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Parasite faunas, testosterone and secondary sexual traits in male red-winged blackbirds

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Summary. We examined associations among parasite infections, secondary sexual traits and testosterone in male red-winged blackbirds sampled at the start of the breeding season. Parasites quantified included ectoparasitic lice and mites and endoparasitic blood protozoans, nematodes, trematodes and cestodes. Secondary sexual traits that we quantified included body size, epaulet size and color, song repertoire size and song switching rate, and behavioral responses to male and female models. Overall we found few significant associations between parasites and secondary sexual traits, between secondary sexual traits and testosterone, or between parasites and testosterone. In addition, most parasite taxa appeared to infect birds independently, although the low prevalence (<50%) of many of the parasites meant that our sample sizes were too small to detect weak associations. Our most promising results were obtained for ectoparasitic mites, which tended to occur on birds uninfected with other parasites, on birds with longer epaulets, and on birds with higher levels of testosterone. Epaulet length and testosterone are both probable correlates of dominance in this species. Further research will be required to determine whether there is a causal link between the immunosuppressive effects of testosterone and the mite infections, and between testosterone, epaulet length and male mating success.

Introduction

In recent years interest has grown rapidly in host-parasite relationships, particularly in birds. Much of that increase can be attributed to the idea proposed by Hamilton and Zuk (1982) (and supporting data from birds that they presented) that linked parasites to sexual selection, the latter already having been the focus of growing interest. They proposed that the coevolution of hosts and parasites could maintain heritable fitness differences among individuals that could be the basis for mate choice, and that secondary sexual traits have evolved to signal those differences in genetic quality. Thus, female birds could use the elaboration of males' plumage or courtship behavior to recognize and select as mates those individuals carrying genes for resistance to parasites. Here we explore several aspects of this hypothesis that have heretofore received little attention, using data collected from male red-winged blackbirds (*Agelaius phoeniceus*).

Much of the research spawned by the Hamilton-Zuk hypothesis has attempted to test one or the other of its two central predictions concerning how plumage brightness (or other secondary sexual traits) should vary with parasite load. Interspecifically, the hypothesis predicts that species with the most parasites should have the best developed secondary sexual traits, since the more there is to be resistant to, the more likely it is for traits to have evolved to signal resistance. Tests of this prediction have been equivocal (e.g. Read and Harvey 1989; Weatherhead et al. 1990; Zuk 1991). Intraspecifically, the hypothesis predicts that individuals that are resistant to parasites should have the most developed secondary sexual traits, and tests of this prediction have also produced results both consistent and inconsistent with the model (e.g. Borgia 1986; Weatherhead 1990; Burley et al. 1991; Møller 1991).

In general, both inter- and intraspecific tests of the hypothesis have been been typified by their narrow focus in terms of both the secondary sexual traits and the parasites that have been considered, relative to those to which the hypothesis is theoretically applicable (Clayton 1991). The narrow focus of earlier studies seems to have been a matter of convenience or necessity rather than scientific imperative. For example, interspecific tests have looked primarily for correlations between plumage brightness and haematozoa prevalence, largely because plumage brightness can be quantified for many species in a standardized fashion using field guides, and haemotozoa are the only parasites that have been systematically surveyed for sufficient species of birds to allow comparative analyses. Similarly, intraspecific studies

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have focussed primarily on ectoparasites, haematozoa, or other endoparasites that can be sampled by means that are not lethal to the birds, thus allowing the study of relevant aspects of the birds' behavior. Studies are needed that attempt a more comprehensive assessment of the relationships between parasites and secondary sexual traits within a host species (Clayton 1991; Zuk 1991).

There are several reasons for pursuing a broader approach. First, there are often multiple traits within a species that have been sexually selected (e.g. song, plumage, morphology, behavior). While some or all of those traits may coevolve (Shutler and Weatherhead 1990), little is known about their relationships to one another, so at present it seems prudent to consider a species' complete suite of secondary sexual traits. In the case of parasites, there is an argument to be made for focusing on some taxa more than others, although, as mentioned above, that seems not to have been the overriding basis for the choice of parasites in studies to date. The generation time of the parasite relative to that of the host has been hypothesized to affect the coevolutionary dynamics between the two, and thus the likelihood that heritable variation in resistance can be maintained in the host (Hamilton and Zuk 1982). Balmford and Read (1991) proposed that one of the strongest tests of the Hamilton-Zuk hypothesis would to be assess whether secondary sexual traits are most strongly correlated with those parasites that are most likely to coevolve with the host in ways required by the hypothesis. They suggested that parasites with long generation times are likely to be the best candidates for appropriate coevolution. The central aim of our study was to test this idea by surveying a broad array of parasites in male red-winged blackbirds for which all major secondary sexual traits had also been quantified.

In meeting our central aim we were also able to meet several subsidiary aims. Little is known at present about the interactive effects of different parasites within the same host (Zuk 1991). However, Schall's (1990) study of two species of *Plasmodium* in a rainbow lizard (*Agama*) suggest that parasite interactions could be complex. He found that the total parasitemia in mixed infections was approximately equal to the sum of the parasitemias in single infections, suggesting that when both parasites are present, one parasite has no effect on the other. However, prevalence data showed that mixed infections occurred 2–3 times more often than expected by chance, suggesting that the presence of one of the parasites may affect the lizards' resistance to the other parasite. The second aim of our study was to assess whether infections by the different parasites we ecountered in red-winged blackbirds occurred independently of one another.

Another subsidiary aim of our study concerned the role of testosterone in affecting parasite infections through its influence on the immune system. There is growing evidence of a negative relationship between stress and immunocompetence in general, and between testosterone and immunocompetence in particular (Zuk 1990; Folstad and Karter 1992). Therefore, during the breeding seasion, male birds may face a tradeoff. They can increase their reproductive success by maintaining high levels of testosterone (which should also cause increased expression of secondary sexual traits), or increase their survival by keeping testosterone low and thus not compromising their immune system. If so, then males infected with parasites should maintain lower levels of testosterone to keep their parasites in check, producing a negative correlation between parasites and testosterone. Alternatively, those males with the best opportunity for reproductive success in a given year may elevate their testosterone at the expense of their immune system, thereby producing a positive correlation between parasites and testosterone. Our third objective, therefore, was to determine whether any correlation existed between testosterone, expression of secondary sexual traits and parasite infections in male red-winged blackbirds.

