



How selfish is a cowbird nestling?

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Brood-parasitic young are reared in the nests of different species and can derive no genetic benefit from the survival of host offspring. However, although the nestlings of many parasitic cuckoo and honeyguide species routinely kill host young soon after hatching, nestling brown-headed cowbirds, *Molothrus ater*, tolerate host offspring and are commonly reared alongside them for at least part of the nestling period. I used comparative analyses of data from the literature to investigate whether brown-headed cowbird nestlings gain direct benefits by allowing host young to live. The brown-headed cowbird (44 g) parasitizes many passerines (adult mass range about 5–90 g) and the likelihood that host young survive to fledge from parasitized nests varies between species. In common with previous work, I found that host offspring mortality was highest in species whose offspring were relatively small compared with the cowbird nestling. Furthermore, cowbird nestlings were most likely to fledge when reared alongside host young of intermediate size. In these nests, one or two host young typically fledged as well. I suggest that cowbirds, and other host-tolerant brood parasites, could benefit from the presence of host nestlings through the assistance that host chicks offer in soliciting a higher provisioning rate, and that such benefits might outweigh the costs of having competition for food at each nest visit. Variation in this cost–benefit ratio could explain differences between brood parasite species in their tolerance of host young.

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When offspring compete for limited parental resources, the extent of their selfishness should be determined by the indirect fitness benefits they stand to gain from sharing the resource with relatives (Hamilton 1964; Mock & Parker 1997). At first sight, it appears that the behaviour of avian brood-parasitic young matches theoretical expectations. Dumped as eggs in the nests of different species, and consequently reared with nonkin, the selfishness of the alien offspring should be unconstrained. In some parasitic species, a ruthless self interest is evident soon after hatching: cuckoo nestlings evict host offspring from the nest, and newly hatched honeyguides rip host young apart using a hook on the end of their bill (Davies 2000). But other brood parasites appear puzzlingly tolerant of host nestlings. Young *Clamator* cuckoos, parasitic African estrildid finches and parasitic cowbirds do not kill host offspring directly and are typically reared alongside them for at least part of the nestling period (Davies 2000).

One explanation of this tolerance is that these species have more recently acquired the brood-parasitic habit and have yet to develop the ability to dispense with host offspring directly, although molecular phylogenies suggest that this is plausible only for the cowbird species (Sorenson & Payne 2002). An alternative possibility is

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that host young are tolerated because their presence in the nest brings the parasite direct benefits. In many passerine species, the brood collectively solicits the total amount of care supplied by parents (Kilner et al. 1999). For example, pied flycatcher, *Ficedula hypoleuca*, parents decide how much food to bring to the nest by attending to the summed intensity of their brood's begging behaviour. When von Haartman (1953) hid an extra brood of young in a compartment behind a nest of chicks, the additional begging calls of the concealed offspring stimulated parents to provision the exposed brood more frequently. Similar results have been obtained by broadcasting begging calls during nest visits, both with pied flycatchers (Ottoson et al. 1997) and other species (e.g. Müller & Smith 1978; Davies et al. 1998; Price 1998). Therefore, some brood-parasitic species may tolerate host young because they effectively enslave them, exploiting the assistance that they offer in soliciting a higher provisioning rate from parents (see also Lichtenstein 1997). Providing that host young do not prevent the parasite from taking all the extra resources, by being too numerous or too large, there might be some advantage to parasites if host offspring survive.

As a first step in investigating whether parasites can benefit by allowing host young to live, I analysed data collected from the literature on the brown-headed cowbird, *Molothrus ater* (44 g). This species parasitizes the

parental care of a variety of North American passerine species, ranging from the tiny gnatcatchers (5 g) to the more substantial thrashers (70 g) and meadowlarks (90 g; Ortega 1998). Individual host nests may be singly or multiply parasitized by cowbirds adding their eggs to the host clutch. After incubation for 11–12 days, which is typically shorter than that required by most hosts, the cowbird chick hatches and is reared alongside any host young, or other cowbirds, that survive to hatch.

