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## Brood parasitism by brown-headed cowbirds and the expression of sexual characters in their hosts

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**Abstract** Interspecific brood parasites may use the secondary sexual characters of the hosts to decide which species to parasitize. Hence, species with conspicuous and well-recognisable traits may have higher chances of becoming parasitised. Using North American birds and their frequent brood parasite, the brown-headed cowbird *Molothrus ater*, we tested the relationship between features of song and plumage coloration of hosts and the frequency of brood parasitism while controlling for several potentially confounding factors. Relying on two sets of analysis, we focused separately on the evolutionary view of the parasite and the host. From the cowbird's perspective, we found that males of heavily parasitized species posit songs with low syllable repertoire size, shorter inter-song interval and have brighter plumage. From the host's perspective, a phylogenetic analysis revealed similar associations for features of song, but not for plumage characteristics that were unrelated to brood parasitism. These comparative findings may imply that brood parasites choose novel hosts based on heterospecific signals; and/or host species working against sexual selection escape from brood parasitism by evolving inconspicuous sexual signals. Although our data do not allow us to distinguish between these two evolutionary scenarios, our results suggest that selection factors mediating cowbird parasitism via host recognition by heterospecific signals may

have an important role in the evolutionary relationship between brood parasites and their hosts.

**Keywords** Bird song · Cowbird parasitism · *Molothrus ater* · Plumage coloration · Signal evolution

### Introduction

Evolving various levels of auditory and visual discrimination of heterospecific signals may be adaptive for an obligate avian brood parasitic species when deciding “what to parasitize”, because such abilities may help to locate the nests of potential hosts (Hauber et al. 2002; Payne et al. 2000; Soler et al. 1995). Most of the hosts of such parasites are passerine species (e.g. Friedmann and Kiff 1985; Wyllie 1981) that often advertise and defend their territories acoustically (Catchpole and Slater 1995), and also show considerable variation in plumage brightness (Bennett and Owens 2002). Therefore, individuals and/or species with more conspicuous sexual traits may be more prone to parasitism than birds with less conspicuous signals (e.g. Banks and Martin 2001; Soler et al. 1995, 1999).

The evolution of secondary sexual characters in host species is determined by natural and sexual selection to optimise reproductive success under given environmental conditions (Andersson 1994). However, natural and sexual selection may sometimes involve forces that act in opposite directions on trait elaboration. Hence, in such cases the degree of signal expression observed in nature should strike the optimal balance between conflicting pressures for greater efficiency and lower fitness costs (Endler 1992, 1993; Wiley 1983, 1992). If brood parasites use secondary sexual characters for host recognition, brood parasitism is a potential selection pressure that may raise evolutionary constraints against the products of sexual selection (e.g. Soler et al. 1999). Consequently, selection pressures arising from brood parasitism may have favoured hosts to develop less elaborate sexual

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signals, allowing them to escape this pressure. Such an adaptation of hosts is expected to be particularly important among species that are more sensitive to the costs of parasitism, but not among those host species in which parasitism has a minor effect on fitness. Surprisingly, the evolutionary impact of brood parasitism, as a natural selection force, in shaping bird song or plumage coloration has largely been ignored, in spite of its obvious potential role for modulating host life history (e.g. Soler et al. 2001).

Here, we used the brown-headed cowbird *Molothrus ater* and their hosts across their breeding range in North America as a model system to determine the interspecific relationship between sexual signals of hosts and the level of brood parasitism. It has been shown previously that cowbirds are able to discriminate between the songs of different host species (Hauber et al. 2002), and may select a host based on its vocalisation (Banks and Martin 2001; Ueyhara and Narins 1995). If this is a general phenomenon for the brood parasitic relationship between cowbirds and their hosts, we predicted an interspecific association between signal expression of hosts and the level of brood parasitism. In other words, heavily parasitized host species should have well recognisable, conspicuous sexual characters, if cowbirds use sexual signals of hosts to locate the nest they intend to parasitize. In particular, interspecific brood parasitism should be higher in vocally active species as reflected by their longer songs and shorter silent intervals between songs. Cowbirds may also respond to the complexity of host songs by increasing their level of parasitism in species with large repertoires. However, it is also possible that less complex songs may be easier to recognise heterospecifically. Cowbirds may be successful in nest localisation when they use cues that are easy to classify and allow accurate discrimination between potential host species. For example, they can rely on the presence of specific syllables or motifs, which are repeated frequently in small repertoires. In addition, low song complexity will lead to lower variation within species that may also be useful for cowbirds in heterospecific song recognition. If either mechanism of song cue apply to cowbirds, there should be an interspecific relationship between the level of cowbird parasitism and song type and/or syllable repertoire sizes. We also predicted a positive relationship between plumage conspicuousness and cowbird pressure across species. Plumage brightness of males and females of the host species should be higher in heavily parasitized species on the premise that both male and female passerine birds concentrate their activities in a small area around their nests.

