Research article

Relationship between nest predation suffered by hosts and brown-headed cowbird parasitism: a comparative study

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Abstract. There are at least four main hypotheses that may explain how the evolution of host selection by avian brood parasites could be linked to nest predation among their potential hosts. First, selection may have favoured parasite phenotypes discriminating among hosts on the basis of expected nest failure. Second, parasitized nests may be more easily detected by predators and extra costs of parasitism may accelerate the evolution of host defences. Third, selection may have favoured predator phenotypes avoiding parasitized nests because parasitism enhances nest defence. Fourth, female brood parasites may directly or indirectly induce host nesting failures in order to enhance future laying opportunities. We collected data on brood parasitism and nest failure due to predation to test these hypotheses in a comparative approach using North American passerines and their brood parasite, the brown-headed cowbird *Molothrus ater*. Under the hypotheses 1 or 3 we predicted brood parasitism to be negatively associated with nest predation across species, whereas this relation is expected to be positive if hypotheses 2 or 4 are true. We demonstrate that independent of host suitability, nest location, habitat type, length of the nestling period, body mass and similarity among species due to common ancestry, species experiencing relatively high levels of nest predation suffered lower levels of cowbird parasitism. Our results suggest a previously ignored role for nest predation suffered by hosts on the dynamics of the coevolutionary relationships between hosts and avian brood parasites.

Key words: brood parasitism, comparative analysis, cowbirds, host selection, nest predation, passerines

Introduction

Parasites and their hosts are parts of complex ecological communities where other species may affect the dynamic of their specific coevolutionary relationships (e.g. Thompson, 1994, 1999; Benkman, 1999). Studies in avian brood parasitism have provided us with some good examples of ongoing coevolution (reviewed in Davies, 2000), but they have often neglected the possibility that other species may have been shaping the dynamics of the coevolutionary

relationship between hosts and parasites. A major factor affecting avian brood parasite fitness is nest predation suffered by hosts while caring for parasite offspring. Nest predation typically accounts for the loss of the entire host clutch or brood, and if parasitized, also for the loss of parasite offspring. Current evidence suggests that nest predation is a major source of nestling mortality in birds (Ricklefs, 1969; Nilsson, 1984) affecting their life history traits (Slagsvold, 1982; Martin, 1995; Martin and Clobert, 1996; Martin *et al.*, 2000). Hence, it seems reasonable to argue that predators may affect the co-evolutionary relationships between avian brood parasites and their hosts.

The aim of this paper was to study interspecifically the relationship between nest failure due to predation and level of parasitism. As a model system, we used the brown-headed cowbird *Molothrus ater* and its hosts across their breeding range in North America. The brown-headed cowbird is a common and widespread obligate brood parasite species known to utilize more than 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 (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 (Woolfenden *et al.*, 2003). Moreover, it has been shown that cowbirds are able to discriminate between the songs of different host species (Hauber *et al.*, 2002), and may select hosts based on their vocalization (Uyehara and Narins, 1995; Banks and Martin, 2001).

There are at least four hypotheses that predict covariation between levels of parasitism and nest failure among species. First, host's mean probability of producing fledglings (a generic estimate of ''host quality'') may have influenced the evolution of host selection in cowbirds (e.g. Davies, 2000). Accordingly, the level of predation suffered by a host species may have determined its suitability to parasitism and therefore the level of brood parasitism it may suffer. Selection may then have acted to reduce the relative fitness of parasite phenotypes that do not discriminate among hosts on the basis of expected nest failure. This hypothesis proposes that those host species suffering higher levels of nest predation should be relatively less suitable hosts, because they provide the parasites with lower chance of successfully rearing a viable offspring, than host species that suffer less from nest predation. Therefore, under this hypothesis we predict a negative association between the levels of nest predation and brood parasitism across species. Second, parasitized nests may be more predated due to their increased conspicuousness as compared to unparasitized nests. Noteworthy, this possibility may affect the coevolutionary process between cowbirds and their hosts since the extra cost of parasitism via predation would make parasitism avoidance particularly selective for cowbird hosts. A study by Dearborn (1999) revealed that the begging calls at indigo bunting *Passerina cyanea* nests parasitized by brown-headed cowbirds were louder and more

