 0.3	−4.16	<0.0001
tibia (mm)	21.5 $\pm$ 0.8	24.2 $\pm$ 1.0	−1.89	0.06
tarsus (mm)	17.4 $\pm$ 0.7	18.5 $\pm$ 0.9	−0.72	0.45
weight (g)	7.1 $\pm$ 0.4	14.7 $\pm$ 1.1	−3.96	<0.0001

¹Results of a two-tailed Mann-Whitney *U*-test comparing measurements of both chick types.

(i) hand-feeding until satiation with a mixture of raw minced-meat and egg; (ii) depriving the host or the parasite of food for 1 h by removing them from the nest, and filming without manipulating the hunger level (control). The experimental treatments were done twice (once for each chick) and the control treatment was done once. The treatments were used for another experiment (Lichtenstein 1998). Filming took place between 06:00 and 20:00 h (CST). The results of the 2 h segments corresponding to the control period were used to describe the chicks' begging behaviour and determine the distribution of food. The results of all 10 h of filming were used for the logistic regression analysis to provide sufficient visits to the nest in which both chicks were begging simultaneously.

(d) *Video analysis*

Films were analysed frame by frame with a Sony Nicam video cassette recorder. For each visit by the host parents, nestlings were ranked in terms of sequence of begging initiation (start rank), and relative height (height rank) (see details in §2e). These measures were estimated during the 'aiming phase' (Bengtsson & Rydén 1981), when parents froze at the nest rim before feeding the nestlings. The begging intensity was scored on an arbitrary scale from 0 to 4, using the criteria of Redondo & Castro (1992): 0, did not beg; 1, gapes, tarsi flexed; 2, neck stretched, tarsi flexed; 3, tarsi extended; 4, same as (3) plus wing flapping.

(i) *Feeding success*

This was calculated as the number of successful feeds given to a chick (i.e. food swallowed) divided by the total number of offers given to the brood for the trips in which both chicks were begging.

(e) *Statistical methods*

To avoid pseudoreplication (Hurlbert 1984), we analysed only mean values for each index of begging intensity from each chick, so that each nest contributed one data point per chick to the analysis. When non-parametric tests were used, they were two-tailed.

The height reached and latency to start of begging were measured in ranks. The rank assigned to one chick depended on the rank given to its nest companion (for example, the chick that reached higher was assigned 1 and its nest companion 2; if both

Figure 1. Proportion of feeds given to the brown-headed cowbird chicks and the yellow warbler chicks. Mean bars ($\pm$ s.e.) are shown ($n=15$).

chicks reached the same height, both were given a rank of 1.5). In order to analyse these data statistically, we compared the ranks obtained by the brown-headed cowbird chicks against the null hypothesis of no difference between the chicks (rank 1.5) with a two-tailed Sign test. The same procedure was followed to compare the feeding success with the null hypothesis of 0.50 (equal food offers given to both chicks).

We performed a logistic regression analysis using Genstat 5 (Genstat 5 Committee 1993), on data from the brown-headed cowbird chicks to identify the most important variable that determined their feeding success. Each chick contributed to the analysis with an average value of start, height, and begging intensity, and its probability of getting fed. Average values of start rank, height rank, and begging intensity were obtained for each chick by multiplying the number of times that it begged at a certain rank by that rank, and then dividing the total sum by the total number of visits. Initially, the 'maximal' model was fitted to the data. This comprised the complete set of measures to be considered as possible explanatory variables. The significance of the full model was tested using the deviance which is distributed approximately as χ^2 , with degrees of freedom equal to the change in the residual degrees of freedom. Terms were dropped if this did not reduce the explanatory power of the model. This process was continued until no more terms could be dropped. The significance of each variable was tested by examining the change in deviance associated with dropping that particular variable from the model. All dropped terms were then tested to see if their reinstatement in the model would significantly improve it. The 'minimal model' was reached when no terms could be added or dropped.

3. RESULTS

At the age that nestlings were filmed, the cowbird chicks had significantly larger gapes, and weighed significantly more than yellow warbler chicks, but there was no difference in the tibiae and tarsi lengths (table 1).