These expected associations may represent different evolutionary stages in the arms race between cowbirds and their hosts. On one hand, signal elaboration of hosts may affect the choice of the parasite species that uses suitable cues for nest location. However, if parasites rely on the expression of sexual signals of their hosts, intensively parasitized hosts may benefit, on an evolutionary time scale, by decreasing the expression of those

signals that attract parasites. Accordingly, the current evolutionary stage may *also* reflect the evolutionary counteradaptation by hosts to parasitism. In line with this second mechanism, the association between sexual traits and parasite pressure may be particularly strong in species where cowbirds have a relatively higher impact on host fitness. Thus, the inclusion in the analysis of a factor reflecting host sensitivity to brood parasites should sharpen the relationship between cowbird parasitism and trait expression in hosts. In general, both causal mechanisms reveal an evolutionary role for heterospecific signal recognition of a brood parasite relying on the secondary sexual traits of hosts, albeit as two successive stages in the arms race between cowbirds and their hosts. Primarily, we did not aim to disentangle these two stages, but we considered these scenarios at the level of analysis. Reflecting the different evolutionary perspective of the two participants, we performed our analysis using both hosts and parasites as the units of interest. In these analyses, we assessed the importance of research effort, host suitability and relative distributional overlap with host species on reported cowbird parasitism. We also controlled for habitat preferences of hosts and parasites, and for migratory habits of hosts that may potentially confound the relationship between brood parasitism and host sexual signalling.

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## Materials and methods

### The brood parasite

The brown-headed cowbird is a common and widespread obligate brood parasite species known to utilise >220 passerine species as hosts in North America (Friedmann and Kiff 1985). It has for a long time been regarded as more or less a generalist in its choice of hosts (Orians et al. 1989; Rothstein and Robinson 1998). However, recent genetic analyses have revealed that it may well be that there is a combination of generalist and specialist females laying up to 13 eggs in a single season (Woolfenden et al. 2003). The negative effects on hosts through brown-headed cowbird parasitism includes reduction in clutch size (Rothstein 1990), reduced hatching success of remaining eggs due to damage during parasitism (Røskaft et al. 1990; Spaw and Rohwer 1987) and/or the inability of hosts to incubate all eggs in enlarged mixed clutches (Petit 1991).

### Data set

The data set consisted of 53 North American bird species with quantitative information on brood parasitism, song and plumage coloration (see Appendix). We have used the relative frequency of cowbird parasitism for a particular host species as a measure of brood parasitism, defined as the number of nests parasitized by the total number of nests observed. Data for brood parasitism

were retrieved from Appendix B and C in Ortega (1998) and completed from the Handbook of the Birds of North America (Poole et al. 1993–2002). We only considered species for which at least one report was available, because it is difficult to decide whether a lack of evidence for cowbird parasitism in a given species indicates that brood parasitism is equal to zero or that observers have failed to report it. As differences in research effort in different species may cause bias in the data, we estimated research effort by using the number of studies published since 1972 on each species as cited in the ISI Web of Science (<http://isi1.newisiknowledge.com/>). We found that in species for which song data were available but evidence for brood parasitism was not reported, the mean number of papers published was significantly smaller than in species for which song and brood parasitism data were available (respective means  $\pm$  SE,  $10.83 \pm 31.54$  vs.  $63.65 \pm 11.34$ ;  $t$ -test on  $\log_{10}$ -transformed data,  $t_{51} = 2.87$ ,  $P < 0.01$ ). Hence, we can reasonably conclude that a lack of evidence for cowbird parasitism is probably the result of a lower research effort instead of this having biological meaning. In some species, estimates of cowbird parasitism were available for more than one population. Based on such multiple information for a single host species, a one-way ANOVA revealed consistently greater variance among than within species, which is an important prerequisite for comparative analyses ( $F_{38,193} = 2.46$ ,  $P < 0.01$ ). Therefore, we assumed that despite considerable intraspecific variation, the level of brood parasitism can be viewed as a species-specific characteristic, which can be reliably estimated. Consequently, if more than one estimate was available for a species, we used the mean estimate in the analyses from all studies where more than five host nests had been monitored. Brood parasitism was arcsine-square root transformed prior to further analyses. The relationship between mean brood parasitism and research effort indicated that after excluding species with no information on brood parasitism, the remaining dataset was not confounded by research effort (see Appendix). However, we included research effort in our analysis to control for any potential bias.

The frequency of cowbird parasitism may be affected by host suitability. We divided species into three groups regarding their suitability as cowbird hosts according to data obtained from the Handbook of the Birds of North America (Poole et al. 1993–2002). Species were classified as unsuitable as cowbird hosts (score of 3) either because: (1) they are hole-nesting birds or build their nests in concealed places which makes egg laying difficult for the parasite, (2) because they feed their chicks with food unsuitable for the parasite chick (mainly seed eaters) (Eastzer et al. 1980; Kozlovic et al. 1996), (3) or because they have eggs or chicks very dissimilar in size with those of the parasite (Kilner 2003; Ortega 1998). Two species, the American robin *Turdus migratorius* and the house finch *Carpodacus mexicanus* can be regarded either as suitable or unsuitable hosts, since in some part of their range they are available as hosts, but in other

parts are unavailable. For our analyses we included these two species in an intermediate group of partially suitable hosts (score of 2). The rest of the species were handled as suitable hosts (score of 1). We predicted higher levels of brood parasitism in suitable hosts as compared to non-suitable hosts.

Cowbirds have expanded in North America across the last century (Mayfield 1965; Rothstein 1994), thus counteradaptations to cowbird parasitism should be more frequently reported in those species having experienced a longer exposure to parasitism. Thus species were classified into three different groups according to the overlap between their historical distributional ranges and that of the brown-headed cowbird: (1) allopatric species with  $> 75\%$  of their current distribution differing from the current distribution of brown-headed cowbird (score of 1); (2) recent sympatric species with  $> 75\%$  of their current distribution overlapping with the current brown-headed cowbird distribution, but whose distribution differed by  $> 75\%$  from the distribution of the brown-headed cowbird as reported in 1929 (Friedmann 1929) (score of 2); (3) old sympatric species, with current distribution overlapping at least the 75% of the brown-headed cowbird distribution as reported in 1929 (score of 3). Cowbird distribution in relation to host distribution along our three-scale categorisation can be regarded along a continuous axis, since intermediate states are biologically meaningful. Since overlapping distributions of the host and their brood parasites may result in increased levels of brood parasitism, we predicted that demographic transitions toward sympatry would be accompanied by augmented brood parasitic pressure by cowbirds.

