



Why brown-headed cowbirds do not influence red-winged blackbird parent behaviour

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Brown-headed cowbirds, *Molothrus ater*, frequently parasitize red-winged blackbirds, *Agelaius phoeniceus*. The presence of a brood parasite, unrelated to both host nestlings and parents, has provoked speculation regarding within-brood food allocation and parental provisioning. This study is the first to compare directly the effect of brood parasitism on host parent and offspring behaviour in younger and older broods. We videotaped 28 unparasitized red-winged blackbird broods and compared them to 22 parasitized broods. Red-winged blackbird nestling begging appears largely unaffected by cowbird parasitism. The presence of the cowbird in the nest affected neither the latency nor duration of host nestling begging, but stimulated more frequent begging by red-winged blackbird nestlings following food distribution. Begging by cowbirds was unique in two ways: (1) cowbirds maintained a consistent begging effort throughout the nestling period (but did not receive a consistent food share); and (2) cowbirds begged longer and more frequently following the allocation of food. Persistent begging by the cowbird following the allocation of food has implications for the division of parental care, if by doing so the brood parasite is able to provoke the foster parent to increase provisioning, at the expense of brooding. We found no evidence for the adjustment of parental care. Neither the foraging rates nor the lengths of the parental feeding visits differed markedly between parasitized and unparasitized broods.

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Avian brood parasites lay their eggs in the nests of other birds and leave all further parental care to the host (Rothstein 1975). As brood parasite nestlings are unrelated to their host nestmates, and are therefore theoretically unconstrained by kin selection (Hamilton 1964), they are considered models for the evolution of selfishness. In particular, the conspicuous and persistent begging displays of nestling brood parasites (Nice 1939; Gochfeld 1979; Eastzer et al. 1980; Woodward 1983; Broughton et al. 1987; Briskie et al. 1994) have been the focus of this work.

Empirical work on altricial passerines shows that nestlings may adjust their begging effort in accordance with the duration (e.g. Smith & Montgomerie 1991; Price & Ydenberg 1995; but see Cotton et al. 1996) and intensity (e.g. Price & Ydenberg 1995; Leonard & Horn 1998; but see Kacelnik et al. 1995; Cotton et al. 1996; Leonard & Horn 1996) of begging by nestmates, although results vary (see recent reviews in Budden & Wright 2001; Wright & Leonard 2002). Whereas begging games among relatives are expected to be tempered by kin selection

(review in Mock & Parker 1997), game theoretical models predict greater begging intensity by brood parasites because they are unrelated to host nestlings (Harper 1986; Motro 1989). The brown-headed cowbird, *Molothrus ater*, is a generalist, obligate brood parasite, meaning that the female lays its eggs in the nests of other species, and leaves the foster parents to rear the foreign nestling (Rothstein 1975). Brown-headed cowbird nestlings begin begging sooner; beg longer; and beg at a higher intensity than host nestlings of similar age, regardless of the relative size difference between species (Dearborn 1998; Lichtenstein & Sealy 1998). Furthermore, there is evidence that host nestlings in parasitized broods increase their begging effort relative to unparasitized broods, to which parents respond by increasing provisioning (e.g. Dearborn et al. 1998).

Red-winged blackbird, *Agelaius phoeniceus*, parents reduce the time they spend at unparasitized nests midway through the nestling period, evidently in response to the escalated demands that accompany brood homeothermy (Hill & Beaver 1982; Olson 1992; Glassey 2000). If parents use nestling begging effort to schedule food deliveries, the brood parasite may provoke the foster parent to increase provisioning, at the expense of brooding. As multiple

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parasitism is rare (see below) cowbirds generally remain in the minority within the brood. Consequently, for the brood parasite to effect an increase in parental foraging, it must provoke a concerted increase in brood begging effort, either indirectly, through a reduction in food intake of host nestlings, or directly, by stimulating a behavioural response through its own begging efforts. Otherwise, the brood parasite must mimic an increased group effort through its own vocal begging behaviour, as occurs in cuckoos (Davies et al. 1998).

In this paper we examine the begging behaviour of a brood parasite, the brown-headed cowbird, and one of its many hosts, the red-winged blackbird, during two stages of the nestling period. Most studies that have assessed cowbird behaviour have focused on older nestlings or fledglings (Nice 1939; Gochfeld 1979; Eastzer et al. 1980; Woodward 1983; Broughton et al. 1987; Briskie et al. 1994; but see Dearborn et al. 1998; Lichtenstein & Sealy 1998), and a direct comparison between broods of different ages has been lacking. Consequently, little is known regarding the ontogeny of begging by cowbirds, or whether the presence of a cowbird affects the behaviour of host parents and offspring differently across the nestling period. Here we address three questions. First, does the begging behaviour of a cowbird differ from that of the host nestling, and if so, how? Second, does the presence of a cowbird directly or indirectly influence the begging behaviour of host nestlings, and if so, is the effect consistent in younger and older broods? And third, does the presence of a cowbird alter schedules of parental behaviour? Do, for example, parents provision more and brood less at parasitized broods?

METHODS

We studied red-winged blackbirds in wetlands near Winnipeg, Manitoba during late April–late July, 1993–1999. Five to 15% of clutches were naturally parasitized by cowbirds each year. Daily observations of clutches were made during the incubation period. An egg was considered to have been removed by a female cowbird if it was missing on the same day that the cowbird egg appeared in the nest. We surveyed broods daily after the eggs hatched, and recorded nestling mass to the nearest 0.1 g using an electronic balance. We studied the behaviour of nestlings and parent blackbirds by videotaping 22 parasitized broods and 28 unparasitized broods ranging in age between 2 and 8 days (hatch=day 0). None of the 22 parasitized nests contained more than one cowbird nestling. Of the 22 parasitized broods, six were parasitized experimentally as a control for potential preferential selection of host broods by cowbird females (e.g. Smith 1981), although a review by Lea & Kattan (1998) suggests that cowbirds deposit their eggs randomly in red-winged blackbird nests. A single host egg was removed by us from one of the six (16.7%) experimentally parasitized nests to mimic the behaviour of the cowbird. Host eggs were removed from the remaining four (25%) naturally parasitized broods, presumably by the cowbird female. Although egg removal resulted in significantly fewer red-winged blackbird nestlings in parasitized broods

(independent t test: $t_{51} = -4.19$, $P < 0.001$; $\bar{X} \pm \text{SE}$: parasitized: 2.56 ± 0.14 ; unparasitized: 3.32 ± 0.12), the addition of the cowbird maintained the total brood size (independent t test: $t_{51} = 1.31$, $P = 0.20$; $\bar{X} \pm \text{SE}$: parasitized: 3.56 ± 0.14 ; unparasitized: 3.32 ± 0.12) near that of unparasitized broods.

Brood age was standardized as the age of the oldest red-winged blackbird nestling. We classified broods as 'younger' (oldest red-winged blackbird nestling < 5 days) or 'older' (oldest red-winged blackbird nestling ≥ 5 days) following Hill & Beaver (1982), Clark & Lee (1998) and Glassey (2000). Video cameras were set up 1.5–3 m from nests and 2 h of videotape was recorded at each nest. Each nest was videotaped only once, between 0900 and 1500 Central Standard Time, so that each nest represented one independent data point. Parasitized and unparasitized broods were videotaped during the same time period (mid-June to mid-July), under fair-weather conditions. Independent t tests revealed no detectable difference in ambient temperature between days on which parasitized and unparasitized broods were filmed ($t_{41} = -0.51$, $P = 0.61$; $\bar{X} \pm \text{SE}$: parasitized: 18.8 ± 1.03 ; unparasitized: 18.0 ± 1.0), or between naturally and experimentally parasitized brood taping days ($t_{18} = -1.03$, $P = 0.32$; $\bar{X} \pm \text{SE}$: experimentally parasitized: 18.0 ± 1.14 ; naturally parasitized: 20.2 ± 2.1). Mean daily ambient temperatures were supplied by Environment Canada, Winnipeg Airport substation, about 3 km from the field sites.

The videotapes were analysed using a ColorTrak stereomonitor, with a remote-control and freeze-frame mechanism. We analysed only the second hour of taping, when the adults were presumably habituated to the presence of the camera (in most cases, parents resumed feeding of nestlings within minutes of the camera being set up near the nest). In a minority of cases, the female parent was 'camera-shy' and the taping session was discontinued. These data are not included here.