frequent than those at non-parasitized nests (see also Briskie *et al.*, 1994). Interestingly, a higher predation of parasitized nests relative to non-parasitized ones was also reported in that study (Dearborn, 1999; see also Burhans *et al.*, 2002). Hence, under this hypothesis we predict that measures of level of parasitism are positively associated with nesting failures due to predation. Third, the causal association between level of parasitism and nest predation may have acted in the opposite direction. Selection may have favoured avoidance of parasitized nest by predators if the parasite enhances nest defence of parasitized nests. According to this causal scenario the level of brood parasitism would correlate with level of defence against predators in the close vicinity of the nest. This hypothesis would predict that preferred hosts on average will suffer lower than average probabilities of nesting failure. Finally, female brood parasites may directly or indirectly induce host failures to enhance future laying opportunities (Arcese *et al.*, 1996, Cowbird predation hypothesis). Cowbirds regularly depredated song sparrow *Melospiza melodia* nests that were found too late in breeding cycle to be suitable for parasitism, resulting in a positive association between the occurrence of parasitism and nest failure at the intra- and inter-annual scale (Arcese *et al.*, 1996). Whether parasites preferentially depredated on defensive against parasite host phenotypes this may decelerate the evolution of host defences (e.g. Soler *et al.* 1995, 1999a). The interspecific consequence of this mechanism is that species suffering a higher rate of predation are also more frequently parasitized.

Materials and methods

Data collection

Complete information on nest predation rate and level of brood parasitism was collected for 63 North American passerines (see Appendix). Only species with open nests were used in our analyses, since hole nesters might be exposed to different selective forces than open nesters (e.g. Lack, 1968). Estimates of nest failure due to predation were obtained from data reported in Martin (1995) and used as an index of the constraint exerted by predation. Nest predation was expressed as the simple percentage of nests lost to predation to avoid possible biases in determining causes of partial brood losses, and because predation often causes loss of the entire brood (Martin, 1995; Martin and Clobert, 1996). Martin (1995) pointed out the inability to examine within-species variation in nest predation in his data set due to a large number of species with information for only a single study population. Confidence in the nest failure data as representative of the true mean values for a particular species is reduced for those species represented by a single study because nest failure due to predation may

vary geographically. However, we assume that any such biases are randomly distributed across species such that statistical noise is increased and observable patterns must be robust (Martin, 1995; Martin and Clobert, 1996).

We have used percentage of parasitized nests in a particular host species as a measure of level of brood parasitism. Data regarding 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 of parasitism was available, because it is difficult to decide whether lacking evidence for brood parasitism in a given species indicates that brood parasitism is equal to zero or the absence of observers to report it. In some species, the rate of parasitized nests was available for more than one population. A one-way analysis of variance revealed consistently greater variance among than within species ($F_{38,193} = 2.461$, $p < 0.001$). Therefore, we assumed that despite considerable intraspecific variation, the level of brood parasitism can be viewed as a species-specific characteristic (see also Soler and Møller, 1996), and 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. Finally, it could be argued that parasitism rate may be a biased proxy of parasitism level if the eggs of the brood parasite do not hatch equally in different hosts species. Indeed, there is some evidence showing that hatching rates of the European cuckoo eggs when parasitizing the hole-nesting redstart *Phoenicurus phoenicurus* may be weakly smaller than that when parasitizing open nesting passerines (Avilés *et al.* 2005), which suggests that nesting site may account for variation in hatching rate among European cuckoo hosts. To control for this potential source of bias we considered host suitability that accounted for the kind of nest (see below) in our comparative analysis. Brood parasitism was arcsine-squareroot transformed prior to further analyses.