Red-winged blackbirds are ideally suited to this study. They are highly sexually dimorphic and males have an array of both morphological and behavioral secondary sexual traits. Furthermore, extensive research on our study population and on others suggests that male secondary sexual traits have little influence on the competition among males for territories, the principal mode of male-male competition in this species (Eckert and Weatherhead 1987a, b, c; Beletsky and Orians 1989; Shutler and Weatherhead 1991a, b, 1992). Thus, it is reasonable to assume that these traits may be important in attracting mates, and therefore appropriately used in investigating Hamilton and Zuk's (1982) parasite hypothesis of sexual selection.

Methods

General. We banded a large sample of males when they first began defending territories in the spring. We then collected behavioral information from those males over a period of several weeks prior to and into the start of the breeding season. We than attempted to recapture as many of those males as we could within a 10-day period to assay other secondary sexual traits, parasites and testosterone. The recapture period was limited to 10 days to avoid potential temporal biases in parasite prevalence or intensity (e.g. Weatherhead and Bennett 1991, 1992). During the recapture period we also captured unbanded territorial males to supplement our data (with the exception of behavioral variables). Unbanded males are much easier to catch than males with recent experience of our traps, mist nets and playbacks.

All males were territory owners and were at least 2 years old based on their plumage. Most males acquire territories in their 3rd year (D. Shutler and P.J. Weatherhead ms.) and approximately 70% of males acquiring territories retain them for only 1 or 2 years (Orians and Beletsky 1989; Weatherhead, unpubl.). Therefore, although the males we studied here were of unknown age, most would have been either 2 or 3 years old.

Male behavior. Data were collected in April and May, 1991, at field sites near the Queen's University Biological Station in eastern Ontario. All the males included in the study held territories either in one large marsh 25 km from the station or in small marshes along roadsides within 15 km of the large marsh. We began capturing and banding the males as soon as they began defending territories in early April. At the time of this initial capture we collected a blood smear (Bennett 1970) for assessment of haematozoa. We also captured and collected blood smears from some males in the study area that had been banded as part of studies done in previous

years (Shutler and Weatherhead 1991a; Metz and Weatherhead 1991). We released all males back on their territories immediately after banding them and then quantified their behavior over the next several weeks.

We measured three features of the males' behavior. Intrasexual aggression was measured by presenting each male with a stuffed male red-winged blackbird accompanied by a tape recording of the territorial singing of an unfamiliar male. All males received the same playback. We placed the model near the center of a male's territory sometime between 0600 and 0900 hours DST and then observed his response for 5 min. Observations were made from outside the territory at a distance of 30–50 m. We recorded the time taken for the male to first respond to the model, the time to the first contact with the model, the number of contacts, the time spent close to (0–2 m), intermediate (2–10 m), and distant from (>10 m) the model, the total number of flight displays with and without song, the total number of song spreads given by the male and the intensity of those song spreads. Song-spread intensity is a measure of the exposure of the epaulets and the associated body postures accompanying the song, and were scored on a four point scale following the method of Metz and Weatherhead (1991). We also presented each male with a female model (without any tape recording) following a similar procedure and recording the same response variables as recorded in the male model presentations. Although males perform many of the same behaviors in response to the two models, contacts with the male model appear to be attacks and contacts with the female model appear to be copulation attempts. Previous analyses have also shown substantial differences in the other responses of males to the two models (Eckert and Weatherhead 1987d).

To quantify song repertoire differences among males, we recorded individuals with Sony WM-D6C Professional Walkman cassette recorders and Audiotechnica AT815 directional microphones. All recordings were made during the 4 h following dawn or during the last hour before nightfall. During these times, most males sang in long, uninterrupted stretches; at other times, males sang only occasionally. Each male was recorded for at least 30 min on each of two different days. If a male did not sing regularly during either of these periods we made additional attempts to record him. In addition, males were recorded during the male and female model presentations.

Recordings were analysed using a Kay DSP sonagraph. Songs were categorized into song types by visual inspection of sound spectrograms. Songs were composed of two to seven brief (0.02–0.2 sec) introductory syllables with variable acoustic structure following by a long (0.4–0.8 sec) frequency modulated trill. Syllables were categorized into discrete types by visual inspection. Songs were considered the same type if all syllables were the same. In general, song types were highly stereotyped. Recognition of different renditions of the same song type was unambiguous because different song types were almost always composed of entirely different syllable types. Because different song types were so clearly identifiable based on major differences in syllable composition, we considered songs with either of two types of minor variation to be of the same type. The types of minor variation allowed within song types were (1) some variation in the length of the long trill that occurs at the end of all red-winged blackbird songs, and (2) presence or absence of a brief, faint syllable as the first syllable of some songs. The length of the terminal trill was somewhat variable for all song types, and no discrete differences in trill length were identifiable. Some songs began with a very short, faint syllable, and in some cases, this syllable was apparently not given.

To determine song repertoires, we analysed all songs from all recordings of each male. As has been reported for red-winged blackbirds elsewhere (Smith and Reid 1979; Yasukawa 1981), males sang in bouts where the same song type was repeated many times. We concluded that we had recorded the complete repertoire of a male if all recorded song types were repeated in different, independent bouts. We considered bouts independent if they were separated by bouts of different song types of if they were given on different days or different times (morning or evening) of the same day. If all but one song type was repeated independently, and most repeated several times, we considered it unlikely that the male had additional songs and so we assumed that we had also recorded the entire repertoire for these males. For other individuals we assumed that the recorded repertoire was a minimum estimate of the true repertoire.

Singing pattern, including how frequently song types are switched, as well as the song repertoire, can determine the apparent vocal versatility of a male, and might indicate male quality. Following Searcy and Yasukawa (1990), we calculated song type switching frequency as $X/c/(n\text{-}1)$, where X is the number of song switches in a sample and n is the number of songs in the sample. As discussed by Searcy and Yasukawa, this measure gives an index of song type switching that can be based on an entire sample of songs, and which is not confounded by singing rate. We calculated song type switching separately for each of the two or three samples for each male, and assigned the mean of these values to the male. Recordings made during model presentations were not used to determine song switching rates.