We analysed nestling behaviour from all feeding visits during the second hour of taping (with the exception of those few visits on which the parent blocked the nestling from view) from each videotaped brood on a frame-by-frame basis, and used the mean hourly data from each nest for analysis.

Natural History

Red-winged blackbirds are an 'acceptor' species, meaning that eggs are not normally removed and rates of host nestling success are high (Rothstein 1975; Weatherhead 1989; Røskaft et al. 1990). Despite the frequent removal of one host egg by the cowbird female, the number of red-winged blackbird nestlings fledged from parasitized broods is generally equal to or greater than the number fledged from unparasitized broods in the same population (Weatherhead 1989; Røskaft et al. 1990). Similarly, despite the size advantage of its host, the cowbird is generally able to fledge successfully from nests of red-winged blackbirds (Ortega & Cruz 1988, 1991; Weatherhead 1989; Røskaft et al. 1990). Red-winged blackbirds are moderately larger than cowbirds and both species are sexually dimorphic (Fiala & Congdon 1983;

Weatherhead 1989). The cowbird reaches a mass asymptote comparable to the female blackbird, but less than that of the male (Williams 1940; Norris 1947; Orians 1980), although considerable geographical variation exists. By day 6 a cowbird is roughly the same size as a female red-winged blackbird nestling.

Parental Behaviour

We measured (1) hourly number of visits and (2) visit duration. Visits were identified as thermal visits (female broods or shades nest) or feeding visits (visits on which food was provided by the female or male, or on which the female provided both food and thermal care). Provisioning by males accounted for 8% of feeding visits to unparasitized broods, and 2% of feeding visits to parasitized broods. Nestling behavioural data were gathered from two phases of the feeding visit: (1) the feeding phase, between the parent's arrival and allocation of the last food item; and (2) the nonfeeding phase, from allocation of the last food item until the departure of the parent.

Nestling Behaviour

For each visit during a 1-h span we measured four indices of 'primary begging response' (sensu M. L. Leonard & A. Horn, personal communication), defined as begging behaviour (gaping and/or neck stretching) initiated in response to the arrival of a food-bearing parent at the nest. Although begging was often accompanied by vocalizations, we were unable to reliably determine which specific nestling called in each case. Therefore, we did not differentiate between begging while vocalizing and begging silently. First, latency to beg was defined as the amount of time between the arrival of the parent on the nest rim and the initiation of begging. A negative latency indicates that begging commenced before the parent's arrival at the nest. Second, frequency of begging was defined separately for the feeding and nonfeeding phases as the proportion of visits/h during which a nestling begged (proportion of visits with begging/h), and the proportion of visits/h during which a nestling continued to beg following the allocation of food (proportion of visits with continued begging/h). Third, the duration of begging was defined as the total length of time that a nestling begged during a visit. Begging duration was subdivided into two measurements: the length of time that nestlings begged during the feeding phase (pretotal begging duration); and the length of time nestlings continued to beg during the nonfeeding phase (continued begging duration). Fourth, the intensity of begging was scored when the parent arrived at the nest, as follows: 0 (not begging), 1 (gaping), or 2 (gaping with neck stretched) (e.g. Cotton et al. 1999). The sides of the nest cup often blocked leg and wing activity, precluding the use of a scoring system that included these measures.

A feeding visit was defined as the arrival of a parent carrying food to the nest, and the foraging rate was defined as the number of hourly feeding visits. Food loads usually consisted of one large, or primary item, although

sometimes smaller prey items or fragments that had broken off from the primary item were also distributed. We did not attempt to identify prey. Individual food consumption was measured as the number of primary food items consumed, because in this population, mass gain is positively correlated with consumption of the primary food item (see Glassey & Forbes 2002).

We randomly selected a red-winged blackbird nestling from each parasitized brood for comparison with the cowbird nestling and then compared the mean begging behaviour of the nestlings over a 1-h observation period. We performed a second, separate analysis on a subset of older, parasitized broods to compare directly the cowbird nestling with a randomly selected female blackbird nestling. Nestlings were sexed using mass at day 8 obtained from census data (Forbes & Glassey 2000). Given that some broods were comprised solely of males, and other broods did not survive to day 8, this analysis was limited to seven broods.

Nestlings sometimes initiate begging in response to jostling of the nest by the departing parent or to external stimuli in the absence of the parent (Clemmons 1995; Budden & Wright 2001; Leonard & Horn 2001). As our study focused specifically on begging initiated by the arrival of a food-bearing parent, we deliberately excluded these types of begging from our analysis.

To avoid pseudoreplication (Hurlbert 1984), we averaged the values for each behavioural variable for each nestling over the entire 1-h observation period. We also generated a single, average value per brood for the host nestlings for each behavioural index. All values are reported as $\bar{X} \pm \text{SE}$. All *P* values are two tailed. Proportions were arcsine square-root transformed prior to analysis.

RESULTS

Parental Behaviour

Experimental versus naturally parasitized broods

An independent *t* test revealed no discernable differences between experimentally and naturally parasitized broods in terms of total brood size ($t_{20} = -1.127$, $P = 0.273$), brood age ($t_{20} = 0.094$, $P = 0.92$), or parental behaviour (visits/h: $t_{20} = 1.66$, $P = 0.11$; length of parental visits (min): $t_{20} = -1.00$, $P = 0.33$; thermal care/h (min): $t_{20} = -1.61$, $P = 0.12$), although with modest sample sizes, we cannot reject the possibility of subtle differences as statistical power was low ($1 - \beta$ ranged between 0.14 and 0.49). The age spread was significantly wider in naturally parasitized broods ($\bar{X} \pm \text{SE}$ difference = -0.83 ± 0.35 ; $t_{20} = -2.37$, $P = 0.028$). Parents fed nestlings on all visits; thermal care was infrequently provided following the distribution of food (feeding visits with thermal care/h: $t_{20} = -0.71$, $P = 0.49$). To provide more power in differentiating parasitized and unparasitized categories, we pooled the data from naturally and experimentally parasitized broods.

In a second analysis, restricted to parasitized broods and using pooled data, we compared the hatching status of the cowbird nestling relative to the oldest host nestling. The cowbird was ranked as -1 (hatching after

Table 1. Results of multiple regression analysis to determine which characteristics (brood age, presence of cowbird, hatch spread, total brood size, mean daily temperature) contributed to visit length and foraging rate

Parameter	B	SE	t	P
Visit length (min)				
Brood age (days)	-0.15	0.04	-4.03	<0.001
Presence of cowbird	0.14	0.11	1.22	0.23
Brood size	-0.19	0.11	-1.70	0.10
Hatch spread	0.02	0.08	0.23	0.82
Average daily temperature (°C)	-0.01	0.012	-0.54	0.59
Overall adjusted $R^2=0.24$, $P=0.004$				
Best-fit adjusted $R^2=0.233$, $P<0.001$				
Foraging rate (visits/h)				
Brood age (days)	1.52	0.55	2.75	0.01
Presence of cowbird	1.55	1.67	0.93	0.36
Brood size	2.48	1.66	1.49	0.14
Hatch spread	-0.84	1.24	-0.67	0.50
Average daily temperature (°C)	0.26	0.18	1.44	0.16
Overall adjusted $R^2=0.09$, $P=0.100$				
Best-fit adjusted $R^2=0.08$, $P=0.030$				

host nestling), 0 (hatching on same day) or +1 (hatching prior to host nestling). Generally, cowbirds hatched on the same day as the oldest host nestling (Mann-Whitney U test: $U=37.50$, $N_1=16$, $N_2=6$, $P=0.39$).

Parasitized versus unparasitized broods

We assessed the relationship between two dependent variables, the length and frequency of feeding visits, against the following independent variables: brood age (as determined by the age of the oldest host nestling); total brood size (redwing plus cowbird); total hatch spread (in days between hatching of the first and the last nestling, cowbird included); mean daily ambient temperature (°C); and brood type (parasitized versus unparasitized entered as a dummy variable) using multiple regression. Cowbirds consistently hatching before (hatch rank = +1) or after (hatch rank = -1) host nestlings would change the total hatch spread. We therefore used the total hatch spread to measure indirectly whether the hatch rank of the cowbird affected parental behaviour. Parents made longer visits to younger broods (Table 1). Similarly, parents foraged more frequently when broods were older, regardless of whether a cowbird was present in the nest (Table 1). Consistent with previous studies of red-winged blackbirds (Hill & Beaver 1982; Glassey 2000), a reduction in the length of the parental visits occurred on day 5 (Fig. 1), which resulted in parents spending significantly less time at the nest when broods were older, regardless of whether or not a cowbird was present (Table 2).

