

# Begging and cowbirds: brood parasites make hosts scream louder

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Avian brood parasites have evolved striking begging ability that often allows them to prevail over the host progeny in competition for parental resources. Host young are therefore selected by brood parasites to evolve behavioral strategies that reduce the cost of parasitism. We tested the prediction that the intensity of nestling begging displays functioning to attract parental care increases across species with the frequency of parasitism by the brown-headed cowbird (*Molothrus ater*). This was expected because host young should try to prevail over highly competitive parasitic broodmates in scramble interactions, act more selfishly when frequency of parasitism is high because brood parasites often affect more severely host condition than conspecific broodmates, and discount the kin selection costs of subtracting resources to unrelated parasites. Across 31 North American host species, begging loudness positively covaried with parasitism rate in Passerines, and such effect was stronger in species with small compared with large clutches. Begging loudness increased with brood parasitism and nest predation among the most suitable host species. These results held after controlling for concomitant ecological factors and for common ancestry effects. Our results support the hypothesis that avian brood parasitism has played a role in the evolution of begging behavior of host young. *Key words:* begging, brood parasitism, host–parasite coevolution, kin selection, scramble competition. [*Behav Ecol* 20:215–221 (2009)]

Parasites obtain the resources they need at the expense of host individuals, without causing their death in the immediacy (Price 1980). Nonetheless, hosts are entailed by the parasites with a severe decrease of their Darwinian fitness, in terms of reduced growth, viability, or reproductive success (reviewed in Lehmann 1993; Möller 2006), being thus selected to evolve more efficient mechanisms of antiparasite defense.

Among birds, obligate brood parasites have lost during their evolution the capability to build nests and incubate their eggs, which are laid in the nests of heterospecific hosts. Host species are usually altricial and raise the parasitic young until fledging (Lyon and Eadie 1991). The main cost experienced by host parents is mediated by nonadaptive allocation of limiting resources to the parasite, as is the case for parasitism by cowbirds, *Vidua* finches, and black-headed ducks (*Heteronetta atricapilla*), or the complete failure of the reproductive attempt due to the killing of host progeny by the parasite, as is the case for honeyguides and several cuckoo species (Davies 2000). In addition, brood parasites can negatively affect host fitness in other ways by, for example, removing or puncturing host eggs (Ortega 1998; Davies 2000) or increasing the risk of predation of parasitized broods (Dearborn 1999).

In altricial birds, parent–offspring communication and competition among broodmates for limiting resources (e.g., food) are mediated by begging behavior (Kilner and Johnstone 1997; Wright and Leonard 2002). Begging displays include visual and vocal signals (gape coloration, jostling, and calling), which increase in intensity according to hunger, allowing the nestlings to obtain more food from their parents as the

level of signalling increases (Kilner and Johnstone 1997). Variation in individual competitive ability via begging displays (i.e., scramble competition) may determine a hierarchy among the progeny, whereby the most “competitive” nestlings are better able to subtract care to their broodmates compared with the “noncompetitive” ones (Mock and Parker 1997). However, because the individual benefit from receiving additional food decreases as satiation increases (Godfray 1995a) and such acquisition may result in depressed condition and viability of the broodmates, kin selection should tend to reduce the level of scramble competition when closely related broodmates (e.g., siblings or half-siblings) are involved (Hamilton 1964). Consistently with this prediction, a comparative study of begging behavior in relation to extrapair paternity in birds (Briskie et al. 1994) and an intraspecific study of barn swallows (*Hirundo rustica*) (Boncoraglio and Saino 2008) have shown that the loudness of begging calls uttered by the nestlings is higher when relatedness among broodmates declines.

Brood parasites are selected to display their begging signals at an exaggerated level compared with other species to increase food provisioning by foster parents and to outcompete their heterospecific broodmates, if present in the nest. This is because the individual fitness of a parasite depends on the quantity of resources acquired from its host (Price 1980) and because the young of brood parasites do not suffer a reduction in the indirect component of their inclusive fitness by subtracting resources to their unrelated broodmates (Dearborn and Lichtenstein 2002). Several studies have confirmed that parasites are exceptional beggars (e.g., Davies et al. 1998; Kilner et al. 1999; Tanaka and Ueda 2005; Sicha et al. 2007; Grim 2008). The differences in begging behavior between brown-headed cowbird (*Molothrus ater*) young and their hosts, in particular, are well known. Cowbirds have been shown to outcompete their heterospecific broodmates in terms of begging loudness and rate (reviewed in Dearborn and Lichtenstein 2002). Moreover, their presence in the nest significantly reduces the number of feedings received and the growth rate of broodmates, thus reducing their survival prospects (Dearborn and

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Lichtenstein 2002). Parasitism by cowbirds can have behavioral and physiological consequences for the young of their hosts to reduce the risk of being outcompeted, in terms of, for example, louder calls uttered by hosts in parasitized nests (Dearborn 1999; Pagnucco et al. 2008) and higher growth rate of nestlings of highly parasitized species (Remeš 2006).

