

SEXUAL SELECTION AND PARASITES IN WOOD-WARBLEDERS

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ABSTRACT.—We used data on the prevalence of blood parasites in approximately 5,000 individuals of 10 warbler (Parulinae) species captured in New Brunswick and Newfoundland to test the prediction that parasitism and plumage brightness should be positively correlated. We used independent subjective assessments of plumage brightness and two subjective and one objective estimate of plumage dimorphism. No significant correlations were found between parasitism and any index of plumage. We found inconsistencies in our estimates of parasite prevalence for the same species sampled at two different sites and between males and females of the same species. These inconsistencies may be due to sampling error or to ecological differences between sites that produced different patterns of exposure of the birds to the parasites' vectors. Inability to quantify parasites accurately and consistently will make the testing of the Hamilton and Zuk hypothesis of sexual selection more difficult. *Received 20 February 1990, accepted 21 August 1990.*

HAMILTON and Zuk (1982) proposed that secondary sexual traits (e.g. elaborate plumage and song in birds) have evolved as reliable signals of parasite resistance. They argued that, because parasites are costly, only resistant males can afford to produce elaborate secondary sexual traits. Thus, females prefer ornamented males because they sire parasite-resistant offspring. This hypothesis is of importance to evolutionary theory because it provides a novel mechanism for Darwin's (1871) theory of sexual selection. A prediction of Hamilton and Zuk's (1982) hypothesis is that secondary sexual traits should be better developed in species subjected to higher levels of parasitism. This follows because traits that advertise parasite resistance are more important to females that choose mates where the threat from parasites is high. Here we present a test of this prediction and examine some of the pitfalls that potentially affect tests of this sort.

Hamilton and Zuk (1982) provided the first test of their parasite hypothesis when they compared plumage brightness and song with parasite levels in North American passerine birds. Read (1987) demonstrated that the support for the parasite hypothesis provided by these data held even after he had eliminated potentially confounding taxonomic artifacts and ecological variables. Subsequently, Read and Harvey (1989a) questioned Read's earlier results be-

cause they found that those results were dependent on which subjective estimates of plumage brightness they used. Because those analyses remain contentious (Hamilton and Zuk 1989, Read and Harvey 1989b, Zuk 1989), it is timely to bring new data to bear on the issue.

There are many problems with the analyses of plumage brightness and parasites (Read 1990), and we focus on two of the key problems. The first involves quantifying plumage brightness. Hamilton and Zuk (1982) and Read (1987) relied on a subjective assessment of plumage brightness using a combination of illustrations from field guides and first-hand knowledge of the birds. Because of substantial variation in the assessment of brightness by different observers (Read and Harvey 1989a), there is uncertainty as to how well any human assessment conforms to how the birds themselves assess brightness. We compared the subjective assessments made by human observers with an objective assessment based on an analysis of plumage. We also broadened the analysis to consider sexual dimorphism of plumage in addition to plumage brightness. Because mating preference by females is assumed to drive the evolution of plumage coloration (Hamilton and Zuk 1982), plumage dimorphism rather than plumage brightness may be the most appropriate index of the intensity of sexual selection.

Another potential problem with the analyses

of Hamilton and Zuk (1982) and Read (1987) is the parasite data they used. They relied on a variety of reports of hematozoa prevalence collected over a broad geographic area by different observers for an ecologically diverse array of species. Given the substantial inadequacies in our knowledge of even the basic natural history of avian blood parasites (Ender and Lyles 1989, Cox 1989), the best data to use will be those collected in the most standardized fashion. Here we use data collected over several years at the same sites by the same observer (G. F. Bennett). All our data are for wood-warblers (Parulinae), which are small, primarily insectivorous species found principally in wooded habitat (Perrins and Middleton 1985). We sampled parasites from the same warbler species from two ecologically distinct sites. This allowed us to assess whether particular warbler species have the same parasite prevalence, both absolutely and relative to each other, in the two sites.

METHODS

Plumage.—To obtain an objective assessment of plumage dimorphism we used information on feather coloration taken from 19 body regions. These data were provided by E. H. Burt Jr. Burt had assigned the plumage in each of the 19 regions to 1 of 14 colors based on reflectance spectra obtained from fresh museum specimens. Details of the methods are provided in Burt (1986). For our dimorphism index we determined the percentage of body regions for which males and females of a species had been judged to have different colors. We did not attempt to weight the degree of difference between colors.