We used a two-way analysis of variance (ANOVA) to test for effects of brood type (parasitized versus unparasitized) and brood stage (younger versus older) on parental behaviour. The presence of a brood parasite did not significantly affect parental effort ($1 - \beta < 0.22$ in all cases), and there was no significant interaction. Parents made significantly more foraging trips to older broods, but remained for less time (Table 2). The majority of parental visits to both parasitized and unparasitized broods involved food delivery to the brood. Females provided little thermal care, even when broods were young.

Roughly 35 s of thermal care per hour was provided to young broods, an amount that decreased significantly to a maximum of about 5 s/h at older broods. With the exception of one 4-day-old brood, at which exclusively thermal care was provided on two visits, females brooded or shaded the nest only after feeding the nestlings.

Offspring Behaviour

Host nestling behaviour: parasitized versus unparasitized broods

We assessed whether host nestlings in younger and older broods modified their behaviour in response to the presence of a cowbird by comparing the begging behaviour of a randomly selected red-winged blackbird nestling from unparasitized broods to a randomly selected red-winged blackbird nestling from parasitized broods.

We used a two-way ANOVA to test for effects of brood type (parasitized versus unparasitized broods) and brood stage (younger versus older) on nestling begging behaviour. We found no difference between the begging behaviour of red-winged blackbird nestlings from parasitized and unparasitized broods, with the exception of continued begging duration (pretotal begging duration: $F_{1,50}=0.12$, $P=0.73$; latency to beg: $F_{1,50}=0.43$, $P=0.51$; proportion of visits with begging: $F_{1,50}=0.95$, $P=0.33$; proportion of visits with continued begging: $F_{1,50}=0.92$, $P=0.34$). Specifically, nestlings from parasitized broods tended to beg longer after feeding than those from unparasitized broods, a difference that approached significance (brood type: $F_{1,50}=3.35$, $P=0.074$, $1 - \beta=0.43$, interaction: $F_{1,50}=0.18$, $P=0.67$).

The majority of behaviours showed age-related changes in performance, probably due to changes in nestling physiology, which accompany age. Nestlings from older broods responded to the arrival of the parent by begging on proportionately more visits (brood stage: $F_{1,50}=8.86$, $P=0.005$; brood type: $F_{1,50}=0.95$, $P=0.33$; interaction: $F_{1,50}=0.012$, $P=0.91$; Fig. 2a), and continued to beg on a

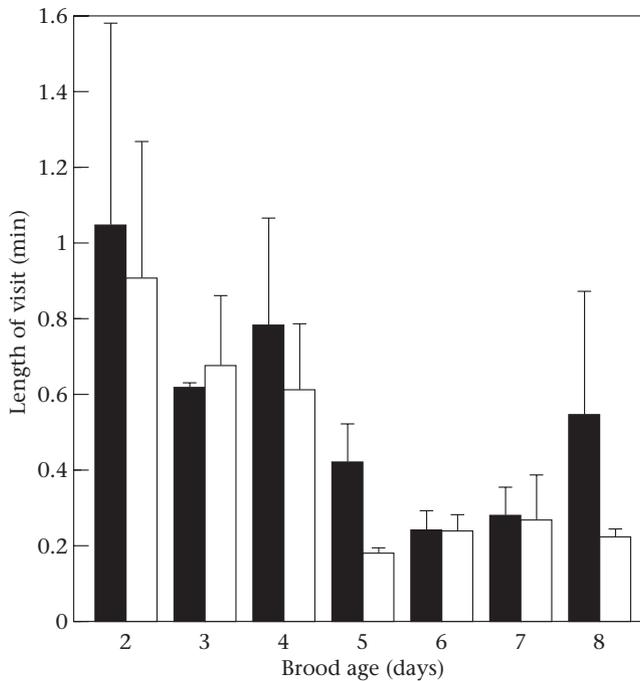


Figure 1. The length ($\bar{X} \pm SE$) of parental feeding visits to parasitized (■) and unparasitized (□) red-winged blackbird broods over the nestling period.

greater proportion of visits following the allocation of food (brood stage: $F_{1,50}=9.06$, $P=0.004$; brood type: $F_{1,50}=0.92$, $P=0.34$; interaction: $F_{1,50}=0.001$, $P=0.98$; Fig. 3a). There was a nonsignificant tendency for nestlings in older broods to stretch their necks higher while begging (Wilcoxon matched-pairs signed-ranks test: younger:

$T=-1.27$, $N=10$, $P=0.20$; older: $T=-1.76$, $N=18$, $P=0.078$; Fig. 2b).

In contrast, begging latency (brood stage: $F_{1,50}=0.86$, $P=0.36$; brood type: $F_{1,50}=0.43$, $P=0.51$; interaction: $F_{1,50}=0.40$, $P=0.53$; Fig. 2c), and the length of time nestlings begged, both while food was being allocated (brood stage: $F_{1,50}=2.68$, $P=0.11$; brood type: $F_{1,50}=0.12$, $P=0.73$; interaction: $F_{1,50}=1.92$, $P=0.17$; Fig. 2d) and after (brood stage: $F_{1,50}<0.001$, $P=0.99$; Fig. 3b), remained consistent across stages.

Brood behaviour: parasitized versus unparasitized broods

We used a two-way ANOVA to test for effects of brood type (parasitized versus unparasitized) and brood stage (younger versus older) on the behaviour of the brood. There was no brood type effect for any behavioural variable, with the exception of the frequency of continued begging (pretotal begging duration: $F_{1,50}=0.615$, $P=0.44$; latency: $F_{1,50}=0.07$, $P=0.79$; proportion of visits with begging: $F_{1,50}=0.27$, $P=0.60$; proportion of visits with continued begging: $F_{1,50}=0.27$, $P=0.60$; intensity: Mann-Whitney U test: $U=278.50$, $N_1=28$, $N_2=22$, $P=0.56$; Figs 4a–d, 5a, b). Specifically, proportionately more nestlings continued to beg following the allocation of food in parasitized broods relative to unparasitized broods (brood type: $F_{1,50}=6.37$, $P=0.015$; interaction: $F_{1,50}=0.49$, $P=0.49$; Fig. 5a). The effect was maintained when the analysis was restricted to a comparison of the average begging frequency of host nestlings from parasitized broods against unparasitized broods (brood type: $F_{1,50}=4.39$, $P=0.042$), indicating that it was not solely the behaviour of the cowbird that contributed to this result.

Table 2. The frequency (visits/h) and duration (min) of parental care (thermal and feeding visits) to younger and older parasitized and unparasitized broods

Parental behaviour	Younger broods $\bar{X} \pm SE$	Older broods $\bar{X} \pm SE$	$F_{1,50}$	P
Thermal visits				
Frequency (during a feeding visit or exclusively)				
Parasitized	1.45±0.55	1.00±0.82	0.09	0.769
Unparasitized	2.00±0.45	0.17±0.12		
Duration				
Parasitized	0.41±0.18	0.09±0.06	11.36	0.002
Unparasitized	0.34±0.11	0.01±0.01		
Feeding visits				
Frequency (with thermal care or exclusively)				
Parasitized	15.36±1.72	17.55±1.27	5.01	0.030
Unparasitized	12.00±1.28	17.39±1.72		
Duration				
Parasitized	0.83±0.11	0.37±0.11	15.85	<0.001
Unparasitized	0.63±0.12	0.23±0.09		
Total				
Frequency				
Parasitized	15.36±1.72	17.55±1.27	4.09	0.049
Unparasitized	12.50±1.29	17.39±1.72		
Duration				
Parasitized	0.83±0.20	0.37±0.07	17.86	<0.001
Unparasitized	0.70±0.11	0.23±0.04		

ANOVA values given for analysis of younger versus older broods.

