Sexual selection and the evolution of bird song: A test of the Hamilton-Zuk hypothesis

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Summary. Hamilton and Zuk (1982) suggested that secondary sexual characters evolve because they allow females to assess a potential mate's ability to resist parasites. A prediction of this theory is that the degree of elaboration of secondary sexual characters should be positively correlated with parasite load across species. In support of their hypothesis, Hamilton and Zuk reported a correlation across North American passerine species between haematozoa prevalence and both brightness and song "complexity and variety", scored on a subjective six point scale. Here we show that this relationship is confounded by phylogenetic associations. We use quantitative data on song duration, inter-song interval, song continuity, song rate, song versatility, and song and syllable repertoire size for 131 species of European and North American passerines to test the Hamilton-Zuk hypothesis. Across species, there are significant *negative* relationships between haematozoa prevalence and song continuity, contrary to the direction predicted by Hamilton and Zuk. In accordance with their prediction, there is a positive correlation with song versatility. However, these relationships come about through taxonomic associations: within taxa there are no consistent relationships between any of the song variables and haematozoa prevalence. None of the other song variables correlate with haematozoa prevalence. We conclude that there is no evidence of an association between song elaboration and parasites.

Introduction

Darwin (1871) suggested that apparently deleterious secondary sexual characters, such as the bright

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colours and elaborate ornaments of many animals and the complex songs of birds, evolved as a result of sexual selection through female choice. Today, this view has considerable empirical and theoretical support, but the question of why such preferences should evolve is contentious (Bradbury and Andersson 1987; Kirkpatrick 1987). One answer, proposed by Hamilton and Zuk (1982), is that females use a male's secondary sexual characters to assess his ability to resist parasites exploiting the host population at the time. By mating with such males, females obtain resistance genes for their offspring. Hamilton and Zuk envisaged a never-ending coevolution between host and parasite genotypes, so that female preferences and male secondary sexual characters are maintained in the host population by the continuing need to assess which males have genotypes currently conferring resistance. Parasites are broadly defined to include parasitic viruses, bacteria, protozoans, helminths and arthropods.

Hamilton and Zuk (1982) predicted that in species that are more vulnerable to parasite invasion, sexual selection should favour greater development of characters that allow females to judge a male's past and present parasite load, and therefore that sexual showiness should correlate positively with parasite burden across species. In support of their hypothesis, Hamilton and Zuk (1982) reported that, across 109 species of North American passerines, species with higher haematozoa prevalences tended to be brighter and to have more variable and complex songs.

However, a major problem with interspecific comparisons of this kind is the problem of statistical non-independence of species points. This arises where species share characteristics, not through convergent evolution, but because of shared ancestry (Harvey and Mace 1982; Ridley 1983; Pagel and Harvey 1988). For example, an interspecific association between parasite prevalence and the

elaboration of secondary sexual characters might be found. But imagine that the life history of a particularly species-rich taxon in the sample predisposes members of the taxon to infection by parasites. If, for some unrelated reason, the members of that taxon also have particularly elaborate secondary sexual characters, then an association between parasites and the character may be found across all species in the analysis: the difference between the parasite loads and elaborate characters of species within that taxon and all the other species in the analysis could, on its own, account for the association. If so, then any unique feature of that taxon could in principle explain the association between the trait and parasites, and the Hamilton-Zuk hypothesis need not be invoked.

Recent comparative analyses of passerine colour (Hamilton and Zuk 1982; Read 1987) have provided equivocal support for the hypothesis, in part because of problems with phylogenetic associations (Read and Harvey 1989; Read, in press). Zuk (in press) demonstrates a relationship between colour and haematozoa prevalence across 500 species of Neotropical birds when phylogenetic associations are controlled for, but she was unable to control for any ecological factors that might independently covary with colour and parasite load and explain the reported correlation.

Here we test Hamilton and Zuk's prediction that passerine species with higher parasite loads will have showier songs: first, by reanalysing the subjective rankings of song "variety and complexity" used by Hamilton and Zuk in their analysis (1982), here controlling for phylogenetic associations, and second, by using quantitative measures of song showiness gathered from the literature.

