

BEGGING BEHAVIOUR AND HOST EXPLOITATION IN PARASITIC COWBIRDS

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ABSTRACT

In this chapter we explore the begging behaviour of cowbirds, obligate brood parasites that are typically raised in mixed broods with host young. As ‘strangers in the nest’, cowbird nestlings present both challenges and opportunities to evolutionary biologists. After a brief overview, we delve into four main topics: (1) the means by which cowbird young achieve success in host nests; (2) the differences between cowbirds and non-parasitic nestlings in the way that natural selection limits the exaggeration of begging behaviour; (3) the extent to which cowbird nestlings are perceived and treated as host young by the provisioning adults; and (4) the extent to which the begging signals of cowbird young are honest indicators of need. The most striking conclusions from our synthesis are that cowbird nestlings do not always successfully manipulate host adults and that begging by cowbirds can be informative of their level of need.

INTRODUCTION

The theoretical focus of studies of begging behaviour has centred on parent-offspring conflict, sibling competition, the honesty of signals and the associated need for signals to be costly (R.A. Johnstone & H.C.J. Godfray this volume). One of the most fascinating systems in which to study begging behaviour is brood parasitism, an uncommon but successful life history strategy present in one percent of the world’s bird species (Davies 2000). Interspecific brood parasites lay their eggs in nests of other species (the

hosts), which then incubate the eggs and care for the young. Brood parasites provide an interesting context in which to examine theoretical issues in begging behaviour because brood-parasitic nestlings are not related to the adults that provision them or to their nestmates (except in the case of multiple parasitism). This lack of relatedness has the potential to change the costs, and hence the honesty, of signals produced by brood-parasitic young.

Obligate brood parasitism occurs in cuckoos (Neomorphinae and Cuculinae, T. Redondo & J.M. Zuñiga and M. Soler this volume), cowbirds (Icterinae), the cuckoo-finch (*Anomalospiza imberbis*), the whydahs (Vidulinae, R.B. Payne & L.L. Payne this volume), the honeyguides (Indicatorinae) and the black-headed duck (*Heteronetta atricapilla*, Davies 2000). In this chapter, we examine the begging behaviour of three species of cowbirds. We show how cowbird begging may have been shaped by selective forces that are unique to brood parasites, and we also discuss how cowbird behaviour can provide insights into the evolution of begging.

Cowbirds provide an ideal opportunity for the study of begging behaviour. Unlike the common cuckoo (*Cuculus canorus*, Wyllie 1981), these brood parasites are raised with the host young. Thus, cowbirds allow the study of nestling competition and adult allocation decisions involving nestlings that are not related to each other and that often exhibit behavioural or morphological phenotypes different from the host's own young. Cowbirds also parasitize host species of different sizes, which permits a comparison of the begging behaviour of parasitic nestlings when receiving different amounts of food and competing with different sized host nestlings. Lastly, one cowbird species mimics the host young, which allows comparative tests of the importance of exaggerated begging as a means of offsetting the disadvantage of looking dissimilar to host young.

Cowbird Natural History and Host Specificity

Recent evidence indicates that the five brood-parasitic cowbird species comprise a monophyletic group (Lanyon 1992; Johnson & Lanyon 1999), and in our discussion we will follow the nomenclature that reflects the best-supported phylogeny (Johnson & Lanyon 1999).

The brood-parasitic cowbirds vary tremendously in the extent to which they specialize on particular host species (Table 1). The screaming cowbird is a specialist brood parasite. Although there are some records of screaming cowbirds parasitizing other hosts (brown-and-yellow marshbird, *Pseudoleistes virescens*, Mermoz & Reboreda 1996; Chopi blackbirds *Gnorimopsar chopi*, Fraga 1996), their main host is the bay-winged cowbird. A recent phylogeny based on mitochondrial DNA suggests that the bay-

winged cowbird is not in a monophyletic group with the parasitic cowbirds (Johnson & Lanyon 1999). Screaming cowbird young are almost identical to the host young in appearance and vocalizations, even though adult plumage and calls of both species are very different (Hudson 1920; Fraga 1979) and adult screaming cowbirds are larger (Lichtenstein 1997). The similarity remains through the fledgling period until the parasitic nestlings attain nutritional independence, and therefore, may be considered a true case of mimicry.

Table 1. General characteristics of the cowbirds (modified from Davies 2000).

Species	Distribution	No. hosts	Main hosts	Mean adult mass (g) ^{a,b,c}
Screaming cowbird <i>Molothrus rufoaxillaris</i>	Bolivia, Paraguay, Uruguay, southern Brazil, Argentina	1	bay-winged cowbird	male: 58.0 female: 48.4
Giant cowbird <i>M. oryzivora</i> ¹	Northern Argentina to Mexico	7	icterids (caciques & oropendola)	male: 219 female: 162
Bronzed cowbird <i>M. aeneus</i>	Colombia through Mexico; and across southern USA	87 ^d	passerines (20% are icterids)	male: 66.7 female: 57.4
Shiny cowbird <i>M. bonaeriensis</i>	South America, the Caribbean, Florida	214	passerines	male: 55.5 female: 44.9
Brown-headed cowbird <i>M. ater</i>	North America	226	passerines	male: 49.0 female: 38.8
Bay-winged cowbird <i>Oreopsa badius</i> ²	Bolivia, Paraguay, Uruguay, SE & NE Brazil, Argentina ^c	0	non-parasitic	male: 46.6 female: 43.7

¹formerly *Scaphidura oryzivora*; ²formerly *Molothrus badius*; ^a Dunning 1993; ^b Mason 1987; ^c Fraga 1986; ^d Sealy et al. 1997.

The giant cowbird is known to parasitize seven species of oropendolas and caciques (Icterinae, Ortega 1998). Giant cowbird young have a beak and face-iris coloration similar to that of oropendola nestlings, that disappears after the young have attained nutritional independence (Redondo 1993).