Male morphology. All the males that we used in the parasite analysis were recaptured (or captured, in the case of the unbanded males) between 10 and 20 May. Birds were caught early in the morning, transported to the biology station and then processed within 1–4 h. The birds were held in large outdoor aviaries while awaiting processing. We weighed each bird and measured the lengths of a wing and tarsus, and the length of the bill.

To quantify variation among males in the red portion of their epaulets we scored each male by holding an epaulet against standard colour chips (Smithe 1975) to find the best match. We measured the length of an epaulet as the distance from the bend in the wing to the furthest extent of the red feathers (Searcy 1979). We also measured the area of one of each male's epaulets by placing a piece of clear plexiglass over the exposed epaulet while the wing was held closed against the body. The small fringe of yellow feathers at the bottom of the epaulet was traced separately. Tracings were transferred to paper and the areas of red and yellow then calculated separately by computer.

Parasites. After completing the measurements of morphological features we collected a blood smear from each male. For the males that had been banded earlier for the collection of behavioral data this was the second blood smear collected. Unless otherwise specified, all analyses of haematozoa are from these second smears. Smears were air-dried and fixed in absolute ethanol prior to shipping to the International Reference Centre of Avian Haematozoa for quantification of blood parasites by GFB. All haematozoa were quantified by counting the number of parasites in 100 fields under oil at ×40 for leucocytozoids and ×100 for *Haemoproteus* and *Plasmodium*.

We collected ectoparasites by suspending each bird for 10 min in a jar containing cotton soaked in chloroform (Wheeler and Threlfall 1986). The top of the jar was covered by a rubber membrane with a slit large enough to allow a bird's head through. We held the bird's head and bill while its body was fumigated. All ectoparasites that dropped from a bird were examined and counted under a dissecting microscope. Following fumigation the birds were sacrificed and the skin around the eyes and cloaca was examined and any additional ectoparasites were counted.

Immediately thereafter we initiated the dissection. We first collected two 50-µl capillary tubes of blood directly from the heart. These tubes were then centrifuged sufficiently to achieve separation of the plasma and erythrocytes, the interface of the which was examined under a microscope for the presence of microfilaria. We subjectively scored the microfilaria infections on a scale of 1–4, with 4 being most heavily infected. We then dissected all the major organs (brain, heart lungs, gastro-intestinal tract, liver, gall bladder) and examined them microscopically for macroparasites (trematodes, cestodes, nematodes), which were counted individually. All dissections and identification of parasites was done by GFB. Specimens of mites that we collected were identified by H.H.J.

Nesbitt. We were unable to identify all parasites to species. However, all specimens have been retained at the International Centre for Avian Haematozoa. Hood and Welch (1980) have provided a detailed analysis of the parasites known to infect red-winged blackbirds at two other locations in their range.

Testosterone and testes. We collected blood for testosterone assays at the time we captured birds for processing. All samples were collected within 10 min of the birds being captured, a necessary condition to avoid testosterone levels being confounded by the stress of capture (Wingfield et al. 1982). We collected 100–200 µl of blood from a wing vein in 50 µl heparinized capillary tubes. These samples were immediately placed on ice and were centrifuged to separate the plasma within 3 h of collection. Once centrifuged, the samples were frozen in the original capillary tubes until they were analysed. We analysed total testosterone in the plasma by radioimmunoassay using a "Coat-a-Count" kit from Diagnostic Products Corporation. The calibration curve indicated that estimated testosterone values ≤ 3 ng/ml or ≥ 20 ng/ml had variances $>25\%$ and we therefore classified all estimated values in those ranges as 'low' or 'high', respectively. We used the actual values for all intermediate estimates. When the birds were dissected we removed the testes and recorded their total fresh weight to assess how variation in testes weight correlated with variation in testosterone levels and with the variation in the expression of secondary sexual traits and with infection by parasites.

Results

General

We collected behavioral data from an initial sample of 40 territorial males, 22 of which we were able to recapture for the parasite analysis. We supplemented those 22 birds with an additional 23 unbanded territorial males for which no behavioral data were collected. In subsequent analyses, minor deviations from these sample sizes are attributable to missing values for some individuals.

To simplify the behavioral data we first used principal components analysis (PCA). All variables were normalized by log transformation prior to analysis. We used the entire set of male model presentations ($n=40$) and female model presentations ($n=37$) in the respective PCAs and then used the factor scores from the first three factors for subsequent analyses. For the response to the male model the first three factors collectively explained 57% of the variation. Factor 1 had strong positive loadings of attack rate and time spent <2 m from the model, factor 2 had strong loadings of song spread intensity and the rate of flight displays, and factor 3 had strong loadings of song spread rate and intensity and moderate loading of time spent >10 m from the model. The first three factors from the analysis of responses to the female model explained 51% of the variation. Factor 1 was characterised by high rates of contact with the model, high intensity song spreads, and time spent close to the model. Factor 2 had moderate loadings of time spent 2–10 m from the model, song spread intensity and flight song rate. Factor 3 had moderate loadings of flight song rate and a negative loading of song spread rate.

As our measure of body size we used scores from the first axis of a PCA on tarsus length, bill length and wing length. Because body mass was not significantly correlated with this measure of body size ($r^2=0.032$, $P>0.30$), we used body mass as our index of condition. Body mass did not vary with the date a bird was captured ($r^2=0.014$, $P>0.50$), so it was not necessary to correct for capture date.