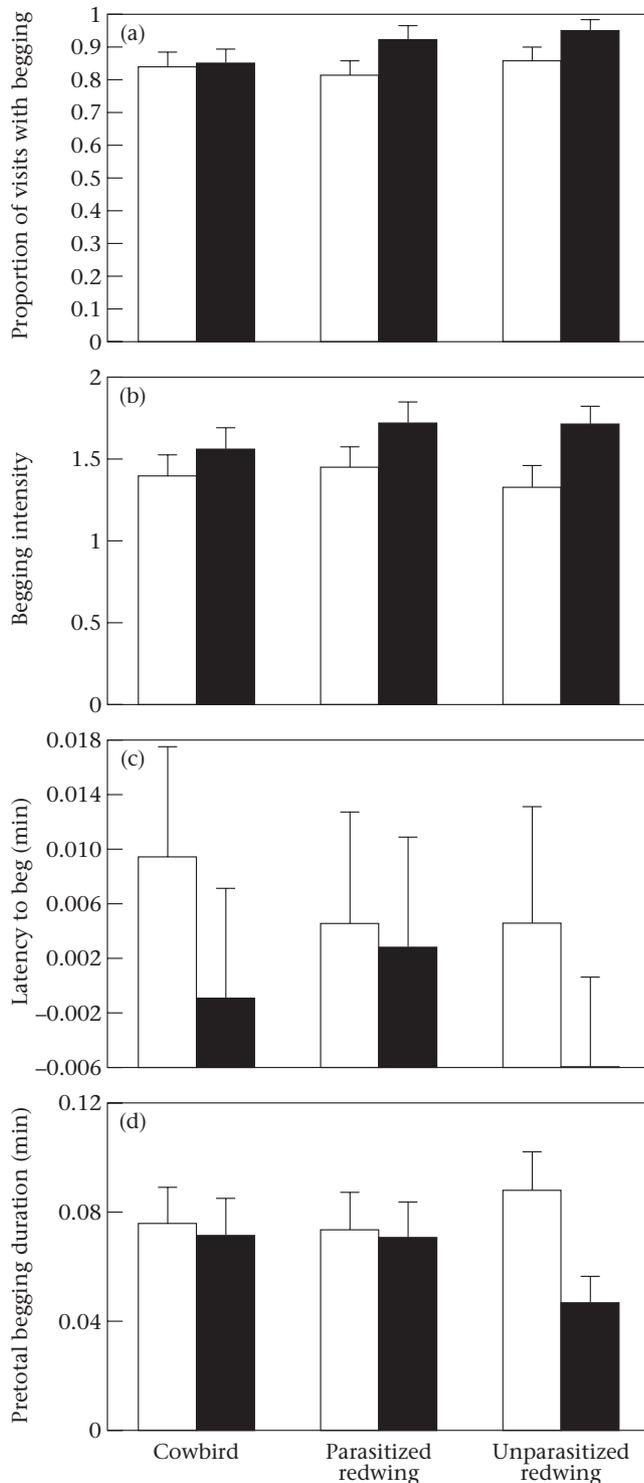


Figure 2. The mean+SE begging behaviour by cowbird nestlings and parasitized and unparasitized red-winged blackbird nestlings from younger (\square) and older (\blacksquare) broods during the feeding phase. Begging was measured as: (a) the proportion of visits with begging; (b) begging intensity; (c) latency to beg (min); and (d) pretotal begging duration (min).

On average, a greater proportion of nestlings begged, and at higher intensity, in older broods (pretotal begging duration: $F_{1,50}=3.39$, $P=0.072$, $1-\beta=0.44$; proportion of

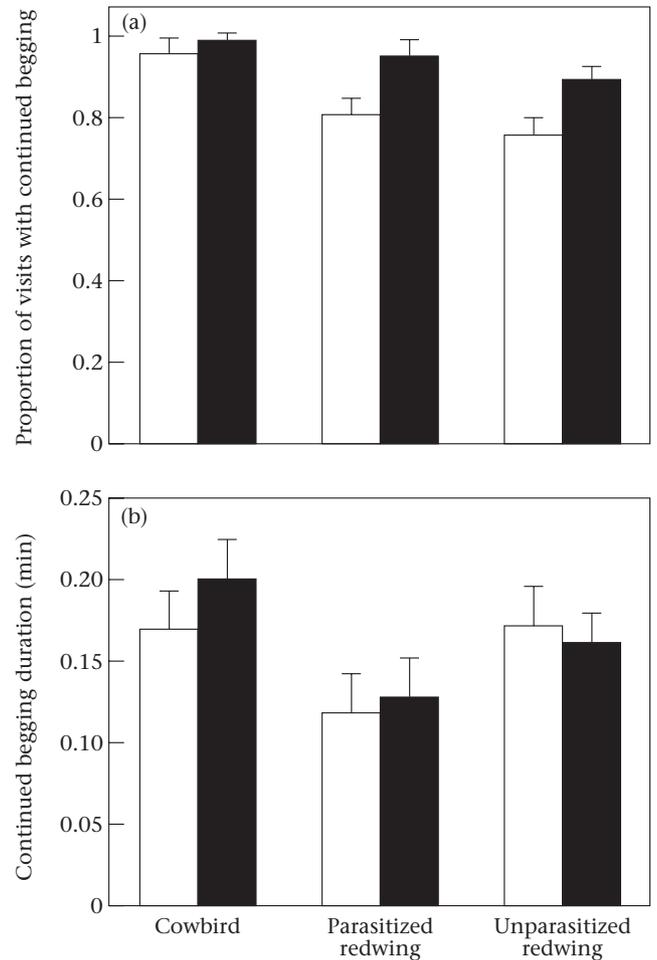


Figure 3. The mean+SE begging behaviour by cowbird nestlings and parasitized and unparasitized red-winged blackbird nestlings from younger (\square) and older (\blacksquare) broods during the nonfeeding phase. Begging was measured as: (a) the proportion of visits with continued begging and (b) continued begging duration (min).

visits with begging: $F_{1,50}=10.33$, $P=0.002$; proportion of visits with continued begging: $F_{1,50}=14.38$, $P<0.001$; begging intensity: Mann-Whitney U test: $U=143.50$, $N_1=28$, $N_2=22$, $P=0.021$; Figs 4a, b, d, 5a). The latency to beg did not change significantly with brood age, and continued begging duration was consistent over the nestling period (latency to beg: $F_{1,50}=2.98$, $P=0.09$, $1-\beta=0.39$; continued begging duration: $F_{1,50}=0.23$, $P=0.64$; Figs 4c, 5b).

Behaviour of host versus cowbird nestling within parasitized broods

Begging behaviour of the cowbird versus a randomly selected redwing. We used a paired-samples t test to compare directly begging behaviour of the cowbird and a randomly selected host nestling within younger and older parasitized broods. Cowbird nestlings were virtually the same size ($\bar{X} \pm \text{SE}$ difference: younger: -0.21 ± 1.63 g; paired t test: $t_{10} = -0.13$, $P=0.90$; older: 2.68 ± 2.15 g; $t_{10}=1.25$, $P=0.24$) and age (younger:

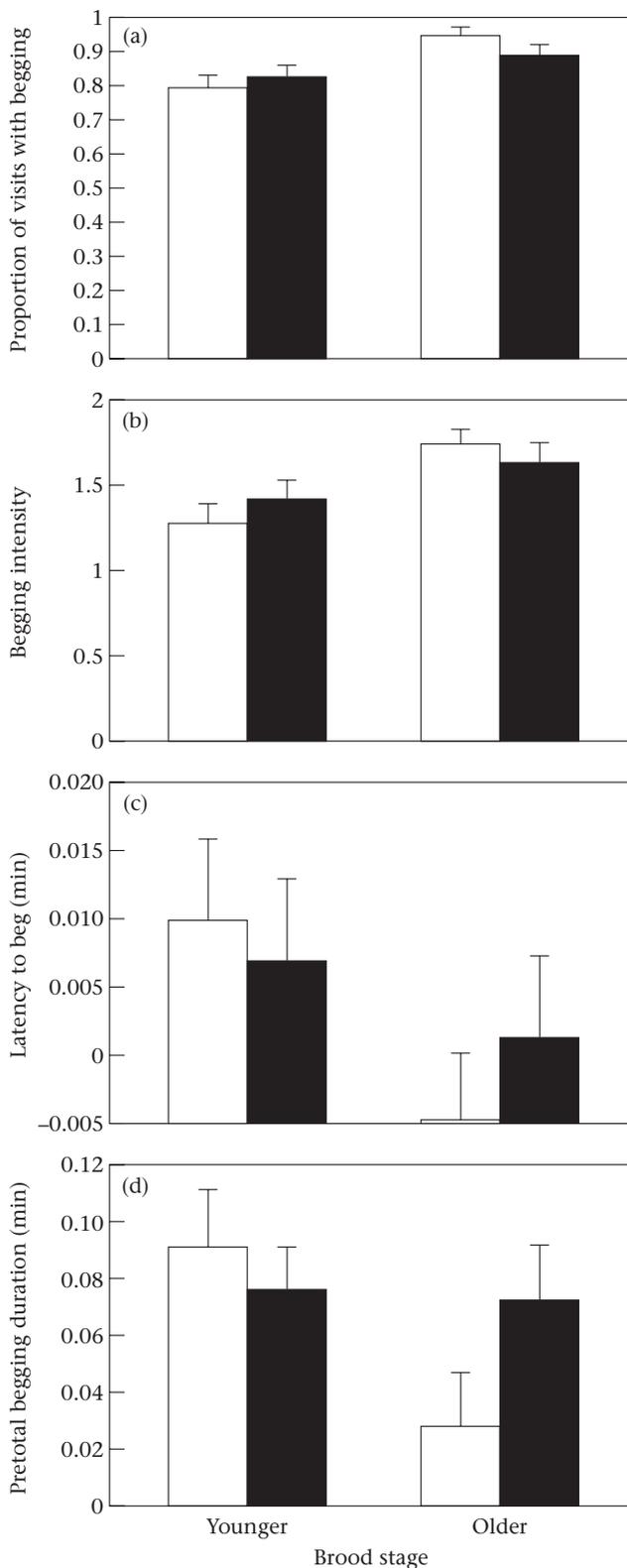


Figure 4. The mean+SE cumulative begging behaviour by parasitized (■) versus unparasitized (□) red-winged blackbird broods during the feeding phase. Begging was measured as: (a) the proportion of visits with begging; (b) begging intensity; (c) latency to beg (min); and (d) pretotal begging duration (min).

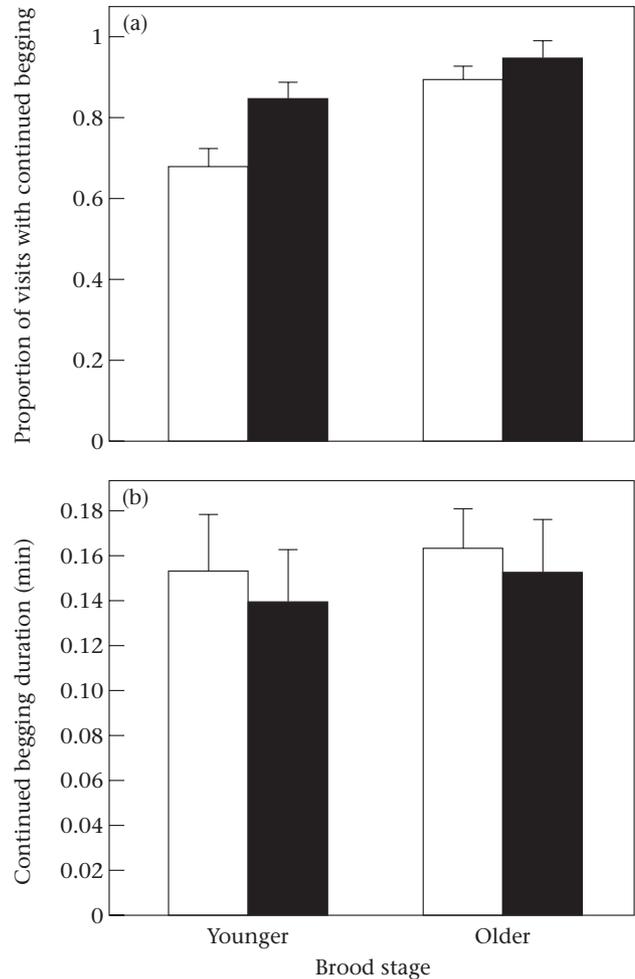


Figure 5. The mean+SE cumulative begging behaviour by parasitized (■) versus unparasitized (□) red-winged blackbird broods during the nonfeeding phase. Begging was measured as: (a) the proportion of visits with continued begging and (b) continued begging duration (min).

-0.27 ± 0.33 days; $t_{10} = -0.82$, $P=0.43$; older: -0.18 ± 0.30 days; $t_{10} = -0.61$, $P=0.55$) as the paired redwing nestling in both younger and older broods.

We found no detectable difference between the mean begging behaviour of randomly selected host nestlings and the behaviour of the cowbird nestling during the feeding phase. The frequency with which host and cowbird nestlings responded to the arrival of the parent remained consistent over the nestling period (younger: $t_{11} = -0.83$, $P=0.43$; older: $t_{11} = 1.34$, $P=0.21$; Fig. 2a). Similarly, latency to beg was short for both species, as all nestlings within a brood generally began begging when the parent arrived on the nest rim (younger: $t_{11} = -0.41$, $P=0.69$; older: $t_{11} = 1.42$, $P=0.19$; Fig. 2c). Begging intensity did not change with age, as both species stretched their necks while gaping (Wilcoxon matched-pairs signed-ranks test: younger: $T = -0.10$, $N=11$, $P=0.92$; older: $T = -1.26$, $N=11$, $P=0.21$; Fig. 2b). Nestlings did not differ significantly in the amount of time spent begging while food was being allocated (paired t test:

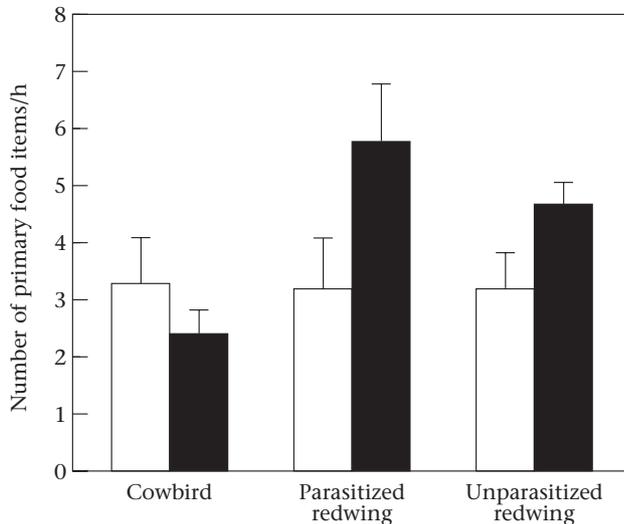


Figure 6. Food reception ($\bar{X} \pm SE$) by cowbird nestlings and parasitized and unparasitized red-winged blackbird nestlings from younger (□) and older (■) broods. Food consumption was measured as the number of primary food items/h received by a nestling.

younger: $t_{11} = -0.18$, $P=0.86$; older: $t_{11} = -0.40$, $P=0.70$; Fig. 2d).

In contrast, there was a substantial difference between the begging behaviour of cowbirds and redwing nestlings during the nonfeeding phase, particularly in older broods. Cowbirds more frequently continued begging after food was allocated (younger: $t_{11} = -2.62$, $P=0.026$; older: $t_{11} = -2.34$, $P=0.041$; Fig. 3a). As well, the duration of continued begging by the cowbird consistently exceeded begging by host nestlings (younger: $t_{11} = -2.16$, $P=0.056$; older: $t_{11} = -3.85$, $P=0.003$; Fig. 3b), which resulted in lengthier overall begging by the cowbird (younger: $t_{11} = -2.13$, $P=0.059$; older: $t_{11} = -4.31$, $P=0.002$). The begging behaviour of the cowbird was consistent across the nestling period (multiple regression: continued begging duration: $F_{1,23}=0.23$, $P=0.63$; pretotal begging duration: $F_{1,23}=2.31$, $P=0.14$; latency to beg: $F_{1,23}=0.46$, $P=0.51$; proportion of visits with begging: $F_{1,23}=1.03$, $P=0.32$; proportion of visits with continued begging: $F_{1,23}=0.60$, $P=0.45$; Spearman rank correlation: begging intensity: younger versus older $r_s=0.08$, $N=22$, $P=0.38$).