The bronzed cowbird, shiny cowbird and brown-headed cowbird are all host-generalists. These cowbirds parasitize between 87 and 226 host species (although not all of these hosts are able to rear cowbirds). Suitable hosts of all three cowbird species comprise an enormously diverse group of passerines that vary in body size, nestling behaviour, adult behaviour, nestling diet and decision rules used by adults when allocating food. Generally, brown-headed cowbirds tend to parasitize smaller hosts whereas shiny cowbirds apparently prefer to parasitize hosts larger than themselves (Mason 1980; Wiley 1988; but see Lichtenstein 1998).

The distinction between host-specialists and host-generalists is an important one, in part because it affects the predictability of the competitive environment in which the cowbird nestlings must solicit food. Generalist cowbird young may require behavioural flexibility to acquire food from a host that could exhibit a wide range of behavioural and morphological phenotypes. High fecundity and cheap egg production (Kattan 1995) might enable female generalist cowbirds to pursue an opportunistic strategy, laying eggs in nests of poor hosts in the absence of higher quality hosts. Specialist cowbird nestlings do not experience such variation in host phenotype, but they face a host that may have evolved defences against the parasite (Rothstein 1990).

This chapter reviews our current understanding of nestling behaviour by both generalist and specialist cowbirds. First, we examine the success of cowbirds in mixed broods of parasite and host young to test for benefits of exaggerated begging. Second, we examine the predation costs associated with exaggerated begging by cowbirds. Third, we ask whether cowbirds are treated differently from host young. Fourth, we address whether the apparently exaggerated level of begging by cowbirds is an honest reflection of their hunger. We conclude with suggestions for future work.

SUCCESS OF COWBIRDS IN MIXED BROODS

It is especially fascinating to consider the mechanisms underlying the success of cowbird nestlings because: (1) cowbirds do not face the inclusive fitness costs that potentially shape the begging behaviour of non-parasitic young and (2) cowbirds must acquire food from, and usually compete against, individuals of a different species. These unique circumstances raise many exciting questions. Under what conditions are cowbird young

successful and what mechanisms are involved in this success? How does cowbird behaviour affect host young? In this section, we will explore these issues, using data collected mainly from brown-headed cowbirds.

Ejection of Host Nestmates

In most brood-parasitic species of cuckoos and honeyguides, the parasitic nestling ejects or kills the host eggs or young, leaving the parasite as the sole occupant of the nest (Payne 1977; Rothstein 1990). There is one documented case and several suspected cases of a brown-headed cowbird nestling ejecting a host nestling from the nest (Dearborn 1996), but this behaviour is the exception rather than the rule among cowbirds. Thus, cowbird young typically spend part or all of the nestling period in the company of host young. Consequently, a main determinant of the success of cowbird nestlings is their ability to acquire food in the presence of host nestmates.

Early Hatching by Cowbirds

Early hatching relative to host hatching is one factor that appears to facilitate the success of cowbird nestlings, and this trait is widespread among the brood-parasitic cowbirds. The specialist screaming cowbird has a shorter incubation time than its host, the bay-winged cowbird (Fraga 1986; Briskie & Sealy 1990), and for the three generalist species (brown-headed, shiny and bronzed) examined by Briskie and Sealy (1990), the incubation period is shorter than expected based on body size analysis of parasitic and non-parasitic members of the Icterinae. Thus, for both generalist and specialist cowbirds, the nestling is predisposed to early hatching. The likelihood, however, of hatching before the host nestlings depends also upon the timing of laying by the female cowbird and upon the incubation period of the host species.

When a cowbird nestling hatches before its host nestmates, the head start afforded the parasite can create a large asymmetry in size (e.g. Marvil & Cruz 1989). Hosts accept cowbird nestlings even when they hatch many days earlier than host young (McMaster & Sealy 1998), and early hatching means an early start at food acquisition. Brown-headed cowbird nestlings receive food almost immediately after hatching, and they can double in mass during the first 24-hour period (Hatch 1983). In addition, early hatching by cowbird young may cause a delay in hatch date of the last-laid host egg (McMaster & Sealy 1999), which could create a further size disadvantage for last-hatched host nestlings.

In general, if a cowbird hatches early in the nest of hosts that are similar or smaller in body size, the cowbird nestling is all but assured of remaining larger than its nestmates. Several mechanisms may maintain or exaggerate this size asymmetry. Adults of some host species may preferentially provision larger nestlings (Price & Ydenberg 1995), or allocate food in response to a begging cue that is partially size-dependent (Teather 1992; Kilner 1995; Dearborn 1998) or more readily produced by nestlings that are developmentally advanced (Lee 1995). The persistence of size and/or developmental asymmetries can lead to the death of host nestlings due to either trampling by the cowbird (Friedmann 1929; Nolan 1978) or starvation of host young that cannot compete with the much larger cowbird (Marvil & Cruz 1989). In contrast, when parasitizing larger hosts, the cowbird's advantage of earlier hatching may not be enough to overcome the size advantage of the host young (Lichtenstein 1998).

Effects of Nestmates on Cowbird Growth

The death of host nestmates is potentially advantageous for cowbird nestlings. Studies of an array of non-parasitic species have shown that individual nestlings exhibit lower growth rates when reared in unmanipulated broods with many nestmates (Henderson 1975; Emms & Verbeek 1991; Filliater & Breitwisch 1997) or when broods were experimentally enlarged (Nur 1984; Smith et al. 1989; Sanz 1997). Few researchers, however, have looked at the effect of nestmates on cowbird growth. D.C. Dearborn and D.E. Burhans (unpublished data) studied the growth of brown-headed cowbirds in nests of the indigo bunting (*Passerina cyanea*), a small host (adult mass of 14.5g versus 43.9g for cowbirds; Dunning 1993). Both the mass gain and structural growth of cowbird nestlings was markedly reduced by the presence of another cowbird in the nest, but was unaffected by the presence or number of host nestmates. In general, we might expect a greater impact on cowbird growth from large host nestmates, but this dynamic is complicated by the tendency for large hosts to experience multiple parasitism more frequently than small hosts (Lorenzana & Sealy 1999).

