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Blood parasites and dominance in captive blackbirds

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Evidence of the pathogenicity of haematozoa in wild bird populations is limited, possibly because infected birds alter their behavior to avoid the costs of being parasitized. We tested this hypothesis by examining dominance relationships relative to parasite status in captive Red-winged Blackbirds *Agelaius phoeniceus*, and Brown-headed Cowbirds *Molothrus ater*. There was some evidence that uninfected individuals tended to be dominant to infected individuals, but the pattern was variable, even within two studies involving male Red-winged Blackbirds. Dominant parasitized individuals were not consistently larger than the uninfected individuals they dominated, although other, untested asymmetries might have allowed the infected birds to overcome any cost associated with being parasitized.

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The demonstration by Hamilton and Zuk (1982) that haematozoa infections may be linked to the evolution of secondary sexual traits in birds prompted a proliferation of research into bird-parasite relationships in general, and bird-haematozoa relationships in particular (e.g., Loye and Zuk 1991). Underlying the proposed link between parasites and sexual selection is the assumption that parasites are truly parasitic (i.e., reduce host fitness). Evidence documenting the pathogenicity of haematozoa in birds is sketchy, with most positive evidence drawn either from studies of domestic species or from wild species challenged with an exotic parasite (Atkinson and Van Riper 1991, Bennett et al. 1993). In a study of free-living Red-winged Blackbirds *Agelaius phoeniceus*, Weatherhead (1990) found no evidence that haematozoa affected body condition or survival, and Weatherhead and Bennett (1992) reported similar negative results for free-living Brown-headed Cowbirds *Molothrus ater*.

One reason that correlational studies of free-living birds may fail to detect any cost to parasitism is that infected birds may alter their behavior to minimize the cost of being parasitized (Weatherhead 1990, Forbes 1993). For example, a parasitized male might avoid competitive interactions if competing compromises his ability

to keep the infection in check. To assess this possibility, one must place birds in a situation where their options for modifying their behavior are limited and easily detected. Here we examine dominance relationships relative to parasite status among Red-winged Blackbirds and Brown-headed Cowbirds that were maintained in aviaries and forced to compete for food. We predicted that if haematozoa infections are costly, infected birds should generally be subordinate to uninfected birds to avoid the cost of fighting for dominance.

Methods

In nearly all cases the data that we report come from a series of studies that used dominance relationships among birds maintained in aviaries to test various hypotheses unrelated to those we consider here. Because these studies were conducted coincidentally with studies of haematozoa in wild blackbirds, blood smears were collected as part of a general protocol employed in our laboratory at that time.

The data come from two studies of male Red-winged Blackbirds, one of female Red-winged Blackbirds, and

Table 1. Mean (\pm S.E.) percentage of total encounters won by parasitized and unparasitized individuals.

Study	Parasitized			Unparasitized			t	P
	\bar{x}	S.E.	N	\bar{x}	S.E.	N		
Male Red-winged Blackbird ^a	42.6	11.11	7	49.3	9.84	13	0.45	0.66
Male Red-winged Blackbird ^b	31.5	3.10	12	57.7	7.39	15	-3.00	0.006
Female Red-winged Blackbird ^c	53.6	8.50	10	42.2	5.48	24	1.13	0.27
Male Brown-headed Cowbird	20.1	11.29	4	50.6	8.10	14	-1.85	0.08

^aShutler and Weatherhead (1991). ^bMetz (1991). ^cMuma and Weatherhead (1991).

one study of male Brown-headed Cowbirds. The first study of male Red-winged Blackbirds used dominance relationships to assess the competitive abilities of territorial males relative to floaters (Shutler and Weatherhead 1991). No evidence of competitive differences or differences in parasitism between owners and floaters was found. The second study, conducted in a different year from the first and using birds from different local populations, assessed whether leg-band color affected dominance relationships among male Red-winged Blackbirds captured on their territories and found no effect (Metz 1991). The study of female Red-winged Blackbirds examined whether plumage variation influenced dominance and found no evidence that it did (Muma and Weatherhead 1991). Finally, the study of male Brown-headed Cowbirds was conducted specifically for the present purposes (i.e., to assess the effect of haematzoa on dominance). To reduce possible confounding effects of age on dominance (Searcy 1979, Weatherhead and Teather 1987) or parasite status (Weatherhead and Bennett 1991, 1992), we only used males that were at least two years old in the cowbird study and only considered data for males at least two years old from the Red-winged Blackbird study that included some yearling males (Shutler and Weatherhead 1991). All birds were captured and tested early in the breeding season when all infected individuals would have been in a similar stage of their infection.