We also used several subjective estimates of both plumage brightness and plumage dimorphism. Read provided us the estimates of plumage brightness used by Read and Harvey (1989a). These were assigned by six ornithologists using field guides. Males of each bird species were scored from 1 (dull) to 6 (very striking). We refer to the mean values across the six ornithologists as the "Oxford brightness scores." Zuk provided us the plumage brightness scores used by Hamilton and Zuk (1982). Their scoring system was similar to Read and Harvey's (1989a) but included scoring the brightness of both males and females of each species. We use their values for male brightness as the "Hamilton-Zuk brightness scores." We also used their data to generate a dimorphism index, calculated as the difference in brightness scores for males and females of each species (the "Hamilton-Zuk dimorphism score"). Finally, our own panel of five biologists used illustrations in two field guides (Peterson 1980, National Geographic Society 1983) to assign brightness scores on a scale of 1 to 5. Although some

of our panelists study birds, none were "birders," and they were all unaware of our specific purpose. Details of the individual results of our plumage scores are presented elsewhere (Shutler and Weatherhead 1991). In this paper we use the means for all our observers using both field guides to generate the "Carleton brightness scores" and the "Carleton dimorphism scores" (as for Hamilton-Zuk) for each species.

Parasites.—Bennett mist-netted warblers from two sites during the breeding season. The New Brunswick sample was collected from 1972–1978 in the Tantram marsh area located near Sackville, New Brunswick. The study area is an area of alders (*Alnus rugosa*) fringing a lakeshore that provided an interface between marsh, hay fields, and oat fields (see figure 1 in Bennett et al. 1975: 1434). The net sites were not moved >50 cm during the study period. Some of the hematozoa results used in the present study were initially reported by Bennett et al. (1975). The identical study area and net sites were used subsequently for a study of habitat relationship of passerines (Beauchamp 1985), and blood parasites sampled from birds caught in that study contributed the balance of our New Brunswick sample.

The Newfoundland sample was obtained from 1978–1983 as part of a monitoring program on the impact of the pesticide Matacil (for control of spruce budworm) or nontarget organisms. The study areas, near the town of Gander, are in two blocks, one of which was aerially sprayed with Matacil at a 2-week interval in each year of the 6-yr study; the other block was an unsprayed control. As with the New Brunswick study, net sites were unchanged for the duration of the study. The control and sprayed blocks were similar ecologically and represented a typical boreal balsam fir (*Abies balsamea*)/black spruce (*Picea mariana*)/white birch (*Betula papyrifera*)/aspen *Populus* sp. second-growth forest following initial logging operations. Net sites were located along logging roads in the alder (*Alnus* sp.)/pin cherry (*Prunus pensylvanicus*) roadside cover. Matacil had no effect on the prevalence of hematozoa in the passerine population (Bennett et al. 1988). There was little habitat similarity between the New Brunswick and Newfoundland study areas.

Smears were made from a drop of blood taken from the brachial vein (Bennett 1970). All hematozoa (predominantly *Haemoproteus* spp. and *Leucocytozoon* spp.) were quantified by counting the number of parasites per 100 fields ($\times 100$ objective for haemoproteids; $\times 40$ for leucocytozoids). All blood smears were placed in the collection of the International Reference Centre for Avian Haematozoa. We classified all birds as either infected or uninfected.

For all correlation analysis we used one-tailed tests because all correlations had predicted outcomes.

RESULTS

Plumage.—There were varying levels of agreement between the different plumage in-

TABLE 1. Spearman rank correlations between indices of plumage brightness and dimorphism for the 10 warbler species for which parasite data were obtained. * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

	Brightness		Dimorphism		
	Oxford	Carleton	Burt	Hamilton-Zuk	Carleton
Brightness					
Hamilton-Zuk	0.78**	0.92***	0.37	0.83**	0.60*
Oxford		0.91***	0.80**	0.75**	0.83**
Carleton			0.61*	0.85***	0.77**
Dimorphism					
Burt				0.60*	0.80**
Hamilton-Zuk					0.80**

* See text for derivation of indices.

dices (Table 1). Interestingly, the agreement among indices of brightness and among indices of dimorphism was much the same as between indices of brightness and dimorphism. Thus, species in which the males were judged to be bright are also the species judged to be dimorphic. In addition, our objective measure of plumage dimorphism (the Burt index) was significantly correlated with the Hamilton-Zuk and Carleton subjective indices of dimorphism (Table 1). In spite of this general agreement between indices, we have no basis to prefer one

over another. Therefore, we retained all six indices for our analysis of plumage and parasites.