The implication of these findings, and those of Kattan (1996), is that the success of cowbirds at soliciting food from small-bodied hosts is unrelated to the presence or number of competitors in the nest, unless those competitors are also cowbirds. Because cowbirds in the nests of small hosts appear to pay a cost for sharing a nest with another cowbird, adult female cowbirds should avoid laying eggs in small hosts' nests that are already parasitized. Although multiple parasitism is common in some study systems

(Elliott 1978 and Trine 1998 for brown-headed cowbird; Lichtenstein 1998, 2001a for shiny cowbird and screaming cowbird, respectively), there is some evidence that brown-headed cowbirds may avoid laying in already-parasitized nests (Ortega et al. 1994). When multiple parasitism does occur, the fitness consequences of competition between cowbird nestmates depends on the relatedness between the cowbirds; multiple parasitism may be due to egg laying by multiple females (Hahn et al. 1999), in which case cowbirds would be unrelated, or repeated laying by one female (Alderson et al. 1999), in which case cowbirds would be full or half siblings.

Relative Success of Cowbird Nestlings with Different Host Species

Some species are inappropriate cowbird hosts because they reject cowbird eggs (Rothstein 1975). Among those hosts that do accept and hatch cowbird eggs, there is still substantial variation in host suitability. The most dramatic examples of this are those host species in which nestling diet is not adequate for the survival and growth of nestling cowbirds. Like most passerines, cowbird nestlings require a high protein diet of arthropods (Lowther 1993). Thus, cowbird nestlings do not survive in the nests of cedar waxwings (*Bombycilla cedrorum*, Rothstein 1976), which feed their young primarily fruit, or American goldfinches (*Carduelis tristis*, Middleton 1977) and house finches (*Carpodacus mexicanus*, Kozlovic et al. 1996), which feed their young primarily seeds. Surprisingly, parasitism rates can still be relatively high for these species in some study areas (e.g. 24.4% for house finches in Ontario; Kozlovic et al. 1996).

Among hosts that can rear cowbirds, incubation period and body size appear to be primary determinants of the success of cowbird nestlings. Cowbirds are quite successful with hosts that are smaller or that hatch later (Robinson et al. 1995), primarily due to their success at food acquisition (Dearborn 1998; Lichtenstein 1998). Cowbirds also do well with similar-sized host species (e.g. shiny cowbirds with yellow-hooded blackbirds, *Agelaius icterocephalus*, Cruz et al. 1990; brown-headed cowbirds with song sparrows, *Melodia melospiza*, Smith 1981). In contrast, cowbirds fare poorly with large and/or early-hatching hosts (e.g. shiny cowbirds with rufous-bellied thrushes, *Turdus rufiventris*, Lichtenstein 1998). Among hosts that are well matched with cowbirds in adult body size, there may still be differences in the size of host and parasitic nestlings. For example, adult brown-headed cowbirds are similar in size to both northern cardinals (*Cardinalis cardinalis*) and red-winged blackbirds (*A. phoeniceus*), but these species differ in egg size and also in hatchling size (cowbird: 3.0g egg, 2.3g

hatchling; cardinal: 4.9g, 3.5g; redwing: 4.0g, 2.3g; Wetherbee & Wetherbee 1961; Lowther 1993; Yasukawa & Searcy 1995; Scott & Lemon 1996). Cowbirds thus start out on a more equal footing with red-wing nestmates than they do with cardinal nestmates. Perhaps as a consequence, cowbirds seem to fare better in red-wing nests than in cardinal nests (Weatherhead 1989; Ortega & Cruz 1991; Scott & Lemon 1996). Later in the chapter, we will explore the details of cowbird food acquisition with hosts of different sizes.

Two alternative hypotheses could explain the differential success of cowbirds with cardinals and red-winged blackbirds (or similar pairs of host species). The first is the likely relationship between phylogenetic relatedness and similarity of begging behaviour. Redwings are close relatives of cowbirds whereas cardinals are not; consequently, there may be a difference in the similarity of begging behaviour between host and parasite and, hence, in the success of cowbirds at soliciting food from host adults. For example, cowbirds in indigo bunting nests sometimes flutter their wings while begging (Dearborn 1998). Indigo bunting adults appeared to ignore this behaviour (Dearborn 1998), but icterid hosts might preferentially feed wing-flapping young, as such behaviour is performed by non-parasitic icterid nestlings when they are very hungry (Lee 1995).

A second alternative explanation for the differential success of cowbird nestlings raised by cardinals and red-wings is similarity of appearance between parasitic and host young (Lichtenstein 1998). Brown-headed cowbird nestlings, which have gapes with red lining and white rictal flanges in most parts of their range (Rothstein 1978), are outcompeted by the slightly larger northern cardinals, which have orange-red lining and white rictal flanges (Scott & Lemon 1996). In contrast, brown-headed cowbirds do well at nests of red-wings and even larger hosts with a similar gape colour (e.g. yellow-headed blackbird, *Xanthocephalus xanthocephalus*, Ortega & Cruz 1992). The idea that parents might discriminate on the basis of gape colour is not new. In 1978, Rothstein hypothesized that the geographical variation in the colour of the rictal flanges of the cowbirds was influenced by the preferential feeding of those nestlings whose gape is most similar to that of the host's own young. This might explain why, when parasitizing larger hosts, shiny cowbirds are more successful at parasitizing species with similar looking young. Icterids, with their red gapes (Ficken 1965), are among the most common hosts of the shiny cowbird (Friedmann et al. 1977; Manolis 1982; Wiley 1988). The more specialist species of parasitic cowbirds also parasitize icterids (reviewed in Lichtenstein 1997).