A number of potentially confounding factors may affect the association between nest predation and level of parasitism. Cowbirds have expanded in North America across the last century (Mayfield, 1965; Rothstein, 1994), thus counter adaptations to cowbird parasitism should be more frequently reported in those species having experienced a longer exposure to parasitism. Cowbirds prefer open habitats and were largely confined to the Great Plains of North America prior to European settlement (Rothstein, 1994). Therefore, hosts in open areas are expected to have been exposed to cowbird parasitism for a longer time than species breeding exclusively in forests (see Hosoi and Rothstein, 2000; Peer and Sealy, 2004). In order to control for such confounding effect we classified species as inhabiting open (score of 1) or forested habitats (score of 3). Species of open habitats include species nesting in open land, old-field, and riparian habitats that are the preferred habitats of brown-headed cowbirds (Lowther, 1993). The forest species are mostly strict forest breeders.

Some species breed in a variable range of habitats comprised of 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 of habitat type was retrieved from Baicich and Harrison (1997).

Nest location may also influence the degree of constraint placed by brood parasitism and nest predation on hosts. Conspicuous nests are arguably more detectable by predators and brood parasites than well-concealed nests (e.g., Götmark, 1992; Weidinger, 2001). Martin and Badyaev (1996) demonstrated that predation suffered by warblers and finches in North America was associated in a parabolic way with nest height: those species mainly nesting in shrubs suffered higher levels of predation than the ones nesting on the ground or the tree canopies. Similarly, nest height may determine the occurrence of brood parasitism since brown-headed cowbirds rarely parasitize strict tree-nester species in forest habitats while it frequently uses species nesting in open areas or close to them (Lowther, 1993). Therefore, differences among species in nest location may determine different exposures to predation and brood parasitism and thus may potentially confound an interspecific association between nest predation and brood parasitism. To control for such confounding effect, species were classified into one of three general nest heights (ground, shrub, subcanopy/canopy). Nests were classified as ground nests (score of 1) if on the ground, shrub nests (score of 2) if off the ground but generally <3 m high, and as subcanopy/canopy nest (score of 3) if >3 m high (see Martin and Badyaev, 1996). Information on nest location was retrieved from Baicich and Harrison (1997). Habitat type and nest location were treated as continuous variables in the comparative analyses. This procedure makes intuitive sense since intermediate states of these variables are biologically meaningful.

The frequency of cowbird parasitism may be affected by host suitability. Therefore we divided species into three groups according to their suitability as hosts after data obtained from the Handbook of the Birds of North America (Poole *et al.*, 1993–2002). Species were classified as unsuitable as brood parasite 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), or (3) because they have eggs or chicks very dissimilar in size as compared to the parasite chick (Ortega, 1998; Rothstein and Robinson, 1998). Some species could be regarded as both suitable or unsuitable hosts (see Røskaft *et al.*, 2002). We included these 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).

A potentially important attribute of host reproduction that can be important for host selection in parasitic cowbirds is the length of the host nestling period. The duration of the nestling care is known to be negatively related to

growth rate of chicks (Lack, 1968). Brood parasites may select hosts based on the growth rate of nestlings, because they need foster parents that are able to provide chicks with sufficient food to yield a high growth rate. Soler *et al.* (1999b) demonstrated in a comparative study of European cuckoo *Cuculus canorus* hosts that increased rate of brood parasitism is associated with shorter nestling period probably reflecting the importance of growth rate in host selection. In our scenario the length of the nestling period may be important because longer nestling periods could increase the risk of predation of parasitized nests. Hence we controlled for the length of the nestling period in our analyses. We extracted information on the length of host nestling period from Baicich and Harrison (1997). In order to obtain a normal distribution, nestling period was squared-root transformed prior to the analyses.

Finally, we entered host body mass in our comparative framework. Weight of adult birds was subtracted from Dunning (1993) and was $\log_{10}$-transformed prior the analyses. Information on variation in nest predation, suitability as host, parasitism rate, habitat type, nest location, body mass and length of the nestling period for all species in which analyses controlled by common descent were based on is summarized in the Appendix.

