

The evolution of virulence in brood parasites

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Abstract Avian brood parasites are virulent, both as adults and as nestlings, because they reduce the fecundity of their hosts. The extent of virulence varies widely, both within and between brood parasite species. Here I review previous explanations for variation in the harm that brood parasites inflict on their hosts, which focus largely on the benefits of virulence, and suggest that each hypothesis is in some way unsatisfactory. I then summarize the evidence that brood parasitic offspring experience costs when host young die. I argue that the virulent behaviours shown by brood parasites are exactly analogous to the virulence shown by pathogens. Both can experience benefits by damaging host fitness, but they come at a price. I suggest that the trade-off hypothesis, developed with some success for understanding the evolution of virulence in pathogens, ought to be adopted in future theoretical and empirical work on the evolution of virulence in brood parasites.

Key words Cowbird, Cuckoo, Nestling, Trade-off hypothesis, Vidua

Brood parasites escape the costs of parental care completely by parasitizing the clutches of others, leaving their egg to be incubated in a foreign nest and their chick to be reared by host foster parents. Obligate brood parasitism is currently thought to have evolved seven times within the birds (Sorenson & Payne 2002). Six of these parasitic families produce altricial young whose nestlings are raised to independence by the host species. They are the old world cuckoos, the *Clamator* cuckoos, three species of new world cuckoo, the honeyguides (*Indicator* spp), the *Vidua* finches and the cuckoo-finch (*Anomolospiza imberbis*), and five species of cowbird (Payne 1997a; Sorenson & Payne 2002).

As adults, all these brood parasites are virulent to some degree. They inflict untargeted harm on host fecundity as nest predators (e.g. Soler et al. 1995, Arcese et al. 1996, Davies 2000). More specifically, they reduce the fecundity of their chosen victims by breaking host eggs as they parasitize the nest (e.g. Soler & Martinez 2000), by removing a host egg before adding their own to the clutch (e.g. Sealy 1992; Davies 2000), and by disrupting the efficiency of host egg incubation with their larger eggs to such an extent that host eggs fail to hatch (e.g. Rothstein 1975).

Perhaps the virulent behaviour exhibited by adult brood parasites is simply for the benefit of their offspring, who may consequently experience a lower risk of rejection by hosts (Soler et al. 1995, 1999) and who will encounter reduced competition for incubation while in the egg and fewer rivals for food after hatching. Perhaps adults also profit by damaging host fecundity, because the host nests constructed to replace those they have destroyed are available for parasitism and because they gain a free meal as they parasitize the nest (Davies 2000).

In some species, the actions of the parasitic offspring greatly compound the damage to host fitness begun by their mothers. For example, the newly hatched Common Cuckoo *Cuculus canorus* nestling further destroys host reproductive success by evicting young from the nest, balancing any unhatched egg or newly hatched chick in the small of its flattened back, before edging backwards up the side of the nest to tip it over the rim (Jenner 1788). The discovery of this remarkable behaviour earned Edward Jenner his Fellowship of the Royal Society in 1789, long before he more famously turned his attention to the virulent actions of the variola virus that causes smallpox. It has since been observed in virtually all the other old world cuckoo species (Payne 1997b).

Young honeyguides and the new world Striped Cuckoo (*Tapera naevia*) dispose of host offspring in

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a more bloody fashion. They hatch bearing sharp hooks on the ends of their bill, which they use for inflicting lethal injuries on their companions in the nest (Morton & Farabaugh 1979; Davies 2000). Host adults then remove the corpses of their young, leaving the parasite the sole recipient of their care.