Effects of Brown-Headed Cowbirds on Host Nestlings and Adults

Cowbird nestlings have a direct negative impact on small-bodied hosts, above and beyond the well-documented effects of host egg removal by adult cowbirds (Sealy 1992) and reduced hatching success of host eggs (Hofslund 1957; Petit 1991). Some effects are directly due to the cowbird's larger size, whereas others are due to the cowbird's success at food acquisition. Cowbird nestlings may reduce the growth or survival of host young (Mayfield 1960; Root 1969; Marvil & Cruz 1989; Weatherhead 1989), and host young that do survive the nestling period may still exhibit a lower recruitment probability than hosts from unparasitized nests (Payne & Payne 1998). Cowbirds can impact host nestlings by trampling them to death (Mayfield 1960; Nolan 1978), out-competing them for food (Dearborn 1998; Lichtenstein & Sealy 1998), stimulating host young to spend more time begging (Dearborn et al. 1998) or causing nestlings to be brooded less as parents spend more time foraging (Dearborn et al. 1998). In addition to these effects on nestlings, host adults may pay a cost for raising a cowbird. For small-bodied hosts that are capable of raising mixed broods (e.g. Wolf 1987), host adults provision parasitized broods at a much higher rate than unparasitized broods (Dearborn et al. 1998). Such an increase in reproductive effort would be expected to impose a cost upon residual reproductive value. Testing for evidence of such costs is often difficult. One study, however, that has examined this issue thoroughly (Payne & Payne 1998) found that indigo buntings raising cowbirds incurred only minimal costs in terms of same season re-nesting, adult survival to the subsequent year and reproductive success in the subsequent year. Costs to large-bodied hosts are much less pronounced, and sometimes there is no impact on host fledging success (e.g. Cruz et al. 1990).

EVOLUTIONARY LIMITS ON BEGGING BY HOSTS AND COWBIRDS

Cowbirds are quite successful at acquiring food in nests of indigo buntings, as outlined earlier, and also in nests of other small hosts (e.g. yellow warblers, *Dendroica petechia*, Lichtenstein & Sealy 1998). Their success may occur in part because cowbirds can afford to beg more intensely than hosts. Although the energetic costs of begging appear minimal (M.A. Chappell & G.C. Bachman this volume) and are not expected to differ between host nestlings and cowbird nestlings, there are likely to be pronounced differences in the inclusive fitness costs (Hamilton 1964) and

the predation costs (Harper 1986; Dearborn 1999) of begging by cowbirds versus non-parasitic nestlings. These differences may allow cowbirds to beg more loudly than non-parasitic nestlings.

Evidence for Loud Brood Parasites

For many years, researchers have noted that cowbird nestlings seem unusually loud (Friedmann 1929; Nice 1939; Hofslund 1957; Carter 1986; Payne 1991; also see Redondo 1993). To more firmly test these anecdotal reports, four studies have now quantified the rate or loudness of begging by brood parasites, and one study has experimentally tested whether the vocalizations at parasitized nests increase the risk of nest predation.

Davies et al. (1998) measured the call rates of common cuckoos raised by reed warblers (*Acrocephalus scirpaceus*) and found that a single cuckoo nestling called as frequently (and was fed an equivalent amount) as the entire brood of reed warblers that it replaced. In an early study of the shiny cowbird, Gochfeld (1979a) found that cowbird begging calls were louder and longer than those of their host nestmates, Loyca meadowlarks (*Sturnella loyca*). In addition, cowbirds were more likely to vocalize spontaneously than were their meadowlark nestmates. Briskie et al. (1994) used a comparative approach to examine the loudness of begging calls in relation to the average level of nestmate relatedness, when controlling for phylogeny. They found that species with low levels of nestmate relatedness (including brown-headed cowbirds and also non-parasitic species with high rates of extra-pair paternity) exhibited louder begging calls than species in which nestmates were usually full siblings. Lastly, Dearborn (1999) found that the rate and loudness of begging calls at indigo bunting nests was higher in nests with a cowbird than in nests without a cowbird. In Dearborn's (1999) study, measurements were made of entire broods. Based upon measures of total time begging by cowbirds and by hosts in parasitized and unparasitized nests (Dearborn 1998; Dearborn et al. 1998), it seemed likely that the louder, more frequent calls at parasitized nests were due to a combination of direct effects of cowbird vocalizations and indirect effects of cowbird behaviour on the calling of bunting nestlings.

For three different species of brood parasites, there is now evidence for louder or more rapid calling by the parasite. For cowbirds in particular, this may carry consequences for nest predation, especially for those species that parasitize hosts which build cup nests.

Predation Cost of Loud Vocalizations at Parasitized Nests

In conjunction with noticing the apparent loudness of cowbird nestlings, many authors have suggested that such noisiness may increase the risk of nest predation (Friedmann 1929; Hofslund 1957; Nolan 1978; Gochfeld 1979a; Payne 1991; Robinson et al. 1995; D.G. Haskell this volume). Comparisons of predation rates at parasitized and unparasitized nests within a given host population, however, have yielded equivocal results. Some studies have found higher predation rates at parasitized nests (Nice 1937; Burhans & Thompson 1999; Dearborn 1999), but others have found no difference (e.g. Mayfield 1960) or a difference in the opposite direction (i.e. unparasitized nests suffering higher predation rates; Arcese et al. 1996). Furthermore, the increase in predation rates at parasitized nests relative to unparasitized nests is not always greater during the nestling period than during incubation (e.g. Dearborn 1999), as would have been expected if cowbird begging calls were responsible for the overall difference in predation risk at parasitized versus unparasitized nests. Few comparisons of predation rates include power analyses, so it is difficult to judge our ability to detect differences that may exist.