All the studies employed the general protocol developed by Eckert and Weatherhead (1987). From three to 10 individuals were placed in a $3 \times 2 \times 1.5$ m aviary for a period of approximately two to four weeks. In addition to having individual color bands, each bird had a unique patch of plumage bleached with a mixture of commercial hair dye and peroxide to facilitate identification on videotape. On three to five occasions during the period of captivity we videotaped interactions at a food dish for one to two hours early in the morning following a night of food deprivation. The food dish used during a trial was only large enough for one bird to feed at a time. At other times food and water were provided ad libitum. From each videotape we recorded all aggressive interactions (physical displacements and avoidance behavior) and assigned a winner and loser. For the purposes of this paper we consider two measures of dominance. The first is the percentage of total interactions won by an individual. The second involves pairs of birds where their pooled interac-

tions over all observation periods indicated a clear ($p < 0.05$) winner by a binomial test.

Blood smears for parasite analysis were collected from each bird either when placed in the aviary or just prior to release at the end of the study (a subset of birds was sampled both at the start and the finish). All scoring of the smears was done by GFB (details in Weatherhead and Bennett 1991). The assessment of dominance relationships and the scoring of blood smears were performed blind with respect to each other.

Results

The three species of parasites we detected in Red-winged Blackbirds were *Leucocytozoon icteris*, *Haemoproteus quisqualis* and *Plasmodium vaughani*. Only the first two parasites were found in Brown-headed Cowbirds. Because of small sample sizes we have classified all birds as either parasitized or unparasitized. Of the 41 birds sampled both at the start and finish of the study, 26 were unparasitized in both samples, 10 either went from unparasitized to parasitized or the intensity of their infection increased, and 5 either lost or decreased the intensity of their infections. Thus, being in captivity did not appear to affect the birds' parasite status in any consistent fashion. We consider individuals that changed status as parasitized because they were infected for at least part of the study.

Unparasitized male Red-winged Blackbirds won significantly more interactions on average than parasitized males in one of the two studies (Table 1). No significant difference was found for females. Unparasitized male Brown-headed Cowbirds won more than double the number of interactions than parasitized individuals, although the difference was not quite significant, at least in part due to the small number of parasitized individuals (Table 1).

Previous research has shown that, in Red-winged Blackbirds, larger individuals tend to dominate smaller individuals (Eckert and Weatherhead 1987). Therefore, it is possible that the parasitized individuals that were dominant in our studies were able to overcome the cost of being parasitized by virtue of their size. To assess this possibility we examined the wing lengths of winners and losers in dyads involving a parasitized and an unparasitized individual. For male Red-winged Blackbirds, in 8 of 12 dyads won by parasitized individuals, the parasitized

males had longer wings than their opponents. Unparasitized males had that advantage in 13 of 26 dyads they won ($\chi^2 = 0.37$, $p > 0.05$). For females, in 11 of the 17 dyads won by parasitized individuals, the parasitized females had longer wings, while unparasitized females had that advantage in only 2 or the 6 dyads they won (Fisher exact test, $p = 0.34$). Thus, for Red-winged Blackbirds, larger body size (as indexed by wing length) does not consistently explain why some parasitized individuals were able to dominate some unparasitized individuals. No wing length measurements were made for Brown-headed Cowbirds.

Discussion

Freeland (1981) found that male laboratory mice experimentally infected with a nematode did not become behaviorally dominant. Here we found that haematzoa infections sometimes had a negative effect on dominance in captive blackbirds. We assume that the parasites affect an individual's dominance rather than the converse (i.e., subordinate individuals being more likely to become infected). The vectors for the haematzoa we studied are biting flies, and it is likely that the birds are exposed to these flies from the time they are in the nest (Weatherhead and Bennett 1991, 1992). Therefore, it is difficult to imagine a plausible scenario whereby subordinate birds suffer increased exposure to the vectors.

Although some of our results did show a negative effect of parasites on dominance, that effect was not uniform either within or among our studies. Indeed, just with male Red-winged Blackbirds, parasites were only clearly associated with dominance in one of the two studies. It is possible that the way in which an individual responds to being parasitized is conditional upon a variety of other factors. We found only weak evidence that infected individuals that had longer wings tended to dominate opponents that were uninfected but had shorter wings. However, there were undoubtedly other, unmeasured asymmetries that may have influenced our results. For example, blackbirds are host to many other parasites, most of which appear to infect birds independently of each other (Weatherhead et al. 1993). These other parasites may account for some of the variability we observed in the effect of haematzoa. Further research with captive birds in which both the asymmetries between opponents and the rewards to the winner are varied experimentally, will be necessary to assess the flexibility of a bird's behavioral response to being parasitized.

Free-living birds presumably have more options for modifying their behavior to reduce the costs of parasites than birds in captivity. In one study of Red-winged Blackbirds, Weatherhead (1990) found that males infected with haematzoa responded less aggressively to a simulated territorial intrusion and tended to court female models less vigorously than uninfected males. However, these effects were not found in a subsequent study

(Weatherhead et al. 1993). This variation in the effect of parasitism may be attributable to variation in environmental conditions affecting the cost of being parasitized. Korpimäki et al. (1993) found that female Tengmalm's Owls *Aegolius funereus*, infected with *Leucocytozoon* reduce their clutches, but only when food was relatively scarce. If wild birds are generally able to reduce the cost of parasitic infections by behavioral means, then the effects of parasitism may often be subtle and only easily detected when environmental conditions are extreme.

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