The brown-headed cowbird is an ideal species with which to investigate the benefits to be derived by allowing host young to live, because the host mortality that results from parasitism varies widely between species (Lorenzana & Sealy 1999). Cowbird nestlings can cause host young to die by consistently outcompeting them for food, and their competitive prowess depends on their size relative to host young (Eastzer et al. 1980). For example, in the parasitized nests of yellow warblers, *Dendroica petechia*, and indigo buntings, *Passerina cyanea*, cowbird nestlings obtain roughly twice as much food as the smaller host young (Dearborn 1998; Lichtenstein & Sealy 1998). But in the nest of the northern cardinal, *Cardinalis cardinalis*, chicks are more evenly matched in size and the cardinals and cowbird are equally adept at obtaining food (Dearborn 1998). With such a wide range of host sizes exploited apparently indiscriminately by brown-headed cowbird females (Ortega 1998), cowbird nestlings present a natural experiment for investigating the direct benefits to be gained from tolerating host nestlings.

I began by looking at the relation between the size of host young relative to the cowbird and estimates of host mortality in the nest, predicting that the more closely that cowbirds and host young were matched in size, the better the survival prospect of the host young would be (see also Lorenzana & Sealy 1999; Hauber, in press). Next, I considered whether the survival of host young benefited cowbird offspring, by testing whether the principal correlates of host mortality were related to cowbird mortality in the nest. I predicted that if cowbirds benefit from the death of nonrelatives, and derive no advantage by allowing host young to live, then they should fare best in nests of hosts that lose all their offspring as a result of parasitism and least well when all the host young survive to compete for food. In contrast, if cowbirds gain any advantage when host nestlings survive, then they should do best when a few host young survive to help demand resources, and less well when forced to solicit care by themselves (cf. Kilner et al. 1999) or when facing intense competition for food from several host nestlings.

METHODS

Host Young Mortality in Parasitized Nests

I reviewed the available literature for data on offspring mortality attributable to starvation through competition with cowbirds, restricting my search to studies where the majority of parasitized nests monitored contained a single cowbird egg (Table 1). In this way, I avoided the potentially confounding effects of host nestlings competing with multiple cowbirds. I excluded mortality that

could be attributable to predators by focusing only on nests reported to have survived until the brood fledged. I assumed that host offspring were neither evicted by the cowbird (but see Dearborn 1996) nor victims of partial brood consumption by predators.

Five methods were used to estimate host mortality in parasitized nests (Table 1), as follows. (1) When it was reported that no young survived to fledge, I scored host mortality as 100%. (2) Some studies reported percentage of nestlings that failed to fledge because of starvation, and I used this value as the estimate of host mortality. (3) For some species, I calculated mortality as (mean parasitized clutch size – mean number of host young fledged from parasitized nests)/mean parasitized clutch size. This method accounted for damage to host eggs and egg removal by adult cowbirds during parasitism. (4) Where possible, I calculated (mean parasitized brood size at hatching – mean number of host young fledged from parasitized nests)/mean parasitized brood size at hatching. The advantage of this method is that it also accounts for host mortality caused by hatching failure, which is often the result when smaller host eggs are incubated with a larger cowbird egg (Rothstein 1975). (5) Finally, I calculated host mortality as (experimental brood size – mean number of host young fledged)/experimental brood size. For some species, more than one study reported host mortality. To combine data from different studies, which may have used different methodologies for calculating host mortality, I simply derived the mean of the values obtained for each species.

Relative Size of Host Young

I estimated the size of host young in relation to the cowbird with two variables: (1) mass of adult host and (2) duration of the host incubation period in relation to that of the cowbird (Lorenzana & Sealy 1999; Davies 2000; Hauber, in press). For consistency, all values of host adult mass used were taken from Sibley (2000), and the relative durations of the host's incubation period were calculated from data in Baicich & Harrison (1997). Where the incubation period was given as a range (e.g. 11–12 days in the case of the cowbird), I used the midpoint (in this case 11.5 days). The incubation period for Bullock's oriole is given as 11.5 days (Table 1), because cowbird nestlings were experimentally added to the nest on the day of hatching of host young. Data on host clutch sizes were similarly collected from Baicich & Harrison (1997).

I investigated how much variation in host mortality could be explained by two variables: log adult host mass and (cowbird – host incubation period). Ideally, an analysis of proportional data should use a generalized linear model with a logit link function and a binomial error structure. However, with several methods used to calculate host mortality, the data were not available in a form that made this approach feasible. Instead, I fitted a multiple regression model where each species was weighted by its sample size, and controlled for phylogenetic effects in subsequent analyses.