Nestlings of the remaining brood parasitic species, (the *Clamator* cuckoos, the parasitic estrildids and the parasitic cowbirds) do not show such targeted chick-killing behaviours. Their presence in the nest may impose some collateral damage to host fitness, by depriving host young of food for example, or by slowly squashing them into the nest lining. Here, virulence could simply be a by-product of the parasite's larger body size. It might be argued that brood parasitic adults strategically select hosts that are much smaller than themselves, or that have longer incubation periods than the parasitic nestling, to create competitive conditions in the nest which favour their own offspring. The deaths of host young that occur merely as a consequence of the parasitic nestling's superior body size ought then be viewed as a strategy of virulence employed by adult brood parasites, rather than their offspring. Alternatively, or in addition, the young parasites themselves might pursue different strategies of virulence. For example, they may adjust their competitive ability by changing their begging behaviour to best suit the host that is rearing them. Either way, the fate of host young ultimately depends on the feeding decisions made by host parents. The hundred or so species of obligate avian brood parasite can therefore be split roughly evenly into those whose offspring are active chick-killers and those whose nestlings are more tolerant of host young.

PREVIOUS EXPLANATIONS FOR VARIATION IN THE VIRULENCE OF YOUNG BROOD PARASITES

How can we explain why brood parasitic offspring should vary so much in the damage they inflict on host fecundity? Previous hypotheses have focused on the benefits that young parasites might stand to gain from their behaviour. Variation in the extent of offspring virulence can then only be explained by suggesting different types of benefit for the different offspring behaviours observed. For example, the offspring-killing behaviours shown by the cuckoos and honeyguides are beneficial because they allow the parasite to dispense efficiently with the competition for food (Mock & Parker 1997).

It is harder to think of benefits associated with tolerance of host offspring. In cases of single parasitism, the parasitic nestling cannot gain any genetic benefit by allowing its rivals for resources to live. However, multiple parasitism of individual host nests is common amongst the parasites with host-tolerant young. In these species, parasitic offspring might avoid attacking nest-mates because they run the risk of killing kin, and losing indirect fitness benefits (Davies 2000). Nevertheless, this is unlikely to be a general theory for the evolution of the more benign brood parasitic young because it assumes that the parasite's mother habitually lays more than one egg in the same nest. Female Great Spotted Cuckoos (*Clamator glandarius*) might routinely add eggs to nests they have themselves already parasitized (Martinez et al. 1998), but Brown-headed Cowbirds do not (Fleischer 1985; Alderson et al. 1999). Variation in the virulence of parasitic young therefore cannot be solely explained by variation in the benefits they experience from their behaviour towards host offspring.

If the *Clamator* cuckoos, parasitic cowbirds and parasitic estrildid finches cannot gain any benefits from their decision to tolerate companions in the nest, then perhaps their behaviour is best explained by evolutionary lag. After all, the parasitic finches and cowbirds most recently acquired the brood parasitic lifestyle (Sorenson & Payne 2002) and so might be more likely to lack special adaptations for parasitism. Two lines of evidence stand against this non-adaptive explanation. First, the Asian Koel (*Eudynamis scolopacea*) and Channel-billed Cuckoo (*Scythrops novaehollandiae*) are species in which benign brood parasitic young have evolved from an ancestor with more virulent offspring, a transition that is unlikely to have occurred if it involved the loss of significant benefits to the parasite. Second, a Brown-headed Cowbird (*Molothrus ater*), though most typically regarded as a host-tolerant brood parasite, has been caught on film evicting a host indigo bunting from the nest (Dearborn 1996). Variation in the virulence of brood parasitic offspring therefore cannot be explained by variation in the duration of natural selection either.

VIRULENCE IN PATHOGENS VERSUS VIRULENCE IN BROOD PARASITES

Brood parasite nestlings are not alone in varying in the extent of their virulence. Both within and between

species, pathogens are well-known for differing in the harm they do to their hosts (Bull 1994; Read 1994). Working as a local doctor, Edward Jenner must have been aware of the variation in mortality resulting from infection by the variola virus, for example. On some occasions, it caused 'ordinary' smallpox, which carried a mortality rate of roughly 30%. More rarely, it also caused 'flat' smallpox or 'haemorrhagic' smallpox, and both forms almost always resulted in the death of the patient.

In the epidemiological literature, a cost-benefit analysis lies at the heart of most theoretical approaches to understanding the evolution of virulence, and it is based on a life history trade-off (Bull 1994; Messenger et al. 1999). In these models, pathogen fitness is calculated as the product of two variables that cannot be maximized simultaneously: the fecundity of the parasite (its transmission rate) and its persistence within a host (the duration of infection). For example, a pathogen might increase its fecundity with a greater level of virulence, but only at the cost of reduced persistence within its host. Natural selection favours pathogens that gain most fecundity benefits for least costs, and variable optima yield variation in the extent of virulence, both in theory and in practice (see reviews by Day 2003; Galvani 2003).