Comparative analyses of song diversity

There are several potential difficulties with interspecific analyses of song diversity. First, it is well-known that songs of closely related species are more similar than those of more distantly related species; indeed, song characteristics can be useful for phylogenetic reconstruction (Payne 1986). There is thus a very real possibility that taxonomic associations could produce (or obscure) any trends. Second, there is the 'comparability problem' (Krebs and Kroodsma 1980; Kroodsma 1982), where the degree of elaboration of song complexity and variety may be difficult to determine for different types of song. For example, "the discrete songs of many discontinuous songsters are quite different from the ramblings of many continuous singers" (Kroodsma 1982, p. 141) yet they

may both be examples of sexual elaboration through female choice. Three approaches have been used previously in an attempt to overcome these problems. Hartshorne (1973) and Hamilton and Zuk (1982) used an intuitive notion of what constitutes an elaborate song to arrive at subjective estimates of song complexity and showiness; Harvey et al. (in press) discuss the difficulties of reconciling the two sets of scores. Using quantitative measures, Weary and Lemon (1988) compared only close relatives, on the assumption that the songs of closely related species are more likely to have been elaborated in similar ways. Kroodsma (1982) suggests that it may be possible to combine different measures of complexity and variety into a summary statistic. In our analyses below we use all three approaches.

A third potential difficulty is that of the confounding effect of habitat. An association between habitat and song characteristics has been noted across and within species by several authors and attributed to differences in the sound transmission properties of forested and open habitat (reviewed by Krebs and Davies 1987). There are also likely to be consistent differences in parasite burdens associated with habitat, especially where the parasites are vector-borne.

A further problem facing any interspecific analysis of song as a test of the Hamilton-Zuk hypothesis is choosing the appropriate way of quantifying song showiness and in predicting the directions in which parasite prevalence and the song variables should covary. Several intraspecific studies have presented either correlational or experimental evidence that suggests that song rate (number of songs per unit time), song continuity (proportion of time spent singing), song versatility (the extent to which the same song type is sequential repeated), and song and/or syllable repertoire size are involved in female choice (eg. Kroodsma 1977; Payne and Payne 1977; Baker et al. 1986; Gottlander 1987; Catchpole 1987; Radesäter et al. 1987; Searcy 1988). However, these features of song are only relevant to this analysis if the more extreme values are more costly to produce. The Hamilton-Zuk hypothesis assumes that secondary sexual characters are handicaps (Zahavi 1975), which reduce a male's survival chances but act as a mating signal by advertising genetic resistance (Maynard Smith 1985). For traits to act as honest indicators of genetic quality, they have to be costly to produce or maintain (Kodric-Brown and Brown 1984). Unfortunately, there are little direct data on the costs of producing, or developing the ability to produce, different types of bird song. Here, we

extrapolate from the results of several anuran studies (reviewed by Halliday 1987 and Ryan 1988) and assume that producing longer songs is more expensive than producing shorter songs, and that more continuous singing is more expensive than less continuous singing. Several avian studies provide circumstantial evidence that song output (both song rate and song continuity) is energy limited (reviewed in Reid 1987; Cuthill and MacDonald, in press); Searcy (1979), for example, found a positive association between body condition and song rate in red-winged blackbirds (*Agelaius phoeniceus*). Similarly, song complexity and variety can only honestly advertise genetic quality if more complex and variable songs are more expensive to produce. For the purposes of testing the parasite hypothesis we assume this to be true. We know of no direct evidence that bears on this assumption, but the finding that the ability to sing complex songs is associated with more neurones and greater synaptic and dendritic development in the forebrain nuclei involved in song control (Nottebohm et al. 1981, 1986; Canady et al. 1984) suggests that there is a cost to producing and using the necessary neuronal apparatus.

From these assumptions, then, we follow Hamilton and Zuk's (1982) conclusion that their hypothesis predicts that species with higher parasite prevalences should sing more and/or have more complex and variable songs (species "with most evident sexual selection are most subject to attack by debilitating parasites"; Hamilton and Zuk 1982, p. 385). Hamilton and Zuk's comparative prediction was explicitly one-tailed because they argued that continuous antagonistic coevolution between host and parasite is never ending, so that species vulnerability to parasite attack is unaffected by female choice for parasite resistance. However, a negative association could be viewed as supporting evidence if the hypothesis was only slightly modified: female choice for characters that reveal genetic resistance might lead to an increase in the proportion of resistant individuals in a population and consequently to a decrease in species vulnerability (Borgia 1986; Read, in press). We concentrate on the direction originally predicted, and report one-tailed *P*-values, but in any case the conclusions are the same if two-tailed *P*-values are employed.