Table 1. The data set used in the analyses

Species	Mass (g)	Clutch size	Incubation period (days)	Parasitized nests studied	Total cowbird chicks	'Starved' cowbird chicks	Cowbird mortality (%)	Host chick mortality (%)	Source
Acadian flycatcher, <i>Empidonax vireescens</i>	13.0	3	13.5	16	6	0	0	100 ¹	Walkinshaw 1961
Willow flycatcher, <i>Empidonax traillii</i>	13.5	3.5	12.5	11	2	0	0		Sedgwick & Knopf 1988
Bell's vireo, <i>Vireo bellii</i>	8.5	4	14.0	44	3	0	0	100 ¹	Parker 1999
Red-eyed vireo, <i>Vireo olivaceus</i>	17.0	4	12.5	7				15.9 ⁴	Dececco et al. 2000
Warbling vireo, <i>Vireo gilvus</i>	12.0	4	12.5	29				100 ¹	Ward & Smith 2000
Solitary vireo, <i>Vireo plumbeus</i>	18.0	4	15.0	26	22	4	18.2	87.2 ²	Marvil & Cruz 1989
Blueheaded vireo, <i>Vireo solitarius</i>	16.0	4	15.0	20				98.2 ⁴	Dececco et al. 2000
Brown thrasher, <i>Toxostoma rufum</i>	69.0	4.5	12.5	3	3	1	33.3		Nickell 1955
Blue-grey gnatcatcher, <i>Poliophtila caerulea</i>	6.0	4.5	15.0	63				100 ¹	Goguen & Mathews 1996
				6				100	Root 1969
California gnatcatcher, <i>Poliophtila californica</i>	5.0	4	14.0	53				100 ¹	Braden et al. 1997
Song sparrow, <i>Melospiza melodia</i>	20.0	4	13.0	200				16.5 ⁴	Smith & Arcese 1994
Dark-eyed junco, <i>Junco hyemalis</i>	19.0	4	12.5	8				37.5 ³	Wolf 1987
Chipping sparrow, <i>Spizella passerina</i>	12.0	4	12.5	4				0 ³	Ortega & Ortega 2001
Field sparrow, <i>Spizella pusilla</i>	12.5	4	10.5	16	4	0	0	5.1 ³	Burhans et al. 2000
Abert's towhee, <i>Pipilo aberti</i>	46.0	3	14.0	22	6	4	66.7	11.0 ²	Finch 1983
Yellow-breasted chat, <i>Icteria virens</i>	25.0	4	11.5	13				25.8 ⁴	Whitehead et al. 2000
Common yellowthroat, <i>Geothlypis trichas</i>	10.0	4	12.0	7	3	0	0	0 ²	Hofslund 1957
Louisiana waterthrush, <i>Seiurus motacilla</i>	20.5	5	13.0	9	3	0	0	70.0 ²	Eaton 1958
Prothonotary warbler, <i>Protonotaria citrea</i>	16.0	5	13.0	36	24	0	0	24.5 ⁴	Petit 1991
Yellow warbler, <i>Dendroica petechia</i>	9.5	4.5	11.0	94	5	3	60.0	48.3 ⁴	Weatherhead 1989
Red-winged blackbird, <i>Agelaius phoeniceus</i>	52.0	4	11.0	132	32	6	18.8		Weatherhead 1989
				48				20.0 ⁴	Clotfelter & Yasukawa 1999
Bullock's oriole, <i>Icterus bullockii</i>	36.0	4.5	11.5	12	12	0	0	11.9 ⁵	Røskaft et al. 1993
Orchard oriole, <i>Icterus spurius</i>	19.0	4.5	13.5	4	4	0	0	36.4 ²	Wiens 1963
Indigo bunting, <i>Passerina cyanea</i>	14.5	3.5	12.5	414	78	4	5.1	86.8 ⁴	Payne & Payne 1998
Painted bunting, <i>Passerina ciris</i>	15.5	3.5	11.5	6				0 ⁴	Whitehead et al. 2000
Blue grosbeak, <i>Guiraca caerulea</i>	28.0	4	12.0	6				32.0 ⁴	Whitehead et al. 2000
Dickcissel, <i>Spiza americana</i>	27.0	4	12.0	14	2	0	0	100 ¹	Hill 1976
Northern cardinal, <i>Cardinalis cardinalis</i>	45.0	3.5	12.0	230	35	15		10.2 ²	Scott & Lemon 1996;
				55	4	0		3.7 ³	Eckerle & Breitwisch 1997
					39	15	38.5	7.0	

Numbers in bold in the 'total cowbird chicks' and 'starved cowbird chicks' columns were used to calculate cowbird mortality. Numbers in bold in the 'host chick mortality' column are the values used in the analyses. Superscripts refer to the method used for calculating host chick mortality in parasitized nests (see Methods).