However, to date, no study has addressed whether parasitism by cowbirds has consequences for the evolution of begging behavior of host young. It can be predicted that parasitism by cowbirds has selected for louder begging calls by their young via at least 2 mechanisms. First, host young should beg loudly to contrast the individual direct fitness cost of being outcompeted by the parasites, which are extremely efficient beggars (see above). This mechanism has also another implication for hosts that are smaller than cowbirds. Because individual host young of small species tend to be in poorer conditions when reared with a parasite compared with conspecific broodmates (Lichtenstein and Sealy 1998; Dearborn and Lichtenstein 2002) and the return of gaining access to additional food is expected to increase as young deviate from optimal condition (Godfray 1995a, 1995b), the inclusive fitness advantage of acquiring more resources by begging loudly, thus increasing the "direct" component of individual fitness even at the expense of "related" broodmates (i.e., siblings), will be relatively high. Second, because female cowbirds often replace host eggs with their own ones at laying (Davies 2000) and always reduce the average relatedness of the brood (*sensu* Briskie et al. 1994; Boncoraglio and Saino 2008), individual host young should increase the loudness of their begging calls because they will experience a reduced indirect fitness cost from subtracting resources to broodmates when unrelated parasites are replacing related siblings in the nest. The latter mechanism differs from the first because in the first case, the benefit of begging loudly will arise via a direct effect on the ability to outcompete the parasite, rather than via a reduction in the individual indirect fitness cost of monopolizing the resources when the presence of parasites lowers the average relatedness in the brood.

Here, we tested the specific prediction that nestling begging calls of cowbird hosts in unparasitized nests are louder as the frequency of parasitism increases across species. That is, the selective pressure exerted by cowbirds on host begging behavior would lead to the evolution of, for example, neurological and physiological traits that result in louder begging calls even in the absence of the parasite in the nest. This prediction parallels that in a study by Remeš (2006), who could show that growth rates of host young increases with the frequency of parasitism independently of host nest being currently parasitized by cowbirds. To this aim, we extracted from the published literature data on begging loudness in unparasitized broods and cowbird parasitism rate for 31 potential host species while predicting a positive relationship between begging loudness and parasitism rate across species. Because both variables can be influenced by several potentially confounding factors (e.g., host body size, habitat and nest type, nest predation rate, and clutch size; Briskie et al. 1994, 1999; Horn and Leonard 2002), we controlled for a number of ecological factors and host life-history traits in our analyses. Finally, because species data cannot be considered as independent of common ancestry and because we formulated our predictions from the evolutionary perspective of the hosts, we used host species as the experimental units and ran the analyses while controlling for their phylogeny.

Although both of the proposed mechanisms predict a positive interspecific relationship between brood parasitism and begging loudness, we tentatively discriminated among them by investigating the effects of the concomitant covariation between brood parasitism and body mass or clutch size on beg-

ging loudness. We hypothesized that a scramble competition-driven evolutionary pathway (i.e., mechanism 1 above) should result in a stronger positive effect of brood parasitism on begging loudness in small compared with large species because individual offspring should compensate for their size-related competitive disadvantage against cowbirds by begging louder particularly in species with small body size (Lichtenstein and Dearborn 2004; Rivers 2006; see also Hauber 2003). Conversely, a kin selection-driven pathway (i.e., mechanism 2) should lead to a stronger positive effect of brood parasitism on begging loudness in species with small compared with large clutches. This is the case because the presence in the nest of a parasite instead of a host has a weaker negative effect on the average relatedness among broodmates in species with large compared with small clutches.

