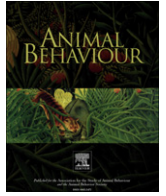


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Forum

Have brood parasitic cowbird nestlings caused the evolution of more intense begging by host nestlings?

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Obligate avian brood parasites rely entirely on host species to raise their offspring, a unique behaviour that has made them an ideal group for a wide variety of ecological and evolutionary topics (Rothstein 1990; Davies 2000). Because brood parasites are raised by heterospecific parents and often share the nest with unrelated host nestlings (Rothstein 1990; Davies 2000), they are typically influenced only by the direct costs of begging (i.e. predation and growth costs; Dearborn 1999; Chappell & Bachman 2002; Haskell 2002; Johnstone & Godfray 2002) and have served as a model for studies of parental care, parent–offspring conflict and nestling begging behaviour. Theory predicts that brood parasitic offspring should evolve more exaggerated begging displays than nonparasitic species for a given level of need (Harper 1986; Motro 1989; Holen et al. 2001), and a number of investigations have confirmed that parasitic nestlings show exaggerated begging vocalizations and postures relative to host species (Davies et al.

1998; Kilner et al. 1999; Lichtenstein 2001; Tanaka & Ueda 2005; Rivers 2007). However, as nestlings also beg in response to the behaviour of their nestmates (Forbes 2002; Rivers 2009) and because brood parasites often outcompete host young (Lichtenstein & Sealy 1998; Kilner et al. 2004; Rivers 2007), brood parasites have the potential to influence the evolution of host begging behaviour. In other words, host species (or populations) subjected to high levels of brood parasitism might be expected to evolve more intense begging displays than infrequently parasitized host species.

Recently, Boncoraglio et al. (2009, hereafter Boncoraglio et al.) tested whether parasitism by the brown-headed cowbird, *Molothrus ater* (hereafter cowbird) influenced host begging behaviour by correlating parasitism rate with host begging call amplitude for potential host species recorded by Briskie et al. (1994, 1999). Boncoraglio et al. found that begging call amplitude positively covaried with parasitism rate in passerines and they concluded that this pattern supported the hypothesis that cowbird parasitism has shaped the nestling begging behaviour of their hosts (i.e. brood parasites selected for increased host begging call amplitude). Although this result has the potential to improve our understanding of host–parasite interactions, we argue that the conclusion reached by Boncoraglio et al. is unsupported for five reasons: (1) some categorizations of cowbirds and their hosts were not supported by the literature, (2) an inappropriate proxy was

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used for selection pressure by cowbirds on host nestlings, (3) inappropriate methodology was used to calculate cowbird parasitism rates, (4) the majority of begging vocalizations were recorded in host populations that had little or no selection pressure from cowbirds, and (5) rates of extrapair young were not controlled in the analysis. Unfortunately, these issues prevent an adequate test of the hypothesis and lead us to conclude there is currently no evidence that cowbirds have shaped host begging behaviour over evolutionary timescales.

Some Categorizations by Boncoraglio et al. Appear to be in Error

The value of a comparative study depends on the validity of its assumptions and the correct categorizations of species and their attributes. Boncoraglio et al. made a number of categorizations that appear to be in error. First, they classified three species (*Hirundo rustica*, *Pipilo chlorurus*, *Pheucticus melanocephalus*) as unsuitable hosts although these species have no intrinsic biological features that would warrant such a classification. One species (*H. rustica*) was even listed by Ortega (1998) as known to have reared a cowbird. Another species, *P. chlorurus*, is a regular host in some regions (Friedmann 1963) and is known to have reared cowbirds (Chace & Cruz 1996). Second, Boncoraglio et al. categorized *Troglodytes aedon* as an egg rejecter even though it typically accepts foreign eggs and is a major host of another *Molothrus* cowbird species in some parts of its range (Friedmann 1963; Kattan 1996). Third, to control for variables related to habitat, Boncoraglio et al. placed all species into one of three habitat categories, yet some of these categorizations are inaccurate. For example, they categorized *Agelaius phoeniceus*, *Melospiza melodia*, *Passerina cyanea*, *Piranga ludoviciana* and *Catharus guttatus* as occupying mixed open–forested habitats. We doubt that anyone familiar with North American birds would equate the open country habitats of the first three species with the primarily forested habitats of the last two. Such errors may seem trivial but are likely to influence the outcome of comparative studies with a relatively small number of species where errors in categorization of one or a few species could have a disproportionate effect on the analyses.