Methods

Data sources

The subjective song scores used by Hamilton and Zuk (1982) were available for 113 species of North American passerine (Hamilton and Zuk, unpublished). Quantitative song data on European and North American passerines were gathered from the literature and are given elsewhere (Read and Weary, in preparation). Major sources were Dobson and Lemon (1975), Hindmarsh (1984), and Weary and Lemon (1988). Further data were collected by searching *Zoological Record* 1980–1987 and the references of relevant papers found there. Where song data for different times of year is given for a species, only data on the advertising song during the premating and laying periods were included, irrespective of whether the author considered that the song was primarily a mate attraction song or a territorial song.

Following Hamilton and Zuk (1982), parasite data were from a large number of studies in which blood smears taken from wild birds were searched for various blood parasites (microfilarial worms and several protozoan genera, the numerically most important being *Leucocytozoon*, *Plasmodium*, *Trypanosoma*, and *Haemoproteus*). The prevalence of haematozoa (proportion of birds sampled that were infected with any protozoan blood parasites) for each bird species was used as a measure of species vulnerability to parasite invasion. Sources of data on parasite infections are given in Read (1987). To reduce one source of sampling error, we excluded all species for which fewer than ten individuals had been assayed for blood parasites. [Across European passerines for which fewer than ten individuals had been sampled for parasites, Read and Harvey (1989) found an association between passerine brightness and parasite prevalence. There are no such relationship between parasite prevalence and any of the song measures considered here.] The parasite data are drawn from over 200 studies from a wide range of locations throughout Europe and North America and come from smears from about 25000 birds, covering 131 species for which we had data on at least some quantitative song variables. For our reanalysis of the Hamilton and Zuk scores, we included all species for which their scores were available whether or not few individuals had been sampled for parasites, so as to make the species in our data set comparable to that of Hamilton and Zuk (1982). However, we have used a considerably larger parasite data set (130 published studies and 5000 unpublished records on blood smears taken from 23624 individuals).

Avian taxonomy follows Howard and Moore (1980) for species and genera, and Sibley and Ahlquist (1985) at higher levels. Following Bennett and Harvey (1985), species were categorised as living in forest, woodland, scrubland, tundra/mountainlands, grassland and marsh; the latter four were treated as open habitats. Several species in the data set are regularly found in both wooded and open habitats (eg. *Melospiza melodia*); these were exluded from the habitat analyses.

The variables

Hamilton and Zuk's song ratings were scored on a six point scale, on the basis of male song "variety and complexity" (Hamilton and Zuk 1982, p. 385), with the species having the most varied and complex song ranked the highest.

Species means for each of the following variables were collected (terminology follows Weary and Lemon 1988):
1. Song duration(s)
2. Inter-song interval(s)
3. Continuity: proportion of time spent making sound during a song bout; $1/(1+2)$
4. Song rate: number of songs sung per minute during a song bout; $60/(1+2)$
5. Song repertoire size: number of song types possessed by an individual. Species with essentially infinite repertoire sizes, such as the North American robin (*Turdus migrator-*

ius), were given a repertoire size equal to one greater than the maximum recorded in our data set. When non-parametric statistics are used (see the following), this ensures that they fall at the extreme end of data range. The same procedure was used for species with essentially infinite syllable repertoire sizes.

6. Syllable repertoire size: mean number of different syllable types within a song
7. Song showiness: A combination of continuity and both repertoire size measures. This summary statistic was developed in an attempt to overcome the comparability problem (discussed previously); however, in the absence of any information on the costs of singing the various possible combinations, or on which combinations might be more preferred by females (eg. continuous song composed of many different syllables or constructed from the same syllable repeated), our weighting of the three components is necessarily arbitrary. Continuity and song and syllable repertoires have very different means and variances; therefore, all three variables were z-transformed, following logarithmic transformation, and then summed. Species with essentially infinite song ($n = 13$ species) or syllable repertoire sizes ($n = 2$ species) were excluded from the song showiness analyses because of the difficulties of including them in such a measure.
8. Versatility: Species were categorised as being either immediately versatile, where song types are rapidly switched (ABCDBDAC...), eventually versatile, where song types are repeated several times before switching (AAAABBBBCCCC....) or nonversatile, where a single song type is repeated throughout a song bout (AAAAAAA...).

Hamilton and Zuk's subjective scores of "variety and complexity" are significantly correlated with syllable and song repertoire sizes, continuity and our summary statistic of all three, but not with inter-song interval or song rate (Table 1). There is also a significant association between Hamilton and Zuk's song scores and our three category song versatility measure (Kruskal-Wallis $H_{[2]} = 7.13$, $P < 0.05$; mean song score of immediately versatile singers $= 3.96$, $n = 24$; for eventually versatile $= 3.29$, $n = 17$ and for nonversatile $= 3.13$, $n = 16$).