Comparative and statistical analyses

Because comparisons across species are potentially confounded by varying degree of common phylogenetic ancestry (Harvey and Pagel, 1991) we controlled for similarity among species due to common descent by performing regression analyses based on statistically independent contrasts (Felsenstein, 1985; Harvey and Pagel, 1991) using PDAP 6.0 (Garland *et al.*, 1993, 1999). Statistically independent linear contrasts were calculated for nest predation, host suitability, log-body weight, log-nestling period, parasitism rate, habitat type and nest location. Moreover, to check whether the contrasts were adequately standardized, we plotted absolute values of standardized contrasts versus their standard deviations (square roots of sums of corrected branch lengths) (see Garland, 1992). Absolute values of contrasts were not related to their standard deviations for any of the traits analysed ($p > 0.05$). The phylogenetic hypothesis was based on a composite phylogenetic tree derived from molecular data (DNA hybridization; Sibley and Ahlquist, 1990), with additional information from the literature (Fig. 1, sources available from the authors upon request). We did not have consistent estimates of branch lengths because data were retrieved from studies using different methods. Therefore, we assume all polytomies to be unresolved, and branch lengths were set as constant ($=1$). Linear contrasts were normally distributed and standardized contrasts for each variable were then used to perform stepwise multiple regression analyses (F value to enter in the model $=1$) through the origin (Garland *et al.*, 1992). All the tests were two-tailed.
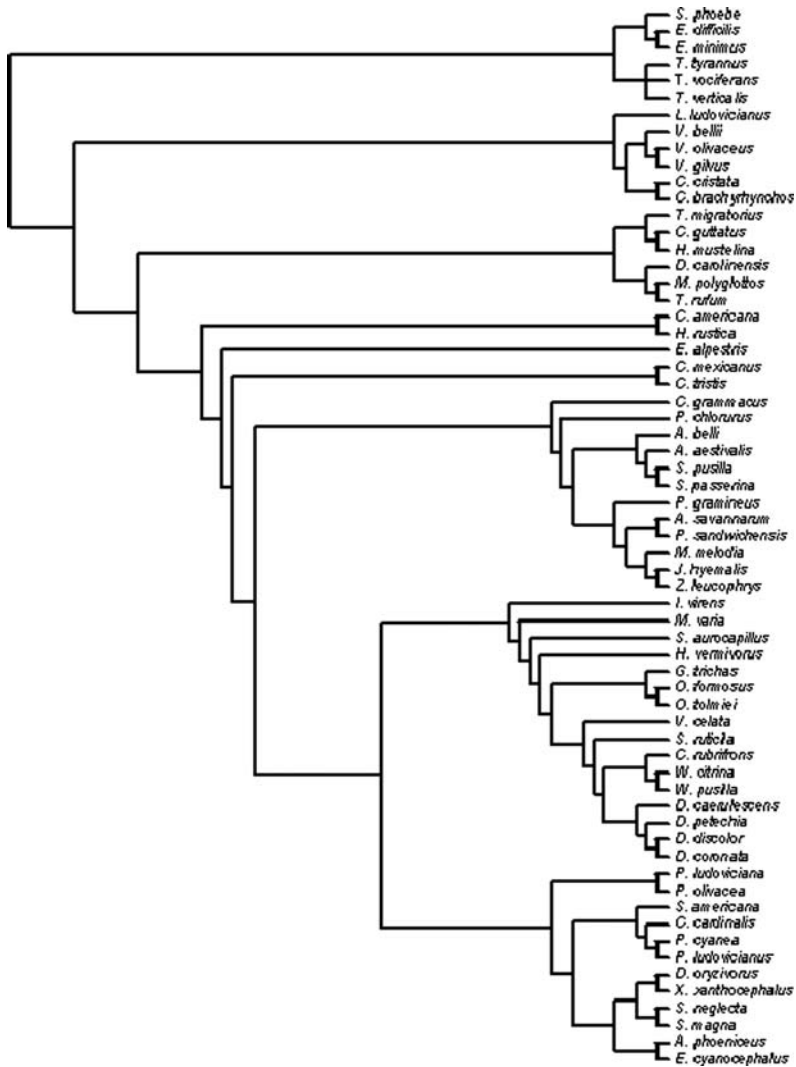
Figure 1. Phylogenetic relationships among passerine birds used in the analyses.