(a) Food distribution in the parasitized nests

The provisioning rate per hour was ($\bar{x} \pm$ s.e.) 10.43 ± 0.84 trips ($n=15$ nests). The food brought to the nest consisted mainly of single geometrid larvae, chironomids, and, to a less extent, other Diptera. In most of the parental visits,

Figure 2. Mean $\pm$ s.e. of (a) the begging intensity, (b) the start rank, and (c) the height rank of the brown-headed cowbird and yellow warbler chicks ($n=15$). All comparisons were significant. The dashed line represents equality between the chicks.

only one chick was fed. Brown-headed cowbird chicks were fed significantly more times than yellow warbler chicks (Sign test: $n=15$, $p=0.01$; figure 1).

(b) Begging behaviour of the brown-headed cowbird and host chicks

The parasitic chicks begged more intensively than the yellow warbler chicks (Wilcoxon signed-ranks test: $z=2.12$, $n=15$, $p=0.03$; figure 2a), started begging significantly earlier (Sign test: $n=15$, $p=0.02$; figure 2b), and reached significantly higher (Sign test: $n=15$, $p=0.002$; figure 2c).

Table 2 *Logistic regression analysis for the brown-headed cowbird chicks*

term	deviance	d.f.	<i>p</i>
start ($\bar{x}$)	1.71	1	n.s.
beg ($\bar{x}$)	0.53	1	n.s.
height ($\bar{x}$)	27.43	1	<0.001
residual	11.67	11	—
total	41.33	14	—

Figure 3. The probability that the brown-headed cowbird chicks got fed for cases in which they reached higher than the yellow warbler chicks (Most), the same height (Equal) and lower (Least). Each of the 15 chicks provided one mean value per category. Standard error bars are shown.

(c) *The parents' response to the chicks' begging*

A logistic regression analysis showed that among the begging variables measured, the most important variable in determining the success of getting fed was relative height (table 2). The chicks' probability of getting fed increased with the increasing relative height that they reached (figure 3). Brown-headed cowbird chicks were fed significantly more than yellow warbler chicks when they reached higher (Wilcoxon signed-ranks test: $z = -3.25$, $p = 0.001$) and significantly less when they were lower (Wilcoxon signed-ranks test: $z = -3.28$, $p = 0.001$), whereas there was no difference in the probability that a chick got fed when they reached the same height (Wilcoxon signed-ranks test: $z = -0.54$, $p = 0.59$). Thus, at equal heights, brown-headed cowbirds were no better at eliciting parental care than the host's young.

The feeding success of brown-headed cowbird chicks that hatched one or two days before yellow warbler chicks was significantly greater than that of brown-headed cowbirds chicks that hatched on the same day as the host's young (figure 4a). The greater success of older cowbird chicks was not related to their begging more intensively (Wilcoxon signed-ranks test: $z = -0.40$, $p = 0.69$; figure 4b) but to their size advantage, because the greater the age difference between the parasite and

Figure 4. Comparison between brown-headed cowbird chicks that were born the same day as the yellow warblers ($n=9$) versus chicks that were born one or two days before ($n=6$). Graph (a) shows the mean probability ($\pm$ s.e.) that the cowbird chicks of both groups got fed, (b) shows the difference in the mean begging intensity, and (c) shows the mean weight difference (cowbird weight minus warbler weight).

the host's young, the greater the mass difference ($z = -2.85$, $p = 0.004$; figure 4c).

4. DISCUSSION

In this study, the chick that reached higher was more likely to be fed, regardless of its species. Thus, parents seemed to follow a 'laissez-faire' strategy and fed the nearer chick (Teather 1992; McRae *et al.* 1993; Leonard *et*

al. 1994). The relative height reached by a chick is influenced by its size and begging intensity. When both chicks were placed at the same distance to the parent they had the same chances of getting fed, which indicates that neither body size nor begging intensity alone could explain who got fed. Cowbird chicks did not get fed preferentially unless they were the closest to the parent, and the same was true for the yellow warbler chicks.

The 'laissez-faire' strategy followed by yellow warblers was exploited by the parasitic chicks for their own advantage. Due to their bigger size and intense begging, the parasitic chicks always managed to place themselves close to the parents. Brown-headed cowbird chicks begged more intensively and started begging earlier than the host's young even though they received most of the feeds. This result (see Lichtenstein 1997) is consistent with the prediction of signalling models that suggest that greater level of solicitation is expected from individuals that do not have to pay the indirect cost of decreasing parental fitness (Johnstone & Grafen 1992; Godfray 1995), and it conforms to recent data demonstrating an increase in the begging levels when relatedness between nestmates is lowered (Briskie *et al.* 1994).