We used four variables to represent song output and song complexity from the literature. These estimates were derived from Read and Weary (1992) and MacDougall-Shackleton (1997). Song output was measured as: (1) song duration (seconds), and (2) inter-song interval (seconds). Song complexity was measured as: (1) song type repertoire size (the mean number of different song types possessed by an individual which represents a measure of between-song complexity), (2) syllable repertoire size (the mean number of different syllable types within a song which represents a measure of within-song complexity). For species having tremendous song complexity, summaries of repertoire size provide near-infinite data, because it is difficult to estimate their potential repertoires (MacDougall-Shackleton 1997; Read and Weary 1992). In such cases, song elements, such as syllables are combined randomly and thus a particular combination occurs rarely, which leads to the detection of numerous song types. Following a common practice, in species with infinitely large song type repertoire size ( $> 100$ ) we assigned an arbitrary value of 1,000 (see Garamszegi and Møller 2004; Read and Weary 1992). Birds with an infinitely large syllable repertoire size were treated as having a syllable repertoire size of 100 (this value is fitted to the range of this variable). Analyses of the reliability of song traits showed that song type rep-

ertoire size is highly repeatable within species ( $R < 0.90$ ), and that syllable repertoire size is predictable by alternative measures of short-term song complexity (Garamszegi and Møller 2004; Garamszegi et al. 2003). All song variables were  $\log_{10}$ -transformed before analyses.

Providing references (National Geographic Society 2000) and keys for definition, we asked an independent observer unaware of the hypotheses under test to score males and females on a brightness scale ranging from 1 to 6, with 1 being “very dull” and 6 “very striking”. Plumage coloration was scored simply with respect to all forms of coloration. We are aware that our method of estimating plumage brightness based upon human vision does not account for UV wavelengths that birds can perceive (Andersson and Amundsen 1997; Bennett et al. 1996; Cuthill et al. 2000). However, as Bennett et al. (1994) suggested “for heuristic purposes, it may be useful to express colour patterns in subjective terms that humans can readily understand”, especially if these are repeatable and standardized as our estimations. If the modes of human sensual assessment are very different from those normal for the animals, a biological phenomenon could exist but fail to be detected by human appreciation. However, interspecific variation in plumage coloration visually assessed from handbooks and field guides have been repeatedly found to show biologically relevant patterns in relation to other variables (see Bennett and Owens 2002; Møller and Birkhead 1994).

A number of confounding factors may influence the potential interspecific association between brood parasitism and sexual traits. For example, species may differ with respect to their sensitivity to cowbird parasitism. Sensitivity is defined as different degrees of evolutionary constraint by the brood parasite. More sensitive species are expected to have suffered cowbird parasitism to a higher extent and thus be more likely to evolve adaptations to overcome it. Host proneness to suffer the cost of parasitism is linked to host body size, with larger hosts suffering relatively fewer costs of parasitism (Lorenzana and Sealy 1999; Trine et al. 1998). Therefore, to reflect host sensitivity, we entered body mass in our comparative framework. Host weight of adult birds was extracted from Dunning (1993) and was  $\log_{10}$ -transformed prior the analyses.

Because cowbirds prefer open habitat and rarely penetrate deeply into forest, species inhabiting open habitats are assumed to have higher levels of cowbird parasitism as compared to forest species (see Hosoi and Rothstein 2000). Habitat-dependent patterns of brood parasitism have been detected in the European cuckoo, *Cuculus canorus*, which prefers parasitizing forest species (Røskaft et al. 2002). In addition, habitat-dependent selection potentially leads to predictable habitat-dependent acoustic characteristics and parallel divergence in song and habitat-dependent fitness (Slabbekoorn and Smith 2002). Species inhabiting open grassland habitats have been reported to have lower song rates and song versatility than species of forested habitats (Read and Weary 1992), because of different sound transmission

properties, and varying bird diversity and density in these two kinds of habitats (Ryan and Brenowitz 1985; Wiley 1991; Wiley and Richards 1978). Taken together, an alternative mechanism through habitat preferences may induce an interspecific association between song and brood parasitism, without there actually being a causal link. To control for these potential confounding effects we classified species as inhabiting open (score of 1) or forested habitats (score of 3). Species of open habitats include species nesting in open lands, old-field, and riparian habitats that are the preferred habitats of the cowbirds (Lowther 1993). The forest species are mostly strict forest breeders where the cowbirds rarely penetrate to parasitize. Some species breed in a variable range of habitats comprising both forested and open habitats. Birds inhabiting both kinds of habitats, or preferring scrubs, clearings or forest edges were categorized as living in “mixed” habitats (score of 2). Information for habitat type originated from Poole et al. (1993–2002).