Taxonomic artefacts

Several methods have been used in an attempt to avoid taxonomic artefacts in comparative studies (Pagel and Harvey 1988). Interspecific relationships that are not due to one or a few species-rich taxa should have arisen many times during the course of evolution (Ridley 1983; Pagel and Harvey 1988). Thus the associations between parasites and song showiness should occur within taxa, as well as across species. Read (1987) asked whether male brightness was associated with haematozoa prevalence within a significant proportion of genera; here we extend this approach, by estimating generic means by averaging the constituent species values, tribal means by averaging the constituent generic means, subfamily means by averaging the tribal means and, finally, family means by averaging the constituent subfamily means. Then, for each song variable, we calculated correlation coefficients with haematozoa prevalence for species within genera, generic means within tribes, tribal means within subfamilies, subfamilies within families and families within superfamilies. Because each taxon is assumed to be derived from a single ancestral species, any interspecific association has to re-arise within each taxon. This approach assumes that the factors being considered are just as likely to be associated at all taxonomic levels. At least in its current form, the Hamilton-Zuk hypothesis proposes that female choice for resistant males is a general phenomenon, and therefore the hypothe-

sis should apply to differences in sexual ornamentation between higher taxa, as well as within them.

Analysis

Parasite prevalences, as well as song and syllable repertoire sizes, are highly skewed and are not normalised by simple transformations; therefore, non-parametric statistics were used throughout. To deal with possible confounding influence of habitat type, we separated our data set into species living in forests and those living in more open habitats, and repeated our analyses.

To test whether associations between haematozoa prevalence and a particular song variable arose within taxa more often than expected by chance, we calculated the z-scores associated with the intra-taxon Spearman rank correlation coefficients (r_s) for each intra-taxon relationship. To test whether these were more positive or negative than expected by chance alone, they were compared with a mean of zero using a one-sample t-test. The z-transformation at least partly overcomes the difficulties associated with the non-normal distribution of the Spearman rank correlation coefficients, which arises because of the small sample sizes within some taxa. This test also has the additional advantage of giving more weight to those taxa within which there are more species or higher taxa (because the z-transformation is in part dependent on the sample size).

Results

Subjective song scores and parasite prevalence

Across all species, Hamilton and Zuk's subjective score of male song complexity and variety is positively and significantly related to parasite prevalence ($r_s = 0.30$, $P = 0.004$, $n = 113$). However, within taxa, there is no evidence of a consistent relationship: only half (13 of 26) intra-taxon associations are positive (mean intra-taxon $r_s = 0.03$, $P = 0.98$). This suggests that the across species association is the result of a taxonomic artefact. Across taxa analyses provide support for this view. If the species values are averaged for each genus, the association across these generic means is still significant ($r_s = 0.32$, $P = 0.008$, $n = 67$). But if these generic means are averaged to give tribal values, the association across the tribes is not significant ($r_s = 0.15$, $P = 0.50$, $n = 22$). Similarly, across subfamily and family means (calculated in the same way) the association is not significant ($r_s = 0.17$, $P = 0.50$, $n = 17$, Fig. 1; and $r_s = 0.05$, $P = 0.88$, $n = 13$, respectively). Thus one or two species-rich higher taxa could explain the across-species correlation.

Indeed, the interspecific association apparently arises because of two taxa, the Turdinae (thrushes) and the most species-rich family in the sample, the Fringillidae (finches, buntings and tanagers), which contain species with both high parasite prevalences and elaborate songs (Fig. 1). If these taxa are removed, there is no significant correlation ac-

ross the remaining species ($r_s = 0.01$, $P = 0.98$, $n = 44$). Within the Turdinae, the association between male song and parasite prevalence is negative ($r_s = -0.83$, $P = 0.12$, $n = 6$). Within the
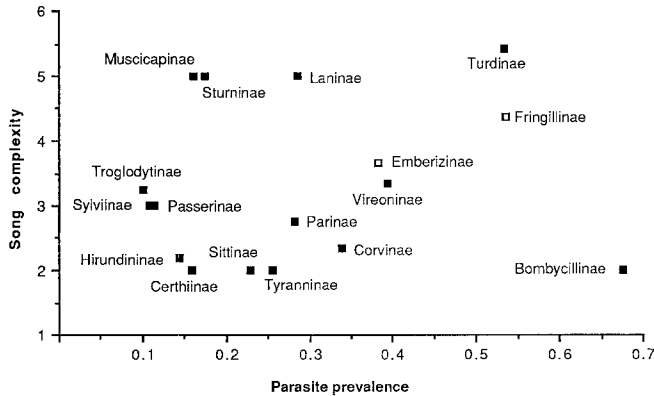