Although the evidence from nest-monitoring studies is equivocal, experimental work by Haskell (1994, 1999, this volume) has shown that nestling vocalizations can indeed affect predation risk. In the one experimental test conducted thus far that deals explicitly with brood parasites, Dearborn (1999) compared predation rates at artificial nests broadcasting cowbird begging calls (loud and frequent), indigo bunting begging calls (less loud, less frequent) and silent nests. There was an overall trend towards more frequent predation at nests playing cowbird calls, followed in turn by nests playing indigo bunting calls and then silent nests. Despite several methodological shortcomings, this study demonstrates the possibility for nest predation to set an upper limit to begging behaviour in a manner that differs between cowbirds and non-parasitic species. Because predator identity can vary among nest sites and even among microhabitats within nest sites (Thompson et al. 1999; Dijak & Thompson 2000), the possible effects of predation on the evolution of begging calls are likely to exhibit much variation (e.g. Haskell 1999), and such variability likely extends to the potential for cowbird and host begging behaviour to be differentially shaped by predation risk.

ARE COWBIRDS TREATED AS HOST YOUNG?

The sight of a parasitic nestling being fed by its foster parents appears to

confound our understanding of adaptive animal behaviour. Why are cowbird nestlings accepted by their hosts and in some cases raised even to the exclusion of the host young? Unlike the hosts of evicting parasitic species, (1) cowbird hosts have their own young for comparison; (2) the benefits of discrimination are high, as the parents could save the present brood (as well as future ones; Davies & Brooke 1988); and (3) parents could learn to recognize their offspring, paying a relatively low cost of misimprinting (Lotem 1993). In the following sections, we examine whether host adults treat cowbird young as though they were host young. As mentioned before, body size appears to be a primary determinant of the success of cowbird nestlings, thus our discussion will be organized according to the relative size of host and parasitic nestlings.

Interaction Between Cowbird Nestlings and Host Young in Nests of Smaller Host Species

As we have pointed out, brown-headed cowbird nestlings fare especially well in the nests of smaller hosts. What mechanism underlies their success? Is it mainly a matter of their larger size or their ability to manipulate the parents by producing exaggerated begging signals? Experiments comparing the feeding success of brown-headed cowbirds and host nestlings in yellow warbler nests showed that the nestling that reached the highest was more likely to be fed, regardless of its species (Lichtenstein & Sealy 1998). Thus, parents seemed to follow a 'laissez-faire' strategy and fed the closest nestling (Teather 1992; McRae et al. 1993; Leonard et al. 1994). The relative height reached by the nestlings was influenced by their size and begging intensity. When both nestlings were placed at the same distance to the parent they had the same chance of getting fed, which indicates that neither body size nor begging intensity alone could explain who got fed. Cowbirds did not get fed preferentially unless they were the closest to the parent, and the same was true for the yellow warbler nestlings. The laissez-faire strategy followed by the yellow warblers was exploited by the parasitic nestlings, which, because of their larger size and intense begging, were generally closer to the parents. In the same experiment, the feeding success of brown-headed cowbird nestlings that hatched one or two days before yellow warbler nestlings was significantly greater than that of cowbird nestlings that hatched the same day as the host young. The greater success of older cowbirds was not related to more intense begging, but to the size advantage gained from earlier hatching.

The importance of relative size in determining the feeding success of cowbirds was also found in a study of brown-headed cowbirds parasitizing

indigo buntings (Dearborn 1998). In this study, cowbirds received more than twice as much food as bunting nestlings in parasitized nests. Cowbirds outperformed their bunting nestmates in the production of several size-dependent begging cues (e.g. height reached) that were correlated with food acquisition by buntings in unparasitized nests. In addition, a nestling transfer experiment showed that six-day-old indigo buntings (which are the same size as two-day-old cowbirds) received more food than their two-day-old bunting nestmates and did not receive a different amount of food than did two-day-old cowbirds. Dearborn's (1998) study, however, also suggested that signal exaggeration might contribute to cowbird success in bunting nests. Cowbirds begged during more parental visits and for more total time than did their bunting nestmates, and in a given feeding visit cowbirds usually begged sooner and stopped begging later than their bunting nestmates. These results suggest that the duration or intensity of begging is also a component of cowbird success with small hosts.

Interaction Between Cowbird Nestlings and Host Young in Nests of Similar-Sized Host Species

Empirical data show that nestlings of similar-sized host species are not outcompeted by cowbirds. The same is true for larger hosts with longer incubation periods (e.g. brown-and-yellow marshbird; Mermoz & Reboresda 1994), in which case host young and cowbird nestlings hatch at a similar size. Observations of cowbirds parasitizing a similar-sized host species, such as cardinals, showed that brown-headed cowbird nestlings did not differ from host nestlings in food acquisition (Dearborn 1998). Experiments looking at the interaction between cowbirds and similar-sized species would enable us to examine how food acquisition is affected by appearance (e.g. gape colour) or behaviour when size differences are eliminated.

Interaction Between Cowbird Nestlings and Host Young in Nests of Larger Host Species

Shiny cowbirds and rufous-bellied thrushes provide an opportunity to examine the interactions between a cowbird nestling and a larger host (Lichtenstein 2001b). Shiny cowbird nestlings do not mimic these host young either in appearance or in vocalizations. In addition to weighing half as much as the host young, the cowbirds are proportioned very differently, plus the bright red of the cowbird gape contrasts with the bright yellow of the thrush gape.

Videotapes were taken of parasitized nests containing one host nestling and one parasite, and of non-parasitized nests containing a big and a small thrush that mimicked the size difference between the host and the parasitic nestlings. Shiny cowbirds did badly in comparison with both large and small host nestlings. Far from being fed preferentially, cowbird nestlings were in fact disfavoured and shiny cowbird nestlings starved in 68.7% of the parasitized broods. Considering that in a natural situation shiny cowbirds must compete with between one and three thrush nestlings, this result probably overestimates cowbird success.