## MATERIALS AND METHODS

### Begging loudness and brood parasitism

The data set concerns 31 North American species (26 Passerines and 5 Picidae species; see Appendices B and C of the Supplementary material). We could locate quantitative information on begging loudness and brood parasitism for 21 Passerine species, whereas we could not find any study which directly estimated the intensity of brood parasitism for at least one population of the remaining 10 species (5 Passerines and 5 Picidae). According to the literature (Poole et al. 1993–2002, <http://bna.birds.cornell.edu/BNA/>; hereafter BNA; Ortega 1998), evidence of brood parasitism for such species is only anecdotal or was never reported. Nonetheless, because our analyses of repeatability of parasitism rate for species where data on more than one population were available suggested that our results could have been sensitive to power issues (see below), the inclusion of species with very low or null parasitism rate was desired to increase sample size. We therefore decided to assign to these species an arbitrary value of parasitism of 0, assuming that the actual parasitism rate in these cases was close to 0 and that we therefore introduced only a small source of noise in the data set. In fact, such species were woodpeckers (5 species), nuthatches (3 species), treecreepers (1 species), or tits (1 species); all of them are strongly unsuitable hosts for cowbird parasitism (BNA; Ortega 1998; Davies 2000) because of their nesting habits (they are all hole nesters and, except woodpeckers, they have considerably smaller body size than cowbirds, implying that cowbirds are usually prevented from entering inside their nests to lay parasitic eggs), diet, or chicks' feeding method (woodpeckers regurgitate food directly inside the beak of their nestlings, being incompatible as foster parents for cowbird nestlings). In any case, when we repeated the analyses while excluding the species to which we arbitrarily assigned zero prevalence of parasitism (see also below), or excluding only the Picidae, we obtained qualitatively identical results. All the results we present in the main text of the paper are from analyses including only Passerines; the results of the analyses based on different selections of species including also Picidae are shown in Appendix A of the Supplementary material.

Data on begging loudness of unparasitized broods were obtained via an exhaustive search of the literature published before 1 January 2007 using the ISI Web of Science (<http://isiknowledge.com>). We identified 2 comparative studies (Briskie et al. 1994:  $n = 10$  host species; Briskie et al. 1999:  $n = 24$  species), where the authors used very similar methods for recording and analyzing the calls, with special reference to the age of recording. In fact, in both studies, the developmental stage of the nestlings was standardized by recording the begging calls invariably on the day when the primary feathers

emerged from the sheaths, with a microphone that was posed 15 cm above the center of the nest and calibrated with the tones of a digital metronome during each recording (Briskie et al. 1994, 1999). Two American Arctic species (*Calcarius pictus*; *Calcarius lapponicus*) and one European species (*Prunella modularis*) whose breeding range does not overlap with cowbird's one (BNA) were discarded. Additional comparative studies on begging calls could not be considered because quantitative data on begging loudness were not presented (Popp and Ficken 1991; Haskell 1999). Papers reporting data for single species were unsuitable for our comparative purposes because of the great heterogeneity in recording protocols adopted across studies (e.g., age of recording, microphone position, recording equipment, etc.), which may seriously affect estimates of begging loudness.

Data on brood parasitism by cowbirds were obtained from the Appendices B and C of Ortega (1998) and from the BNA database. Parasitism rates were estimated as the number of parasitized nests (i.e., either clutches or broods, although in many records authors did not specify host developmental stage for parasitism rate) divided by the total number of observed nests. We acknowledge that, for the specific purpose of our study, assessing specific parasitism rates based only on reports of parasitism in the middle of nestling stage would have provided a more accurate estimate of the intensity of selection exerted by cowbirds on host begging behavior. However, such standardized information was not available in many cases, and restricting our analysis to the reports that estimated parasitism rates only at this stage would have markedly reduced the number of species and the number of parasitism records. Because parasitism rates of clutches or broods in the same population are strongly positively correlated (Ortega 1998; Davies 2000), we decided to use the largest data set available and we considered for each study the total number of parasitized and observed nests, irrespectively of host developmental stage when parasitism was recorded. Only reports from studies including at least 5 host nests were considered. When data for more than one population of the same species were found, we weighed the mean estimate of parasitism rate by sample size. We could find quantitative information on parasitism rate for 21 out of the 31 species for which begging call data were available. A repeatability test on parasitism rate showed greater variance among than within species (1-way analysis of variance:  $F = 3.94$ , degrees of freedom [df] = 20, 162,  $P < 0.001$ ,  $R = 0.597$ ). For species where evidence of brood parasitism was only anecdotal or never reported (Ortega 1998; BNA) and not supported by quantitative information (i.e., sample sizes and parasitism rates), we arbitrarily assigned a value of parasitism of 0 (see also above). Research effort (i.e., number of published studies available in the ISI Web of Science; see, e.g., Nunn et al. 2003) did not differ among species depending on whether quantitative information on parasitism was available ( $n = 21$ ) or not ( $n = 10$ ) ( $t = 1.46$ , df = 29,  $P = 0.16$ ). Confirmatory analyses were carried out while considering maximum rather than mean parasitism rate to control for moderate repeatability of brood parasitism rate across different populations of the same hosts.