The cost-benefit approach developed by epidemiologists might be fruitfully adopted to explain variation in the virulence of brood parasitic young, because recent experimental work has revealed that parasitic offspring not only gain benefits when they damage host fecundity, but sustain costs as well.

COSTS OF KILLING HOST YOUNG

1) Loss of assistance in soliciting care

One of the first indications that brood parasitic nestlings might suffer by being raised alone in the nest came from a study which compared the rates of provisioning by host Reed Warblers (*Acrocephalus scirpaceus*) to a Common Cuckoo chick with the rate at which these parents delivered food to a typical brood of their own young. To their surprise, Brooke and Davies (1989) discovered that cuckoo nestlings and host broods were provisioned with the same types of prey at roughly the same rate and, consequently, that cuckoos attracted a far less rapid rate of food delivery than might be expected from a parasite that is unconstrained by kinship in its demands for food. Similar observations have since been made using a different population of Reed Warblers (Grim

& Honza 1997).

The relatively slow provisioning rate of the cuckoo chick is unlikely to be explained by a constraint on the part of the Reed Warblers, at least in the short term. When presented with a hungry brood of eight Reed Warbler young, temporarily housed in a Blackbird (*Turdus merula*) nest so that each chick had room to beg, Reed Warbler parents almost doubled the number of food items they brought to the nest each hour (Brooke & Davies 1989). Brooke and Davies (1989) suggest that, instead, the constraint might lie with the cuckoo nestling. Perhaps the single gape it reveals as it demands food is a poor stimulus for parents more usually confronted with four open chick mouths at each nest visit.

Detailed experiments on Reed Warbler provisioning behaviour have since demonstrated that two key aspects of the begging display independently influence the rate at which food is brought to the nest. They are the expanse of brightly coloured flesh revealed as the brood gapes for food, and the rate at which the brood produces begging calls (Davies et al. 1998; Kilner et al. 1999) and they are equally important in determining the frequency of food delivery. Furthermore, Reed Warbler parents follow exactly the same provisioning rules whether they are feeding a brood of their own young, a cuckoo nestling or a young Blackbird placed experimentally in their nest (Kilner et al. 1999). The experiments therefore confirm Brooke and Davies (1989) earlier suspicion: by evicting host young from the nest soon after hatching, the cuckoo nestling immediately reduces the potency of the visual begging display to provisioning hosts. The cuckoo partially solves this signalling problem by compensating with a supernormal begging call but, even so, the two aspects of the begging display combine merely to elicit a provisioning rate roughly equivalent to that achieved by a brood of host young (Kilner et al. 1999).

It might be argued that the cuckoo is doing rather well by this arrangement and certainly much better than a single Reed Warbler chick, who will receive roughly one quarter of the food acquired by the cuckoo during its first 11 days of life. But the cuckoo is a much larger nestling, presumably with greater needs. Once the difference in need is accounted for, there is no clear evidence that the cuckoo nestling gets any more food than a young reed warbler (Kilner & Davies 1999). In fact, it seems that the cuckoo chick may even have reduced its needs in response to the constraints it faces in demanding care. Compared

with the similarly sized Blackbird nestling, at least, it grows at a far slower rate (Kilner & Davies 1999), and spends much longer in the nest. Furthermore, cuckoo species that are raised alone in host nests in general grow more slowly than their closest non-parasitic relatives (Payne 1997b). The evidence from the cuckoos therefore suggests that extreme virulence in brood parasitic young carries the associated cost of a reduced capacity to solicit care.