Fig. 1. Hamilton and Zuk's score of song "complexity and variety" plotted against haematozoa prevalence for subfamilies of North American passerines. Open boxes represent members of the Fringillidae (finches, buntings and tanagers). The association is not significant ($r_s = 0.17$, $P = 0.25$, $n = 17$ subfamilies calculated from data on 113 species), whereas the across-species relationship is significant ($r_s = 0.30$, $P = 0.004$, $n = 113$)

Table 1. Relationship between interspecific measures of song and the subjective song ratings of Hamilton and Zuk (1982). Variables defined in text

Variable	r_s	n
Song duration	0.29*	63
Inter-song interval	−0.16	51
Continuity	0.37**	51
Song rate	0.07	51
Song repertoire size	0.42***	57
Syllable repertoire size	0.36**	59
Song showiness	0.48***	46

* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$

Fringillidae, the song-parasite association is significantly positive ($r_s = 0.30$, $P = 0.04$, $n = 64$), but this association is also apparently the result of taxonomic associations! Members of the Emberizinae have low song scores and low parasite prevalence relative to other Fringillids (Fig. 1). Within the Fringillinae and within the Emberizinae, there is no significant relationship ($r_s = 0.16$, $P = 0.30$, $n = 44$; $r_s = 0.41$, $P = 0.14$, $n = 14$, respectively). It is entirely possible that each of the these outlying taxa does represent the independent evolution of complex song in response to high parasite loads. But if so, it has not happened often. In any case, the significant relationship between Hamilton and Zuk's subjective score of male song showiness and parasite prevalence found across all species cannot be separated from taxonomic associations: selective factors associated with any unique feature of the taxa just mentioned could, at least in principle, provide a rival and more parsimonius explanation of the across species association than the Hamilton-Zuk hypothesis.

Quantitative song measures and parasite prevalence

Across species, only two of the relationships between haematozoa prevalence and the seven song continuous variables are in the direction predicted by the parasite hypothesis (Table 2). The only song variables that are significantly related to parasite prevalence are continuity and our song showiness summary statistic, and both correlations are in directions opposite to that predicted by the hypothesis. For all the continuous variables, the proportion of taxa within which there are relationships with prevalence in the predicted direction is, on average, almost 50%, as might be expected by chance alone (Table 2). Even when the magnitude

Table 2. Relationship between parasite prevalence and song variables across species and within taxa. Song variables and calculation of within taxa P-values discussed in text. Tabulated values in left hand column are Spearman rank correlation coefficients, with number of species given in brackets

	Relationship across species	Predicted direction of relationship	Proportion of taxa with relationships in predicted direction	mean r_s	P
Song duration	−0.09 (106)	+	25/42	0.21	0.31
Inter-song interval	0.17 (80)	−	11/32	0.14	0.22
Continuity	−0.24* (80)	+	18/32	0.09	0.58
Song rate	0.01 (80)	+	13/33	−0.15	0.19
Song repertoire size	0.03 (94)	+	14/29	0.02	0.49
Syllable repertoire size	−0.08 (114)	+	22/45	0.06	0.93
Song showiness	−0.30* (70)	+	14/30	−0.06	0.66

* $P < 0.05$

Table 3. Relationship between parasite prevalence and song variables across forest-dwelling species and within taxa. Song variables and calculation of within taxa P-values discussed in text. Tabulated values in left hand column are Spearman rank correlation coefficients, with number of species given in brackets

	Relationship across species		Predicted direction of relationship	Proportion of taxa with relationships in predicted direction	mean r_s	P
Song duration	−0.13	(68)	+	11/36	−0.16	0.39
Inter-song interval	0.23	(51)	−	8/19	0.05	0.49
Continuity	−0.32*	(51)	+	7/19	−0.07	0.18
Song rate	−0.14	(51)	+	7/19	−0.14	0.27
Song repertoire size	0.05	(59)	+	10/22	−0.02	0.97
Syllable repertoire size	−0.02	(69)	+	13/28	−0.19	0.91
Song showiness	−0.27*	(45)	+	9/19	0.003	0.96