Results

Correlation analysis based on phylogenetically independent contrasts showed a significant negative relationship between nest predation and brood parasitism across the considered host species (r_p (SE) $= -0.26$ (0.12), $F_{1,61} = 4.33$, $p = 0.041$, Fig. 2). When we used stepwise multiple regression analyses to re-analyse the interspecific association between nest predation and brood parasitism together with the effect of habitat type, nest location, nestling period, body mass and

host suitability, the more parsimonious model included nest predation, body mass and host suitability as main predictors of cowbird parasitism (Table 1). Nest location, the length of the nestling period and habitat type were excluded from the definitive model (Table 1). Partial correlation analyses showed that once we controlled for possible confounding factors the negative pattern of association remained robust and nest predation remained as the only variable significantly contributing in explaining variation in brood parasitism among the considered cowbird hosts (Table 1).

Discussion

It has been suggested that host's mean probability of producing fledglings may have influenced the evolution of host selection in cowbirds (e.g. Davies, 2000). Nest predation, the indicator of host quality examined here, is a key factor affecting reproductive success in passerines, but it has previously been neglected as a factor contributing in explaining the occurrence of brood parasitism among hosts of avian brood parasites. The main finding of the present study was that interspecific variation in brood parasitism suffered by North American hosts of the brown-headed cowbird was negatively associated with variation in nest predation. This association appeared to be unaffected by the fact that species were classified as ground, shrub, or subcanopy/canopy nester (nest location). In addition, the results were unaffected by the fact that species were inhabiting open, forested or mixed habitats (habitat type), which is a variable assumed to reflect different levels of exposure to cowbird parasitism
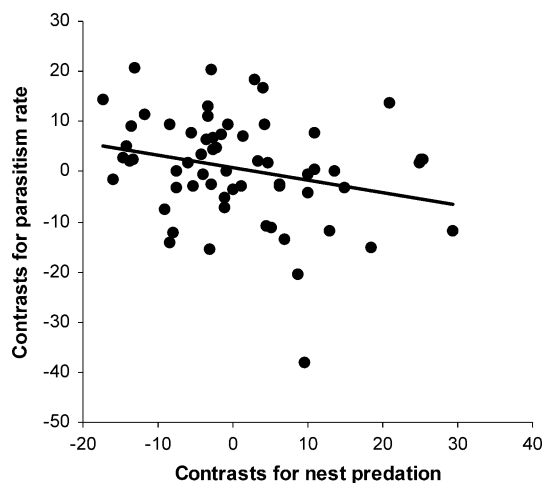

Figure 2. Relationship between level of parasitism (% of parasitized nests) and nest predation (% of predated nests). Values are phylogenetically independent contrasts and the line is calculated from the regression between the contrasts of the two variables.

Table 1. Level of parasitism (dependent variable) in relation to nest predation rate, habitat type, nest concealment, suitability as cowbird host, length of the nestling period and body mass in a forward stepwise multiple linear regression model

Source	r_p (SE)	Slope (SE)	t	p
Model: $r^2 = 0.16$, $F_{3,59} = 3.82$, $p = 0.014$				
Predation	**−0.26 (0.11)**	−0.25 (0.11)	−2.22	**0.029**
Body mass	−0.18 (0.12)	−11.73 (7.78)	−1.50	0.137
Host suitability	−0.21 (0.12)	−6.77 (3.79)	−1.78	0.079
Variables not in the model				
Nest location	−0.02		−0.12	0.90
Nestling period	0.04		0.24	0.80
Habitat type	−0.10		−0.84	0.40

Results are shown after considering the phylogenetical relationships among species (i.e., the multiple regression model is forced through the origin based on phylogenetically independent contrasts). Significant slopes are highlighted. Degrees of freedom were corrected by subtracting the number of polytomies in the phylogenetic trees.