Comparative evidence from Brown-headed Cowbirds is also consistent with this view. Brown-headed Cowbirds have exceptionally broad tastes in the host species they select for exploitation, ranging from the tiny gnatcatchers to the larger thrashers and meadowlarks. The damage to host fecundity that results from cowbird parasitism varies from host species to host species, partly as a consequence of the substantial variation in host body size and host incubation period (Lorenzana & Sealy 1999; Hauber 2003b; Kilner 2003). For example, the cowbird is typically raised alone in a Blue-Gray Gnatcatcher's (*Poliophtila caerulea*) nest, but with two companion host young in an Ovenbird (*Seiurus aurocapillus*) nest and alongside over three host Northern Cardinal (*Cardinalis cardinalis*) offspring. Cowbird nestling growth rates also vary between host species, but not as a function of the host's body mass or usual clutch size (Kilpatrick 2002). However, the number of companions with whom the cowbird nestling shares the nest can account for a significant amount of the variation in its growth (Kilner 2003; Kilner et al. 2004). Cowbird growth rates peak when they share the nest with roughly two host offspring (Kilner 2003; Kilner et al. 2004). With more companion host offspring, cowbirds grow more slowly, perhaps because they face more intense competition for food (Glassey & Forbes 2003). With fewer nestmates, the cowbird grows relatively poorly perhaps because it then faces the same constraints as a lone cuckoo chick and struggles to attract a high provisioning rate (Kilner 2003).

The latter suggestion was tested experimentally by examining just one host species, the Eastern Phoebe (*Sayornis phoebe*). At unmanipulated nests, the number of phoebe young surviving to fledge with the cowbird varies from none to three, with 62% of parasitized nests fledging at least one host nestling (Hauber 2003a). At manipulated nests, cowbird nestlings that were raised alongside two phoebe nestlings grew more rapidly and attained a greater weight before fledging than cowbirds reared alone. The higher growth rate of the accompanied cowbird

nestlings was associated with a higher rate of food delivery by the phoebe parents. With host young in the parasitized nest as well, parents were stimulated to visit the nest more frequently. Cowbird chicks gained disproportionately from the higher brood provisioning rate because they overpowered host young to take more than their fair share of resources. By contrast, the lone cowbirds suffered from the lack of assistance in soliciting care and, even though they had no competition for food, obtained less food from host parents than cowbirds raised with companions (Kilner et al. 2004).

2) Rejection by hosts

In one extreme case, by killing host young, the parasite abolishes the hosts' inclination to deliver food at the nest entirely (Langmore et al. 2003). In other words, by destroying host offspring, young parasites may also suffer the cost of rejection by their hosts.

Ironically, it was once thought that parasitic offspring could reduce the risk of recognition and abandonment by hosts if they killed host young (see also Lawes & Marthews 2003). Lack (1968) implied as much when he attempted to explain why cuckoo eggs often closely resemble host eggs in colour and patterning whereas cuckoo nestlings typically do not mimic host young at all. He suggested that hosts recognize parasitic offspring in the nest only if they appear odd in relation to their own offspring. Therefore any parasitic eggs or chicks that are commonly viewed alongside those belonging to the host are subjected to selection for mimicry. Parasitic nestlings that kill host young simultaneously remove the means of comparison by which host parents might identify them as foreign. Consequently, there is no risk of rejection by hosts and no selection for them to resemble host young.

We now know that birds use a different set of psychological rules for recognizing foreign offspring in their nest to those envisaged by Lack. Experimental studies have shown that hosts can recognize foreign eggs even if none of their own clutch is available for comparison (reviewed by Davies 2000). For example, Village Weaverbirds (*Ploceus cucullatus*) are very good at recognizing and rejecting foreign eggs, and their skills are not significantly improved by the presence of their own eggs in the nest (Lahti & Lahti 2001). Hosts apparently accomplish these extraordinary feats of recognition by memorizing the appearance of their clutch during their first breeding attempt and then rejecting eggs that differ from this mental

image (Lotem et al. 1995).

However even with these different host rules for detecting foreign offspring, parasitic offspring can still benefit from virulent behaviour because it still reduces the risk that they will be recognized by their hosts and consequently rejected. (Lotem 1993). To see why, consider a host that is unlucky enough to be victimized by a brood parasite in its very first breeding attempt. If the host offspring have been killed, then our naïve host parent will mis-imprint on the parasitic nestling. In subsequent breeding attempts, it will reject its own young in the mistaken belief that they are foreign. The cost of making this sort of recognition error is so high for hosts that it outweighs any benefit they might gain from learning to recognize their own offspring correctly. So by killing host young, the parasite makes chick recognition unprofitable for host parents, and it cannot evolve. The parasite effectively shuts down one psychological avenue by which its victims might detect it.