Different rates of migration have been hypothesised to affect the dynamics of the evolutionary relationship between hosts and their brood parasites (e.g. Martínez et al. 1999). Indeed migratory species have also been reported to have large song repertoires and large syllable repertoires (Read and Weary 1992). Migratory behaviour was scored on a three-point scale as: (1) resident (score of 1), (2) partial migrant [(species having resident and migratory populations) (score of 2)], or (3) migrant (score of 3). Information originates from Poole et al. (1993–2002) and the National Geographic Society (2000). Suitability, distribution overlap, habitat type, migration and plumage coloration were treated in a continuous scale in our analysis. The statistical reason behind this choice is that although these variables may appear discrete, intermediate states are biologically meaningful, and different states are thus arbitrary points along a continuum (Sokal and Rohlf 1995). In addition, in an evolutionary context, a transition between two states of these variables follows non-discrete evolutionary changes. Therefore, the continuous treatment is generally applied in comparative studies that are constrained to use non-quantitative data for a larger set of species (Bennett and Owens 2002; Harvey and Pagel 1991). Thus as a result, one can show qualitatively that a given trait plays a role on the evolution of another, but cannot assess its quantitative importance. Hence, any finding appearing with these variables should be interpreted with caution. It is worth noting that the pair-wise correlations for these traits based on the non-parametric rank correlation coefficients are very similar to those reported in Appendix 3 and based on parametric Pearson correlation coefficients.

#### Data analysis

We tested whether passerine bird species inhabiting North America that have evolved conspicuous sexual

signals had higher levels of brood parasitism by the brown-headed cowbird. As we considered evolutionary relationships acting in both directions (see Introduction), we performed our analysis using both hosts and parasites as the units of interest. We assessed the importance of research effort, host suitability and relative distributional overlap with host species on reported cowbird parasitism, and we also controlled for the potentially confounding factors arising from habitat preferences of hosts and parasites, and from migratory habits of hosts. When considering the evolutionary view of hosts, we included body mass in the analyses to reflect host sensitivity to cowbird parasitism and checked whether this variable had modulator effects on the relationships of interest.

Considering the causality in which the level of cowbird parasitism is affected by trait elaboration of the host, we regarded cowbirds as the unit of analysis. From this view, we assumed that cowbirds are generalists; or if specialists, different races of cowbirds parasitizing different host species are statistically independent data points. Therefore, in the light of the scenario that predicts cowbirds to respond to hosts' traits, we performed our analyses on the raw species data. There were several, statistically significant correlations among the traits considered (see Appendix). To control for the covariation among traits and also for their potentially confounding effects, we performed a single multiple regression analysis in which we included all variables of interest together with the confounding variables. We used an approach from which we excluded non-significant effects by stepwise deletion procedure in which the threshold  $P$  value was set to 0.1. We used the 10% threshold, because we intended to capture marginally significant tendencies of biological relevance that may appear in our limited sample of birds.

Conversely, in accordance with the causal mechanism in which avian species are affected by cowbird parasitism on an evolutionary scale, we performed our analyses using host species as the unit in focus. Evidently, species cannot be considered as statistically independent data-points, and associations between biologically important variables may be confounded by common ancestry (Felsenstein 1985; Harvey and Pagel 1991). We applied the comparative method to distinguish between effects of common descent and convergent evolution. We constructed a composite phylogeny based on number of sources that estimated phylogenetic relationships by using molecular techniques. We used Sibley and Ahlquist (1990) as a basic source of information at the family level. To assess the phylogenetic relations within families we used information from Grapputo (2001), Johnson and Lanyon (1999), Klicka et al. (2000), and Lovette and Bermingham (2002). We applied branch lengths from the tapestry tree of Sibley and Ahlquist (1990) for higher taxonomic levels. Within families the distance between different genera was set to  $3.4 \Delta T_{50} H$  units, and we used  $1.1 \Delta T_{50} H$  units between species

within genera (Bennett and Owens 2002; Sibley and Ahlquist 1990). The entire phylogeny is given in the appendix.

Relying on the reconstructed phylogenetic associations, we investigated the relationship between brood parasitism and song and plumage characteristics of the host while controlling for the confounding variables with special interest in the mediator effect of body mass. For this investigation we adopted the general method of comparative analysis for continuous variables that is based on multiple regression of statistically independent standardised linear contrasts, as originally suggested by Felsenstein (1985). Using this approach, evolutionary relationships between different traits can be assessed by regression through the origin, where the expected value of the slope of the regression line equals the true relation between two variables in the absence of phylogenetic effects (Harvey and Pagel 1991; Purvis and Rambaut 1995). We have chosen this phylogenetic framework, because we involved numerous variables in our analysis, and we intended to perform similar multivariate analyses from both the host's and the cowbird's evolutionary perspective. We used the computer program CAIC (Purvis and Rambaut 1995) to generate statistically independent contrasts that were subsequently entered into a multiple regression forced through the origin, and from which non-significant effects were removed by stepwise deletion with a  $P=0.1$  threshold. An important assumption of the independent contrast method is that values of contrasts should not be correlated significantly with the SD of the contrast (Purvis and Rambaut 1995). We checked for this prerequisite, and we found that only syllable repertoire size showed such a significant correlation. However, this effect was caused by an outlier, and when we excluded this data point we found very similar results to those we report below (see also Fig. 2b). In addition, when we analysed the pair-wise relationship between syllable repertoire size and cowbird parasitism relying on an alternative phylogenetic approach using generalised least square models implemented in the program Continuous (Pagel 1999), we detected that this relationship was independent of the phylogenetic method used. Hence, the significant relationship between the contrasts of syllable repertoire size and its SD does not have an effect on the relationship in question.

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## Results

A multiple regression model using the raw species data representing the evolutionary view of the parasite revealed that the frequency of brood parasitism by the brown-headed cowbird in North America was dependent on the syllable repertoire size, inter-song interval and male coloration in the host, while distributional overlap, habitat type and research effort also explained a significant amount of variance on cowbird parasitism (Table 1, Fig. 1).