Table 1. Comparison of individuals receptured and those not recaptured with respect to body size, body mass (g), and epaulet length (mm)

	Recaptured	Not recaptured	t[a]	P
Body size[b]	-0.27 ± 0.75 (22)	0.42 ± 1.14 (18)	-2.34	0.026
Body mass[c]	$67.2\ \pm2.6$ (14)	$69.0\ \pm4.4$ (17)	-1.35	0.187
Epaulet – red	$38.0\ \pm2.5$ (14)	$38.4\ \pm2.5$ (18)	-0.45	0.658
Epaulet – total	$39.4\ \pm4.7$ (14)	$41.9\ \pm3.9$ (18)	-1.68	0.103

Values are means ± 1 SD (sample size in parentheses)
[a] Pooled variances t-test
[b] Scores along the first axis from a PCA on tarsus, bill and wing lengths
[c] Analysis based on measurements taken upon initial capture

Because we were only able to recapture approximately half of the birds we initially banded, it was important to assess whether our recaptured sample was biased. We compared the morphology, behavior and haematozoa status (based on blood smears taken when the birds were banded) of the recaptured birds with those birds we were unable to recapture. Recaptured birds were significantly smaller than those we failed to recapture, but did not differ in body weight or epaulet length (Table 1). The colour of neither the red nor the yellow portions of the epaulets of recaptured birds differed from those of birds we did not recapture (Mann-Whitney U-tests, both Ps $>$ 0.22). We used multiple analysis of variance to compare the scores from the first three factors of the PCA analyses of the male and female model presentations. Males that we recaptured did not differ significantly from those we did not recapture ($F=0.888$, $df=6,30$, $P=0.516$). In the blood smears taken when the birds were banded we found four types of haematozoa (leucocytozoids, *Haemoproteus*, *Plasmodium*, and microfilaria). Fisher exact tests showed no significant differences in the prevalence of infections between recaptured and unrecaptured males for any of the four parasites (all Ps >0.44). Overall, therefore, the males we recaptured differed little from those we did not recapture, particularly with respect to the traits of interest in this study.

The parasites

We collected a diverse array of parasites from the 45 males that we screened (Table 2). The ectoparasites included both lice (Mallophaga) and mites (Acarina). Mites were only detected by the fumigation technique. Specimens of these mites were identified as *Dermanyssus* sp., a common genus of avian blood-feeding mites. We obtained lice both by fumigation and by visual examination of the skin around the ears (but not the cloaca).

Table 2. Summary of the parasites found on the 45 individuals for which complete parasite data were available

	No. birds infected	Percent infected	Intensity[a]			
			Mean	SD	Median	Range
Ectoparasites:						
Lice (jar)	45	100.0	17.0	15.8	8	2–67
Lice (ear)	33	73.3	7.1	11.7	3	0–65
Mites	20	44.4	1.5	2.6	0	0–10
Total	45	100.0	18.6	16.3	12	2–67
Protozoa:						
Haemoproteus	5	11.1	2.9	15.0	0	0–100
Leucocytozoon	23	51.1	12.0	23.4	1	0–100
Plasmodium	17	37.8	47.8	97.2	0	0–470
Total	32	71.1	62.6	97.4	21	0–485
Microfilaria:						
Smear	12	26.7	0.49	0.94	0	0–3
Tube	14	31.1	0.76	1.37	0	0–5
Other:						
Tapeworms	14	31.1	3.1	6.7	0	0–30
Flukes (gut)	10	22.2	1.5	4.5	0	0–25
Flukes (gall bladder)	18	40.0	0.9	1.3	0	0–4

[a] See Methods for details of different collection and quantification techniques

Fumigation produced lice from every individual, while by visual examination we only detected lice on 73% of the birds. By Spearman rank correlation, the intensities of lice infections determined by the two techniques were not significantly correlated ($r_s = 0.07$, $P > 0.50$). Therefore, we only used the measures determined by fumigation in subsequent analyses.

In the blood we found *Haemoproteus quiscalus*, a protozoan parasite transmitted by ornithophilic ceratopogonid midges. *Haemoproteus* have a 10–14 day sexual cycle in the fly, a 2-week prepatent (first asexual cycle) period in the host bird, followed by somewhat shorter asexual cycles (Garnham 1966). Also in the blood were *Leucocytozoon* spp., most often *L. icteris* (erroneously cited as *L. fringillinarum* by Weatherhead and Bennett 1991). *Leucocytozoon* are protozoans that are transmitted by ornithophilic blackflies (Simulidae). They have a 5–7 day sporogonic cycle in the backfly and a 5–7 day asexual cycle in the birds (Garnham 1966). The third protozoan parasite in the blood was *Plasmodium vaughani*, which is reproductively similar to *Haemoproteus* described above, but is transmitted to the birds by mosquitoes. Finally, we found microfilaria in both the blood smears and in the capillary tubes of blood collected and centrifuged specifically for this purpose. The microfilaria were principally the embryos of the nematode *Eufilaria hibleri*, although a few *Splendidofilaria quiscali* were also present, the former transmitted to the birds by ceratopogonid midges and the latter by blackflies. The microfilaria are picked up by the flies from infected birds and after 10–12 days new birds can be infected when the fly feeds again. Once back in the avian host the adult filarid worm matures in 6–12 months, producing at best a single generation per year.

For the purposes of analysis we have combined the data for the two species of microfilaria. The capillary tube method identified 14 of the 45 birds as infected with microfilaria, 12 of which (86%) were also detected by blood smears. This agreement between the two techniques is much higher than that (45%) reported by Kirkpatrick et al. (1991). Because of its greater sensitivity, we used the data from the capillary tube method in subsequent analyses.

Although we detected some microfilaria of *S. quiscali*, we did not find any adults in the birds' brains, the tissue in which the adult resides. We did find adult filarid worms in the body cavity of a single bird. These were probably *Diplotraenia bargusinica*, a worm that infects a variety of invertebrate hosts and enters a bird when the invertebrate is eaten. Given that only a single bird was infected, we have excluded this parasite from further analysis.

We found trematodes in both the hind gut and in the gall bladder. the former were *Plagiorchis* sp. (probably *nobeli*) and the latter were *Conspicuum* sp. (probably *icteridorum*). Both types of trematodes infect snails as their first intermediate hosts and odonates as their second intermediate hosts. The life cycle of these parasites through the three hosts probably requires at least 1 year. We also found cestodes (probably *Ananchotaenia* sp.) in the intestines of some birds. The sexual stage of these tapeworms occurs in the birds, with asexual stages in invertebrates. These parasites also have a 1-year life cycle.

We failed to detect any parasites in the brains, lungs, hearts or livers of any of the birds we examined.