Food reception by the cowbird versus a randomly selected redwing. Food reception by host and parasite differed in younger and older broods. Whereas the number of primary food items received by the cowbird and redwing were virtually equivalent in younger broods (paired t test: $t_{10}=0.001$, $P=1.00$), host nestlings received a significantly greater share than the cowbird in older broods ($t_{10}=2.60$, $P=0.027$; Fig. 6). In contrast to cowbird nestlings that received the same number of primary food items, regardless of brood stage ($\bar{X} \pm SE$ difference: younger versus older broods: 0.91 ± 0.93 ; independent t test: $t_{20}=0.98$, $P=0.34$), there was a nonsignificant tendency for the number of primary food items received by red-winged blackbird nestlings to increase in older broods

(younger versus older broods: -2.55 ± 1.35 ; $t_{20} = -1.89$, $P=0.074$; Fig. 6). This tendency was also apparent in unparasitized broods, where nestlings received significantly more primary food items in older broods (younger versus older broods: -1.52 ± 0.71 ; $t_{26} = -2.157$, $P=0.040$; Fig. 6).

To determine whether nestlings were offered more food than they consumed, we differentiated between the number of food items that were placed in a nestling's gaping mouth, but subsequently removed and fed to another nestling (offered first), and food items that were placed in a nestling's mouth, and swallowed (fed first). Cowbird nestlings were offered essentially the same number of primary food items per hour as they consumed in both younger broods (offered first: 3.36 ± 0.83 ; fed first: 3.18 ± 0.84 ; paired t test: $t_{10}=1.491$, $P=0.167$) and older broods (offered first: 2.55 ± 0.45 ; fed first: 2.27 ± 0.38 ; $t_{10}=1.40$, $P=0.19$). Redwing nestlings, conversely, were offered more food items per hour than they consumed, and in older broods, the difference approached significance (younger broods: offered first: 3.45 ± 0.87 ; fed first: 3.18 ± 0.80 ; $t_{10}=1.94$, $P=0.082$; older broods: offered first: 6.36 ± 1.05 ; fed first: 5.55 ± 1.05 ; $t_{10}=2.17$, $P=0.055$).

Begging behaviour and food reception by the cowbird versus a female redwing from older broods. With the exception of continuing to beg for a longer duration than a similarly sized female red-winged blackbird nestling, the begging behaviour of the cowbird did not differ from that of the host (Table 3). Similarly, both the cowbird and female redwing received the same food share. These results should be interpreted with caution, however, as the power of the analysis was low due to the small sample sizes (Table 3).

DISCUSSION

Do Cowbirds Affect Host Nestling Behaviour?

Begging by cowbirds differed from that of nestling blackbirds in two ways. First, cowbirds begged longer, particularly following the allocation of food. Second, cowbirds more frequently continued to beg following allocation of food.

Did this affect the behaviour of host nestlings? Prior to food distribution, the answer is no. But begging by the cowbird did have an effect on host behaviour following food distribution. Cowbirds persisted in begging after the brood was fed, often by themselves. This continued begging by the parasite induced host nestlings to beg after food was allocated more often than in unparasitized nests, although they sustained the effort for less time than the cowbird. Nestling blackbirds may have stopped begging earlier because they were physiologically unable to sustain the effort, particularly when young (Choi & Bakken 1990), or because they were satiated (e.g. Price 1994). Host nestlings in younger broods may pay an energetic cost for begging more frequently following the distribution of food (Leach & Leonard 1996; McCarty

Table 3. The begging behaviour of a cowbird versus a female red-winged blackbird nestling from older parasitized broods

Variable	$\bar{X} \pm \text{SE}$	Paired t_6	P	Power (1- β)
Mass				
Redwing	23.36 \pm 1.33	1.57	0.168	0.36
Cowbird	18.67 \pm 2.82			
Number of primary food items received				
Redwing	6.43 \pm 1.51	2.00	0.092	0.14
Cowbird	2.43 \pm 0.57			
Behaviour: feeding phase				
Pretotal begging duration (min)				
Redwing	0.06 \pm 0.02	-0.61	0.563	0.05
Cowbird	0.06 \pm 0.02			
Proportion of visits with begging				
Redwing	0.92 \pm 0.04	0.74	0.486	0.56
Cowbird	0.86 \pm 0.07			
Latency to beg (min)				
Redwing	0.01 \pm 0.01	1.89	0.108	0.13
Cowbird	0.00 \pm 0.01			
Begging intensity*				
Redwing	1.65 \pm 0.17		0.686	0.06
Cowbird	1.56 \pm 0.23			
Behaviour: nonfeeding phase				
Continued begging duration (min)				
Redwing	0.13 \pm 0.02	-2.37	0.056	0.83
Cowbird	0.19 \pm 0.01			
Proportion of visits with continued begging				
Redwing	0.93 \pm 0.03	-2.09	0.081	0.05
Cowbird	0.99 \pm 0.01			

*Wilcoxon matched-pairs signed-ranks test: $T = -0.41$, $N = 7$.

1996; Bachman & Chappell 1998). However, given that cowbird parasitism has virtually no impact on the growth, fledging or survival rates of red-winged blackbirds (e.g. Weatherhead 1989; Røskaft et al. 1990; Clotfelter & Yasukawa 1999), we suspect that the cost to host nestlings is either negligible (e.g. Dearborn 1998; Dearborn et al. 1998) or compensated for by 'catch-up' growth later in the nestling period.

Continuing to beg more frequently after food is distributed cannot be attributed to increased hunger of the host nestlings since, if anything, they received more food than in unparasitized broods. Rather, this effect on host nestling behaviour is probably attributable to the evolutionary game played between nestmates. The begging level of an individual may be influenced by the begging level of others around it independent of hunger levels (von Haartman 1953; Ryden & Bengtsson 1980; Bengtsson & Ryden 1983; Smith & Montgomerie 1991; Price 1996; but see Cotton et al. 1996; Leonard & Horn 1996). Thus, our result accords well with earlier observational and experimental work on conspecific nestlings. We further note that the physical act of begging, which includes jostling among nestlings, is sufficient to induce begging by other nestlings; vocal begging is not essential (McRae et al. 1993).

Continued begging by the cowbird may represent a selfish attempt to induce the parents to deliver more food or it may be an honest indicator of need. Given that

cowbirds received less food than a host nestling of similar size in older broods, we suspect that hunger was a contributor at this stage of brood development. However, cowbirds in younger broods received the same food share as host nestlings, suggesting that other factors may have contributed to this behaviour. Cowbirds grow at a faster rate than both sexes of red-winged blackbird nestlings (Williams 1940; Norris 1947; Olson 1992), which may require a greater intake of food by the brood parasite relative to host nestlings, particularly during early development (e.g. Soler & Soler 1991). Consequently, despite receiving a food share equivalent to that of a similar-sized redwing, it does not follow that that amount of food necessarily met the cowbird's nutritional needs.

Lengthy begging has been noted in great spotted cuckoo chicks, *Clamator glandarius*, that parasitize broods of magpie, *Pica pica*, nestlings (Redondo 1993). When matched to a host nestling at the same stage of development, the great spotted cuckoo continued to beg for a longer period than did a magpie nestling with the same degree of need (Redondo 1993). In addition, being fed did not deter the cuckoo from continuing to beg and accepting more food, despite a full gape. The author attributed this lack of satiation to the cuckoo's enlarged esophagus and gizzard, which allow for increased food storage. The consistent begging effort of the cowbird nestling, combined with its relatively large gape relative to that of the yellow-head blackbird, *Xanthocephalus xanthocephalus*

(Ortega & Cruz 1992), another icterid blackbird, hints at the potential for similar physiological modifications.

Lengthy, persistent begging is common among brood-parasitic nestlings, including various species of cuckoos and cowbirds (review in Redondo 1993), suggesting an adaptive function. Redondo (1993) hypothesized that exaggerated begging (loud, persistent, lengthy or intense) by nonmimetic brood parasites may be a compensatory, adaptive behaviour to manipulate host parents into caring for them either directly, by improving individual feeding success, or indirectly, through an increase in the amount of food delivered to the brood. The cowbird did not receive a greater food share than a host nestling for a given age, suggesting that the behaviour of the cowbird does not provide a direct competitive advantage (see also Lichtenstein & Sealy 1998; Lichtenstein 2001). Indeed, despite begging longer and more frequently, the cowbird was fed less often than host nestlings in older broods, contrary to the predictions of brood parasite begging models (Harper 1986; Redondo & de Reyna 1988; Motro 1989; Briskie et al. 1994). A potential cost associated with continued begging is the removal and redistribution of prey items by the parent (e.g. Lichtenstein 2001). However, we found no evidence that the host parent actively discriminated against the cowbird by selectively removing food from its gape.