When we controlled for phylogenetic relationships of hosts to reflect their evolutionary perspective, we found in the final model that the frequency of cowbird parasitism was significantly related to song type repertoire size, and syllable repertoire size, and inter-song interval of the host together with research effort, habitat type and distribu-

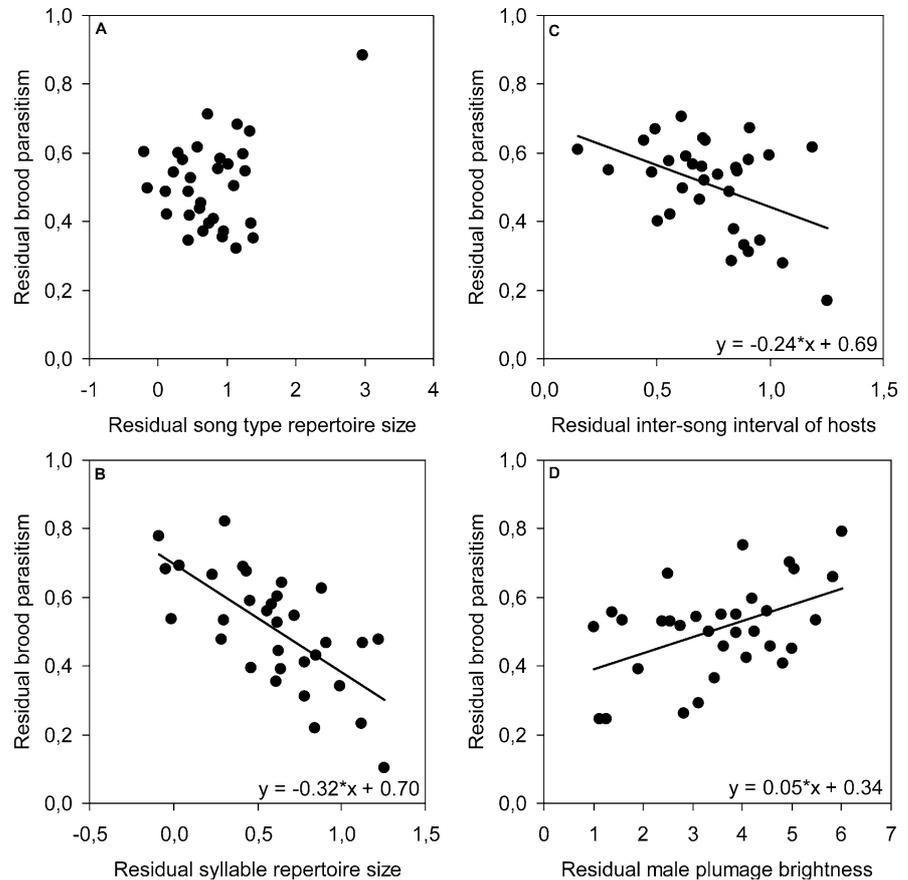
tional overlap (Table 2, Fig. 2). Body mass, which is a potential measure of host sensitivity to costs of parasitism, was not included in the final model (Table 2). Contrary to the results that are based on the raw species data, male plumage brightness was not included in the final model.

**Table 1** A multiple regression of the frequency of brood parasitism by the brown-headed cowbird in relation to song and plumage characteristics of the host species together with confounding variables. An analysis based on raw species data representing the evolutionary view of the cowbird

	Slope ( $\pm$ SE)	F
Dependent variable: Frequency of brood parasitism		
Overall model, $R^2 = 0.68$		$F_{7,31} = 7.30, P < 0.01$
Intercept	0.51 ( $\pm 0.14$ )	$F_{1,31} = 11.81, P < 0.01$
Independent variables:		
Song type repertoire size	0.07 ( $\pm 0.04$ )	$F_{1,31} = 2.95, P = 0.10$
Syllable repertoire size	-0.32 ( $\pm 0.07$ )	$F_{1,31} = 21.18, P < 0.01$
Song duration	Not in the model <sup>a</sup>	
Song interval	-0.24 ( $\pm 0.10$ )	$F_{1,31} = 5.67, P = 0.03$
Male coloration	0.05 ( $\pm 0.02$ )	$F_{1,31} = 7.22, P = 0.01$
Female coloration	Not in the model <sup>a</sup>	
Body mass	Not in the model <sup>a</sup>	
Distributional overlap	0.07 ( $\pm 0.03$ )	$F_{1,31} = 4.49, P = 0.05$
Habitat type	-0.12 ( $\pm 0.05$ )	$F_{1,31} = 7.27, P = 0.01$
Migration	Not in the model <sup>a</sup>	
Suitability	Not in the model <sup>a</sup>	
Research effort	0.15 ( $\pm 0.06$ )	$F_{1,31} = 7.34, P = 0.01$

<sup>a</sup> Not selected by the stepwise procedure

**Fig. 1** The relationship between some sexually selected traits of hosts (a song type repertoire size, b syllable repertoire size, c inter-song interval, d male plumage brightness) and the relative frequency of cowbird parasitism representing the view of the parasite. The figures are based on the raw species data. Residuals were taken from the relevant multiple regression of the statistically transformed raw species data, in which covariation among traits and the effect of confounding factors were held constant (Table 1). Lines and equations are linear regression lines between the residuals of the considered traits, given if the corresponding effect in the multiple regression was significant



**Table 2** A multiple regression forced through the origin of the frequency of brood parasitism by the brown-headed cowbird in relation to song and plumage characteristics of the host species together with confounding variables. An analysis based on phylogenetically independent contrasts representing the evolutionary view of the hosts