Host suitability to parasitism has been categorized according to published literature (BNA; Ortega 1998; Davies 2000; see also Garamszegi and Avilés 2005; Remeš 2006). All hole nesters (Ortega 1998; Davies 2000; but for an exception, see Petit 1991) and egg rejecters were classified as unsuitable hosts (suitability = 1). Three species (*H. rustica*, *Pipilo chlorurus*, and *Pheucticus melanocephalus*) whose life histories do not fit with cowbird requirements (because of their nest sites, diet, etc.; BNA; Ortega 1998), but for which reports of unsuccessful parasitism events are documented, were classified as partially suitable hosts (suitability = 2). All the other species were clas-

sified as suitable (suitability = 3). We also applied 3 additional categorizations of host suitability, which slightly differed from that illustrated above. First, we splitted unsuitable hosts into egg rejecters (*Turdus migratorius* and *Troglodytes aedon*), which are secondarily unsuitable species that have coevolved with the parasite from a former condition of suitability to current unsuitability because of egg rejection, and hole nesters, which are primarily unsuitable hosts that have never been parasitized by cowbirds during their evolutionary history because of their peculiar nesting habit. Egg rejecters were therefore moved either to the partially suitable (suitability = 2) host subsample, in the suitability classification 2, or to a fourth category (suitability = 0) including only these 2 rejecter species (classification 3). In classification 4, we simply categorized host suitability based on a 2-level variable, according to the likelihood for parasitic eggs to reach the early-mid nestling stage in the nests of each host species. To this aim, we assigned a new suitability score of 1 to the species that formerly were considered as totally suitable hosts (i.e., previous value of suitability = 3) and a score of 0 to all the others. However, all these 4 ranking systems for suitability led to virtually identical results, as the alternative inclusion in statistical models of the 4 factors accounting for host suitability did not change the main conclusions of our study (the supplementary analyses based on suitability classifications 2–4 are reported in Appendix A of the Supplementary material). Suitability scores were assigned in all cases independently on the frequency of brood parasitism occurring within species, but we obviously predicted that higher levels of brood parasitism should occur in suitable hosts. Species were also classified according to whether their nest is open (score = 1), semiclosed (=2; as in *H. rustica*), or closed (=3) (BNA).

### Ecological correlates and life-history traits

We collected species-specific data on nest predation, mean nestling body mass, mean clutch size, breeding habitat (open, mixed, or closed habitat), and historical exposure to cowbird parasitism.

Nest predation has been shown to influence the evolution of acoustical features of bird begging calls (Haskell 2002). For each species, data on nest predation at the nestling stage were obtained from Martin (1995) and Remeš and Martin (2002). Nest predation rate was expressed as the number of depredated broods divided by the total number of observed broods.

Nestling body mass and clutch size influence the loudness of begging calls (e.g., Briskie et al. 1999). Data on mean clutch sizes were obtained from Martin (1995). Data on nestling body mass were obtained directly from Briskie et al. (1999) or from Martin (1995).

Vegetational features of breeding habitat may influence the frequency of parasitism by cowbirds and the acoustic features of begging calls (BNA; Ortega 1998; Haskell 1999). According to BNA, species were classified as open (score of 1), mixed (score of 2), or forested (score of 3) habitat breeders. Species breeding in both habitats were assigned a score of 2, according to published literature (e.g., Garamszegi and Avilés 2005).

Historical exposure to cowbird parasitism, which may have affected the evolution of host traits according to the selection pressure exerted by the parasite across the time (Garamszegi and Avilés 2005; Remeš 2006), was scored with 1 for the species with small overlap with the current breeding range of the cowbird, 2 for the species showing extensive but recent overlap (i.e., recent sympatric species), and 3 for the old sympatric species, according to Garamszegi and Avilés (2005) criteria.