Using Cowbird Parasitism Rate as a Proxy for Selection Pressure

Boncoraglio et al. correlated nestling begging call amplitude of potential cowbird hosts from Briskie et al. (1994, 1999) with the parasitism rate on these species as reported in Ortega (1998) and the Birds of North America accounts. This approach makes the assumption that parasitism rate is a good proxy for the intensity of selective pressure that cowbirds exert on their hosts. Although parasitism rate has been used as a proxy for the selective pressure from brood parasites by authors of previous comparative studies (e.g. Soler & Møller 1996; Aviles et al. 2006; Remes 2006), it has also long been recognized that the selective pressure exerted by brood parasites depends on both parasitism rate and the fitness cost incurred by a parasitized host (Rothstein 1975). While parasitism rate may be a reasonable surrogate of fitness costs for hosts that raise no young because of directed killing of host offspring by parasitic nestlings (e.g. honeyguides: Friedmann 1955; *Cuculus* cuckoos: Wylie 1981; Davies 2000), this is not the case with cowbird hosts because cowbirds do not show directed killing of host young, and host reproductive success instead typically varies with host life history traits such as body size and host incubation period (Hauber 2003). Indeed, a previous comparative study by one of us (S.I.R.) found no support that the rate of cowbird parasitism was a useful proxy for the effectiveness selection has had in bringing about host nest desertion as a defence against parasitism

(Hosoi & Rothstein 2000). The latter study found that the extent of a long-term history of parasitism and the level of costs incurred by parasitism when it occurs were important correlates of the level of host defences (i.e. desertion of parasitized nests).

The importance of differences in the costs of parasitism among host species can be illustrated by comparing two host species used by Boncoraglio et al., the red-winged blackbird, *Agelaius phoeniceus* (hereafter blackbird) and the cordilleran flycatcher, *Empidonax occidentalis* (hereafter flycatcher). Both species were considered by Boncoraglio et al. to be under similar selective regimes on host begging behaviour because their rates of parasitism were similar (blackbird: 10.4%; flycatcher: 6.6%). However, there appears to be little fitness cost to parasitism in the blackbird, aside from host egg removal by adult cowbirds, because blackbirds and cowbirds differ little in body size (42–44 g for female blackbirds versus 32–38 g for cowbirds; Lowther 1993; Yasukawa & Searcy 1995) and incubation period (11 days for each species; Baich & Harrison 1997). As a result, blackbird nestlings can compete successfully when raised with a cowbird (Glasse & Forbes 2003). In marked contrast, the flycatcher is smaller (11 g; Lowther 2000) and has a longer incubation period than the cowbird (14–15 days; Lowther 2000; Baich & Harrison 1997). Although data on the outcome of parasitism are limited in the flycatcher (Lowther 2000), the success of parasitized nests of other temperate *Empidonax* flycatchers is near zero, with most parasitized nests fledging only cowbirds. For example, among 4 *Empidonax* spp., host young fledged from only 2/26 parasitized nests, with only two host nestlings fledging in each of the two successful nests (Norris 1947; Berger 1951; Walkinshaw 1961, 1966; Sedgwick & Knopf 1988; Tarof & Briskie 2008; see also Whitfield & Sogge 1999). This gives a per-nest productivity of 0.15 (4/26) host young/parasitized nest, whereas the figure for blackbirds may be an order of magnitude higher (e.g. Weatherhead 1989; Røskaft et al. 1990). Thus, the cost of parasitism and intensity of selection for host defences is roughly 10× greater in the flycatcher than in the blackbird (assuming similar frequencies of parasitism), yet both were considered to be under similar selective regimes by Boncoraglio et al.

The sources that Boncoraglio et al. used for data on rates of parasitism show similar differences in the cost of parasitism among other host species. For example, the warbling vireo, *Vireo gilvus*, typically suffers complete reproductive failure when parasitized (Gardali & Ballard 2000), whereas the song sparrow, *Melospiza melodia*, and western tanager, *Piranga ludoviciana*, experience little cost when their nestlings compete with cowbirds (Hudon 1999; Arcese et al. 2002). As these examples illustrate, the use of parasitism rate alone is an inappropriate proxy for the selective pressure of cowbird parasitism on host fitness. Although Boncoraglio et al. tried to account for such differences in cost by controlling for host body mass and clutch size statistically, even variation between hosts of similar size suggests that more direct measures are needed. For example, the yellow warbler, *Dendroica petechia* (10.0 g) is able to fledge one to two host young in parasitized nests, while the equally sized least flycatcher, *E. minimus* (10.6 g) always shows complete failure (Briskie et al. 1990). Accounting for differences in the cost of parasitism is particularly important in any comparative study of cowbird hosts, as the cost varies greatly across host species, ranging from almost no impact on the number of host young produced to complete reproductive failure (Lorenzana & Sealy 1999; Hauber 2003).