	Slope ( $\pm$ SE)	F
Dependent variable:		
Frequency of brood parasitism		
Overall model, $R^2 = 0.74$		$F_{6,30} = 11.54$ , $P < 0.01$
Intercept	Zeroed	
Independent variables:		
Song type repertoire size	0.11 ( $\pm 0.05$ )	$F_{1,30} = 4.34$ , $P = 0.05$
Syllable repertoire size	-0.25 ( $\pm 0.07$ )	$F_{1,30} = 13.10$ , $P < 0.01$
Song duration	Not in the model <sup>a</sup>	
Song interval	-0.29 ( $\pm 0.10$ )	$F_{1,30} = 7.93$ , $P = 0.01$
Male coloration	Not in the model <sup>a</sup>	
Female coloration	Not in the model <sup>a</sup>	
Body mass	Not in the model <sup>a</sup>	
Distributional overlap	0.10 ( $\pm 0.03$ )	$F_{1,30} = 9.64$ , $P < 0.01$
Habitat type	-0.18 ( $\pm 0.05$ )	$F_{1,30} = 15.20$ , $P < 0.01$
Migration	Not in the model <sup>a</sup>	
Suitability	Not in the model <sup>a</sup>	
Research effort	0.17 ( $\pm 0.05$ )	$F_{1,30} = 10.16$ , $P < 0.01$

<sup>a</sup> Not selected by the stepwise procedure

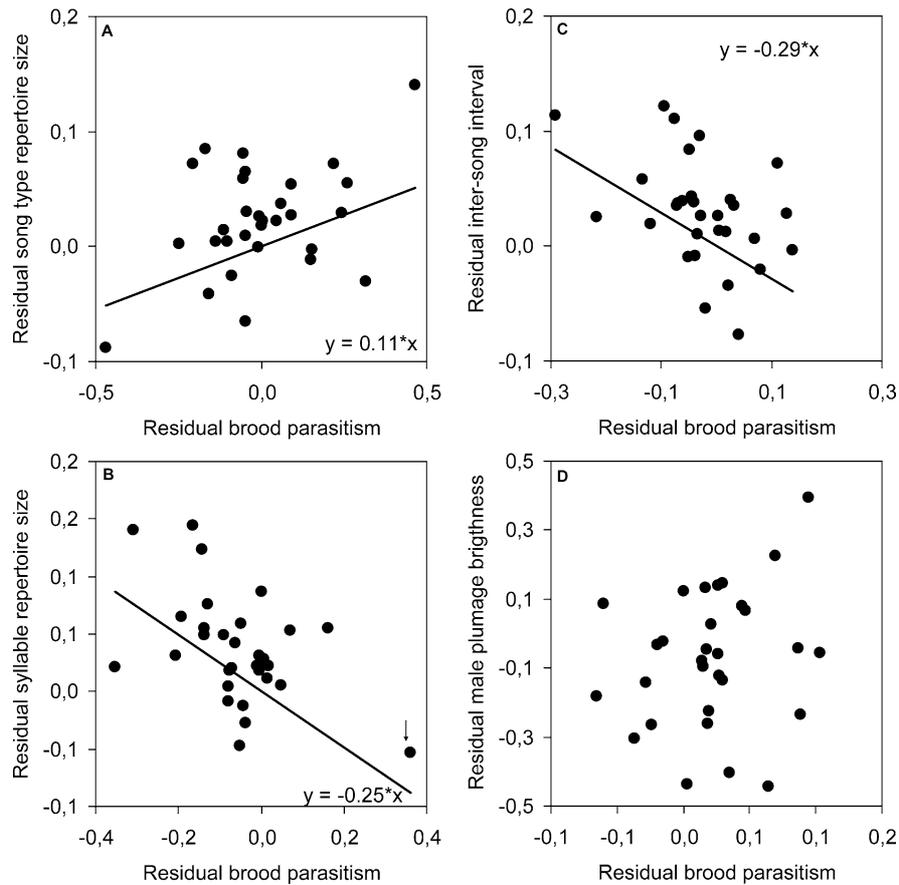
## Discussion

In both analyses, corresponding to the two sides of evolutionary relationship between cowbirds and their North American hosts, we found that some aspects of the song of the host species were significantly related to the reported frequency of cowbird parasitism. In addition, there was a significant association between male coloration and brood parasitism when we used the raw species data, but this relationship disappeared when we controlled for the phylogenetic relationship among hosts. These associations appeared to be independent of several confounding factors, such as research effort, host suitability, relative distributional overlap, habitat type and host migratory behaviour. While studies have suggested that hosts may evolve defence mechanisms against their brood parasites (e.g. Briskie et al. 1992; Davies and Brooke 1988; Rothstein 1990; Soler and Møller 1990), and that the evolution of brood parasites is constrained by selection from both ecological pressures and host defences (e.g. Krüger and Davies 2002), we are only aware of a single study that aimed to quantify the interspecific variation in brood parasitism and relate this to host behaviour including the number of vocalisations (Banks and Martin 2001). We investigated this interspecific relationship further by determining the extent to which host song output, song complexity and plumage brightness co-varied with the

level of cowbird parasitism by concentrating on both sides of the potential evolutionary relationship: the hosts and the parasite.