Associations among parasites

To determine whether the different parasites we found infect the birds independently of one another, we per-

Table 3. Tests of association among parasites within birds

	Lice[a]	Mites	*Haemoproteus*	*Leucocytozoon*	*Plasmodium*	Microfilaria	Tapeworm	Fluke (gut)
Lice	–							
Mites	0.04	–						
Haemoproteus	0.22	−0.16	–					
		0.36						
Leucocytozoon	0.06	−0.26	0.13	–				
		0.02 (−)	0.35	–				
Plasmodium	0.15	−0.11	0.09	−0.02	–			
		0.37	0.35	1.00	–			
Microfilaria	0.15	−0.15	−0.12	−0.10	0.03	–		
		0.20	1.00	1.00	0.74	–		
Tapeworm	0.11	0.11	−0.08	−0.08	0.07	−0.14	–	
		0.75	1.00	0.53	0.74	0.49	–	
Fluke (gut)	0.16	−0.29	0.15	−0.11	0.23	0.46[b]	−0.13	–
		0.03(−)	0.31	1.00	0.14	0.005(+)	0.47	–
Fluke	−0.01	−0.02	−0.28	−0.12	0.10	0.13	−0.13	−0.07
(gall bladder)		1.00	0.07	1.00	0.54	0.51	0.20	1.00

Upper values are correlation coefficients from Spearman rank correlations of infection intensities. Lower values are probabilities from 2-way Fisher exact tests of infection prevalence. Symbols in parentheses following probabilities indicate whether significant associations are positive or negative

[a] Because lice occurred on all birds, no tests of prevalence could be done.
[b] $P<0.01$

Table 4. Comparison of parasitized and unparasitized individuals with respect to mean (±1 SD) body size based on PC1 scores; sample sizes in parentheses

Parasite	Parasitized	Unparasitized	t[a]	P
Mites	−0.05±0.85 (20)	−0.26±0.94 (25)	0.78	0.441
Haemoproteus	−0.26±1.03 (5)	−0.16±0.90 (40)	−0.25	0.807
Leucocytozoon	−0.06±0.82 (23)	−0.29±0.98 (22)	0.90	0.374
Plasmodium	−0.11±0.81 (17)	−0.21±0.96 (28)	0.35	0.731
Microfilaria	−0.11±1.00 (14)	−0.20±0.87 (31)	0.31	0.757
Tapeworm	−0.28±0.78 (14)	−0.12±0.96 (31)	−0.55	0.585
Fluke (gut)	−0.57±0.91 (10)	−0.05±0.88 (35)	−1.62	0.113
Fluke (gall bladder)	−0.09±0.96 (18)	−0.22±0.87 (27)	0.45	0.658

[a] Pooled variance *t*-test

formed pairwise Spearman rank correlations of infection intensities and Fisher exact tests of infection prevalences for all the parasites (Table 3). Overall, there were few significant associations among parasites. Microfilaria were positively associated with gut flukes, both by prevalence and intensity. In addition, we found some evidence that the two types of ectoparasites were associated with other parasites. In pairwise analyses, mite prevalence was negatively associated with the prevalence of both *Leucocytozoa* and gut flukes. Also, 6 out of 7 correlation coefficients between mites and internal parasites were negative, suggesting that mites may be more likely to infect birds that are otherwise healthy. By contrast, 6 out of 7 correlation coefficients between lice intensities and those of the internal parasites were positive. This result suggests that lice infections were heavier on birds that were also infected by other parasites. In spite of these different patterns for lice and mites, however, the correlation between these two ectoparasites was very weak. Because we found no evidence of strong associations among most of the parasites, we treat all the parasites independently in subsequent analyses. We also calculated the total number of parasite taxa with which each bird was infected (maximum = 9). Because all birds were infected with lice, all values were ≥1. Thus, as with lice, we analysed total parasites as a continuous variable.

Parasites and secondary sexual traits

Male morphology. The mean body size of infected birds did not differ significantly from that of uninfected birds for any of the parasites for which there were both classes of birds (Table 4). In addition, the intensity of lice infections was not significantly correlated with body size ($r_s = -0.01$, $P>0.50$), nor were the total parasite scores ($r_s = 0.15$, $P>0.20$). Similarly, body mass did not differ significantly between infected and uninfected males (Table 5), nor was body mass significantly correlated with the intensity of lice infections ($r_s = -0.003$, $P>0.50$) or with total parasite scores ($r_s = 0.11$, $P>0.20$). Thus, if any

Table 5. Comparison of parasitized and unparasitized individuals with respect to mean (±1 SD) body mass (g); sample sizes in parentheses

Parasite	Parasitized	Unparasitized	t[a]	P
Mites	65.6±3.0 (20)	64.4±3.3 (25)	1.29	0.205
Haemoproteus	65.3±4.1 (5)	64.9±3.1 (40)	0.29	0.771
Leucocytozoon	64.8±3.6 (23)	65.0±2.8 (22)	−0.29	0.771
Plasmodium	66.0±3.0 (17)	64.3±3.2 (28)	1.80	0.079
Microfilaria	64.3±2.9 (14)	65.2±3.3 (31)	−0.82	0.417
Tapeworm	65.8±2.5 (14)	64.5±3.4 (31)	1.21	0.234
Fluke (gut)	63.3±3.0 (10)	65.4±3.1 (35)	−1.86	0.070
Fluke (gall bladder)	64.4±3.9 (18)	65.3±2.6 (27)	−0.95	0.347

[a] Pooled variance *t*-test

of these parasites affect the birds' health, it was not reflected in the infected individuals being in poorer condition.

From the tracing of the epaulets we calculated the area of the red feathers and the total epaulet area (red plus yellow). Mean values of these two measures did not differ significantly between infected and uninfected birds, for any of the parasites for which some birds were uninfected (pooled variance *t*-tests, all $Ps > 0.05$). Similarly, neither the intensity of lice infections nor total parasite scores were significantly correlated with either measure of epaulet area (Spearman rank correlations, all $Ps > 0.50$).