These results are consistent with the observation that a reduction in clutch size is the primary cost to host species larger than a brood parasite; the growth and survival of host nestlings is little affected, primarily due to the relatively poor competitive abilities of the smaller brood parasite (e.g. Smith 1981; Eckerle & Breitwisch 1997; Clotfelter & Yasakawa 1999; Lichtenstein 2001).

Effect on Host Parental Behaviour

The presence of cowbirds had no obvious effect on host parental behaviour as measured by brood-provisioning levels, or the amount of thermal care provided, although modest sample sizes may have precluded detection of subtle differences, if any. If cowbird nestlings were behaving selfishly, this did not translate into any obvious food rewards, as per capita food shares did not exceed that of host nestlings. Indeed, they lagged behind at older ages. Our results do not support the hypothesis that exaggerated begging manipulates host parents into providing more food through an increase in foraging rate (Redondo 1993).

Previous work on red-winged blackbird nestlings showed that begging after food distribution seemed to accelerate the next meal because parents leave almost immediately to forage rather than remaining at the nest (Glassey 2000). Why then did parents not always return more food to parasitized broods, as cowbirds showed this postfeeding begging quite consistently? First, parents leave to forage almost immediately when the majority of the brood continues begging for a prolonged period. For the cowbird's strategy to work, it needs to recruit host nestlings to a sustained effort. It did this, but only in part; host nestlings continued to beg more frequently, but for less time in younger broods.

Lengthy begging, a behaviour interpreted as signalling hunger (Smith & Montgomerie 1991; Mondloch 1995; Price & Ydenberg 1995; Cotton et al. 1999; Smiseth 1999), has also been observed in broods of indigo buntings, *Passerina cyanea*, parasitized by the brown-headed cowbird (Dearborn et al. 1998). In contrast to our system, the smaller, less successful and presumably hungrier host-nestling majority sustain their begging effort for as long as the cowbird, and parents respond to the increase in overall brood begging by increasing provisioning (Dearborn 1998; Dearborn et al. 1998).

Second, the presence of a cowbird did not elevate the mean begging intensity of the brood, which other studies have shown contributes to an increase in parental provisioning to hungry passerine broods (von Haartman 1953; Ryden & Bengtsson 1980; Smith & Montgomerie 1981; Bengtsson & Ryden 1983). In fact, we found no detectable difference between the begging intensity of host and cowbird nestlings (see also Lichtenstein & Sealy 1998). Our results should be interpreted with caution, however, given the relatively coarse measure of begging intensity used in this study. The lack of an increase in both the cumulative begging intensity of the brood and parental activity at the nest site might explain why parasitized red-winged blackbird broods do not attract more predators than unparasitized broods (e.g. Weatherhead 1989; Clotfelter & Yasukawa 1999). Conceivably, persistent begging by the cowbird alone following the allocation of food may not impose a predation cost that is shared by the brood (but see Dearborn 1999).

Another possible component to the answer can be framed as a simple question. If a cowbird nestling begs, does a blackbird parent hear? It is not at all clear to us that cowbirds and blackbirds are sending and receiving information on the same 'channel'. A cowbird nestling's call differs markedly in rate and volume from that of a blackbird (Eastzer et al. 1980; Briskie et al. 1994) and is, to the human ear, easily distinguished from that of a blackbird nestling. Unlike common cuckoos, brown-headed cowbirds are generalist brood parasites and do not practice vocal mimicry (Broughton et al. 1987; Redondo 1993), so that begging by the cowbird may not augment the cumulative vocalizations of the brood. Parents require a minimum threshold level of vocalizations by their own offspring in order to initiate and maintain foraging (Nottebohm & Nottebohm 1972; Miller & Conover 1979). A failure to register a cowbird call would reduce the effective size of the begging brood after food distribution, and would help to explain the failure to affect increased provisioning to the brood in parasitized nests. Presumably the effect would be exacerbated in those broods from which a host egg was removed.

These results are in accord with earlier work in the same system, where experimental muting of a single red-winged blackbird nestling resulted in significantly reduced provisioning of the brood (Glassey & Forbes 2002), supporting the hypothesis that feeding events are not independent (Cotton et al. 1996). Rather, continued begging during the nonfeeding phase appears to represent both a cooperative group effort by siblings to induce

parents to increase overall levels of provisioning, as well as competition for food by an individual.

Persistent, lengthy begging by the cowbird targets the nonfeeding phase presumably to increase the foraging rate of the foster parent, as opposed to being a competitive behaviour. Because the cowbird is in the minority, the success of this strategy is dependent on the cooperation of host nestlings, which is not guaranteed. The cowbird is unable to manipulate the behaviour of the parent indirectly by stimulating nestlings to beg more frequently following the distribution of food.