Our findings may have biological meaning, if two important assumptions are upheld. First, we assumed that although cowbird parasitism may show some degree of variation among populations of the same host species, it is a host-specific attribute. To support this assumption, we demonstrated that the variance in cowbird parasitism within species was significantly smaller than the variance among species. Hence, the comparison of the mean frequencies of brood parasitism among different host species makes biological sense (see also Hosoi and Rothstein 2000; Øien et al. 1995; Soler and Møller 1996). Indeed, the biologically relevant findings for distributional overlap, habitat type and research effort (Tables 1, 2) may imply that the mean of the reported frequency of nests parasitized provides reliable estimates for the strength of cowbird parasitism in different host species. We relied on similar assumptions regarding both song variables and plumage coloration. This was supported by detailed analyses of the reliability of these traits reported elsewhere (song, Garamszegi and Møller 2004; plumage coloration, Møller and Birkhead 1994). Second, we also assumed that males of the host species showing visual and acoustic displays spend a considerable amount of time near the nest during egg laying, which may help brood parasites to locate their host. We did not perform any analysis to confirm this assumption. However, we can at least take into account that males of many passerines are known to guard their territories or fertile females near the nest by conspicuous sexual displays prior to egg laying (Birkhead and Møller 1998; Møller 1991). Recent evidence in the brown-headed cowbird revealed that this brood parasite may be able to recognise the songs of heterospecific males (Hauber et al. 2002). If this ability is a general phenomenon applied to each host species, it should have evolutionary consequences. The probability of brood parasitism by cowbirds in four host species was found to be higher with increasing male vocalisations near the nest (Banks and Martin 2001).

The comparative analyses using raw species data and representing the parasite point of view revealed that brown-headed cowbirds parasitize a higher proportion of nests in species with lower short-term song complexity indicated by syllable repertoire size (Fig. 1b). There was a tendency for a positive relationship between cowbird parasitism and song type repertoire size, but this correlation appears to be due to an outlier (Fig. 1a). The significant, negative slope for intersong interval indicated that in heavily parasitized species the silent phases between songs are shorter (Fig. 2c). Moreover, male plumage brightness was positively associated with relative brood parasitism caused by cowbirds (Fig. 1d). All these results are in line with the hypothesis that the brown-headed cowbird adjusts its choice for hosts based on the elaboration of their sexual characters. When we analysed the interspecific relationships between the



**Fig. 2** The relationship between brood parasitism caused by the cowbird and some sexually selected traits of hosts (**a** song type repertoire size, **b** syllable repertoire size, **c** inter-song interval, **d** male plumage brightness) corresponding to the evolutionary perspective of the hosts. The figures are based on independent contrasts. Residuals were taken from the relevant multiple regression of the phylogenetically independent contrasts, in which covariation among traits and the effect of confounding factors were held constant, and the intercept was zeroed (Table 2). Lines and

equations are linear regression lines between the residuals of the considered traits, given if the corresponding effect in the multiple regression was significant. In **c** the arrow indicates a residual that corresponds to an outlier contrast (see also Materials and methods). The exclusion of this contrast from the multiple regression analysis results in a very similar model to that presented in Table 2, in which the slope for syllable repertoire size is given by:  $-0.31 \pm 0.09$ ,  $P < 0.01$

expression of sexual traits in hosts and cowbird brood parasitism, using the avian phylogeny as the basis for the comparative analysis, we found remarkably similar results for song traits (Table 2, Fig. 2a–c). However, when we controlled for effects due to common descent, the previous findings in relation to male plumage brightness disappeared (Fig. 2d). These findings, from the host's perspective, are in accordance with the hypotheses suggesting that the evolution of sexually selected characters in passerine birds may be constrained by selection factors arising from brood parasitism.

Comparative results cannot provide insight on the casual evolutionary mechanisms, and this shortcoming is also applicable to the present study. Considering the evolutionary relationship between host and parasites, we proposed two causal mechanisms linking host choice of the cowbird and the expression of sexual characters of the hosts on an evolutionary scale. Apparently, our findings in relation to song traits are in accordance with both mechanisms, because comparative analyses of the

two sides of the evolutionary relationship provided very similar results (Tables 1, 2). Based on such correlative evidence, it remains difficult to separate the evolutionary impact of the two opposite causal mechanisms in mediating the observed interspecific association between brood parasitism and features of song. However, both causal mechanisms predict that parasitic cowbirds use heterospecific signals in host discrimination. Our results thus show that this discrimination ability of the brood parasite may have important evolutionary consequences for both sides of the evolutionary relationship. Below, we investigate these consequences further for both participants.

From the parasite's point of view it may be easier to locate hosts with lower short-term song complexity (as reflected by smaller syllable repertoire size), with shorter pauses between songs (as indicated by shorter inter-song interval) and with more conspicuous plumage characteristics (as shown by male plumage brightness). We found evidence for syllable repertoire size being nega-

tively related to relative cowbird parasitism [we do not discuss results on song type repertoire size, because the marginally significant effects we found are probably caused by outliers (Figs. 1a, 2a)]. Based on these results we assume that brood parasites do not directly select host species with lower syllable repertoire size, but prefer parasitizing hosts with a song attribute that is more likely to be in songs with smaller syllable repertoire size. For example, brood parasites may be sensitive to specific and well recognisable motifs that become typical patterns in less complex songs. Shorter inter-song interval, when controlling for song duration may correspond to the singing activity of species, because with decreasing inter-song interval the relative frequency of vocally active periods increases. Hence, cowbirds when relying on heterospecific acoustic cues may be expected to favour hosts with more active singing behaviour. It is noteworthy that in surveys of animal communities when the aim is to estimate species richness by count data based on the detection of singing bird species, factors associated with species-specific song attributes have been suggested to affect detectability (Richards 1981). We also found some support for the hypothesis that plumage brightness may also be important in the heterospecific context, because in species where males have elaborate plumage colours the frequency of cowbird parasitism was higher. Male rather than female plumage brightness appeared to be associated with increased level of brood parasitism. In our data male coloration showed larger variation than female coloration (range for males, 1–6; range for females, 1–4), and males were consistently more colourful than females ( $t_{38} = 5.15$ ,  $P < 0.01$ ). This may be a general phenomenon among passerine species, since it is usually the male that expresses bright plumages to attract mates (Andersson 1994). Therefore, it is plausible that the conspicuous males of host species provide better cues for nest-searching cowbird females, something which may explain the sex-dependent patterns we found here.