Cowbird nestlings were offered food significantly fewer times than the host young, being fed only when the thrush nestlings did not beg or begged with a low intensity. Only 53.6% of the food items offered to the cowbird resulted in successful feeds. This was a result of parents removing the food from the cowbird's gape to feed their own nestlings if their own young started begging. The greater handling time for large food items might have contributed to the cowbird's low feeding success, as it gave more time to the thrush nestlings to start begging. Most of the food items that parents brought to the nest were, however, small, and the fact that cowbird nestlings were significantly less successful than the thrush nestlings even in acquiring small food provides evidence that the inefficiency of food transfer was not simply related to prey size. An alternative hypothesis is that parents were more reluctant to give the prey items to the cowbirds than to their own young.

The most important variable in determining who got fed was the relative height the nestlings reached, but parents used different rules for feeding nestlings in the parasitized and non-parasitized nests. In non-parasitized nests parents fed the nestling that reached the highest, and if both nestlings reached the same height, they had the same probability of getting fed. In the parasitized nests, however, the host nestlings had a significantly greater chance of getting fed if they were higher or at the same height as the cowbird. When the cowbird was positioned higher than the thrush nestlings, there was no difference in the probability that either was fed. Shiny cowbird nestlings were usually fed only if the host nestlings were not begging. These results suggest that the poor success of shiny cowbird nestlings in nests of rufous-bellied thrushes is not simply due to competition with their larger nestmates, but the result of parental discrimination.

The mechanism for discrimination could be similar to that which operates in cases of brood reduction. If there is enough food available, the larger host young become satiated, and the smaller parasite then has an opportunity to be fed. Alternatively, if there is not enough food available, the host nestlings always beg, so the parasite does not get fed. No experimental study on brood reduction has shown whether the parents actively discriminate against runt young, or whether runts are not fed because of sibling competition alone.

However, the variation in nestling size or appearance has also not been as extreme. As cowbirds were not only smaller than the host young but also looked very different, this study could not determine whether the cowbirds were discriminated against because of their appearance, or a combination of appearance and small size. Experimental studies changing the appearance of different-sized thrush nestlings will be needed, as well as the creation of experimental nests in which cowbirds are larger than their thrush companions.

Cowbird Size and Host Discrimination

The previous results suggest that, if all other costs are equal, discrimination against generalist brood parasites may be more likely to evolve where the cost of a recognition error is low (Lichtenstein 2001a). According to this hypothesis, discrimination would be more likely to evolve in hosts larger than the brood parasite. In these cases, the cowbird is the smallest nestling in the parasitized nest. If a host mistakenly discriminated against its own smallest nestling, the host would lose the nestling with the lowest fitness return. By contrast, discrimination against a generalist brood parasite is less likely to evolve when the cost of a parental mistake is high. Thus, hosts smaller than the parasites are not expected to evolve discrimination. Bigger nestlings promise a larger marginal return (Lack 1954; O'Connor 1978; Parker et al. 1989) than smaller nestlings. The cost of making a mistake in unparasitized nests would be to lose the best nestling. This hypothesis led to the following predictions: (1) generalist parasitic nestlings will be discriminated against at nests of large hosts and (2) generalist parasitic nestlings will do well at nests of smaller hosts. This experiment should be replicated with other large host species (e.g. meadowlarks) to determine if the reluctance to feed shiny cowbird nestlings is widespread.

If we do not assume equal costs, the situation is more complicated. The cost of accepting a parasitic nestling is much higher for a small host than for a large host, because the nestlings of the small host might be outcompeted by the parasitic nestling (Carter 1986; Briskie & Sealy 1987; Marvil & Cruz 1989). So why do small hosts not discriminate against a larger parasitic nestling? One possibility is that large nestlings are a supernormal stimulus (Redondo 1993). Offspring size is important in determining food allocation within a brood (Redondo & Castro 1992a; Price & Ydenberg 1995), and adult birds might be constrained from evolving a rule for refusing to feed the largest nestling. An alternative hypothesis states that for small hosts whose nestlings fail to compete with the parasite, the cost of misimprinting may outweigh the benefits of correct learning (Lotem 1993). If, however, host

and parasite young fledge in nests of larger hosts, learning to recognize nestlings should be adaptive. If the parents were able to discriminate, why was the cowbird fed at all?

The fact that parents still fed the cowbirds was probably the result of conservative decision-making, rather than a perceptual inability. The absence of discrimination does not necessarily mean that an individual is unable to perceive the difference between two items. In a normal situation, it might be adaptive to follow the rule of feeding any nestling in their nest. An example comes from reed warblers that increased the rejection rate of parasitic eggs when they were first presented with a dummy cuckoo (Davies & Brooke 1988). Without evidence of parasitism, the best choice was to accept all the eggs. The additional information provided by the presence of the cuckoo, however, meant that the best response was to reject (Davies et al. 1996). The results of this study fit with the prediction that discrimination is more likely to evolve when foster parents can save most of their young after rejecting the parasite (Davies & Brooke 1988). These higher benefits, along with the smaller cost of misimprinting (Lotem 1993), make discrimination adaptive.

THE HONESTY OF BEGGING SIGNALS

As we have seen in previous chapters, young altricial birds communicate their desire to be fed by begging using postures and calling. For young in any condition, the benefits of gaining more resources are balanced by the direct and indirect costs of the begging signal (Godfray 1995a). As mentioned earlier, the potential direct costs include an increase in energetic expenditure (but see M.A. Chappell & G.C. Bachman this volume) and in the risk of predation (Dearborn 1999; D.G. Haskell this volume). The escalation of begging is also limited by an indirect cost arising from the fact that nestlings are related to their parents and siblings. Depriving present or future siblings of food decreases a nestling's inclusive fitness (Hamilton 1964). In a comparative study, Briskie et al. (1994) demonstrated that the loudness of begging signals increased as the relatedness of brood members decreased.