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References

- Bachman, G. C. & Chappell, M. A. 1998. The energetic cost of begging behaviour in nestling house wrens. *Animal Behaviour*, **55**, 1607–1618.
- Bengtsson, H. & Ryden, O. 1983. Parental feeding rate in relation to begging behavior in asynchronously hatched broods of the great tit *Parus major*. *Behavioral Ecology and Sociobiology*, **12**, 243–251.
- Briskie, J. V., Naugler, C. T. & Leech, S. M. 1994. Begging intensity of nestling birds varies with sibling relatedness. *Proceedings of the Royal Society of London, Series B*, **258**, 73–78.
- Broughton, K. E., Middleton, A. L. & Bailey, E. D. 1987. Early vocalizations of the brown-headed cowbird and three host species. *Bird Behaviour*, **7**, 27–30.
- Budden, A. E. & Wright, J. 2001. Begging in nestling birds. *Current Ornithology*, **16**, 84–117.
- Choi, I.-H. & Bakken, G. S. 1990. Begging response in nestling red-winged blackbirds (*Agelaius phoeniceus*): effect of body temperature. *Physiological Zoology*, **63**, 965–986.
- Clark, A. B. & Lee, W.-H. 1998. Red-winged blackbird females fail to increase feeding in response to begging call playbacks. *Animal Behaviour*, **56**, 563–570.
- Clemmons, J. R. 1995. Vocalizations and other stimuli that elicit gaping in nestling black-capped chickadees (*Parus atricapillus*). *Auk*, **112**, 603–612.
- Clotfelter, E. D. & Yasukawa, K. 1999. Impact of brood parasitism by brown-headed cowbirds on red-winged blackbird reproductive success. *Condor*, **101**, 104–114.
- Cotton, P. A., Kacelnik, A. & Wright, J. 1996. Chick begging as a signal: are nestlings honest? *Behavioral Ecology*, **7**, 178–182.
- Cotton, P. A., Wright, J. & Kacelnik, A. 1999. Chick begging strategies in relation to brood hierarchies and hatching asynchrony. *American Naturalist*, **153**, 412–420.
- Davies, N. B., Kilner, R. M. & Noble, D. G. 1998. Nestling cuckoos *Cuculus canorus* exploit hosts with begging calls that mimic a brood. *Proceedings of the Royal Society of London, Series B*, **265**, 673–678.
- Dearborn, D. C. 1998. Begging behaviour and food acquisition by brown-headed cowbird nestlings. *Behavioral Ecology and Sociobiology*, **43**, 247–257.
- Dearborn, D. C. 1999. Brown-headed cowbird nestling vocalizations and risk of nest predation. *Auk*, **116**, 448–457.
- Dearborn, D. C., Anders, A. D., Thompson, F. R. III & Faaborg, J. 1998. Effects of cowbird parasitism on parental provisioning and nestling food acquisition and growth. *Condor*, **100**, 325–334.
- Eastzer, D., Chu, P. R. & King, A. P. 1980. The young cowbird: average or optimal nestling? *Condor*, **82**, 417–425.
- Eckerle, K. P. & Breitwisch, R. 1997. Reproductive success of the northern cardinal, a large host of brown-headed cowbirds. *Condor*, **99**, 169–178.
- Fiala, K. L. & Congdon, J. D. 1983. Energetic consequences of sexual size dimorphism in nestling red-winged blackbirds. *Ecology*, **64**, 642–647.
- Forbes, S. & Glassey, B. 2000. Asymmetric sibling rivalry and nestling growth in red-winged blackbird (*Agelaius phoeniceus*). *Behavioral Ecology and Sociobiology*, **48**, 413–417.
- Glassey, B. 2000. Resource competition among nestling red-winged blackbirds. Ph.D. thesis: University of Manitoba, Winnipeg.
- Glassey, B. & Forbes, S. 2002. Muting individual nestlings reduces parental foraging for the brood. *Animal Behaviour*, **63**, 779–786.
- Gochfeld, M. 1979. Begging by nestling shiny cowbirds: adaptive or maladaptive. *Living Bird*, **17**, 41–50.
- Hamilton, W. J. 1964. The genetical evolution of social behaviour. I. *Journal of Theoretical Biology*, **7**, 1–16.
- Harper, A. B. 1986. The evolution of begging: sibling competition and parent-offspring conflict. *American Naturalist*, **128**, 99–114.
- Hill, R. W. & Beaver, D. L. 1982. Inertial thermostability and thermoregulation in broods of red-winged blackbirds. *Physiological Zoology*, **55**, 250–266.
- Hurlbert, S. H. 1984. Pseudoreplication and the design of ecological field experiments. *Ecological Monographs*, **54**, 187–211.
- Kacelnik, A., Cotton, P. A., Stirling, P. & Wright, J. 1995. Food allocation among nestling starlings: sibling competition and the scope of parental choice. *Proceedings of the Royal Society of London, Series B*, **259**, 259–263.
- Lea, E. G. & Kattan, G. H. 1998. Reanalysis gives further support to the 'shotgun' model of shiny cowbird parasitism of house wren nests. *Animal Behaviour*, **56**, 1571–1573.
- Leech, S. M. & Leonard, M. L. 1996. Is there an energetic cost to begging in nestling tree swallows (*Tachycineta bicolor*)? *Proceedings of the Royal Society of London, Series B*, **263**, 983–987.
- Leonard, M. L. & Horn, A. G. 1996. Provisioning rules in tree swallows. *Behavioral Ecology and Sociobiology*, **38**, 341–347.
- Leonard, M. L. & Horn, A. G. 1998. Need and nestmates affect begging in tree swallows. *Behavioral Ecology and Sociobiology*, **42**, 431–436.
- Leonard, M. L. & Horn, A. G. 2001. Begging in the absence of parents by nestling tree swallows. *Behavioral Ecology*, **12**, 501–505.
- Lichtenstein, G. 2001. Low success of shiny cowbird chicks parasitizing rufous-bellied thrushes: chick-chick competition or parental discrimination? *Animal Behaviour*, **61**, 401–413.
- Lichtenstein, G. & Sealy, S. G. 1998. Nestling competition, rather than supernormal stimulus, explains the success of parasitic brown-headed cowbird chicks in yellow warbler nests. *Proceedings of the Royal Society of London, Series B*, **265**, 249–254.
- McCarty, J. P. 1996. The energetic cost of begging in nestling passerines. *Auk*, **113**, 178–188.

- McRae, S. B., Weatherhead, P. J. & Montgomerie, R. 1993. American robin nestlings compete by jockeying for position. *Behavioral Ecology Sociobiology*, **33**, 101–106.
- Miller, D. E. & Conover, M. R. 1979. Differential effects of chick vocalizations and bill-pecking on parental behaviour in ring-billed gulls. *Auk*, **96**, 284–295.
- Mock, D. W. & Parker, G. A. 1997. *The Evolution of Sibling Rivalry*. Oxford: Oxford University Press.
- Mondloch, C. J. 1995. Chick begging affects parental allocation of feedings in pigeons. *Animal Behaviour*, **49**, 601–613.
- Motro, U. 1989. Should a parasite expose itself? Some theoretical aspects of begging and vigilance behaviour. *Journal of Theoretical Biology*, **140**, 279–287.
- Nice, M. M. 1939. Observations on the behaviour of a young cowbird. *Wilson Bulletin*, **51**, 233–239.
- Norris, R. T. 1947. The cowbirds of Preston Frith. *Wilson Bulletin*, **59**, 83–103.
- Nottebohm, F. & Nottebohm, M. E. 1972. Vocalizations and breeding behaviour of surgically deafened ring doves (*Streptopelia risoria*). *Animal Behaviour*, **19**, 313–327.
- Olson, J. M. 1992. Growth, the development of endothermy, and the allocation of energy in red-winged blackbirds (*Agelaius phoeniceus*) during the nestling period. *Physiological Zoology*, **65**, 124–152.
- Orians, G. H. 1980. *Some Adaptations of Marsh Nesting Blackbirds*. Princeton, New Jersey: Princeton University Press.
- Ortega, C. P. & Cruz, A. 1988. Mechanisms of egg acceptance in marsh dwelling blackbirds. *Condor*, **90**, 349–359.
- Ortega, C. P. & Cruz, A. 1991. A comparative study of cowbird parasitism in yellow-headed blackbirds and red-winged blackbirds. *Auk*, **108**, 16–24.
- Ortega, C. P. & Cruz, A. 1992. Differential growth patterns of nestling brown-headed cowbirds and yellow-headed blackbirds. *Auk*, **109**, 368–376.
- Price, K. 1994. The behavioural ecology of begging by yellow-headed blackbird nestlings. Ph.D. thesis, Simon Fraser University, Burnaby, British Columbia.
- Price, K. 1996. Begging as competition for food in the yellow-headed blackbirds. *Auk*, **113**, 963–967.
- Price, K. & Ydenberg, R. 1995. Begging and provisioning in broods of asynchronously-hatched yellow-headed blackbird nestlings. *Behavioral Ecology Sociobiology*, **37**, 201–208.
- Redondo, T. 1993. Exploitation of host mechanisms for parental care by avian brood parasites. *Etologia*, **3**, 235–297.
- Redondo, T. & de Reyna, L. A. 1988. Locatability of begging calls in nestling altricial birds. *Animal Behaviour*, **36**, 653–661.
- Røskoft, E., Orians, G. H. & Beletsky, L. D. 1990. Why do red-winged blackbirds accept eggs of brown-headed cowbirds? *Evolutionary Ecology*, **4**, 35–42.
- Rothstein, S. 1975. Evolutionary rates and host defences against avian brood parasitism. *American Naturalist*, **109**, 161–176.
- Ryden, O. & Bengtsson, H. 1980. Differential begging and locomotory behaviour by early and late hatched nestlings affecting the distribution of food in asynchronously hatched broods of altricial birds. *Zeitschrift für Tierpsychologie*, **53**, 209–224.
- Smiseth, P. T. 1999. Social evolution in monogamous families: mate choice and conflicts over parental care in the bluethroat (*Luscinia s. svecica*). Ph.D. thesis, Norwegian University of Science and Technology.
- Smith, H. G. & Montgomerie, R. 1991. Nestling American robins compete with siblings by begging. *Behavioral Ecology Sociobiology*, **29**, 307–312.
- Smith, J. N. M. 1981. Cowbird parasitism, host fitness, and age of the host female in an island song sparrow population. *Condor*, **83**, 152–161.
- Soler, M. & Soler, J. J. 1991. Growth and development of great spotted cuckoos and their magpie host. *Condor*, **93**, 49–53.
- von Haartman, L. 1953. Was reizt den Trauerfliegenschnäpper zu füttern? *Die Vogelwarte*, **16**, 157–164.
- Weatherhead, P. J. 1989. Sex ratios, host-specific reproductive success, and impact of brown-headed cowbirds. *Auk*, **106**, 358–366.
- Williams, M. F. 1940. The sex ratio in nestling eastern redwings. *Wilson Bulletin*, **52**, 267–277.
- Woodward, P. W. 1983. Behavioral ecology of fledgling brown-headed cowbirds and their hosts. *Condor*, **85**, 151–163.
- Wright, J. & Leonard, M. L. (Eds) 2002. *The Evolution of Begging: Competition, Cooperation and Communication*. Dordrecht: Kluwer Academic.