From the host's point of view, if cowbirds use their secondary sexual traits to localise the nest they intend to parasitize, brood parasitism may represent a selection factor that works against the product of sexual selection. If cowbirds show preferences for species with low syllable repertoire size, small inter-song interval and bright male plumages, and brood parasitism incurs considerable fitness costs for hosts, these victims may be under a selective framework which favours expression of sexual traits in a direction less attractive to the cowbird. Our phylogenetic findings corresponding to the evolutionary perspective of the host species with the exception of male plumage brightness are in line with this possible evolutionary scenario. Hence, the interspecific relationship between syllable repertoire size and inter-song interval of the host species and the rate of cowbird parasitism may be regarded as the product of the parasite avoidance mechanisms of hosts (Fig. 2b, c). We predicted that according to the causal relationship that takes evolutionary steps from increasing brood parasitism towards

trait expression of hosts, the correlation between these characters should be more pronounced in species that are most sensitive to the cost imposed by brood parasites. Based on recent suggestions (Lorenzana and Sealy 1999; Trine et al. 1998), we assumed in our analysis that the harmful effect of brood parasites on host fitness is linearly related to host body size. We included body size in our analysis to reflect host sensitivity, but this variable seemed not to have modulator effects on the relationship in question. However, we cannot exclude the possibility that body size is a poor measure of host sensitivity in our context. An efficient approach to demonstrate an evolutionary response of the host to cowbird parasitism would be to study in several species whether they change the expression of their sexual characters before and after contact with cowbirds, and/or to investigate sexual traits across different populations of the same hosts differing in the rate of brood parasitism. Our distributional overlap variable may reveal the importance of the timing of the evolutionary contact with the cowbird (see Materials and methods). Therefore, if brood parasitism works against the product of sexual selection, one can expect remarkable differences in signal elaboration between old and new hosts. Such differences should mediate interspecific relationships between sexual traits and distributional overlap, which was not the case for either of the traits studied (Appendix 3). It is noteworthy that current evidence based on egg and clutch characteristics suggests that cowbirds may not be as strong selective agents regarding host defences as cuckoos (Stokke et al. 2002). The brown-headed cowbird is a relatively young brood parasite for its hosts, which is thought to result in a lack of defence mechanisms, such as egg rejection (Rothstein 1990; Rothstein and Robinson 1998). Hence, as proposed by the “evolutionary lag hypothesis” (Rothstein 1975), time lag in the origin and spread of anti-parasite adaptations in the cowbird-host system may delay hosts from modifying their sexual characters to avoid parasite pressure. Altogether, the exact role of brood parasitism in constraining the evolution of sexual characters remains elusive and needs further investigation.

In addition to the hypothesis posed in the Introduction, we can imagine an alternative evolutionary mechanism, which predicts an interspecific relationship between sexual traits and brood parasitism, and acts along the parasite–host causal line. Brood parasitism may mediate the intensity of sexual selection independent of its direct effects on sexual traits through host recognition. Parasites have been suggested to play an important role in the evolution of sexual traits, as they may have been partly evolved to reflect parasite resistance of males (Hamilton and Zuk 1982). Sexual selection is expected to have favoured trait expression in species experiencing high parasite pressure, because of female mate preferences for males better at coping with parasites. Under this evolutionary scheme, elevated levels of brood parasitism may have evolutionary effects on sexual selection, in which secondary sexual

characters, such as songs or plumage coloration evolve to reveal the quality of a males' territory. Intense brood parasitism may raise competition among males for territories or nest sites differing in exposure to parasitism. If the risk of attracting brood parasites is related to territory quality, sexual selection for territories of superior quality will favour the evolution of secondary sexual characters. These selection pressures will increase the variance of trait elaboration among individuals that leads to directional selection (Møller and Pomiankowski 1993), which would in turn raise an interspecific relationship between the level of brood parasitism and sexual signalling. Note that this alternative mechanism does not predict that cowbirds use heterospecific signals for host localisation, but it does predict intraspecific variance in occurrence of brood parasitism in association with individual quality and thus sexual signalling. Since greater song output and song complexity and also plumage brightness of males have been associated interspecifically with factors that are presumed to produce more intense inter- or intra-sexual selection (Bennett and Owens 2002; Read and Weary 1992), the mechanism predicts a positive relationship between brood parasitism and these sexual traits. However, this was not the case in our study, as the majority of the considered traits showed no significant relationship in this expected direction with relative brood parasitism after taking the phylogenetic history of hosts into account. Therefore, sexual selection mediated by brood parasitism acting on the considered traits is unlikely. Our results rather support our main hypotheses, in which cowbird parasitism adjusted to heterospecific signals, as a result of natural selection, potentially represents evolutionary pressures for both the hosts and the parasites.

In conclusion, we found that a measure of short-term song complexity, intersong interval and male plumage brightness of hosts were significantly associated with the level of interspecific brood parasitism. These findings are in accordance with the hypotheses that predict that host selection of cowbirds may rely on the expression of sexually selected signals of the hosts. Considering the evolutionary relationship between cowbirds and hosts, these hypotheses may involve two potentially functioning causal mechanisms that could explain the observed correlations. At this moment, it would be premature to disentangle these evolutionary scenarios. However, our results raise the prospect of an important evolutionary role for sexually selected characters of hosts in species recognition of cowbirds and that this may have implications for the evolutionary relationship between brood parasites and their hosts.

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