A growing number of empirical studies support the argument that begging is an honest indication of need (Redondo & Castro 1992b; Kilner 1995; Cotton et al. 1996). What happens when a parasitic nestling disrupts this stable signalling system? Parasitic nestlings do not share any genes with the foster parents nor with their nestmates, so their begging intensity is constrained only by the direct costs of begging. In theory then, this enables parasitic young to exhibit a higher intensity of solicitation than the host

young for the same degree of need. As parents are accustomed to a stable signalling system, they should interpret the intense begging of the parasites as a signal of intense hunger. Theoretical studies suggest that cheating by parasites can be part of a stable signalling system provided that its incidence is very low (Grafen 1990; Dawkins & Guilford 1991; Johnstone & Grafen 1993). In accordance with this theory, the begging calls of parasitic nestlings belonging to 12 genera have been described as intense, exaggerated or conspicuous (Redondo 1993). Furthermore, an experimental study controlling the degree of food deprivation showed that great spotted cuckoos (*Clamator glandarius*) begged significantly more than their magpie hosts (*Pica pica*) for the same degree of need (Redondo 1993). In the common cuckoo, nestlings begged as frequently as an entire brood of host young (Davies et al. 1998) and demanded a higher provisioning rate than the host young in relation to their daily energy budget (Kilner & Davies 1999).

Signal Exaggeration in Brown-Headed and Shiny Cowbirds

Anecdotal observations (Friedmann 1929; Nice 1939) have suggested that cowbird nestlings beg more intensively than host young, and this result has been substantiated by recent experimental studies (Gochfeld 1979b; Briskie et al. 1994; Dearborn 1998; Lichtenstein 1998). As the hunger level of the nestlings was not controlled in any of these studies, it is impossible to draw conclusions about the influence of hunger on the begging signal. There are three possible scenarios: (1) intense begging behaviour of cowbirds is not related to hunger; (2) intense begging behaviour is an honest indicator of hunger; (3) begging of parasitic nestlings is dishonest, but still informative.

To test these hypotheses, Lichtenstein (1997) studied cowbird begging behaviour when the parasitic nestling was significantly smaller than the host young (shiny cowbirds parasitizing rufous-bellied thrushes) and when the parasitic nestling was significantly larger than the host young (brown-headed cowbirds parasitizing yellow warblers). Hand-feeding and food deprivation experiments were conducted with the parasite and host young. If parasitic nestlings beg as predicted by the signalling models, both species of cowbirds are expected to beg more intensively than the host young, but their begging will vary with hunger level. Alternatively, if the parasites do not beg informatively, the prediction is that both species of parasites would beg more intensively than their hosts, but there would be no variation in their begging intensity following the experimental manipulations of their hunger. If begging was only an expression of hunger, both species of parasite should beg with intensities similar to host young for the same degree of food deprivation.

The results of the study showed that both species of cowbirds varied their begging intensity relative to their hunger. Parasitic nestlings decreased their begging intensity after being hand-fed and increased it after being food deprived. Shiny cowbird nestlings begged more intensively than the thrush nestlings during all the experimental treatments, which suggests that their begging behaviour was not an honest indication of their short-term need. Their begging behaviour fits with the prediction of signalling models as it is not honest, but is still informative. On the other hand, brown-headed cowbirds begged as intensively as the host young, which might suggest that their begging honestly reflected their short-term need. These results suggest that the intensity of begging by parasitic nestlings is influenced both by their lack of kinship with the hosts and by their hunger, which is influenced by the relative size of the host young with which they compete for food.

Differences in the cost of begging may also partially explain the results of this experiment. That is, assuming that the energetic costs of begging are the same for the two species of parasite, the high risk of predation (54.6 %; Hebert & Sealy 1993) for brown-headed cowbird nestlings may have limited the escalation of loud begging. A reduced begging intensity is predicted for populations that suffer high risks of predation (Godfray 1995b). Shiny cowbirds, on the other hand, were in relatively safer nests, in an environment with lower predation pressure (34.3%; Lichtenstein 1998). In addition, shiny cowbirds had to beg very intensively in order to get as close to the feeding adults as their larger nestmates. The begging intensity was probably also influenced by hunger. As they were getting such small amounts of food, the benefit of getting more food may have outweighed the risk of predation.

Signal Exaggeration in Screaming Cowbirds

The ideal situation for studying the relationship between begging intensity and hunger level is the interaction between the specialist screaming cowbird and its almost exclusive host, the bay-winged cowbird. Screaming cowbird nestlings coexist with the host young, ruling out the possibility that their intense begging occurs because they are the only occupants of the parasitized nest. Second, they look the same as the host young, so they do not need to compensate for their odd appearance. Third, they are similar in size and weigh as much as the host young during the nestling period, so presumably they have the same metabolic rate and would not be hungrier than the host nestlings after receiving the same amount of food.

Hand-feeding experiments done in the laboratory showed that the begging behaviour of bay-winged cowbirds was influenced by their hunger level. As the period of food deprivation increased, both cowbird species decreased

their latency to start begging and increased their begging intensity, the period they spent begging and the number of pellets consumed (Lichtenstein 1997). A positive correlation between begging intensity and hunger is consistent with other studies (Redondo & Castro 1992b; Price & Ydenberg 1995; Leonard & Horn 1998). The novel result here was that the begging intensity of the parasitic nestlings was also influenced by their hunger. Both species of cowbird exhibited long latencies to start begging following brief periods of food deprivation and the latencies got shorter as the nestlings became hungrier. These results contrast with those reported by Redondo (1993) for great spotted cuckoos, which did not vary their begging behaviour in relation to their hunger, and support the prediction of signalling models for informative begging signals in both parasitic and host nestlings (Johnstone & Grafen 1992; Godfray 1995b).

