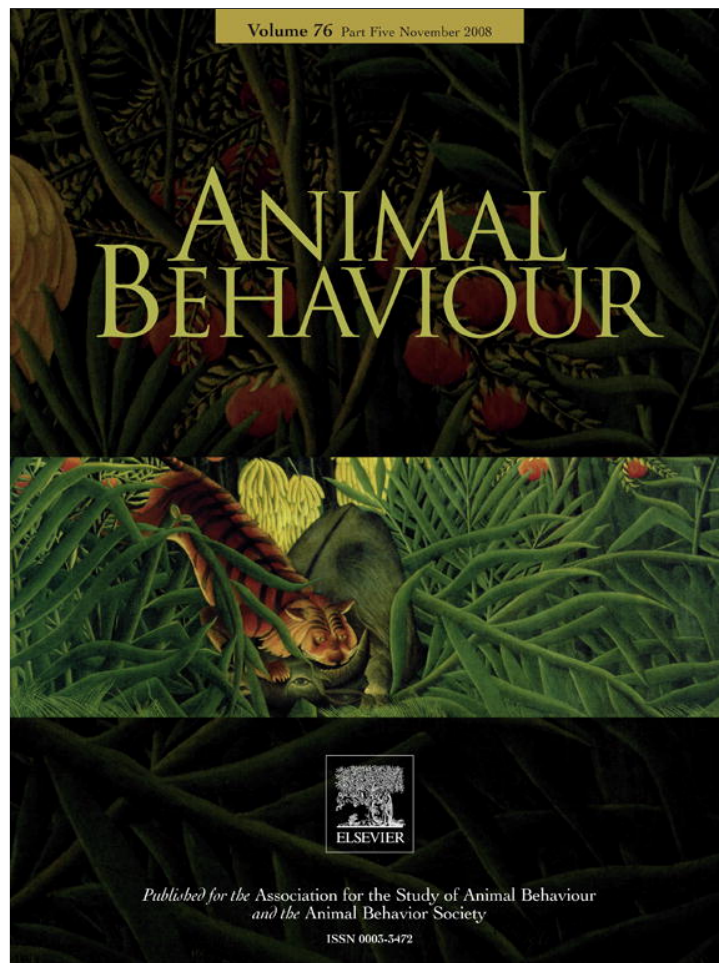


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Do hosts of interspecific brood parasites feed parasitic chicks with lower-quality prey?

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Brood parasites avoid the costs of parental care by laying their eggs in the nests of other species, the hosts. Because brood parasitism reduces host fitness, rejecting the parasitic eggs and/or nestlings is expected to be advantageous. In the absence of egg rejection, nestling discrimination is the most obvious host defence against parasitic chicks and evidence of this discrimination has been recently reported in several host–parasite systems (reviewed in Grim 2006; Anderson & Hauber 2007). However, another more subtle type of defence has been described, namely, reluctance by foster parents to feed parasitic chicks when they share the nest with host chicks, mainly because parasitic chicks are less effective at eliciting parental care than host nestlings rather than the host recognizing the parasite and choosing not to feed it (Gaston 1976; Davies & Brooke 1988; Fraga 1998; Lichtenstein 2001; Payne et al. 2001; Martín-Gálvez et al. 2005; M. Soler, G. Moreno-Rueda, J.G. Martínez, T. Pérez-Contreras & J. J. Soler, unpublished data). Here, I suggest a new possibility that adult foster parents could defend against brood parasitism by provisioning the parasitic chicks with food items of lower quality. This behaviour would decrease the cost of parasitism because providing lower-quality prey would lower parental effort, since there is a trade-off between the quality and quantity of food items delivered by parents to the rest (see below).

Type of Prey

There is abundant information in the literature supporting the possibility that foster parents feed parasitic chicks with different prey. For instance, reed warblers, *Acrocephalus scirpaceus*, feeding European cuckoos, *Cuculus canorus*, provide a higher percentage of Coleoptera to parasitic

than to host chicks (82.6% of cuckoo faeces contained Coleoptera remains, whereas in unparasitized nests Coleoptera appeared in only 33.9% of the reed warbler faeces; Brooke & Davies 1989). Grim & Honza (1997) also found that reed warblers provided cuckoo chicks with more Coleoptera (30.4% versus 8.5% of prey numbers) and more Gastropoda (30.4% versus 5.3% of prey number) than host chicks. In another study, Grim & Honza (2001) reported a smaller average size of food items delivered by reed warblers to large cuckoo nestlings. Furthermore, as cuckoo chicks became older, parents became less selective when capturing prey, decreasing prey length (Grim & Honza 2001).

