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The exaggerated begging behaviour of an obligate avian brood parasite is shared with a nonparasitic close relative

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Offspring signalling models predict that the begging displays of obligate brood parasites are more intense than nonparasitic species because parasitic young are never reared by their genetic parents and often compete against unrelated host young during development. The brown-headed cowbird, *Molothrus ater*, has been described as having exaggerated begging relative to nonparasitic species, but an effective test of this idea is lacking because previous studies have not controlled for evolutionary history while simultaneously standardizing rearing conditions. We quantified the begging intensity of cowbirds and the closely related, nonparasitic red-winged blackbird, *Agelaius phoeniceus*, when both species experienced identical rearing conditions in two distinct nest environments: reared alone by a small cowbird host, or reared with two host young by a moderate-sized cowbird host. Against theoretical predictions, we found that in both nest environments four components of the cowbird begging display were similar to (or less intense than) blackbird begging displays (i.e. latency to beg, begging score, call rate and call amplitude) when nestlings were tested across a gradient of short-term need. Our results provide the first experimental evidence that a closely related, yet nonparasitic, species shares an exaggerated begging display with a brood-parasitic species when reared under conditions typically experienced by parasitic offspring. We discuss three nonexclusive explanations for our findings: (1) relatedness among cowbird nestmates reduced cowbird begging intensity (kin selection hypothesis), (2) reduced body condition of blackbirds elevated their begging intensity (body condition hypothesis) and (3) intense competition in blackbird nest environments led to increased blackbird begging intensity (competitive environment hypothesis).

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Begging is part of a dynamic behavioural interaction in which dependent offspring solicit critical resources from care-giving adults, and adults use begging displays to decide how resources should be distributed to offspring (Kilner & Johnstone 1997; Budden & Wright 2001). For a wide range of animals, begging is the primary means by which offspring acquire food resources (Weygoldt 1980; Budden & Wright 2001; Smiseth et al. 2007; Madden et al. 2009), especially for species with altricial development that are unable to forage independently until after leaving the nest (Kilner & Johnstone 1997; Budden & Wright 2001). Thus, begging serves as a behavioural means for obtaining food resources

that are critical to fitness while in the natal environment, making it perhaps the most important behaviour of nest-bound offspring.

Signalling models of offspring begging posit that dependent young honestly signal their need to provisioning adults, who, in turn, use those signals to make decisions about their degree of parental investment (Godfray 1991, 1995). Signalling models assume that the honesty of begging signals is maintained by three costs that rise with a concomitant increase in begging intensity: growth, nest predation and inclusive fitness (Mock & Parker 1997; Johnstone & Godfray 2002). Growth costs are based on reallocating energy from growth and development towards increased energetic expenditure that stems from elevated begging intensity (Chappell & Bachman 2002), whereas nest predation costs are based on a greater likelihood of a nest being detected and depredated due to more intense begging (e.g. louder or more frequent begging vocalizations; Haskell 2002). Inclusive fitness costs are due to decreased reproductive value of close kin that rise with an increase

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in begging intensity (Johnstone & Godfray 2002). Although empirical estimates of begging costs have been elusive (Chappell & Bachman 2002; Haskell 2002; Johnstone & Godfray 2002), such costs are thought to place an upper limit on the intensity of begging displays in dependent young (Mock & Parker 1997; Johnstone & Godfray 2002).

Obligate brood parasites are unique among birds because they are reared by unrelated adults and, in most cases, occur alone in the nest or compete against unrelated young for critical food resources during development (Payne 1977; Rothstein 1990; Davies 2000). Brood-parasitic young are therefore thought to be free of inclusive fitness costs during development, so their begging intensity is more intensive and exaggerated than nonparasitic species, all else being equal (Harper 1986; Motro 1989; Holen et al. 2001). In accordance with this notion, several empirical studies have confirmed that parasitic nestlings beg more intensively than nonparasitic species under similar conditions in a range of brood-parasitic species (e.g. Davies et al. 1998; Kilner et al. 1999; Lichtenstein 2001). In particular, several studies have found that nestlings of the brown-headed cowbird, *Molothrus ater* (hereafter cowbird) show begging displays that are more intense and exaggerated than those of nonparasitic species; cowbirds respond faster, beg longer, call louder and more frequently, and attain a greater begging posture than do nonparasitic young (Briskie et al. 1994; Dearborn 1998; 1999; Glassey & Forbes 2003; Rivers 2007; Pagnucco et al. 2008). Despite these clear differences, only a handful of studies have compared cowbird begging to close relatives to control for differences in evolutionary history (i.e. Briskie et al. 1994; Glassey & Forbes 2003; Rivers 2007), and none has examined parasitic and nonparasitic species in a standardized rearing environment where both species were cared for by heterospecific 'parents'. Nevertheless, both factors must be controlled for experimentally because rearing environments can greatly affect begging behaviour (e.g. Kedar et al. 2000; Rodríguez-Gironés et al. 2002) and because species-specific parent–offspring signals may lead to differential treatment of host young and parasitic offspring (Glassey & Forbes 2003; Schuetz 2005).