What happens if the parasite is more benign? This time, the risk that hosts will mis-imprint on the parasite is much smaller. With several host young in the nest as well, the average offspring image learnt by hosts will always more closely resemble a host nestling than a foreign chick. In future breeding attempts, hosts will then never mistakenly reject their own young. Therefore, when they are exploited by relatively benign parasites, the benefits that hosts gain from learning to recognize their young are greater than any potential recognition costs. In these circumstances, hosts can evolve the ability to discriminate against odd-looking chicks (Lotem 1993; Rodriguez-Girones & Lotem 1999).

Lotem's argument is so elegant that it seems a shame to dismiss it with mere empirical observation. At first sight, the circumstantial evidence appears consistent with his hypothesis. If chick recognition has evolved amongst hosts of the more benign parasites, then Lotem's ideas suggest that these hosts should discriminate against odd-looking offspring in their nest. Hosts of more virulent parasitic nestlings, however, should be happy to raise any chick, no matter how different it looks from their own young. As predicted, Red-billed Firefinch (*Lagonosticta senegalensis*) hosts of the relatively benign Village Indigobird (*Vidua chalybeata*) have a relatively high fledging success whether raising either their own broods, or broods which contain a mimetic parasitic nestling. They are much less likely to fledge any offspring that look unlike their own (Payne et al. 2001). Further-

more, host-tolerant Shiny Cowbird (*Molothrus bonariensis*) chicks have low fledging success in the nests of Rufous-bellied Thrushes (*Turdus rufiventris*), and do not resemble host young in either size or appearance (Lichtenstein 2001). By contrast, Reed Warbler hosts of the virulent Common Cuckoo will supply food to nestling Reed Buntings (*Emberiza schoeniclus*), Dunnocks (*Prunella modularis*) and Blackbirds even though they do not look at all like host offspring (Davies & Brooke 1989; Davies et al. 1998).

There is another way of interpreting these data, though. It is possible that when chick mimicry has evolved among the benign brood parasites, a key part of success in the competition for food depends on resembling host offspring. Even when parasites are raised alone in the nest, they must tune into the usual host offspring-parent communication system to extract care. To influence host provisioning rates, they typically exploit only the vocal channel of communication (Fry 1974; Davies et al. 1998; Kilner et al. 1999; Butchart et al. 2003). However, the more benign parasitic offspring face a different set of challenges in obtaining food because they must compete with host offspring. Here visual cues are likely to play a greater role in successful communication with host parents (Leonard et al. 2003). Thus parasitic nestlings may resemble host young because they are attempting to use the same signals when they demand care, rather than because they are trying to outwit hosts that are adept at recognizing odd-looking chicks. Equally, nestlings which do not resemble host young may suffer lower fledging rates, not because they have been recognized and rejected by their hosts, but simply because they are less effective at acquiring food. In short, these observations do not necessarily show that chick discrimination is confined to hosts of the more tolerant brood parasites. They might simply indicate the different begging tricks required by virulent and benign parasitic offspring to extract sufficient resources from their hosts.

A more serious challenge to Lotem's (1993) hypothesis comes from recent experimental work on an Australian cuckoo host: the Superb Fairy-Wren (*Malurus cyaneus*). Fairy-wrens are co-operative breeders and live in groups comprising one female and between one and four males. The female alone builds the nest and incubates the eggs, but all group members help raise young, usually three or four nestlings. The group's provisioning behaviour is exploited by the Horsfield's Bronze-Cuckoo (*Chalcites*

basalis), a parasite which specializes in victimizing malurids. More rarely, the Shining Bronze-Cuckoo (*C. lucidus*) may add its egg to a fairy-wren clutch but it more typically targets thornbills (*Acanthiza* spp.).