Cowbird Mortality

I searched the literature for data on cowbird mortality, using only those studies where the majority of parasitized nests monitored contained a single cowbird egg (Table 1). For studies reporting data separately for each year of the study, I included data only from years with, on average, singly parasitized nests (e.g. Hofslund 1957). By using this approach, I avoided the potentially confounding effects of cowbirds competing with each

other. I excluded studies that involved the experimental parasitism of a typically unused host (e.g. yellow-headed blackbird, *Xanthocephalus xanthocephalus*; Ortega & Cruz 1991) or that examined a host whose diet made it unsuitable for parasitism by the cowbird, in the view of the study's authors (e.g. house finch, *Carpodacus mexicanus*; Kozlovic et al. 1996). For nests that did not succumb to predators, I estimated percentage cowbird mortality attributable to starvation by calculating:

number of cowbird chicks reported missing during the nestling period/total number of cowbird eggs that successfully hatched $\times 100\%$.

Estimates of cowbird mortality therefore do not include the effects of host defences seen at the egg stage (Rothstein 1975; Hosoi & Rothstein 2000) and assume that chick disappearance was caused by starvation and not partial depredation of the brood. There is no evidence to suggest that cowbird mortality might be the result of host discrimination (Lichtenstein 2001). Where more than one study was available for a particular species, I summed the total number of cowbird chicks reported missing and the total number of cowbird young that successfully hatched before calculating cowbird mortality (Table 1).

To explain variation in cowbird mortality, I used two approaches. I initially used a generalized linear model with logit link function and binomial error structure to fit the following terms: log adult host mass, (log adult host mass)², (cowbird – host incubation period), (cowbird – host incubation period)² and the interaction between log adult host mass and (cowbird – host incubation period) (i.e. their product; Hair et al. 1995). Nonsignificant terms were then dropped from the model. Log adult mass and (cowbird – host incubation period) were treated as independent variables because they were not significantly correlated ($F_{1,26}=2.62$, $P=0.12$). The squared terms were included to test for the predicted U-shaped relationship between relative host size and cowbird mortality. The interaction term was included because the effect of hatching after the cowbird is likely to have a bigger effect on host mortality in small hosts than in large hosts (e.g. Hosoi & Rothstein 2000; i.e. if cowbirds gain directly from host young in the nest, then host mortality will, in turn, influence cowbird mortality).

Each species was treated as an independent data point. In subsequent analyses, I controlled for potential confounding phylogenetic effects by analysing independent contrasts calculated by the application CAIC 2.0 (Purvis & Rambaut 1995). It was not possible to use a similar generalized linear model to analyse the independent contrasts (Mayhew & Pen 2002), which instead were analysed with a multiple regression. Therefore, for comparison, I also analysed the species data using a multiple regression.

Control for Phylogeny

Analyses that treat species as independent data points are potentially flawed, because the behaviour of an individual species may not represent a unique response to the correlated variable in question, and may instead be heavily influenced by the species' evolutionary history. For example, cowbird mortality rates in vireo nests may be entirely unrelated to the relatively small size of host young, and may owe more to a common provisioning rule inherited from an ancestral vireo. To attempt to overcome this problem, I used the CAIC 2.0 application (Purvis & Rambaut 1995), which uses a

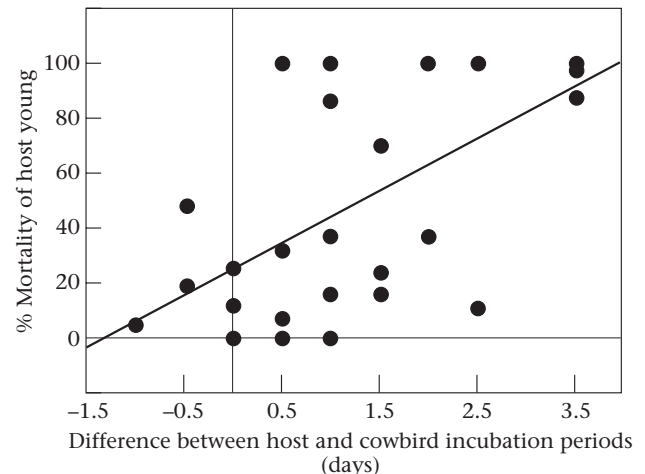


Figure 1. The relation between the mortality of host young in singly parasitized nests and the difference between host and cowbird incubation periods. The least squares regression line is shown. Each data point represents a different species.