(Hosoi and Rothstein, 2000; Peer and Sealy, 2004), or by the phylogenetic relationships among the studied species.

Comparative results cannot provide insight into the causal evolutionary mechanisms, and this shortcoming is also applicable to the present study. Considering the relationships between parasites and predators, we proposed four causal mechanisms linking the host choice of the cowbird (level of parasitism) and the nest failure of hosts induced by predation on an evolutionary scale. Apparently, our findings are in accordance with two of these mechanisms. Firstly, selection may have selected predator phenotypes avoiding parasitized nests because parasites enhance global nest defence. Evidence supporting the existence of nest defence by brood parasites, is scarce. Soler *et al.* (1999) have shown that great spotted cuckoos *Clamator glandarius* scolded researchers in their regular visits to parasitized magpie *Pica pica* nests, but never in those to unparasitized ones. However, scolding did not reduce predation in that magpie population (Soler *et al.* 1999). The brown-headed cowbird is an extremely prolific egg layer with females laying up to 40 eggs in a single breeding season, in which parental effort has been largely assumed to be devoted to search host nests and only consist of the laying of the eggs by the female (e.g., Payne, 1977; Davies, 2000). However, Hahn and Fleischer (1995) noted that females of the brown-headed cowbird associated with their own juvenile offspring at feeding sites more often than would be expected by chance. This finding may be interpreted as evidence of parental care, but also as an innate attraction of the young cowbird to the sight and sound of cowbird visual and vocal cues. Arcese *et al.* (1996) found that song sparrow nests parasitized by brown-headed cowbirds survived until hatching more frequently than unparasitized nests. However, this was due to female cowbirds depredating unparasitized nests instead of the nests they have laid their own egg in (Arcese *et al.*, 1996).

Our findings are also in accordance with a second mechanism, namely that selection may have favoured parasite phenotypes discriminating among hosts on the basis of expected nest failure. This second hypothesis is based on the existence of parasite cognitive abilities to discriminate among hosts on the basis of expected nest failure. Pöysä (1999) reported for the common goldeneye *Bucephala clangula*, a hole nesting species with a frequent occurrence of conspecific brood parasitism, higher prevalence of parasitism in those nests that were not predated during the previous breeding attempt. This suggests that a mechanism of avoidance of nests based on previous experience is likely to be at work at the intra-specific level. In a hetero-specific context, Parejo *et al.* (2005) have recently shown that rollers *Coracias garrulus* and Eurasian kestrels *Falco tinnunculus* sharing similar ecological requirements may compete for nests, but also that one species may benefit when making reproductive settlement decisions of the information provided by the reproductive outcome of the other. Birds may have evolved cognitive capacities to perceive the reproductive outcome of species sharing similar ecological resources, and then use this information as a cue to make decisions on "where to breed". Selection of such cognitive capacities would be particularly strong for an obligate avian brood parasite which shares with its host the nest and parental care of its offspring.

Finally, there is a third methodological explanation for the negative correlation between nest predation and brood parasitism obtained in this study based on how the data were collected. If parasitism leads to an increase in nest predation (Dearborn, 1999; Burhans *et al.*, 2002), it could be argued that for species in which nest predation is high, the fraction of parasitized nests may have been systematically underestimated by researchers. This possibility could be worthy only whether parasitism features (i.e. cowbird eggs broken outside the nests as consequence of ejection of parasite eggs; cowbird chicks begging louder than host ones) may augment conspicuousness of parasitized nest to predators. We cannot discard this possibility, however, some sources of evidence would suggest this scenario as unlikely. Firstly, many of the North American hosts of the brown-headed cowbird are accepters (e.g. Rothstein, 1990), which suggests that cowbirds eggs would remain in the host nests sufficiently long for allowing non-biased detection of parasitism. Furthermore, change in detectability of host nests due to brood parasitism is only expected after the hatching of the brown-headed cowbird chick, but not before.