Although the begging behaviour of screaming cowbird nestlings was a reliable signal, they still exaggerated their need. Hand-feeding and food deprivation experiments indicated that screaming cowbirds begged more intensively and for a longer period than the host young for the same degree of food deprivation (Lichtenstein 2001a). When offered food *ad libitum*, they ate the same number of pellets as host young, indicating that they were not hungrier. Given the similarity in size and appearance between the parasitic nestlings and the host young, and thus similarities in the direct costs of begging (as suggested for the common cuckoo and its hosts, Lotem 1998), the exaggerated begging of the screaming cowbird can be explained solely by its lack of relatedness to its host.

Further evidence in favour of the reliability of the begging signal comes from a result suggesting that the begging of a nestmate did not influence the begging intensity of a focal nestling (Lichtenstein 2001a). Thus, both host and parasitic nestlings begged in accordance with their own need. A similar result was found for yellow warblers, rufous-bellied thrushes, shiny and brown-headed cowbirds (Lichtenstein 1997) and starlings (*Sturnus vulgaris*, Cotton et al. 1996). In contrast, studies on American robins (*Turdus migratorius*, Smith & Montgomerie 1991), yellow-headed blackbirds (Price et al. 1996) and tree swallows (*Tachycineta bicolor*, Leonard & Horn 1998) found that nestlings increased their begging in response to the begging of their nestmates. As this was not tested in a standard way across species, the disparity in results could be due to differences between the species that were tested or to the different experimental designs.

In summary, begging intensity results from an equilibrium between the direct and indirect costs of begging and the benefit of being fed. Whereas parasites are generally not related to their nestmates or to the host parents, and so do not share the indirect costs of begging with the host young, they do have to pay the direct costs of begging. The different species studied may

have reached different equilibria, depending on factors such as the probability of being related to the rest of the brood, the probability of being fed when begging at certain intensities, hunger and risk of predation. The begging intensity exhibited by screaming cowbird nestlings suggests that in situations in which the costs of begging are relatively low (the nests of bay-winged cowbirds have a low risk of predation), parasitic nestlings engage in signal overlap.

These results provide a better understanding of the interaction between host parents and parasitic young. Parasitic nestlings exploit a pre-existing honest signalling system. Hosts are trapped because this system is adaptive as long as signals are, on average, a reliable indication of their own offspring's need. Not feeding young that are begging intensively is a cost they cannot afford. Coevolution between the specialist screaming cowbird and its major host seems to have arrived at a stable equilibrium, in which the parasitic nestlings are winning the arms race. The interaction between the generalist shiny and brown-headed cowbirds and their hosts, however, might still leave room for discrimination by the hosts and for further adaptation (probably in terms of better host choice) by the parasites.

FUTURE DIRECTIONS

Two widely held views are challenged in this chapter. First, it was generally accepted that parasitic nestlings are always successful at manipulating the host parents to feed them: the experiments with shiny cowbirds and rufous-bellied thrushes show that this view is incorrect, as cowbirds were actually fed less than host young by adult thrushes. Second, observations and empirical data previously suggested that parasitic nestlings always beg intensively, independently of their hunger level. This was shown not to be the case for cowbirds, as parasitic nestlings were found to beg informatively to the extent that they increased their begging intensity with their hunger level, as predicted by signalling models. Below we provide some ideas for further research in this area.

Nestling Discrimination

Work with shiny cowbirds and rufous-bellied thrushes supported the notion that discrimination against generalist parasitic nestlings is more likely to occur in nests of large hosts, where costs of recognition errors are lower. Future work could replicate these experiments with other large host species to determine whether discrimination against cowbirds by large hosts is a

widespread phenomenon.

Additional work is also needed to further clarify the role of phylogenetic relatedness in the success of cowbirds with particular hosts. To what extent have cowbirds evolved mimicry *per se*, as opposed to exhibiting similarity to certain hosts more as a matter of phylogeny? This is an important issue in understanding relative success with different hosts and the apparent preference of some cowbird species for parasitizing other icterids.

Solicitation and Provisioning

Higher levels of solicitation result in higher nest visit rates, and this is particularly true at some parasitized nests. After arriving at the nest, however, some host parents prefer to feed their own young. If the host nestlings were able to assess their competitive ability with regard to that of their nestmate, or their feeding success in relation to the effort put into begging, host young could 'free-ride' upon the begging effort of the parasitic nestlings. The parasite makes all the effort to encourage parents to visit the nest frequently, but once the parent is in the nest, the host young are preferred. It would be interesting to compare the begging intensity and fledging mass of host nestlings when accompanied by a similar-sized and smaller nestmate (of the size of a cowbird), or a cowbird under controlled levels of hunger. Bearing in mind, however, that parasitic nestlings are usually accompanied by more than one host young, competition among host young might dilute the benefit of having a noisy cowbird in the nest.

Additional research is also needed on the relationship between begging intensity of brown-headed cowbirds and the nestlings of small hosts. In particular, we need to better assess whether competition with cowbirds might increase the need of host young such that they increase their own begging in a manner that honestly reflects their need.

Brood Parasitism and Nest Predation

Finally, more work is needed on the link between cowbird parasitism and nest predation. This issue is important from the standpoint of signal evolution and also with regard to avian conservation, as the impact of cowbird nestlings on host reproductive success may depend on synergistic effects of food acquisition and nest predation.

Several key questions remain unanswered. To what extent are the louder, more frequent vocalizations at parasitized nests due to direct versus indirect effects of brown-headed cowbird nestlings? How strong is the link between

these vocalizations and predation risk across an array of hosts, nest types and predator communities? And lastly, what is the relative importance of vocal cues in determining food allocation within a nest? This question stems from a general methodological discrepancy between studies of food allocation and studies of nest predation. When studying the allocation of food among nestmates, most researchers examine non-vocal cues (but see A.G. Horn & M.L. Leonard this volume), primarily due to the difficulty of measuring the properties of individual calls and assigning these calls to the correct offspring in the nest; the effect of begging behaviour on nest predation, in contrast, is due to vocal cues. These research areas need to be merged to allow a comprehensive view of the factors shaping the evolution of begging.

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