### Statistical and phylogenetic analyses

Brood parasitism and nest predation rate data were arcsine square root transformed, and nestling body mass and research

Table 1

Phylogenetic relationships between begging loudness and the variables that resulted as significant predictors in the analyses relying on the raw species data (Appendix A, Table 1, of the Supplementary material)

|  | Log likelihood | <i>F</i> | <i>R</i> <sup>2</sup> | <i>t</i> | <i>P</i> | $\beta \pm$ standard error |
|--|----------------|----------|-----------------------|----------|----------|----------------------------|
| Model 1. All Passerines ( <i>n</i> = 26)                     | -83.95         | 12.58    | 0.632                 |          | <0.001   |                            |
| $\lambda$ statistics: 0.000                                  |                |          |                       |          |          |                            |
| Test of $\lambda = 0$ : $\chi^2 = -0.001$ , <i>P</i> = 1.000 |                |          |                       |          |          |                            |
| Test of $\lambda = 1$ : $\chi^2 = 14.26$ , <i>P</i> < 0.001  |                |          |                       |          |          |                            |
| Parasitism rate  |                |          |                       | 3.10     | 0.005    | 25.10 $\pm$ 8.09           |
| Clutch size  |                |          |                       | 2.21     | 0.038    | 2.95 $\pm$ 1.34            |
| Suitability  |                |          |                       | 3.71     | 0.001    | -8.08 $\pm$ 2.18           |
| Model 2. Most suitable hosts ( <i>n</i> = 13)                | -37.11         | 12.14    | 0.713                 |          | 0.002    |                            |
| $\lambda$ statistics: 0.000                                  |                |          |                       |          |          |                            |
| Test of $\lambda = 0$ : $\chi^2 = -0.001$ , <i>P</i> = 1.000 |                |          |                       |          |          |                            |
| Test of $\lambda = 1$ : $\chi^2 = 10.38$ , <i>P</i> < 0.001  |                |          |                       |          |          |                            |
| Parasitism rate  |                |          |                       | 4.38     | 0.001    | 28.28 $\pm$ 6.52           |
| Predation rate   |                |          |                       | 3.72     | 0.004    | 51.73 $\pm$ 13.92          |

Models 1 and 2 were obtained considering either all Passerines or only the most suitable hosts, respectively.

effort data were log<sub>10</sub> transformed before analyses to achieve normality. Host suitability, breeding habitat, nest openness, and historical exposure to cowbird were treated as continuous variables because intermediate states of these variables bear biological meaning and can thus be considered as arbitrary points along a continuum (Sokal and Rohlf 1995). In all models, we included a 2-level random factor accounting for the study from which the data on begging loudness were obtained to correct for any systematic difference in begging sampling methods across the 2 studies. Final models were obtained after sequential exclusion of the nonsignificant (*P* > 0.05) terms. The interactions between brood parasitism and clutch size or body mass were included in the models to control for the combined effects of the covariation between these factors on begging loudness. However, they were included only in the final step of the analyses to reduce the risk of overparameterization.

To control for the common ancestry of species, we applied the general method of comparative analysis for continuous variables based on generalized least squares (GLSs) models (Martins and Hansen 1997; Pagel 1999). We tested our evolutionary hypotheses with likelihood ratio statistics (Pagel 1997), which compare the log likelihood of the model corresponding to a null hypothesis (*H*<sub>0</sub>) with the model for an alternative hypothesis (*H*<sub>1</sub>). The likelihood ratio is defined as  $-2 \log_e[H_0/H_1]$  and is asymptotically distributed as a chi-squared variate with df equal to the difference in the number of parameters between the 2 models. This method also enabled us to estimate the importance of phylogenetic corrections (Freckleton et al. 2002). We conducted all analyses by setting the degree of phylogenetic dependence ( $\lambda$ ) to the most appropriate degree evaluated for each model. These exercises were performed in the R statistical computing environment, with additional unpublished functions by R. Freckleton (University of Sheffield, available on request) for the GLS procedure developed for multivariate models. For simplicity, we only considered confounding factors in the phylogenetic models that had a significant effect in the statistical models relying on the raw species data (see Avilés and Garamszegi 2007). Phylogenetic analyses were carried out on the residuals of begging loudness values after the correction for the variation across data sources at the study level (i.e., Briskie et al. 1994, 1999) on the raw species data.