In previous studies of sexual selection in red-winged blackbirds we have used epaulet length rather than area as our measure of epaulet size (e.g. Eckert and Weatherhead 1987b; Weatherhead 1990; Metz and Weatherhead 1991). This is due in part to convenience (it is easily measured in the field), and because, earlier, Searcy (1979) had shown that epaulet length was correlated with dominance in red-winged blackbirds. Furthermore, males rarely if ever display their entire epaulet, whereas length would be apparent in any display, so length is potentially a more meaningful measure than area. Epaulet length was not significantly correlated with either the area of red or total epaulet area ($r^2 = 0.06$ for both analyses). Comparisons of parasitized and unparasitized birds revealed that individuals parasitized by mites had significantly longer epaulets than birds without mites, while the opposite pattern occurred for microfilaria (Table 6). Correlations between epaulet length and both the intensity of lice infections and total parasite scores were not significant ($r_s = -0.23$ and -0.01, respectively, both $Ps > 0.10$).

The color of the red portion of the epaulets varied from "spectrum orange" to "scarlet" on Smithe's (1975) colour chart, with five discernable intermediates (for more details of these colours, see Metz and Weatherhead 1991). By Mann-Whitney *U*-tests, the mean scores of infected individuals did not differ significantly from those of uninfected individuals for any of the parasites (all $Ps > 0.10$). Similarly, the colour of red was not significantly correlated with either the intensity of lice infections ($r_s = 0.17$, $P > 0.20$) or with total parasite scores ($r_s = -0.11$, $P > 0.20$). The colour of the yellow portion of the epaulet varied from "pale horn colour" to "burnt orange" on Smithe's colour charts, with six discernible intermediates. Variation in the colour was not significantly associated with any of the parasites, although males infected with gall bladder flukes tended to have feathers that were duller yellow (Mann-Whitney *U*-test, $P = 0.06$).

Male behaviour. We used multiple analyses of variance (MANOVA) to determine whether infected and uninfected males differed significantly in their response to the male and female models. Male response was defined by the first three axes of the PCAs for male and female model presentations, respectively. Although the PCAs were developed from all the model presentations (see above), the MANOVAs could only be done using the 21 birds that we recaptured for which we had done presentations of both male and female models. None of these analyses indicated an association between parasites and behaviour (Table 7). For lice and total parasite scores we used Spearman rank correlations with each of the six behaviour variables. None of these correlations was significant at $P < 0.10$.

Males in the recaptured sample sang between three and seven song types. Mean repertoire sizes did not differ between parasitized and unparasitized males for

Table 6. Comparison of parasitized and unparasitized individuals with respect to mean (±1 SD) epaulet length (mm); sample sizes in parentheses

Parasite	Parasitized	Unparasitized	t[a]	P
Mites	43.3±2.1 (20)	41.8±2.5 (25)	2.13	0.039
Haemoproteus	42.0±2.4 (5)	42.5±2.5 (40)	−0.45	0.653
Leucocytozoon	42.6±2.5 (23)	42.3±2.4 (22)	0.42	0.676
Plasmodium	42.2±2.3 (17)	42.6±2.6 (28)	−0.56	0.582
Microfilaria	41.1±2.5 (14)	43.1±2.2 (31)	−2.63	0.012
Tapeworm	42.6±2.8 (14)	42.4±2.3 (31)	0.22	0.824
Fluke (gut)	41.3±2.7 (10)	42.8±2.3 (35)	−1.66	0.103
Fluke (gall bladder)	42.6±2.4 (18)	42.3±2.5 (27)	0.41	0.683

[a] Pooled variance *t*-test

Table 7. MANOVAs to determine whether parasitized and unparasitized individuals are significantly differentiated in the six-dimensional space defined by the behavior variables (scores from the first three factors of the PCA's for male and female model presentations)

Parasite	Wilk's Lambda	F approximation	df	P
Mites	0.823	0.503	6, 14	0.796
Haemoproteus	0.839	0.446	6, 14	0.836
Leucocytozoon	0.861	0.377	6, 14	0.882
Plasmodium	0.645	1.283	6, 14	0.326
Microfilaria	0.818	0.520	6, 14	0.784
Tapeworm	0.564	1.801	6, 14	0.171
Fluke (gut)	0.992	0.020	6, 14	1.000
Fluke (gall bladder)	0.566	1.789	6, 14	0.173

For each analysis sample size = 21

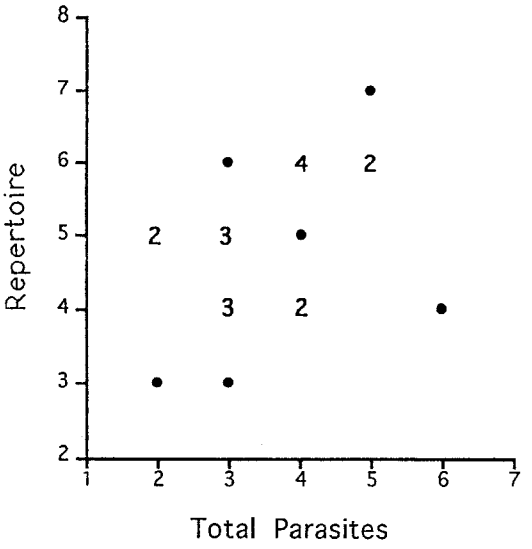

Fig. 1. Repertoire size relative to the number of parasite taxa with which the male was infected. *Numbers* indicate points where more than one male had the same values

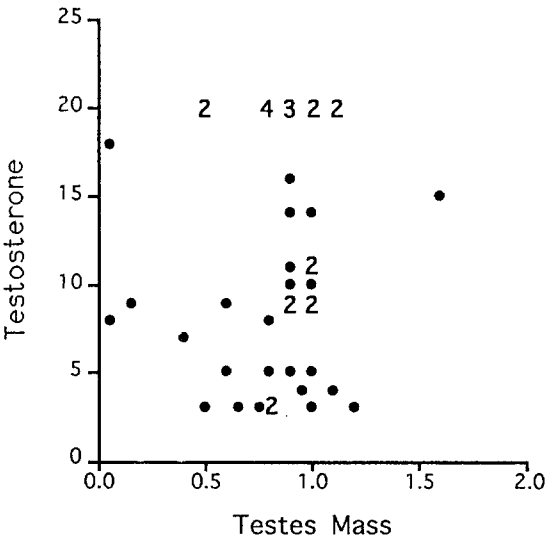

Fig. 2. Testosterone levels (ng/ml) vs. testes mass (mg; both testes combined). *Numbers* indicate points where more than one male had the same values

any of the parasites for which some males were uninfected (t-tests, all $Ps > 0.10$). Repertoire size was also not significantly correlated with the intensity of lice infections ($r_s = 0.18$, $P > 0.20$). However, males that sang more song types were infected with more types of parasites ($r_s = 0.45$, $P < 0.05$, Fig. 1). The rates at which males switched between songs did not differ between between parasitized and unparasitized males (*t*-tests, all $Ps > 0.20$), and were not significantly correlated with either the intensity of lice infections ($r_s = 0.04$, $P > 0.50$) or total parasite scores ($r_s = -0.07$, $P < 0.50$).