Using Inappropriate Methodology to Calculate Cowbird Parasitism Rates

Even if rates of parasitism alone were a reliable indicator of the strength of selection cowbirds impose on host species, the data Boncoraglio et al. used for these rates would still be problematical.

To estimate rate of parasitism, Boncoraglio et al. calculated species-specific parasitism rates by combining records of parasitism from two compilations. This approach can skew estimates if samples are not collected with equal effort across the range of a host. For example, Boncoraglio et al. reported that the western tanager had the highest rate of parasitism in their study. The high rate of parasitism is taken from the Birds of North America account, which cites a large study (Hudon 1999) from New Mexico that reported parasitism at 40/56 western tanager nests. Boncoraglio et al. evidently lumped this sample with a study cited by Hudon (1999), in which 2/39 nests from British Columbia were parasitized, and with two California studies cited in Ortega (1998), in which a total 0/13 nests were parasitized. However, Boncoraglio et al. apparently ignored Hudon's (1999) statement of 'only 4 reports of cowbird parasitism known to Friedmann (1963)'. The latter estimate, included in a classic work on cowbirds, was based on a review of virtually all available literature and suggested this species is rarely parasitized, a result restated in two later compilations (Friedmann et al. 1977; Friedmann & Kiff 1985). The rarity of the western tanager as a host was confirmed when we consulted the Western Foundation of Vertebrate Zoology and found that 0/127 western tanager clutches collected from 1888 to 1983 were parasitized (L. Hall, personal communication). Thus, the western tanager would appear to be one of least parasitized species among the suitable hosts in the data set used by Boncoraglio et al. This species is significant because it not only had the highest rate of parasitism in the data set, it also had the loudest begging call and so probably contributed a great deal to the statistical significance that Boncoraglio et al. reported.

The western tanager is not the only species with marked spatial variation in cowbird parasitism within the sources examined by Boncoraglio et al. Parasitism rates for the warbling vireo also ranged from 0 to 79% (Gardali & Ballard 2000) and from 0 to 76.5% for the red-winged blackbird (Ortega 1998). While combining data over multiple studies gives greater weight to large samples, this approach ignores important spatial heterogeneity that makes it difficult to estimate the impact of cowbirds on their hosts. Although it is clear that over their entire range cowbirds use some host species more than others, summing the results of published studies from only certain parts of a species' range is unlikely to provide the unbiased estimates needed for comparative analyses.

Using Unparasitized Populations to Draw Inferences Regarding Effects of Selection on Cowbird Hosts

As proposed by other authors, Boncoraglio et al. noted that begging incurs costs in the form of expended energy and increased predation risk (Chappell & Bachman 2002; Haskell 2002). Heightened begging intensity could also lower inclusive fitness by reducing the amount of food delivered to siblings (Johnstone & Godfray 2002). Therefore, increased host begging in response to cowbird parasitism would be most adaptive if expressed in the actual presence of cowbirds. Unfortunately, most of the begging amplitude data used by Boncoraglio et al. were recorded from populations that experience virtually no cowbird parasitism. Indeed, only six of the 26 potential passerine host species for which Briskie et al. (1994, 1999) collected amplitude data were recorded in areas where cowbirds were common (southern Ontario) and thus had the potential to exert selection pressure on host begging calls. In contrast, 19 species were recorded at a mature forest site in Arizona where cowbird parasitism is extremely rare (<0.1% of 7000 open-cup nests; T. E. Martin, personal communication) and at which cowbirds are absent in most years (Martin & Martin 2001; T. E. Martin, personal communication). In addition, the begging calls of one species (white-crowned sparrow, *Zonotrichia*

leucophrys) were recorded outside of the northern limits of the cowbird's range in northern Manitoba. Thus, the majority (77%) of the potential host species used by Boncoraglio et al. to test for the effects of cowbird selection on begging call amplitude were recorded in populations that experienced no (or virtually no) parasitism by cowbirds.