Phylogenetic tree of species involving branch length estimations used in the comparative analyses was originated from Sibley and Ahlquist (1990) and supplemented with Lovette

and Bermingham (2002) for Parulidae. The considered phylogenetic hypothesis is given in Appendix B (Supplementary material). When we reconstructed our composite phylogeny based on Barker et al. (2002) and using equal branch lengths, the conclusions of this paper did not change.

In the Results, we report only the results of the phylogenetic analyses of the relationship between begging loudness and brood parasitism in Passerines. For simplicity (see also above), phylogenetic models were obtained by including only the predictors that already showed a significant effect on begging loudness in raw data analyses. The entire set of analyses testing for the effect of cowbird parasitism on begging loudness of host species carried out on the raw data is reported in Appendix A of the Supplementary material.

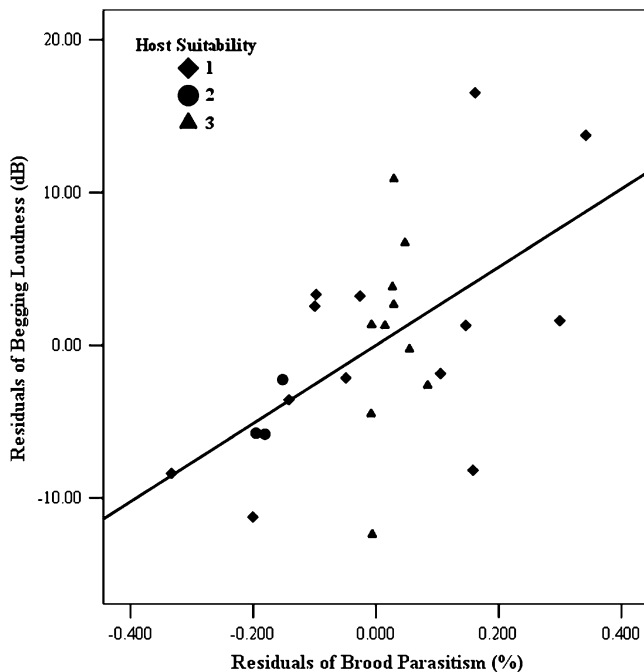
## RESULTS

### Relationship between begging loudness and parasitism while controlling for phylogeny

Phylogenetic analysis on Passerine species (*n* = 26) showed significant effects of brood parasitism, clutch size, and host suitability on begging loudness, consistently with the results of the analysis on raw data (Table 1; see also Figure 1, and Table 1, Model 1 in Appendix A of the Supplementary material). Their effects were significant also when body mass and the interaction between brood parasitism and clutch size were included (full evolutionary model: log likelihood = -79.64, *P* < 0.001,  $\lambda = 0$ ; brood parasitism: *t* = 3.03, df = 20, *P* = 0.007;  $\beta = 157.38 \pm 51.90$ ; clutch size: *t* = 3.68, df = 20, *P* = 0.002;  $\beta = 4.88 \pm 1.33$ ; suitability: *t* = 3.22, df = 20, *P* = 0.004;  $\beta = -6.38 \pm 1.98$ ). This model also showed a significant effect of the brood parasitism  $\times$  clutch size interaction on begging loudness (*t* = -2.59, df = 20, *P* = 0.018;  $\beta = -36.83 \pm 14.23$ ), whereas a positive, nonsignificant effect was detected for body mass (*t* = 1.99, df = 20, *P* = 0.060).

When we considered only the most suitable hosts (i.e., suitability = 3, *n* = 13), the phylogenetic analysis revealed a positive effect of brood parasitism and nest predation rate on begging loudness, consistently with the raw data analysis (Table 1; see also Table 1, Model 2 in Appendix A of the Supplementary material).

Finally, the outcome of the phylogenetic analysis performed on Passerine and Picidae species pooled was consistent with the findings obtained for Passerines only (see Appendix A of the Supplementary materials for all details).



**Figure 1**  
Relationship (simple linear regression) between cowbird brood parasitism (percentage of nests parasitized) and begging loudness in 26 Passerine species. Residuals of the 2 variables were obtained from the model on raw data presented in Appendix A, Table 1, of the Supplementary material, after correcting for the effect of the significant confounding factors. Species are grouped according to their suitability for cowbird parasitism (see Materials and methods). See Appendix C of the Supplementary material for the raw data.