Female fairy-wrens have a line of defence against exploitation by cuckoo nestlings, which is apparently unique among cuckoo hosts. Roughly 40% of Horsfield's Bronze-Cuckoo nestlings are abandoned, typically within four days of hatching. While the cuckoo nestling is still vigorously demanding food, the female stops feeding it and sets about building a new nest, sometimes taking material from the old one still holding the begging cuckoo chick. The males may persist in feeding the cuckoo for a few more hours, but eventually they give up as well and the cuckoo starves to death. During the next day, the corpse is picked apart and carried off by meat ants and all that remains is a slightly dishevelled old nest. The female fairy-wren, meanwhile, is already lining her new nest (Langmore et al. 2003).

Unlike hosts of the *Vidua* finches or the Shiny Cowbird, female fairy-wrens therefore unambiguously reject parasitic nestlings in favour of constructing a new nest. What is more, they can recognize the cuckoo nestling even though it is alone the nest. Whatever the mechanism by which females acquire the ability to identify cuckoo chicks, it seems not to result in mis-imprinting (Langmore et al. 2003). Recall that the rejection costs associated with mis-imprinting were the key factor preventing the evolution of chick recognition in Lotem's (1993) model.

To determine how females recognized the cuckoo in their nest, fairy-wren clutches were experimentally manipulated so that after hatching they contained a single fairy-wren nestling, or a Horsfield's Bronze-Cuckoo nestling or a Shining Bronze-Cuckoo nestling. The fates of the young birds in all three

treatments were then followed after hatching. Every single Shining Bronze-Cuckoo nestling in the experiment was abandoned within a week, sometimes by females who were either previously or subsequently fooled by a Horsfield's Bronze-Cuckoo nestling. The rasping begging call produced by the young Shining-Bronze Cuckoo, which is quite different from the purer begging notes uttered by both nestling Horsfield's Bronze-Cuckoos and Superb Fairy-Wrens, may have revealed the cuckoo's identity.

Fairy-wrens also deserted single nestlings of their own at much the same rate as they abandoned Horsfield's Bronze-Cuckoo chicks, even though they always attempted to raise broods of two or more fairy-wrens to fledging. It suggests that sole occupancy of the nest is another cue determining the female's decision to abandon that breeding attempt (Langmore et al. 2003). So in this case, killing host offspring increases the risk that the cuckoo will be identified by its hosts and deserted. For Horsfield's Bronze-Cuckoos and Shining Bronze-Cuckoos, virulence is costly because it increases the risk of rejection by hosts.

THE EVOLUTION OF VIRULENCE IN BROOD PARASITES

The virulent behaviour exhibited by brood parasitic offspring is therefore exactly analogous to the virulent behaviour shown by pathogens: both can gain by damaging their host's fitness, but these benefits come at a price (see Table 1).

In the brood parasite's case, its fitness depends on the product of two variables that cannot be maximized simultaneously: the total amount of parental investment (PI) that hosts will supply during that breeding attempt and the fraction of that parental investment that can be taken by the parasite. For example, a parasitic chick might increase its share of

Table 1. Costs and benefits of virulence to parasites.

	Pathogen	Brood parasites
Benefits of virulence	Virulence may increase fecundity by increasing transmission rates	Virulence increases the amount of parental investment that hosts devote to the parasite by removing potential competitors
Costs of virulence	Virulence may decrease fecundity by decreasing the duration of infection	Virulence reduces the amount of parental investment that hosts devote to the parasite: <ol style="list-style-type: none"> a) through inadequate stimulation of host parents b) by revealing the parasite's identity to hosts who then stop feeding it completely