Testes, testosterone, parasites and secondary sexual traits

Of the 45 males we assayed for testosterone, 6 were scored as "low" (levels less than 3 ng/ml) and 5 as "high" (>20 ng/ml). For the purposes of analyses we assigned these males values of 3 and 20, respectively. The mean for males with intermediate levels was 6.6 ng/ml, which is slightly higher than the mean of approximately 4 ng/ml reported by Beletsky and Orians (1989) for territorial male red-winged blackbirds in Washington State, that were also sampled early in the nesting season. Testes weights also varied substantially, with three males having extremely small testes. Testosterone and testes weight were not significantly correlated ($r_s = 0.10$, $P > 0.20$), and the three males with very small testes all had intermediate testosterone levels (Fig. 2).

Neither testosterone or testes size was significantly correlated with body size ($r_s = 0.14$ and 0.22, respectively, both $Ps > 0.10$). Males in better condition (i.e. greater body mass) did not have higher testosterone levels ($r_s = 0.163$, $P > 0.20$) but they did have heavier testes ($r_s = 0.35$, $P < 0.05$). Neither testosterone nor testes size was significantly correlated with the area of the red portion of the epaulet ($r_s = 0.06$ and -0.02, respectively, both $Ps > 0.05$), but birds with longer epaulets had higher levels of testosterone ($r_s = 0.36$, $P < 0.02$, Fig. 3) but not larger testes ($r_s = -0.04$, $P > 0.50$). Testosterone was not significantly correlated with the colour of the red ($r_s = -0.27$, $P > 0.10$) or yellow ($r_s = -0.10$, $P > 0.50$) portions of the epaulet. The same was true of testes size ($r_s = -0.06$ and -0.01, respectively, both $Ps > 0.50$).

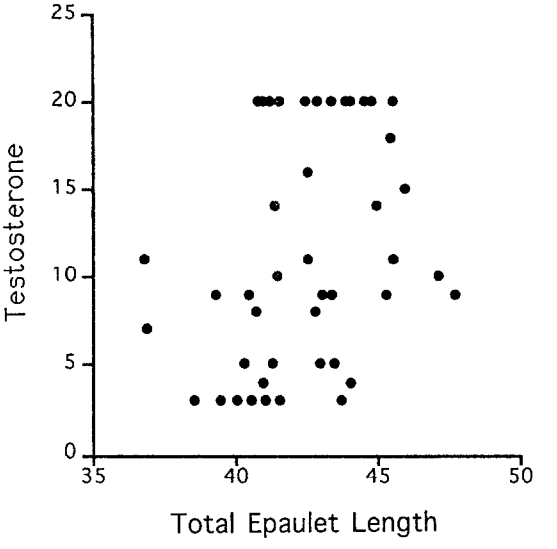

Fig. 3. Testosterone (ng/ml) vs. epaulet length

Testosterone levels were not significantly correlated with any of the behaviors we quantified for the 22 males we recaptured. These include response to the male model ($r_s = 0.16$, 0.24 and -0.10 for scores from PC 1, 2 and 3, respectively, all $Ps > 0.10$) and female model ($r_s = 0.17$, -0.15 and -0.10 for scores from PC 1, 2 and 3, respectively, all $Ps > 0.10$), song repertoire size ($r_s = 0.15$, $P > 0.50$) and song switching rate ($r_s = 0.11$, $P > 0.50$). Similarly, testes size was not correlated with any of these behaviors: response to the male model ($r_s = -0.05$, -0.14 and 0.28 for scores from PC 1, 2 and 3, respec-

Table 8. Comparison of parasitized and unparasitized individuals with respect to mean (±1 SD) testosterone level (ng/ml); sample sizes in parentheses

Parasite	Parasitized	Unparasitized	t[a]	P
Mites	14.8±6.3 (20)	8.8±5.6 (25)	3.39	0.002
Haemoproteus	9.2±5.6 (5)	11.8±6.7 (40)	−0.82	0.420
Leucocytozoon	12.1±6.5 (23)	10.8±6.7 (22)	0.69	0.495
Plasmodium	9.2±5.5 (17)	12.9±6.9 (28)	−1.87	0.068
Microfilaria	11.1±6.7 (14)	11.6±6.6 (31)	−0.27	0.790
Tapeworm	11.7±6.9 (14)	11.4±6.5 (31)	0.17	0.867
Fluke (gut)	9.9±5.6 (10)	11.9±6.8 (35)	−0.85	0.399
Fluke (gall bladder)	11.1±6.7 (18)	11.7±6.6 (27)	−0.29	0.771

[a] Pooled variance *t*-test

tively, all $Ps > 0.10$); response to the female model ($r_s = 0.16$, -0.23 and 0.03 for scores from PC 1, 2 and 3, respectively, all $Ps > 0.10$); song repertoire size ($r_s = 0.03$, $P > 0.50$); song switching rate ($r_s = 0.43$, $P > 0.05$).

To assess the relationship between both testosterone and testes size and parasites, we first compared the mean values of testosterone and testes size of parasitized and unparasitized birds. Males parasitized with mites had significantly higher testosterone than unparasitized males (Table 8). There was also a tendency for males infected with *Plasmodium* to have lower levels of testosterone, but there was no relationship between parasite prevalence and testosterone for the other parasites (Table 8). For all the other parasites for which some males were not infected, there were no significant differences in testes size between infected and uninfected individuals (Pooled variance *t*-tests, all $Ps > 0.25$). Testosterone was not significantly correlated with the intensity of lice infections ($r_s = -0.12$, $P > 0.20$) or with total parasite scores ($r_s = 0.03$, $P > 0.50$). Testes size also was not significantly correlated with either the intensity of lice infections ($r_s = -0.22$, $P > 0.10$) or with total parasite scores ($r_s = -0.03$, $P > 0.50$).