How may predation affect the arms race between avian brood parasites and their hosts?

Shifts in host usage by brood parasites have been unequivocally linked to the evolution of host defences (e.g. Davies, 2000). For instance, once the host has

started to reject eggs unlike their own, parasites may not have the adaptive potential to overcome such a defensive barrier by evolving mimetic eggs. Hence, shifting to another host with a lower level of defence, should be a more likely evolutionary trajectory for the parasite (e.g. Davies, 2000). Our results suggest that an alternative mechanism mediated by predation could result in a change in host usage by the parasite. Nest predation suffered by a host is a potential source of variation in host suitability without being determined by the coevolutionary process. Whether predators start to use a common, and *a priori* suitable host as a prey, this may have a negative effect on the parasite, reducing its fitness dramatically. Loss of parasite fitness linked to predation may induce an adaptive shift towards a new host experiencing lower levels of predation. A basic assumption of this hypothesis is that parasites should show a certain level of specialization to a particular host. Current evidence supports this assumption since the European cuckoo (e.g. Wyllie, 1981; Marchetti *et al.*, 1998; Gibbs *et al.*, 2000; Avilés and Møller, 2004) and to a lesser extent brownheaded cowbird (Alderson *et al.*, 1999, Woolfenden *et al.*, 2003) females show host preferences when laying. This mechanism may potentially explain why some apparently suitable hosts used by brood parasites in the past are not currently being used (Rothstein and Robinson, 1998).

In conclusion, although we can not discern between parasite avoidance and parasite defence as the causal mechanisms rendering a negative association between nest predation and level of parasitism we have provided for the first time evidence that nest predation suffered by hosts of avian brood parasites and the occurrence of inter-specific brood parasitism may co-vary across species. This finding could suggest that predators may have played a previously ignored role in the dynamic of the coevolutionary relationships between avian brood parasites and their hosts.

Acknowledgements

Appendix

Information on nest predation (% of nests lost to predators), brood parasitism (frequency of nests parasitized, %), suitability as host, nesting habitat, nest location, body mass and length of the nestling period for bird species included in this study. See main text for sources of data.

Appendix.