Parasites.—The categorization of the parasite data by sex and study location (Table 2) reveals several important patterns. First, there was considerable variation across species in the prevalence of parasitism, a necessary prerequisite for our analysis of parasites and plumage (below). Second, although the rank orders of the species by prevalence of parasitism at the two sites were positively correlated, the correlation is rather weak (Fig. 1, $r_s = 0.56$, $P = 0.046$). Third,

TABLE 2. Summary of parasite data for males, females, and individuals of unknown gender from New Brunswick and Newfoundland for all study years combined.

Species	Para-sites*	New Brunswick			Newfoundland			Both		
		♂	♀	Un-known	♂	♀	Un-known	♂	♀	Un-known
Black-and-white Warbler (<i>Mniotilta varia</i>)	+ve -ve	1 20	4 14	2 32	38 53	24 36	21 29	39 73	28 50	23 61
Tennessee Warbler (<i>Vermivora peregrina</i>)	+ve -ve	13 35	4 30	54 369	15 26	16 28	34 36	28 61	70 58	88 405
Magnolia Warbler (<i>Dendroica magnolia</i>)	+ve -ve	22 33	7 20	25 65	40 45	29 32	50 31	62 78	36 53	75 96
Yellow-rumped Warbler (<i>D. coronata</i>)	+ve -ve	71 30	39 8	78 87	62 12	45 5	60 26	133 42	84 13	138 113
Blackpoll Warbler (<i>D. striata</i>)	+ve -ve	17 13	5 6	12 1	51 101	52 57	45 38	68 114	57 63	57 39
Ovenbird (<i>Seiurus aurocapillus</i>)	+ve -ve	0 1	0 4	5 6	9 16	6 5	6 19	9 17	6 9	11 25
Northern Waterthrush (<i>S. noveboracensis</i>)	+ve -ve	2 22	0 0	16 22	94 177	77 134	368 276	99 199	77 134	384 298
Mourning Warbler (<i>Oporornis philadelphia</i>)	+ve -ve	2 1	0 0	0 0	24 37	7 12	20 7	26 38	7 12	20 7
Wilson's Warbler (<i>Wilsonia pusilla</i>)	+ve -ve	18 81	6 11	4 28	16 58	5 8	13 19	34 139	11 19	17 47
American Redstart (<i>Setophaga ruticilla</i>)	+ve -ve	104 261	57 227	39 257	8 8	7 19	5 12	112 269	64 246	44 269

* +ve = parasitized; -ve = unparasitized.

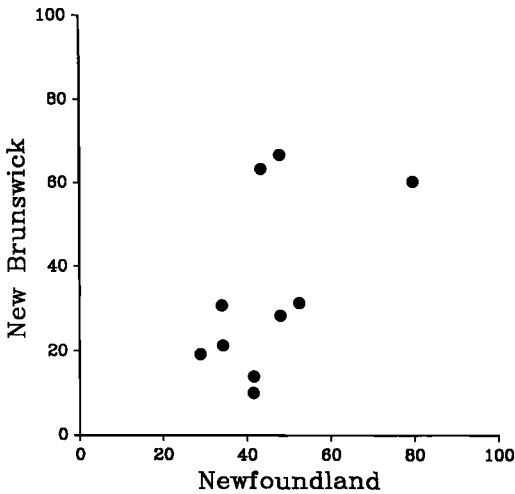


Fig. 1. The percentage of birds parasitized in 10 warbler species sampled in New Brunswick and Newfoundland.

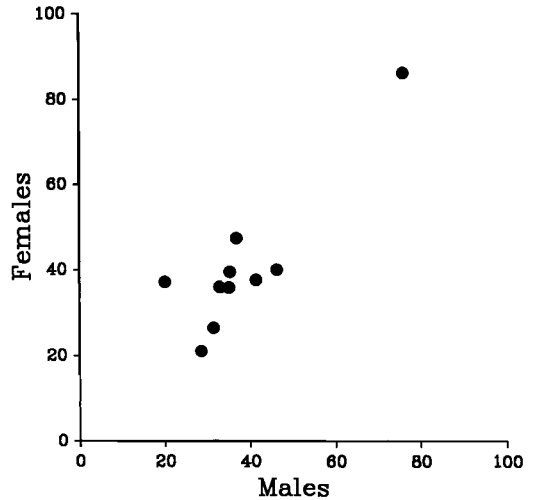


Fig. 2. The percentage of male and females parasitized in 10 warbler species sampled from both New Brunswick and Newfoundland.

within species, the correlation between the prevalence of parasitism of males and females also was not perfect (Fig. 2, $r_s = 0.74$, $P = 0.008$).