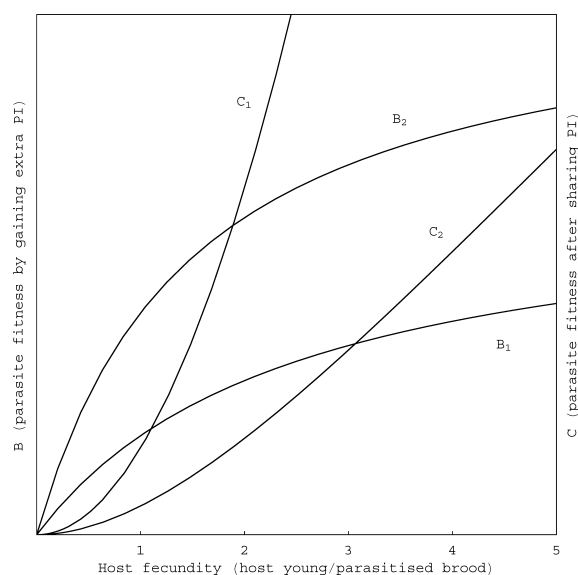


Fig. 1. The fitness costs (C) and benefits (B) to nestling brood parasites in relation to changes in host fecundity. Parasite nestling fitness peaks when they derive maximum benefits for minimum costs (i.e. B/C is greatest). Cost curve C_1 and benefit curve B_1 illustrate a case when selection would favour the evolution of chick-killing, because parasite fitness is greatest when <1 host chick survives per parasitized brood. Cost curve C_2 and benefit curve B_2 illustrate a case where selection favours the evolution of host tolerance. See text for further details.

parental investment by killing host young, but only at the cost of reduced assistance in soliciting care and hence reduced total parental investment. According to this view, the particular strategy of virulence adopted by a brood parasitic nestling depends on the optimal trade-off between the costs and benefits of killing host young (Kilner 2003; Kilner et al. 2004; see Fig. 1). Perhaps for cuckoos and honeyguides, the cost of competing for food outweighs the benefits of retaining assistance in soliciting care. The best strategy for them is to kill host chicks as soon as possible after hatching. Perhaps the reverse is true for the cowbird, *Clamator* cuckoos and *Vidua* finches. Their tolerance of host nestlings may persist because they gain more from the help they get in demanding care than they lose by sharing resources.

FACTORS CAUSING VARIATION IN VIRULENCE AMONG BROOD PARASITES

Virulence differs among the brood parasites in two key ways. The most dramatic distinction is between those species whose offspring kill host companions in

the nest and those whose nestlings are more tolerant. Variation at this level is limited and deeply entrenched phylogenetically, with a couple of rare exceptions at the species level (see above). However, if we confine our attention to the more benign parasites, then we can also see variation in virulence within species, just as in the pathogens, particularly within generalist brood parasites such as the Brown-headed Cowbird (e.g. Sealy 1992). Much of this variation might well be explained by differences in the extent of adult virulence. In theory, both types of variation can be understood by adopting the cost-benefit approach outlined in Fig. 1 (whether this is also true in practice remains open for empirical investigation).

VARIATION IN OFFSPRING VIRULENCE

The sorts of factors that are likely to determine optimal levels of offspring virulence, and whether they influence the cost (C) or benefit (B) curves depicted in Fig. 1, are summarized in Table 2. Of the six variables listed (parasite life history, host life history, co-evolution between parasites and hosts, parasite dispersal distance, kin selection, competition among parasites within hosts), I suggest that the first two are most likely to explain the deep-seated phylogenetic variation in virulence. Perhaps only these factors can tip the cost-benefit trade-off sufficiently to promote the evolution of chick-killing.

Figure 1 shows how different cost and benefit curves might favour the evolution of chick-killing over chick tolerance (and vice versa). The benefit curves show how the increased provision of host care to the parasitized brood, as a function of the number of companion host young, improves parasite fitness. The curves plateau eventually because host parents are limited in their ability to supply food. The cost curves indicate the loss in fitness experienced by the parasite when it must share food with host young. The curves are accelerating because parasite mortality increases sharply once a critical amount of resources is taken by host offspring. Cost curve C_1 and benefit curve B_1 illustrate a case when selection would favour the evolution of chick-killing, because parasite fitness ($B-C$) is greatest when less than one host chick survives per parasitized brood. In general, selection for chick-killing parasites might be expected when it takes at least one host nestling, but fewer than the mean number of young hatching from a parasitized clutch, to compromise the successful growth and development of the parasitic chick. (The

Table 2. Some factors causing variation in virulence among brood parasites.