* $P<0.05$

Table 4. Relationship between parasite prevalence and song variables across species living in open habitats and within taxa. Song variables and calculation of within taxa P-values discussed in text. Tabulated values in left hand column are Spearman rank correlation coefficients, with number of species given in brackets

	Relationship across species		Predicted direction of relationship	Proportion of taxa with relationships in predicted direction	mean r_s	P
Song duration	−0.06	(33)	+	10/16	0.23	0.28
Inter-song interval	0.03	(24)	−	5/13	0.27	0.32
Continuity	−0.16	(24)	+	10/13	0.38	0.08
Song rate	0.19	(24)	+	6/14	−0.17	0.48
Song repertoire size	0.05	(30)	+	9/13	0.35	0.22
Syllable repertoire size	−0.03	(41)	+	8/20	−0.07	0.51
Song showiness	−0.27	(21)	+	8/12	0.24	0.36

of the correlations is taken into account, there were no significant associations (Table 2). If the data set is split into species living in forests and open habitats, similar patterns are found within taxa and across species of forest-dwelling birds (Table 3), but there are no significant associations between the song variables and parasite prevalence within taxa or across species living in open habitats (Table 4). Thus, there are no consistent intra-taxon associations between parasite prevalence and the song variables, suggesting that taxonomic artefacts do not obscure any across species relationships, and that in two cases (continuity and song showiness) they may produce them.

Indeed, the relationship between haematozoa prevalence and continuity across species arises because of the differences between the Fringillidae and all other species. Almost half the species included in this sample are members of the Fringillidae (39/80 species for which we have estimates of continuity). Furthermore, as might be expected for such a species-rich taxon, members of the Fringilli-

dae belong to a large number of higher taxa, and are therefore likely to have a large impact on the relationships across higher taxa. For example, across generic ($r_s = -0.36$, $n=44$, $P<0.01$; Fig. 2) and tribal ($r_s = -0.42$, $n=17$, $P<0.05$) means calculated from all species in the sample, continuity and prevalence are negatively related; when only forest dwelling species are considered, similar but stronger associations are found across genera ($r_s = -0.64$, $n=26$, $P<0.001$) and tribes ($r_s = -0.68$, $n=13$, $P<0.01$). But the Fringillidae are characterised by relatively high parasite prevalences and low song continuity (Fig. 2). When the Fringillidae are removed from the whole data set and from the subset which includes only forest-dwelling species, then these relationships across species are no longer significant ($r_s = -0.09$, $n=41$, $P>0.25$; $r_s = -0.07$, $n=30$, $P>0.35$, respectively). Within the Fringillidae only, there is no significant association between continuity and prevalence across all species ($r_s = -0.08$, $n=39$, $P>0.30$), and although there is a significant relationship within the Fringil-
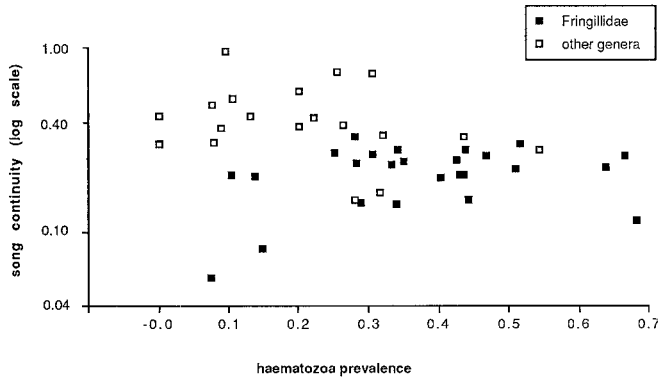
Fig. 2. The relationship between song continuity and haematozoa prevalence across generic means. The relationship is in the opposite direction to that predicted by Hamilton and Zuk (1982) ($r_s = -0.36$, $P<0.01$, $N=44$ calculated from data on 80 species). However, the Fringillidae (closed squares) are characterised by relatively high haematozoa prevalences and low song continuities. Within the Fringillidae, and across the remaining genera, the relationship is not significant ($r_s = +0.20$, $N=25$, $P>0.15$ and $r_s = -0.29$, $N=19$, $P>0.10$ respectively)

Table 5. Mean parasite prevalences of the song versatility categories within three data sets: all species for which we have versatility data, and in the subset of species living in forests and in open habitats. Numbers in brackets are samples sizes