In this study, we investigated whether cowbirds have evolved exaggerated begging behaviour that serves as an adaptation for brood parasitism by comparing cowbird begging displays to those of the red-winged blackbird, *Agelaius phoeniceus* (hereafter blackbird), a closely related, nonparasitic species that is closely allied with the *Molothrus* cowbirds within the family Icteridae (Johnson & Lanyon 1999; Price et al. 2009). We used an approach in which both species were reared in heterospecific host nests that represented two common rearing environments for cowbirds in our study system (Rivers et al. 2010a): (1) reared alone by a small cowbird host and (2) reared with two host offspring by a moderate-sized cowbird host. In both host species, we experimentally controlled for nestling age and brood size, as both are known to influence begging behaviour (Budden & Wright 2001). In the middle of their developmental period we assayed nestling begging behaviour across a gradient of short-term need (Clark 2002) under controlled laboratory conditions. We predicted that the intensity of four components of the begging display of cowbird nestlings (i.e. latency to beg, begging score, call rate and call amplitude) would be greater than that of blackbirds for a given level of need and that this pattern would be consistent across the distinctly different rearing environments.

METHODS

Study Locations and Focal Species

We conducted experiments during the 2004–2007 breeding seasons at Konza Prairie Biological Station, KS, U.S.A., a 3487 ha

tallgrass prairie preserve where the cowbird is abundant, occurs in all available habitats and parasitizes more than 20 host species (Rivers et al. 2010a, 2012). The blackbird is also abundant at this location, nesting in lowland habitats and rearing offspring that are similar to cowbirds in size and appearance during the early nestling period (Weatherhead 1989). The blackbird has a socially monogamous breeding system with extrapair fertilizations that often result in a mixture of full and half siblings in broods (Yasukawa & Searcy 1995). Although genetic data are not available from Konza Prairie, we have no reason to expect that the mean relatedness of blackbird nestling at this site would be different from previous studies that have reported a mean of one to two extrapair young per brood (e.g. Westneat 1993; Weatherhead & Boag 1995; Gray 1997). Long-term research on cowbird–host interactions at Konza Prairie has found that the Bell's vireo, *Vireo bellii* (hereafter vireo), and the dickcissel, *Spiza americana*, are the two primary cowbird host species, harbouring more than 75% of total cowbird offspring found in more than 3000 host nests (Rivers et al. 2010a). However, these two cowbird hosts differ markedly in the rearing environments they provide for parasitic young. Cowbirds are reared alone in parasitized vireo nests because in these nests host young rarely hatch, host nestlings do not survive when competing against cowbirds, and vireos cannot rear more than one cowbird in a single breeding attempt (Parker 1999; Kosciuch & Sandercock 2008). In contrast, cowbirds in dickcissel nests typically compete against slightly smaller host offspring and/or other cowbirds, some of which survive to fledging (Zimmerman 1983). Thus, these two hosts provide two distinct rearing environments that are experienced by cowbird offspring in this host community (Rivers et al. 2010a) and throughout their geographical range (Friedmann 1963; Ortega 1998).

Creation of Experimental Broods

Because of high predation rates we were forced to collect most cowbird and blackbird eggs and place them into incubators (Lyon Electronics, model TX-7) to maximize the number of nestlings for experiments. Nevertheless, we found no difference in the begging behaviour of incubator-hatched and field-hatched individuals for either species (J. W. Rivers, B. D. Peer & S. I. Rothstein, unpublished data), and thus we combined nestlings from both approaches for subsequent analyses. To create vireo broods, we transferred a single cowbird or blackbird into vireo nests that were close to hatching (mean placement = 1.1 days prior to hatch date) to mimic the nest environment experienced by cowbirds in this small host (Parker 1999; Kosciuch & Sandercock 2008); at the same time, any additional nest contents were collected under permit (i.e. 58 vireo eggs, 37 vireo nestlings, 2 cowbird eggs, and 7 cowbird nestlings from 28 nests; nestlings were killed via cervical dislocation and eggs were killed via freezing). For dickcissel broods, we manipulated nests to contain a single focal nestling (cowbird or blackbird) and two dickcissels. We transferred focal nestlings into dickcissel nests on the same day host eggs hatched to ensure that all three nestmates were the same age; any additional nest contents were collected under permit (i.e. 38 dickcissel eggs, 17 dickcissel nestlings, 1 cowbird egg, 1 cowbird nestling from 27 nests; nestlings were killed via cervical dislocation and eggs were killed via freezing). All experimental broods for both hosts were created before noon local time, and a brood size of three was used for the dickcissel because it is a common brood size for parasitized nests in northeast Kansas (Zimmerman 1983; Rivers et al. 2003).

When creating experimental broods, we used only first-hatching 'core' blackbirds (sensu Forbes & Glassey 2000) from original blackbird clutches. This is because testosterone, a hormone that can influence begging behaviour (Schwabl & Lipar 2002),

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