Species	Nest predation (%)	Parasitism level (%)	Host suitability	Habitat type	Nest location	Body mass (g)	Nestling period (days)
Agelaius phoeniceus	44.4	16.2	1	2	2	41.5	10.5
Aimophila aestivalis	45.8	0.2	1	2	1	19.1	10.0
Ammodramus savannarum	58.9	22.6	1	1	1	17.0	9.0
Amphispiza belli	43.2	50	1	2	2	19.3	9.5
Cardellina rubrifrons	48	0	1	4	1	9.8	12.0
Cardinalis cardinalis	54	35.5	1	2	2	43.9	10.0
Carduelis tristis	46.8	4.9	3	3	2	12.6	14.0
Carpodacus mexicanus	45.8	19.4	3	2	2	21.4	15.0
Catharus guttatus	94	8.9	1	3	1	31.0	12.5
Certhia americana	35.3	0.2	3	3	3	8.4	15.5
Chondestes grammacus	38.7	33.3	1	2	1	29.0	9.5
Corvus brachyrhynchos	49.1	0.2	3	3	3	438.0	35.0
Cyanocitta cristata	38.4	0.2	3	3	3	86.8	19.0
Dendroica caerulescens	42.8	17.5	1	3	2	9.8	10.0
Dendroica coronata	53	23.2	1	3	3	12.2	13.0
Dendroica discolor	61.8	18.4	1	3	2	7.3	9.0
Dendroica petechia	34.2	27.1	1	3	2	9.2	10.5
Dolichonyx oryzivorus	29.8	12.4	1	1	1	37.1	12.0
Dumetella carolinensis	31.2	5.9	1	3	2	36.9	11.0
Empidonax minimus	53.3	8	1	3	3	10.3	14.5
Empidonax difficilis	58.9	41.7	1	3	3	10.0	16.5
Eremophila alpestris	24.9	21.8	1	1	1	30.8	10.5
Euphagus cyanocephalus	45.5	16.2	1	3	3	58.1	13.0
Geothlypis trichas	14.5	25.5	1	2	2	9.9	9.5
Helmitheros vermivorus	25.6	31.7	1	3	1	13.0	10.5
Hirundo rustica	0.1	0	3	1	2	16.0	20.0
Hylocichla mustelina	52.5	31.8	1	3	2	47.4	12.5
Icteria virens	66.9	32.5	1	2	2	25.1	10.0
Junco hyemalis	31.7	15.1	1	3	1	18.8	11.5
Lanius ludovicianus	19.4	0	1	3	2	47.4	19.0
Melospiza melodía	28.1	34.9	1	2	2	20.5	10.0
Mimus polyglottos	47.1	0	1	3	2	48.5	13.0
Mniotilta varia	26.3	22.7	1	3	1	10.6	10.0
Oporornis formosus	30	40	1	3	1	13.7	9.0
Oporornis tolmiei	49.3	20	1	3	2	10.4	9.0
Passerculus sandwichensis	43.4	8.8	1	1	1	19.5	11.0
Passerina cyanea	54	38.9	1	3	2	14.1	11.0
Pheucticus ludovicianus	50	4.6	1	3	3	45.6	10.5
Pipilo chlorurus	78	0.2	1	2	1	29.4	11.5
Piranga ludoviciana	46.2	0.2	1	3	3	28.1	10.5
Piranga olivacea	32.6	69.6	1	3	3	28.6	15.0
Pooecetes gramineus	52.9	13.9	1	2	1	24.9	11.0
Sayornis phoebe	15.9	17.3	2	2	2	19.8	16.0
Seiurus aurocapillus	24.5	35.9	1	3	1	19.4	9.0
Setophaga ruticila	37.8	23.4	1	3	2	8.1	9.0
Spiza americana	48.8	46.6	1	2	2	24.6	10.0
Spizella passerina	41.2	20.4	1	3	3	12.3	10.5
Spizella pusilla	60.4	20.4	1	2	2	12.5	8.0

Appendix. (Continued)

Species	Nest predation (%)	Parasitism level (%)	Host suitability	Habitat type	Nest location	Body mass (g)	Nestling period (days)
Sturnella magna	48.6	26.6	1	2	1	76.0	11.5
Sturnella neglecta	46.9	12.7	1	2	1	89.4	11.0
Toxostoma rufum	29	8.4	1	2	2	68.8	11.0
Turdus migratorius	40.2	0.5	3	3	3	77.3	15.0
Tyrannus tyrannus	32.7	2.5	1	3	3	43.6	13.5
Tyrannus verticalis	37.6	0	1	3	3	39.6	13.5
Tyrannus vociferans	42.6	0.2	1	3	3	45.6	14.0
Vermivora celata	50	0.2	1	2	2	9.0	12.5
Vireo bellii	11.4	43.2	1	3	2	8.5	11.0
Vireo gilvus	45	28.9	1	3	3	14.8	14.0
Vireo olivaceus	24.9	40.7	1	3	2	16.7	12.0
Wilsonia citrina	47	0.2	1	3	2	10.1	8.5
Wilsonia pusilla	34.9	27.3	1	2	1	7.7	10.5
Xanthocephalus xanthocephalus	34.4	0.7	1	2	2	49.3	11.0
Zonotrichia leucophrys	51.1	11.6	1	2	1	29.4	10.0

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