Versatility	All species[1]	Forest-dwelling species[2]	Species living in open habitats[3]
Immediately versatile	0.40 (37)	0.44 (29)	0.22 (6)
Eventually versatile	0.30 (30)	0.28 (17)	0.32 (12)
Nonversatile	0.31 (23)	0.33 (13)	0.26 (8)

[1] Kruskal Wallis $H_{[2]}=4.23$, $P>0.10$; [2] $H_{[2]}=7.4$, $P<0.05$; [3] $H_{[2]}=1.99$, $P>0.20$

lidae when only forest dwelling species are considered ($r_s = -0.38$, $n=21$, $P<0.05$), this arises because a single species (*Icterus galbula*) has a very low continuity and a very high prevalence. Across the remaining forest-dwelling Fringillidae there is no such relationship ($r_s = -0.31$, $n=20$, $P=0.14$). Thus the association between continuity and parasites is not found when taxonomic associations are controlled for. The relationship between haematozoa prevalence and our song showiness summary statistic arises in the same way.

Across species, song versatility is not significantly associated with haematozoa prevalence (Table 5) but, as predicted from the parasite hypothesis, species with the most versatile song ('immediately versatile') have significantly higher haematozoa prevalence than eventually versatile (Mann-

Whitney $U=400$, $P=0.034$) or nonversatile ($U=320$, $P=0.054$) species. There is no significant difference between parasite prevalence of eventually versatile and nonversatile species ($U=210$, $P=0.26$). Combined, they still have lower prevalences than immediately versatile species ($U=730$, $P=0.02$). Song versatility of forest-dwelling birds is significantly associated with parasite prevalence (Table 5), and as found across all species, forest-dwelling species with immediately versatile species have a higher prevalence than eventually versatile ($U=140$, $P=0.007$) or nonversatile ($U=121$, $P=0.033$) species. There was no significant difference between the parasite prevalences of eventually and nonversatile species ($U=90$, $P=0.19$). Song versatility and prevalence are unrelated across species living in open habitats (Table 5), and there were no significant differences between the prevalences of any two of the versatility categories.

So, across all species, and across forest-dwelling species, immediately versatile species have higher parasite prevalences than eventually or nonversatile species, as predicted from the Hamilton-Zuk hypothesis. Could these associations be taxonomic artefacts? Across all species, versatility is associated with taxonomy (superfamily by versatility contingency table $X^2_{[4]}=21.1$, $P<0.001$, based on 84 species), suggesting that they might. Furthermore, the across-species relationship is considerably weakened if the Turdinae (10 species) and the tanagers (*Piranga*; 10 species) are removed ($U=573$, $P=0.20$, $n=77$ species). The patterns within the superfamilies containing species which differ in song versatility are quite different. Immediately versatile species have significantly higher prevalences only within one superfamily (Fringilloidea; $U=125$, $n=49$, $P=0.002$); within the Corvoidea there is no significant difference, whilst within the Sylvoidea, there is a significant difference in the *opposite* direction ($U=19$, $n=21$, $P=0.042$).

To control for taxonomic associations, we compared the mean parasite prevalences of immediately versatile taxa with the parasite prevalences of their sister taxa with eventually versatile or nonversatile songs. Phylogeny was inferred from taxonomy. Where sister taxa were genera or higher taxa, generic estimates were taken as the mean of species values, tribal estimates as a means of generic values and so on, to avoid over-representing species-rich taxa in higher taxa means (Harvey and Mace 1982). Pagel and Harvey (1988) provide a general discussion of the use of paired comparisons to control for phylogenetic associations.

Ten sister taxa comparisons are possible when species from all habitats are considered. In five

cases, the immediately versatile taxa have the highest prevalences, whereas in the others they have the lower prevalences. Furthermore, there is no significant difference when the prevalences themselves are compared ($t_{[9]} = 1.04$, $P = 0.33$, based on 63 species). Thus, there is no evidence that a relationship between song versatility and parasite prevalence exists independent of taxonomic associations. Similarly, the association between song versatility and prevalence in forest-dwelling species cannot be separated from taxonomic associations. When the immediately versatile species are compared with their nearest eventually and nonversatile relatives, there is no significant difference ($t_{[5]} = 0.36$, $P = 0.73$, based on 31 species).