procedure developed by Felsenstein (1985) to calculate independent contrasts in the data set. For each variable in the analysis, the program calculates the difference between values at every bifurcation in the phylogeny. These contrasts are independent of evolutionary history and are therefore deemed more suitable for statistical analysis (Felsenstein 1985; Harvey & Pagel 1991). However, Price (1997) argued that the method has limited value in controlling for the effects of phylogeny when interpreting correlations. I follow his suggestion, that the results of analyses that use independent contrast as data points should be reported alongside those that use species.

To derive the independent contrasts using CAIC 2.0, I used Sibley & Ahlquist's (1990) molecular phylogeny, with the branch lengths set to equal. All regressions were forced through the origin, as recommended (Purvis & Rambaut 1995).

Statistics

I checked that the data met the assumptions of the statistical tests used and transformed data where necessary. All P values reported are two tailed.

RESULTS

Correlates of Host Mortality

In keeping with previous findings (Lorenzana & Sealy 1999; Hauber, *in press*) host mortality was higher in nests where the cowbird was larger than the host young. With a weighted regression analysis with species as data points, log host adult mass was individually negatively related to host mortality ($F_{1,25}=5.06$, $P=0.034$). Furthermore, the greater the head start gained by the cowbird through hatching sooner than the host, the higher host mortality became ($F_{1,25}=11.91$, $P=0.0021$; Fig. 1). When analysed together with a weighted multiple regression, the

Table 2. Results of a generalized linear model explaining variation in cowbird chick mortality

Model terms	df	F	P
Log host adult mass	1	4.25	0.039
Cowbird–host incubation period	1	11.30	<0.001
(Cowbird–host incubation period) ²	1	3.76	0.053
Log adult host mass×(cowbird–host incubation period)	1	12.93	<0.001
(Log host adult mass) ²	1	1.53	0.22
Residual	11		
	Average effect		
Minimal model			SE
Constant		-4.16	1.39
Log host adult mass		1.78	0.90
Cowbird–host incubation period		-4.70	1.30
(Cowbird–host incubation period) ²		0.24	0.12
Log adult host mass×(cowbird–host incubation period)		3.11	0.87

Species were treated as independent data points.

difference between cowbird and host incubation periods explained significantly more variance ($t_{23}=2.87$, $P=0.009$) than host mass did ($t_{23}=-1.50$, $P=0.15$).

When the analysis used the independent contrasts calculated by CAIC, the duration of the host's incubation period in relation to the cowbird's was positively related to host mortality ($F_{1,19}=5.92$, $P=0.025$), but adult host mass could not explain a significant amount of variance in host mortality ($F_{1,19}=0.42$, $P=0.53$).

Overall, these analyses suggest that the magnitude of the difference between host and cowbird incubation periods is the better predictor of host mortality. However, the results should be viewed with caution, because it is possible that incubation period and host mass are too closely correlated (see above) to be able to separate their effects statistically.

Correlates of Cowbird Mortality

Of the five independent variables originally fitted in the generalized linear regression model, four were retained in the minimal adequate model (Table 2). After controlling for host adult mass, when cowbirds gained a competitive size advantage by hatching sooner than the host young, they had higher fledging success. When this effect was taken into account, too, cowbird nestlings did best when reared in the nests of hosts whose incubation period was of intermediate duration and markedly worse when hosts hatched at the same time or much later than the cowbird.

A slightly different picture emerged from the multiple regression analyses. Again, four of the five original independent variables significantly explained 63.0% of the variation in cowbird mortality ($F_{4,16}=5.10$, $P=0.012$; Table 3), but this time, host mass was more important than the relative duration of incubation in predicting cowbird mortality (Fig. 2). The results were qualitatively similar when independent contrasts, rather than species, were data points in a further multiple regression analysis.