Plumage and parasites.—We calculated Spearman rank correlations between the prevalence of parasitism and both plumage brightness and plumage dimorphism (Table 3). Collectively these analyses provide virtually no support for the parasite hypothesis. Positive correlations outnumbered negative correlations, but not a single index of either plumage brightness or plumage dimorphism was significantly correlated with parasitism. Interestingly, the two Hamilton-Zuk indices produced the largest correlation coefficients. By contrast, our objective index of plumage dimorphism based on Burtt's analysis of plumage color produced some of the lowest correlations.

DISCUSSION

Using substantial samples ($n = 27$ – 682) collected uniformly from two sites in Atlantic Canada, we found no evidence that hematozoa prevalence was correlated with either male plumage brightness or plumage sexual dimorphism in 10 species of warblers. More significant than the failure of the Hamilton and Zuk (1982) hypothesis in this limited test, however, are the insights provided into some of the difficulties inherent in testing that hypothesis.

First, consider the problem of measuring plumage brightness. According to the Hamilton and Zuk hypothesis, bright plumage has evolved as an honest signal of parasite-resistance in males that females use to select mates. Therefore, ideally we should score brightness by observing courting birds in their natural habitat (Endler and Lyles 1989). Human observers all agree to a reasonable extent on the relative brightness or sexual dimorphism of plumage based on field guide illustrations. Furthermore, these subjective assessments are significantly correlated with an objective assessment of plumage dimorphism based on plumage reflectance using museum specimens (the Burtt index). In spite of this general pattern of agreement, we do not know how well our indices reflect what a female warbler perceives as brightness in a courting male. Although less tractable because of its subjectivity, a Gestalt approach may best approximate what we are trying to measure. Such an approach would use a birder's experience observing a species in the field to assign brightness or conspicuousness, and it would incorporate the contribution of behavior and features such as crests and tails to conspicuousness (see Zuk 1989).

Another difficulty we encountered in testing the Hamilton and Zuk hypothesis concerns the estimation of parasite prevalence. Despite the limitation that we considered only one type of

TABLE 3. Spearman rank correlations between the prevalence of parasitism^a and plumage. For all correlations, $P > 0.05$.

Male Plumage Brightness			Plumage Sexual Dimorphism			
Hamilton-Zuk	Oxford	Carleton	Burt	Hamilton-Zuk	Carleton	
Species (n = 10)						
New Brunswick	0.26	0.17	0.20	0.03	0.45	0.12
Newfoundland	-0.03	0.11	0.11	0.17	0.19	0.14
Overall	0.08	-0.01	-0.01	-0.09	0.19	0.10
Genus (n = 7)^b						
New Brunswick	0.41	0.25	0.32	-0.25	0.51	0.43
Newfoundland	-0.28	-0.16	-0.23	-0.13	0.09	0.07
Overall	0.19	0.07	0.00	-0.21	0.31	0.07

^a Prevalence of parasitism is based on all birds sampled in a species (Table 2).

^b For the two genera with more than one species, each member species was given equal weight in computing the generic mean for both plumage and parasitism.

parasite out of many that could be involved, we did not obtain consistent prevalence scores for the parasites assessed. Although significantly correlated, the rank order of parasite prevalence across species differed between Newfoundland and New Brunswick and between males and females. These results may be due in part to sampling error, particularly given the small samples obtained for two of the species in New Brunswick. However, substantial differences in parasite prevalence between sites and between sexes were also found for species that were well sampled.

Differences in prevalence between sites could reflect the fact that the sites were dissimilar ecologically. In all likelihood this would affect the faunal composition of the biting flies that are the vectors for the hematozoa studied. Differences in parasite prevalence between males and females of the same species could reflect behavioral differences that affect their exposure to the parasite vectors. For example, ground-nesting birds have relatively low hematozoa prevalence (Greiner et al. 1975). Birds nesting in midcanopy may suffer greater exposure to vectors, and that could disproportionately affect incubating females. Two general conclusions can be drawn. First, our results reaffirm our ignorance of the ecology of the parasites, their vectors, and the birds (Endler and Lyles 1989). Second, when the problems we identified are extrapolated to studies that compare parasitism and plumage from a more diverse array of species sampled over broader geographical areas, the potential for the results to be confounded would seem much greater.

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