Following our definition, brown-headed cowbird chicks did not possess supernormal stimulus properties for this host. The success of the brown-headed cowbird chicks in getting fed in preference to the host young was simply related to their better competitive ability, which was due to their size advantage and intense begging. The larger and redder gape of the parasites had no influence upon their feeding success, as was demonstrated above when chicks were observed equidistant from the feeding host. Having a large size *per se* was not a supernormal stimulus either as the larger brown-headed cowbird chicks only got fed preferentially if they were closer to the parent than the yellow warbler chick. Size was important simply because the larger parasitic chicks were able to get closer to the host parent. The greater the age difference between the host and the parasite, the greater the size difference, and therefore the greater the success of the cowbirds.

Clark and Robertson (1981) found that the time of hatching of yellow warbler eggs relative to cowbird eggs is a key determinant of the yellow warbler fledging success. Mayfield (1960) found the same result with Kirtland's warblers (*D. kirtlandii*): chicks of this species were not adversely affected by the presence of the parasitic chick when they hatched two days before the cowbird; however, their survival was reduced if the cowbird hatched first. The success of the parasitic nestlings at nests of different host species depends on the relative size of the host's young in comparison with that of the cowbird nestlings (Weatherhead 1989). Competition with the parasitic chick has no effect on similar sized host species such as the song sparrow, *Melodia melospiza* (Smith 1981), and large ones such as Brewer's blackbirds or red-winged blackbirds, *Agelaius phoeniceus* (Friedmann *et al.* 1977; Weatherhead 1989; Røskoft *et al.* 1990).

(a) *Why brown-headed chicks have not evolved special adaptations to manipulate their hosts*

There has been no evidence in previous studies on the interaction between parasitic chicks and their foster parents to suggest parasitic chicks have to provide the

special stimuli necessary for acceptance. For example, hosts of the European cuckoo (Davies & Brooke 1988, 1989b) and the brown-headed cowbird (Eastzer *et al.* 1980) will accept other species in their nests as readily as those of their respective parasites. Nevertheless, parasitic chicks may have stimuli that increase the rate at which they are fed. Great spotted cuckoo chicks (*Clamator glandarius*) were fed more than smaller and similar sized magpies (*Pica pica*), and equally to much larger host young (Redondo 1993). Their success seems to stem from a combination of intense begging behaviour, conspicuous palatal papillae, and larger size (in natural situations) compared with their host's young (Soler *et al.* 1995a). The palatal papillae seemed to play a key role in their success, as chicks with their gapes painted received less food than the average magpie chick (Soler *et al.* 1995a). In contrast to the system studied here, great spotted cuckoos are specialist parasites, and magpies exhibit some chick discrimination (Soler *et al.* 1995b). Great spotted cuckoos did not fare as well when parasitizing a larger host, the carrion crow *Corvus corone* (Soler 1990), which suggests that they are not equally effective at manipulating all their hosts. Host specificity by brood parasites and discrimination by the hosts might be the requirements for parasitic chicks to evolve special adaptations.

The lack of special adaptations by brown-headed cowbird chicks is probably due to the lack of discrimination (a selective pressure) by their hosts. In the case of the European cuckoo, the degree of egg mimicry attained by different cuckoo species was shown to be related to the discriminatory ability of the hosts (Davies & Brooke 1989a). Dunnocks (*Prunella modularis*) show no discrimination, and cuckoos lay non-mimetic eggs in their nests.

The universal feature that avian parents share is to feed chicks that are begging very intensively (Smith & Montgomerie 1991; Redondo & Castro 1992; Teather 1992; Price & Ydenberg 1995; Leonard & Horn 1996) and chicks that place themselves close to the feeding parent. Large nestlings that beg very intensively get more feeds than their smaller nest companions (Redondo & Castro 1992; Kilner 1995; Price & Ydenberg 1995). In the absence of host discrimination, having a size advantage is enough for the cowbird chicks to elicit parental care and outcompete smaller nestmates.

In summary, the success of brown-headed cowbird chicks in getting fed was simply due to being able to get closer to the feeding adult than the host's young because of their larger size and intense begging. As small hosts seem to be constrained in their ability to discriminate against parasites, and brown-headed cowbirds are generalist parasites (which gives them the option to start parasitizing a new species if a host evolves anti-parasite defences), it is very unlikely that selection will result in special adaptations by brown-headed cowbird nestlings to get fed.

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