Factor	Influences	Variable in Fig 1 affected
Parasite life history	fraction of PI the parasite can afford to share	C
	fraction of total PI available after competing with host young	C
Host life history	total PI supplied during breeding attempt	B
	marginal increase in PI supplied for each additional host young	B
Co-evolution between parasites and hosts	host resistance to brood parasites (e.g. Holen et al. 2001; Langmore et al. 2003)	C
	reduction in total PI supplied in response to parasitism (e.g. Lyon 1998; Hauber 2003b)	B
Parasite dispersal distance	future parasite fecundity: low dispersal distance means that the parasite is destroying potential hosts for its own young by behaving virulently	C
Kin selection	benefits to be gained when related parasites are raised in the same nest	B
Competition among parasites within hosts	costs sustained by sharing a nest with another parasite	C

precise number of host young it takes to impair the parasite's fitness will depend on the total amount of parental investment available.) A situation favouring the evolution of chick-killing might arise when the brood parasite exceeds the demands made by the host young it replaced in its victim's clutch, for example when it is relatively large in relation to its hosts. A general prediction, then, is that the chick-killing brood parasites should be substantially larger than their hosts, whereas the more benign brood parasites and their hosts should be more closely matching in size.

Cost curve C_2 and benefit curve B_1 illustrate a case where selection favours the evolution of host-tolerance. Although the parasite experiences the same benefits (B_1) as in our first example, it sustains less substantial costs from sharing the nest with host young (C_2), which means some degree of host-tolerance is favoured. A third scenario is illustrated by considering cost curve C_1 and benefit curves B_1 and B_2 . It shows that changing only the benefits to the parasite of sharing the nest with host young, while keeping the same cost curve, can also favour the evolution of chick-killing over chick-tolerance. When parents are indulgent, and one extra host offspring substantially increases the amount of investment they will supply, then selection favours host-tolerant parasites over chick-killers.

VARIATION IN ADULT VIRULENCE

What determines the number of eggs a female parasite removes from her victim's clutch as she parasitizes the nest? Perhaps mothers of host-tolerant parasites remove the number of eggs that will leave the optimal number of companions in the nest with her own offspring. If the parasitic nestling cannot afford to share parental investment with many host young, or if host parents are unlikely to increase their provisioning rate much when confronted with one extra gape in the nest or, even, if hosts have reduced the total investment that they are prepared to supply as a co-evolved response to parasitism (see Lyon 1998; Hauber 2003b), then perhaps mothers will remove more host eggs than they would do otherwise.

A different explanation is required to explain why mothers of chick-killing parasites take eggs during parasitism. One possibility is that mother and offspring work as a team to destroy host fecundity, with the mother sparing her offspring the hard work of slaughtering an entire host brood by killing as many as she can herself without increasing the risk that the host will then abandon the parasitized clutch (Davies & Brooke 1988). Why, then, do these parasites vary in the number of eggs they take? (Davies & Brooke 1988; Moksnes et al. 2000). Perhaps because the virulent behaviour shown by adults also brings benefits to the offspring which it cannot otherwise experience. For example, perhaps mothers remove eggs from the clutch in the hope of removing any parasitic eggs that

might already be lurking in the nest. Any chick-killing parasite that hatches ahead of her own offspring poses a severe threat to its well-being and so increases in the incentive for adult virulence. By taking as many eggs as she can from the clutch herself, rather than selectively targeting odd-looking eggs for removal (e.g. Davies & Brooke 1988, 1989), she reduces the risk that her own nestling will be killed by another brood parasite. According to this hypothesis, females should take more eggs from the host nest when there is a greater chance of multiple parasitism. The trade-off hypothesis thus offers new possible explanations for adult behaviours which have previously been difficult to account for.

CONCLUSION

Previous explanations for the virulent behaviours shown by brood parasites have been piecemeal in their approach, are often untestable and are ultimately unsatisfactory. Here, I have suggested a workable alternative, namely the trade-off hypothesis, which has been developed with some success for understanding the evolution of virulence in pathogens. Perhaps future theoretical and empirical work might use this single conceptual framework to explain the evolution of virulence in brood parasites of all ages.

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