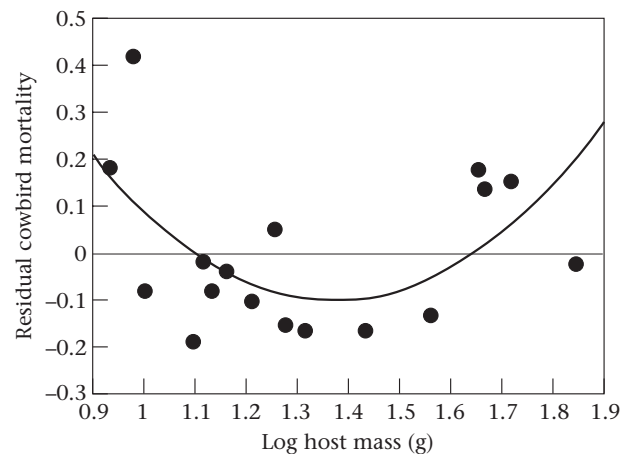
Table 3. Results of a multiple regression model explaining variation in cowbird chick mortality

Model terms	df	t	P
Log host adult mass	1	-2.41	0.032
(Log host adult mass) ²	1	2.42	0.032
Cowbird–host incubation period	1	-3.06	0.010
Log adult host mass×(cowbird–host incubation period)	1	3.23	0.007
Residual	12		

Species were treated as independent data points.

This time, the same four independent variables significantly accounted for 68.5% of the variation in cowbird mortality ($F_{4,14}=5.45$, $P=0.014$; Table 4). Taken together, the results of all three analyses suggest that both the relative duration of a host's incubation period and its adult mass influence the likelihood of cowbird survival, and cowbirds are most likely to fledge when reared alongside host young of intermediate size.

One possibility is that the U-shaped curve relating cowbird mortality and host mass (or relative incubation length) is caused simply by medium-sized birds (or those with incubation periods of intermediate length) typically

**Figure 2.** The relation between cowbird mortality and log host adult mass, after controlling for the difference between cowbird and host incubation periods and its interaction with log host adult mass. The polynomial regression line is shown. Each data point represents a different species.**Table 4.** Results of a multiple regression model explaining variation in cowbird chick mortality

Model terms	df	t	P
Log host adult mass	1	-2.40	0.037
(Log host adult mass) ²	1	2.35	0.040
Cowbird–host incubation period	1	3.06	0.012
Log adult host mass×(cowbird–host incubation period)	1	-3.34	0.008
Residual	10		

Data points were independent contrasts calculated by CAIC 2.0 (Purvis & Rambaut 1995).

rearing more offspring, and so being better able to care for the large cowbird nestling. To test this idea, I performed two separate second-order polynomial regression analyses, which sought to explain variation in host clutch size at unparasitized nests, with either adult host mass or host incubation period as the independent variable. There was no significant curvilinear relation between clutch size and either adult host mass ($F_{2,27}=0.29$, $P=0.75$) or incubation period ($F_{2,27}=0.06$, $P=0.94$), which makes this alternative interpretation unlikely. Perhaps the results are not surprising, given the small range in host clutch size in the analyses (range 3–5; Table 1).

DISCUSSION

From parasitoids to passerines, the level of selfishness displayed by offspring sharing parental resources is correlated with the indirect benefits they gain from allowing siblings to prosper (Briskie et al. 1994; Mayhew & Hardy 1998). This study suggests that, if offspring collectively solicit parental care, they might benefit by further tempering the extent of their selfishness to broodmates, becoming more altruistic than their relatedness alone predicts (see also Wilson & Clark 2002).

Cowbird nestlings were most lethal when reared alongside much smaller host young (Fig. 1) probably because their competitive superiority caused host nestlings to starve (e.g. Parker 1999; Dececco et al. 2000). But cowbird nestlings also suffered high mortality in these nests and in nests containing much larger host young (Fig. 2). It was when reared with host young of intermediate size that cowbirds had the lowest mortality (Fig. 2), and the success of the cowbird was correlated with the survival of one or two host nestlings.

From the slashing of host young by brood-parasitic honeyguides to their eviction by cuckoo species (Davies 2000), the traditional view is that a parasite benefits when host nestlings die (e.g. Rothstein 1975). However, recent work suggests that any benefit gained by parasites through dispensing with host offspring comes at some cost. For example, common cuckoo nestlings, *Cuculus canorus*, reared by reed warblers, *Acrocephalus scirpaceus*, must demand resources with a highly exaggerated begging call to compensate for the deficient visual stimulus they present parents by soliciting food alone in the nest (Kilner et al. 1999). Even then, they fail to behave as selfishly as might be expected (Kilner & Davies 1999). Similarly, the results of the preliminary analyses presented here suggest that cowbirds suffer when host young starve, perhaps because they lose assistance in soliciting a higher provisioning rate.