Similarly, another cuckoo host, the rufous scrub robin, *Cercotrichas galactotes*, provided more Coleoptera to cuckoo chicks in naturally parasitized nests (6.33%) than to nestlings in unparasitized ones (1.41%; Martín-Gálvez et al. 2005). Rufous scrub robins also provided cuckoo chicks with more grapes (16.89%) than they fed to host chicks (3.74%; Martín-Gálvez et al. 2005). In another cuckoo–host system (great spotted cuckoo, *Clamator glandarius* – magpie, *Pica pica*, host), Soler et al. (1995) found that magpies preferentially gave prey insects with a high chitin content to great spotted cuckoo nestlings (Coleoptera 21.3% versus 1.2%; Orthoptera 25.4% versus 2.7%).

Quality of Prey

Coleoptera and Orthoptera, the food items provided more frequently to parasitic than to host chicks, have a higher percentage of chitin than do alternative prey. Chitin is a linear polysaccharide (Zhang et al. 2000) which is very resistant to degradation. In fact, pellets of most corvids (personal observation), as well as those of species such as *Falco tinnunculus*, *Athene noctua*, *Phoenicurus ochruros*, *Oenanthe leucura* and *Lanius excubitor*, contain a high

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proportion of chitinous remains (Soler et al. 1983). In addition I have frequently seen pellets from both great spotted cuckoo nestlings and chicks of their corvid hosts that contained a large amount of chitinous remains. So, there is evidence to suggest that chitin cannot be digested by either adult or immature birds. Obviously, food items with a higher percentage of chitin such as Coleoptera and Orthoptera are less nutritious than other insect foods that contain a lower percentage of chitin and hence a higher proportion of nutritious components (protein, fat, carbohydrates, etc). For instance, the dry protein content of insects varies between 15 and 81%, and the protein and fat contents of food are proportionally higher in species with a lower proportion of chitin (e.g. Ramos-Elorduy et al. 1997). There is some information in the literature about the nutrient composition of insects, but, unfortunately, most of it is based only on commercially reared insects used as food for insectivores (Finke et al. 1989; Barker et al. 1998; Finke 2002). In other cases, the analyses have been done on insects that are traditionally eaten by humans in some populations when immature and only seldom in the adult stage (Ramos-Elorduy et al. 1997; DeFoliart 1999). Studier & Sevick (1992) analysed many insects collected in the U.S.A., but they were interested in insects as prey of aerial insectivores and so most of them were flying insects. Reed warblers, rufous scrub robins and magpies, the host species mentioned above, usually forage on the ground or on vegetation. Thus, very little relevant information on prey is available for these species. In general, it can be stated that larvae have a higher percentage of fat than adult insects (Barker et al. 1998; Finke 2002), and that adults have a higher protein content than larvae (Finke 2002).

With respect to grapes, which were more frequently given to cuckoos than to rufous scrub robin host chicks (Martín-Gálvez et al. 2005), it is clear that fruits are rich in carbohydrates but poor in proteins (Levey & Karasov 1989), whereas insects are good sources of high-quality proteins (Finke et al. 1989; Studier & Sevick 1992; Barker et al. 1998). Thus, grapes are less nutritious than insects.

Another important point here is the digestive capacity of host and parasitic nestlings. Although there is some information available about digestive abilities of nestlings (e.g. Karasov & Wright 2002), no study has compared parasitic and host chicks.

Differential Feeding as a Defence Against Brood Parasitism

There is a trade-off between the quantity and quality of food items delivered by parents to the nest (Wright et al. 1998). When brood size is experimentally manipulated, chicks in large broods usually receive similar rates of feeding, but experience a decrease in the nutritional quality of their food (Wright et al. 1998). Furthermore, when parents stay away longer because the chicks are not hungry, the quality of food the chicks receive increases (larger larvae; Grieco 2001).

In the two examples mentioned above involving hosts of the common cuckoo (reed warblers and rufous scrub robins), the comparison of the quality of food items

received by host and parasitic chicks was between nests. In these cases the presence of a voracious cuckoo chick in the nest could have a similar effect as an increase in brood size, and providing prey items of lower quality but greater availability could be an adaptive strategy, as collecting lower-quality food is less costly when it is more abundant. However, in the third example, involving the great spotted cuckoo and its magpie host, the comparison was within nests. In this case a relevant question is why foster parents do not simply stop feeding parasitic chicks altogether, instead of provisioning them with low-quality food items? Perhaps they do this because this is not a case of discrimination, but a response to an especially voracious nestling that is begging for food continuously. According to parent–offspring conflict theory (Trivers 1974), it would be adaptive for parents to feed low-quality food items to satisfy an especially voracious nestling. This would be an especially adaptive behaviour in areas where the parasitism rate by brood parasites is high and there is a correspondingly high probability that the voracious nestling is a parasite.

Conclusions and Future Directions

Provisioning a parasitic chick with low-quality food items (insects with high chitin content or even vegetable components) may be an adaptive response to begging signals of high intensity as predicted by Holen et al. (2001). This possibility leads to a new line of research in brood parasite–host systems where there is much new research to carry out. Mainly (1) this idea should be evaluated in detail in different brood parasite–host systems, (2) more information is needed about the nutritional value of the different groups of prey and (3) it is necessary to study differences in the relative digestive abilities of both hosts and parasitic chicks.

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