Discussion

As more attention has been focussed on the Hamilton and Zuk (1982) hypothesis, it has become increasingly apparent that the hypothesis is very difficult of falsify, particularly by correlational approaches (Read 1990; Burley et al. 1991). For example, failure to find a correlation between a particular parasite and a particular secondary sexual trait could simply mean that the wrong parasite or the wrong trait was studied (Clayton 1991). One way to assess whether this potential problem is indeed serious is to undertake as comprehensive a survey of parasites and secondary sexual traits as is feasible in a single study. This approach also has the advantage of allowing one to test the hypothesis that parasites with generation times more similar to that of the host are better candidates for the coevolutionary relationship proposed by Hamilton and Zuk than are taxa with much shorter generation times (Balmford and Read 1991). Although we did not include parasites such as microorganisms in our study, we did nonetheless survey a broader spectrum of parasites than has been attempted to date in tests of the Hamilton and Zuk hypothesis. We also quantified most of the features of the males' behavior and morphology that seem likely to constitute secondary sexual traits. Another novel feature of our study involved assaying testosterone of the males scored for secondary sexual traits and parasites. This allowed us to test the recently proposed hypothesis that the high levels of testosterone required to produce secondary sexual traits compromise the immune system resulting in a relationship between testosterone, secondary sexual traits and parasite infections (Zuk 1990; Folstad and Karter 1992). Finally, we also determined whether different taxa of parasites show any evidence of association within hosts, such that infection with one species of parasite might render a host more or less vulnerable to infection with another species of parasite.

Collectively, the results of our study provided only limited support for the hypotheses we tested. Because we found so little evidence of significant associations between any of the parasites and secondary sexual traits (particularly given the number of combinations of variables we analysed), we could not test the hypothesis regarding which parasites should be more likely to be correlated with the secondary sexual traits. We did find that males with the largest song repertoires were infected with the most types of parasites. The most parsimonious explanation for this result, however, is that the males with the largest repertoires may have been the oldest (Yasukawa 1981), and had simply been exposed to parasites longer. Previously, Weatherhead and Bennett (1991) had reported that haematozoa infections became more prevalent in older male red-winged blackbirds, at least over the first 2 years of life.

A negative result that was particularly surprising was the lack of the association between male behavior and parasite infections. In a previous study of the same population, Weatherhead (1990) found that males infected with haematozoa were less aggressive toward a male model and courted a female model less vigorously. We used very similar methods in this study, including a much more comprehensive survey of parasites, but found no association between parasites and behavior. The smaller sample of males in this study may have contributed to the different outcome, although the patterns we found were not close to being statistically significant. The data in Weatherhead's (1990) study were collected over several years, whereas this study was purposely conducted over a short period in a single year. If weather conditions, for example, were not stressful to the birds during the period of our study, the birds' behavior may not have been influenced by parasites. However, since we conducted the study at the time females were choosing mates, females presumably would have shared our difficulty in assessing the parasite status of males from their behavior (or any other trait). For parasites to play an important role in mate choice and

sexual selection, their effect on males must be reliably detected by females.

Testosterone proved to be a very poor predictor of either male secondary sexual traits or of parasite prevalence. It seems unlikely that this result is an artifact of our methods. We caught males by using a simulated territorial intrusion to bring birds into traps or nets and then collected blood samples for analysis within minutes of capturing the bird. Previous research has shown that challenging a male red-winged blackbird with a decoy male does not cause an increase in testosterone (Harding and Follett 1979), a pattern that may be generally true of males of polygynous species (Wingfield et al. 1990). The stress of handling the birds is unlikely to have influenced testosterone levels, given the short handling duration (Wingfield et al. 1982). The lack of correlation between testosterone and male secondary sexual traits may not be unexpected. Although the causal link between testosterone and the development of secondary sexual traits and male sexual behavior are well established, the relationship is not always straightforward (Wingfield et al. 1990). For example, some male birds can exhibit normal sexual behavior even after castration (Moore and Kranz 1983). In the case of immunosuppression, however, we expected a more straightforward relationship between testosterone and parasites. If testosterone does compromise the immune system of male red-winged blackbirds, then either the males with the highest testosterone should have had more parasites (i.e. they were trading off reproductive performance against immunity from parasites) or fewer parasites (i.e. only resistant males could afford to elevate their testosterone). Overall, however, we found little association, either positive or negative, between most parasites and testosterone. Therefore, our results do not provide broad support for the immunocompetence handicap hypothesis (Folstad and Karter 1992).

One of our objectives was to determine whether different taxa of parasites infected hosts independently of one another. Understanding the interactions among parasites that infect the same birds is not only important to research on the role of parasites in sexual selection, but is also fundamental to understanding the community ecology of the parasites themselves. We found that gut flukes were strongly positively associated with microfilaria and weakly negatively associated with mites. Mites were also weakly negatively associated with leucocytozoans and in general appeared to occur most commonly on birds uninfected by other parasites. These results suggest that more detailed investigations of associations among parasites would be worthwhile. Although we sampled parasites from 45 birds, the prevalence of most parasites was less than 50%. Detecting subtle associations among parasites with these samples would not have been possible.

Although the majority of our results were negative, we did obtain several significant results with mites. In addition to the associations with other parasites discussed above, we also found that males infected with mites had longer epaulets, a trait associated with dominance in males (Searcy 1979; Eckert and Weatherhead 1987b). Furthermore, males infected with mites had higher levels of testosterone, also a correlate of dominance in male birds (Wingfield et al. 1990). These results suggest that mites and testosterone could be interacting in accordance with the immunocompetence handicap hypothesis. On the negative side, we did not find any association between mites and male sexual or aggressive behavior. However, in light of the other results, more extensive sampling of male behavior relative to mite infections seems warranted. This suggestion is given further impetus by Møller's (1991, 1992) studies on the interaction between ectoparasitic mites and barn swallows (*Hirundo rustica*). Among other things, he has shown an association between mite infections and the length and symmetry of the males' tails and between those features of males' tails and male mating success. Further research will be required to determine whether a similar relationship exists between mites, epaulets and male mating success in red-winged blackbirds.

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