Discussion

There is considerable circumstantial evidence (Darwin 1871; Catchpole 1982) and some direct experimental evidence (Ericksson and Wallin 1986) that song functions in mate attraction, and, at least in a few species, there is strong evidence that males with more elaborate songs obtain mates earlier and/or more of them (Catchpole 1987; Searcy and Andersson 1986). It therefore seems probable that elaborate song is a secondary sexual character, and that the Hamilton-Zuk hypothesis should apply. However, our comparative analyses show that there is no evidence of the association between parasites and song showiness when the effects of phylogeny are controlled for. There are several possible reasons for this.

The hypothesis could be wrong. A number of other studies, both inter- and intraspecific, have tested the hypothesis (reviewed by Read 1988; Read, in press) and have reported evidence which is largely equivocal or which can be reinterpretated as supporting other theories of sexual selection (Kirkpatrick 1987; Ryan 1988; Read, in press). There are, however, a number of plausible post-hoc rationalisations that proponents of the parasite idea could invoke in response to the analyses reported here in order to save the hypothesis, which illustrates that the hypothesis is easier to support than to refute (Read, in press). Some of these apply to all comparative tests of the hypothesis, while others are specific to comparative studies of song.

Our conclusion might be a type II error (acceptance of a false null hypothesis). A number of factors make this possible. First, the parasite and song data are pooled from surveys from many different locations, covering a variety of sampling techniques. This variation might produce statistical error that obscures any relationships. Second, parasite prevalence is at best only an approximate indication of the extent to which a species is "subject to attack by debilitating parasites" (Hamilton and Zuk 1982, p. 385), since it is a measure of the number of individuals infected, rather than the number exposed to parasites. Unfortunately, data on exposure is notoriously difficult to gather, so that prevalence is likely to remain our best measure of parasite pressure, at least for the foreseeable future (Read, in press). Third, not all of the relevant parasite taxa were assayed.

It may also be that we have failed to adequately characterise those features of song preferrred by females. Our measures do correlate (Table 1) with the intuitive notion of song complexity and variety of Hamilton and Zuk (1982), and we have concentrated on those features of song that others have thought important and for which there is at least some intraspecific evidence of their involvement in female choice (see introduction). Nevertheless, several studies on other species have failed to find evidence that these characteristics are important. For example, there is compelling evidence that repertoire size functions as a cue in female choice in two *Acrocephalus* species (Searcy and Andersson 1986; Catchpole 1987), but several field workers have failed to find a significant relationship between repertoire size and time to mating in great tits (*Parus major*; Krebs et al. 1978; McGregor et al. 1981; Lambrechts and Dhondt 1986) or pied flycatchers (*Ficedula hypoleuca*; Alatalo et al. 1986; Gottlander 1987). In such species, song may have more to do with male-male competition than female choice.

Furthermore, there are many features of song complexity for which we were unable to gather sufficient or acceptable data. Weary and Lemon (1988), for example, were able to quantify the rate of song and syllable switching of 19 species of North American warbler in more detail than is yet possible for a wider range of species. We were unable to gather data on frequency and amplitude modulations. Such variation represents an obvious source of diversity and bird songs, yet has been largely ignored in intraspecific studies of mate attraction. We attempted to gather data on maximum and minimum song frequencies for each species, since frequency has been considered an important cue in female choice in at least one species of anuran (Ryan 1983) and one species of non-passerine (Gibson and Bradbury 1985). However, maximum frequencies depend in part on the sensitivity of the sonogram analyses, which is likely to differ between studies, and both the maximum and

minimum frequency may rarely be sung during a song bout. Probably more relevant are differences in emphasised frequency (those frequencies containing the greatest amount of energy; Morton 1975), but such data were not available for more than a handful of the species in our sample. We consider the inclusion of those components of song complexity associated with frequency and amplitude to be a major challenge for both inter- and intra-specific analyses of song diversity.

Another possible reason for failing to find the predicted associations is suggested by recent genetic models. Female choice for resistant males might lead to runaway elaboration of secondary sexual characters (Pomiankowski 1988), and if so, the point at which the elaboration is halted may be uncorrelated with the parasite load; energetic constraints on sound production (Ryan 1988), for example, could be more important in determining the extent of elaboration. Evaluating such ideas may be difficult until the data on the relative costs of elaborate song in different species become available.

Finally, it is possible that some unknown correlate of song obscures any associations between parasite prevalence and song showiness. Little is known about the ecological and behavioural correlates of interspecific song diversity. Understanding such diversity remains an outstanding problem in ornithology. In the meantime, we conclude that there is no evidence for a relationship between song elaboration and haematozoa prevalence.

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