## DISCUSSION

In this study, we have shown that the loudness of begging calls of cowbird hosts increases across species with the frequency of parasitism. After controlling for the effect of common ancestry of the sampled species, this relationship was significant while considering either only Passerines or both Passerines and Picidae, as well as when considering only the most suitable hosts (see also Appendix A of the Supplementary material). Begging loudness was found to increase with parasitism rate also after controlling for nest type and while considering maximum rather than mean parasitism rate recorded for each species (see Appendix A of the Supplementary material). Because the loudness of begging calls is a reliable index of competition experienced by the nestlings during feeding events (Wright and Leonard 2002), present results suggest that brood parasitism has affected the evolution of competitive behavior in our sample of species.

The increase of begging loudness in unparasitized nests in response to higher cowbird parasitism rate can be viewed as a defense strategy of host species to reduce the fitness costs of parasitism. In species where host nestlings are smaller than parasitic ones, cowbirds can dramatically reduce host fitness, by increasing the risk of starvation of the young during the rearing period (Dearborn and Lichtenstein 2002), decreasing the probability of recruitment of both fledglings and adults (Hoover and Reetz 2006), or skewing the sex ratio of strongly parasitized populations in a potentially nonadaptive way (Zanette et al. 2005). One possibility that the hosts may have to reduce the cost of parasitism would therefore be to enhance the competitive performances of their young in scramble interactions with the parasite. Accordingly, nestling

growth rate has been found to be higher in the species that are more frequently parasitized by cowbirds, thus possibly increasing the chances of host young to prevail over their parasitic broodmates in scramble interactions (Remeš 2006). Because in the present study we found that begging loudness increases across species with the frequency of brood parasitism and louder begging calls should solicit the parents to provide their nestlings with greater care (i.e., more food; Kilner and Johnstone 1997), then louder calls may be the mechanism by which the young of heavily parasitized species attain a faster developmental rate relative to the young of less parasitized species. That is, the offspring of heavily parasitized hosts could invest more energy in anabolic processes, thus enhancing their growth rate, by virtue of the larger amount of food they obtain by begging louder.

Two potential mechanisms could have selected for higher begging intensity in species with higher parasitism risk (see also in the Introduction). First, host young may have been selected to evolve more effective displays to enhance their access to food compared with parasites. This may provide the hosts with a 2-fold advantage in that they reduce the risk of starvation and increase their size relative to the parasite, thus promoting their chances of prevailing in size-mediated scramble interactions (Dearborn and Lichtenstein 2002; Hoover and Reetz 2006; Rivers 2006). According to this scenario, increased risk of brood parasitism may have selected for higher selfishness of host young in scramble interactions with their related siblings too. Individual nestlings of host species commonly experience poorer conditions when reared in parasitized compared with unparasitized nests (Dearborn and Lichtenstein 2002; Hoover and Reetz 2006). Because the fitness return from gaining additional resources by prevailing over the broodmates is expected to increase faster than the return of favoring a sibling as young's general state and condition deviate from their maxima (Godfray 1995a, 1995b), the young of the most parasitized hosts may have been selected to shift their competitive behavior from moderate altruism toward their related broodmates to a condition where it pays more to favor the direct component of their own fitness, due to the potentially detrimental effect of parasitism. Clearly, such adaptation would be more advantageous to the hosts as the chances of being reared in a parasitized nest increase. On the other hand, exaggerated begging escalation among relatives is expected to be prevented by kin selection (Hamilton 1964). Individual nestlings reared alongside unrelated broodmates should experience a smaller indirect cost from monopolizing parental resources and modify their begging behavior accordingly (Briskie et al. 1994; Boncoraglio and Saino 2008). Therefore, relatively weaker constraints imposed by kin selection to the nestlings in highly parasitized species could have selected for more effective begging displays.

Admittedly, we cannot firmly conclude whether superior begging performances in the most parasitized hosts have been selected by a scramble competition-based or a kin selection-based evolutionary mechanism, or both. Because body size and neck length are 2 of the major factors influencing the outcome of scramble competition among nestling birds (Mock and Parker 1997) and the consequences of cowbird parasitism are more negative in small- compared with large-sized species (Lichtenstein and Dearborn 2004; Rivers 2006), it could be speculated that brood parasitism has selected for more conspicuous begging displays (e.g., for louder calls) particularly in small hosts to compensate for their size-related handicap in competitive interactions with the parasites. However, none of our models evidenced a significant effect of the interaction between brood parasitism and body mass on begging loudness. Conversely, we found a strongly negative effect of the interaction between brood parasitism and clutch size on