The inability of cowbirds and other brood parasites to kill host offspring directly may be interpreted as evidence of a more primitive parasitism strategy. An alternative possibility is that the relative costs and benefits associated with the death of host young differ between parasitic species. For example, brown-headed cowbirds, and parasitic estrildid finches (Mines 2002), may gain substantial benefits through not evicting nestmates that outweigh the costs of facing competition for food. A more tolerant attitude to nestmates may bring not only direct benefits,

as I have argued here, but indirect benefits too, because female brown-headed cowbirds and estrildid finches sometimes lay repeatedly in the same host nest (Alderson et al. 1999; Davies 2000). However, generalist parasites, such as the brown-headed cowbird, cannot be perfectly designed for every host that they exploit, which may explain their suboptimal performance when reared with relatively small or relatively large host offspring.

Alternative Interpretations

Of course, it is impossible to infer cause and effect from the correlational analyses reported here. Experiments are required to be certain that the presence of host young was responsible for the lower rates of starvation shown by cowbirds reared alongside nestlings of intermediate size. An alternative interpretation is that cowbirds fared best in these nests because the adults were better at providing food, and their few surviving offspring presented little threat to the cowbird in the competition for food. The relative merits of the two interpretations could be established with a simple experiment. For example, it would be interesting to focus on a single host species of intermediate size and manipulate the number of host young reared with a cowbird nestling. If cowbirds gain a direct benefit from host young, then they should grow or survive best when reared alongside one or two host chicks and fare much worse either when alone in the nest or when competing with more host nestlings for food. In contrast, if cowbirds gain no benefits from the survival of host young, then they should grow best when reared by themselves.

Even in the absence of appropriate experimental data, it seems unlikely that the higher cowbird mortality seen in nests containing smaller host young is simply a consequence of a less optimal diet, or because the smallest hosts could never bring sufficient food to the nest to sustain a cowbird nestling that will grow to be up to nine times their size. All the hosts used in this analysis are known to be capable of rearing cowbird young to fledging (Ortega 1998) which means that diet alone is unlikely to explain the results. Nor does it seem likely that the small size of some hosts will constrain their provisioning ability. First, host adult mass alone did not account for the observed pattern of cowbird mortality. Second, for two of the smallest hosts in this study, Bell's vireo, *Vireo bellii*, and the common yellowthroat, *Geothlypis trichas*, cowbird mortality was reported as 0% after depredated nests were removed. Furthermore, Kilpatrick (2002) found that the amount of energy that hosts were estimated to spend when rearing a cowbird could not be explained by their mass. For example, his calculations show that the blue-grey gnatcatcher, *Poliophtila californica* (6 g) works 36% harder when rearing a cowbird than when rearing an average brood, yet the larger indigo bunting (14 g) works 68% harder when parasitized. Finally, the analysis of clutch size provided no support for the suggestion that medium-sized hosts are simply better able to provision a cowbird and one or two host young because they typically rear more offspring. Further calculations by Kilpatrick (2002) show that it is the largest

hosts, rather than those of intermediate size, that can most easily afford the extra burden of rearing a cowbird nestling.

Sibling Rivalry and Parent–Offspring Conflict

More generally, the results add to suggestions that avian nestlings that are not brood parasites may be less selfish than is conventionally assumed. The results are consistent with previous theoretical analyses that suggest that reduced selfishness in the nest can pay for dominant nestlings, because these chicks stand to gain the direct benefit of assistance in soliciting care (Parker et al. 1989; Rodríguez-Gironés 1999). For example, a model by Forbes (1993) effectively incorporates a direct benefit of companions in the nest, by allowing parents to supply food in proportion to brood size. After the death of a nestling, parents unilaterally reduce the food supply. The prospect of less food curbs the selfishness of dominant offspring, prevents siblicide and thereby substantially reduces parent–offspring conflict over brood size.

In summary, when the supply of parental investment is fixed, as is the case when parasitoid wasp larvae hatch on a host, for example, the extent of offspring selfishness may depend solely on brood relatedness (Godfray & Parker 1991; Mayhew & Hardy 1998). But when offspring collectively solicit parental investment that is then subdivided between brood members, the direct benefit of companions in the nest may encourage more altruistic behaviour and could reduce the potential for conflicts of interest within the family. In common with other social behaviours (Clutton-Brock 2002; West et al. 2002), kin selection alone may not account for the degree of selfishness observed within families.

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