Is it necessary to examine host begging behaviour in areas of cowbird sympatry to test this hypothesis? Or is it feasible to use any population of hosts on the assumption that they display a species-specific level of begging that is related to a species-wide level of brood parasitism? The assumption of a 'species-specific' trait is a common practise in comparative studies (Felsenstein 1985), including several by one of us (e.g. Briskie et al. 1994, 1999). However, a recent paper by Pagnucco et al. (2008) highlights the importance of not only examining host populations that are sympatric with cowbirds, but also emphasizes that future investigations may need to quantify the begging behaviour of host young in nests that are shared with cowbird young. In their study, Pagnucco et al. (2008) found that song sparrow nestlings that were raised with a single cowbird nestling had begging vocalizations that were significantly louder and higher pitched compared to conspecifics raised without cowbirds in the same population. Because increased begging amplitude by song sparrows in parasitized broods may increase the likelihood of nest predation (Haskell 2002), such behaviour should arise only in populations where cowbirds exert a sufficiently strong selective pressure. Based on studies of begging plasticity (e.g. Kedar et al. 2000), the adjustment found in song sparrow nestlings seems likely to occur in other host species. Therefore, comparative studies that only compare host begging calls in populations with no (or virtually no) selection pressure from cowbirds and that do not directly compare host nestlings raised with and without cowbird nestmates will be unable to detect such effects. Assuming that the pattern found by Pagnucco et al. (2008) is typical of other hosts, it suggests that comparative studies using estimates of begging behaviour taken from hosts in areas lacking cowbirds or from hosts that are infrequently parasitized will provide an inadequate test of how cowbirds shape host begging calls. This recent work also suggests that the amplitude of host begging calls recorded by Briskie et al. (1994, 1999) in populations allopatric with cowbirds probably only reflects local selective pressures from predation risk, levels of intraspecific competition, or both, and may be uninfluenced by selective pressure from cowbirds.

Using Begging Call Amplitude as a Response Variable without Controlling for Rates of Extrapair Young

Theory predicts that relatedness is a key factor that constrains offspring begging intensity (Godfray 1991, 1995; Johnstone & Godfray 2002). Although empirical tests of this hypothesis are limited and may suffer from the species-specific assumptions highlighted above, Briskie et al. (1994) examined 11 passerine species and found that species with higher rates of extrapair young had louder begging calls relative to their closest monogamous relatives (or in the case of the blackbird, relative to the parasitic cowbird). This finding supports the prediction that relatedness influences begging intensity across species and indicates that this factor should be considered in comparative studies of nestling begging behaviour. Despite this, Boncoraglio et al. did not control for the rate of extrapair young and assumed that the influence of nestling relatedness on begging call amplitude was similar among hosts. This can be problematic if levels of extrapair paternity are not randomly distributed with respect to levels of brood parasitism, because a high rate of extrapair paternity and the presence of a cowbird are both predicted to increase host begging call

amplitude. To date, no study has attempted to tease apart the influence of extrapair parentage and cowbird parasitism on host begging behaviour. Although the presence of either a cowbird nestling or an extrapair young should both decrease the mean relatedness of nestlings within host nests, each has different implications for the evolution of begging behaviour, because the presence of extrapair nestmates still can provide indirect fitness benefits to host young, whereas the presence of a cowbird nestling does not provide any fitness benefits. Therefore, care should be taken to separate a reduction in mean relatedness within a brood due to cowbird offspring or extrapair offspring because of their different effects on the relative payoffs to host young.

What Conclusions Can Be Drawn at This Point?

Our critique might seem to that takes issue with the general approach taken by comparative studies. On the contrary, we note great value in comparative studies because they can provide important tests of hypotheses that cannot be undertaken by investigations of single species, a view clearly evidenced by the fact that the two comparative studies that acted as the foundation for the Boncoraglio et al. study were conducted by one of us (J.V.B.). It cannot be overemphasized, however, that the value of a comparative study depends on the appropriateness of data used to test hypotheses and the validity of assumptions. Given the problems outlined above, we conclude that the study undertaken by Boncoraglio et al. suffers from both a number of untested assumptions and from inappropriate methodology and data. As a result, we find it premature to conclude that selection pressure from cowbird nestlings has influenced the begging behaviour of hosts over evolutionary timescales. Unfortunately, it appears there are no appropriate data presently available to test this hypothesis in the way proposed by Boncoraglio et al. New data on begging amplitudes of a range host species collected from localities where cowbirds are a significant source of selection, in addition to locations where they are not, could provide suitable data for an appropriate analysis if combined with a more direct assessment of the strength of selection exerted by cowbirds. In the meantime, we also encourage researchers to test this idea using a single-species approach or by comparing the begging behaviour of closely matched, ecologically similar congeners as a first step towards a broader comparative analysis. We note that although manipulative experiments that focus on one or two species do not offer the broad inferences of a comparative analysis, they benefit from being able to control additional sources of variation found among cowbird hosts (e.g. body size, cost of parasitism, rates of extrapair young) that may lead to differences in the strength of cowbird selection on hosts. We suggest that a number of such studies on different species and genera will provide broader inference than a comparative study based on data with questionable relevance to the hypothesis being considered. Moreover, studies focused on begging and cowbird parasitism in a number of species will eventually allow for a comparative study of much greater reliability than is possible with the data used by Boncoraglio et al. Finally, we recommend that researchers conduct additional studies on other brood parasitic species to provide broader inference than is afforded by comparative study of a single species of brood parasite.

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