begging loudness in Passerines. This covariation implies that brood parasitism has a stronger effect in increasing begging loudness in hosts with small compared with large clutches (and thus broods), thus possibly emphasizing the role of kin selection in the evolution of begging of cowbird hosts. Because the presence of a parasitic nestling reduces more severely the average relatedness existing among broodmates in small compared with large broods owing to the presence of a smaller number of host siblings ( $r=0.5$ ) or half-siblings ( $r=0.25$ ) in the nest, the indirect fitness cost of begging selfishness at a given level of brood parasitism is lower to the host in small than in large broods. Therefore, kin selection may favor the evolution of enhanced begging displays in response to parasitism particularly in species with small broods, consistent with our findings. However, these mechanisms are not mutually exclusive and may operate simultaneously.

Irrespective of the effect of brood parasitism, begging loudness of Passerines was also positively predicted by clutch size. Scramble competition models posit that individual nestlings that are begging at the highest level should gain an additional share of resources that is proportional to their own begging level divided by the mean level of the whole brood (reviewed in Mock and Parker 1997). Thus, the effect of a unit increase in individual begging level on access to food would be stronger in large compared with small broods because of a "dilution effect," that is, a greater contrast between the values of the individual and the mean begging levels in such broods (Godfray and Parker 1992). The positive relationship between begging loudness and clutch size we found is therefore consistent with this prediction.

Interestingly, we have found a strong, positive relationship between begging loudness and nest predation rate at the nestling stage when only the species with maximum suitability to cowbird parasitism were considered. We have interpreted this finding as possibly mediated by a conflict between the level of host adaptation to the parasite, reflected by enhanced competitive behavior of the offspring, and the cost of nest predation due to opportunistic exploitation of begging signals by eavesdroppers (Haskell 2002). Thus, the evolution of louder begging calls may be contrasted by predation being more intense on species whose nestlings are selected by brood parasites to beg more loudly (see also Krüger 2007).

Consistent with other studies including larger samples of species (reviewed in Ortega 1998; Davies 2000), we have also found a significant relationship between the rate of cowbird parasitism and the breeding habitat of potential hosts, with parasitism being more frequent in mixed than in forested habitats (see Appendix A of the Supplementary material). The significance of such relationship indicates that our sample of species may have the statistical power to uncover biologically established associations, even if we could not consider a larger number of hosts due to the relatively small number of species for which published data on begging loudness are available (see Materials and methods).

Finally, as comparative studies are based on correlations, certain limitations about causality warrant attention. We tested the prediction that increased parasitism rate selects for louder begging, rather than the reverse. This was the case because cowbirds generally have strong impact on the offspring of their hosts (Dearborn and Lichtenstein 2002), and there is a clear link between begging intensity and competition among broodmates in birds (Kilner and Johnstone 1997). Moreover, as brood parasitism must occur at an early stage of the breeding attempt of hosts, parasites should be selected to locate available nests by eavesdropping, for example, the sexual displays or nest-building activities of breeding adults (Garamszegi and Avilés 2005), rather than the begging calls of host progeny. Although our results support our predictions, it

would be premature to reject alternative scenarios, in which begging loudness could somehow select for brood parasitism. As parasites may hypothetically eavesdrop loud begging calls of their hosts in a habitat patch during a breeding season, they could modify their habitat choice in following years accordingly, thus even increasing the rate of parasitism of such populations. However, either low breeding site fidelity or low recruitment rate of both individual hosts and parasites would prevent this mechanism to operate. Moreover, cowbirds have been shown to induce their hosts to lay replacement clutches by predated the eggs rather than the nestlings (Hoover and Robinson 2007). This may suggest that cowbirds are preferentially selected to eavesdrop other cues than host begging loudness to increase their fitness.

In conclusion, we have shown that, in unparasitized nests, competitive behavior of nestling birds, reflected by the loudness of begging calls, increases across species as the frequency of parasitism by cowbirds increases, and particularly so among species with small clutches. We have interpreted such finding as a mechanism adopted by the host young to reduce the cost of brood parasitism in scramble interactions against the parasites. Our study is consistent with previous literature published on this topic (Remeš 2006; Pagnucco et al. 2008) and emphasizes the importance of brood parasitism as a major factor influencing the evolution of offspring competitive interactions in birds.

## SUPPLEMENTARY MATERIAL

Supplementary material can be found at <http://www.beheco.oxfordjournals.org/>

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