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## Bird song and parasites

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**Abstract** Bird song is a typical sexual trait that may have evolved at least partly to reflect health and vigor. However, the role of pathogens in modulating acoustic communication systems in birds is still less than clear as studies testing the relationship between parasites and song have provided inconsistent results both within and among species. It is often neglected that avian song is complex trait consisting of numerous and variable features with potentially different biological backgrounds. By using meta-analytic approaches to the available intraspecific evidence I demonstrate that different roles are applicable to song traits with different signal design, which could explain, to some extent, the inconsistency of results. I found that condition-dependent, performance-related traits are more closely related to immediate health status, whereas condition-independent features are more likely to be associated with intrinsically determined parasite resistance. Hence, parasitism may mediate the evolution of different acoustic features. Considering the signal function of songs, a communication system depends on the reaction of the receivers, but little is known about how mate choice and male–male competition are affected by parasite-mediated song production. This review of the literature thus suggests that receivers of songs may benefit by responding to these acoustic signals of health through the acquisition of resistance genes, paternal care of superior assistance, success in territory disputes, and the avoidance of directly transmitted parasites.

**Keywords** Bird song · Handicap · Immune response · Immunocompetence · Parasites · Repertoire size · Secondary sexual characters · Testosterone

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### Introduction

Bird song is usually considered to have evolved via sexual selection, because of its dual function in female choice and male–male competition (Searcy and Andersson 1986; Searcy and Nowicki 2000). Females may prefer mates with the most vigorous displays, because, for instance, such males prove their relative resistance to and therefore freedom from devastating parasites (Hamilton and Zuk 1982). Therefore, according to the theories of parasite-mediated sexual selection, bird song may also have evolved at least partly to reveal health status of males.

One particular hypothesis addressing the influence of parasites on the evolution of sexually selected characters suggested that female preference is mediated by resistance genes (Hamilton and Zuk 1982). If the expression of songs reflects the parasite load of the male, and if hosts coevolve continuously with their parasites and, as a result, build up partially heritable resistance to parasites, females will benefit from basing their mate choice on song traits by acquiring resistance genes for their offspring. Because hosts continuously evolve genetically determined defense mechanisms to minimize the effects of parasites, and because parasites continuously evolve new modes of exploiting their hosts, coevolution between hosts and parasites by frequency-dependent selection will generate stable limit cycles in the gene frequencies of both hosts and parasites, and thus maintain heritable genetic variation in fitness (Eshel and Hamilton 1984; Hamilton 1984). Hence, the Hamilton-Zuk hypothesis prevents depletion of genetic variance for resistance and for the selected trait even under strong directional selection by choosy females.

However, the Hamilton and Zuk hypothesis is not the only one that offers a link between parasites and sexual characters, such as songs. The parasite avoidance hypothesis, which applies to horizontally transmitted parasites (ectoparasites, venereal diseases, and directly transmitted microparasites), suggests that females reduce the probability of catching parasites by direct transmission if they choose parasite-free males (Freeland 1976; Borgia 1986; Borgia

and Collis 1989). Selection is suggested to favor exaggerated sexual characters such as bright plumage because these make ectoparasites more visible. Females could hence acquire direct fitness benefits by discriminating among males based on their parasite load, causing sexual characters to evolve by natural selection. According to the parasite avoidance hypothesis, the degree of development of the male trait does not vary among individuals. However, direct avoidance of parasitized males would still lead to rapid changes in the frequency of resistance genes among hosts because of sexual selection, although this would not explain the presence of and variability in the expression of sexual ornaments. Hence, this hypothesis lacks generality as a model of parasite-mediated sexual selection, because it does not apply to variable traits. In addition, it is difficult to imagine how song could help females to see and count parasites directly.

These constraints are relaxed in the contagion indicator hypothesis, in which the degree of expression of variable male traits indicates the male's load of transmittable parasites that a female—or her offspring—risks to acquire by direct transmission (Able 1996). Based on the relationship between parasite load and trait expression, the contagion indicator hypothesis states that females by preferring males with elaborate sexual characters will avoid the damages caused by transmittable parasites. Hence, according to this theory, the association between mating success, parasite load and trait expression is governed by sexual selection.

The efficient parent hypothesis suggests that the advantage of female preference for extravagantly ornamented males is the higher parental care that they provide, as they can allocate more resources to paternal care than parasitized males (Hamilton 1990; Price et al. 1993). While the Hamilton-Zuk hypothesis suggests a mechanism for choosy females to accrue indirect fitness benefits through resistance genes (good-genes), the other alternatives provide mechanisms entirely based on direct fitness benefits. There is no general agreement about the relative importance of these hypotheses, and they are not necessarily mutually exclusive (Møller et al. 1999).

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### **Predictions of theories of parasite-mediated sexual selection for bird song**

A number of different predictions follow from the hypotheses that assume a link between parasites and sexual characters within species (Møller 1990c; Hillgarth and Wingfield 1997; Møller et al. 1999), and these can also be applied to song traits. Full support for the Hamilton and Zuk hypothesis requires that (i) parasites should affect the expression of songs; (ii) receivers of songs should adjust their response according to the information they perceive about the parasite burden of the singer; (iii) parasites should affect host survival and/or reproductive success; (iv) parasite resistance and the expression of song should be heritable. For the alternative models hypothesizing direct fitness benefits gained by females preferring parasite-free males, the prediction concerning the heritability of traits is not necessarily

required. The original parasite avoidance hypothesis predicts no effect of parasites on the expression of ornaments, nor female choice based on such parasite-mediated sexual traits (Borgia 1986; Borgia and Collis 1989). On the other hand, the contagion indicator hypothesis allows variable song traits to signal parasite burden, which in turn predicts the existence of such correlations (Able 1996). These hypotheses predict that females of highly parasitized males should suffer from higher parasite pressure due to the horizontal transmission of parasites, and hence that the parasite load of pair members should be positively correlated. If parasite-mediated song signals the parental quality of males, song traits that can be affected by parasites should be correlated with measures of male paternal effort, with parasitized males providing inferior paternal care.

Here I review studies assessing the relationship between bird song and parasitism under the framework of parasite-mediated sexual selection. Although, several studies investigated the role of pathogens in sexual signaling (review in Møller et al. 1999), there is currently no synthesis focusing on the specific characteristics of bird song.

The hypothetical relationships applied to the parasite-mediated selection of song traits, are presented in Table 1 together with supporting or conflicting evidence. In the following sections I will examine the general validity of these predictions and relationships. First, I will investigate the associations predicted by the Hamilton and Zuk hypothesis, by the efficient parent hypothesis, and by the contagion indicator hypothesis. In this context, based on constraints of signal design, I will consider two possible mechanisms that may generate a functional link between bird song and parasitism. Second, I will review the evidence for the relationship between potential acoustic signals of male health and the receivers' behavior. The Hamilton and Zuk hypothesis, the efficient parent hypothesis and the contagion indicator hypothesis all predict that receivers of parasite-mediated songs should adjust their response according to the information they acquire on parasitism. In this review it is very important to consider the dual function of bird song in female choice and male-male competition. Third, I will focus on the effects of parasites on host fitness. It is implicit in all three hypotheses that parasites entail fitness costs to the hosts, which may be reflected in trade-offs between immune function and reproduction. Fourth, as the Hamilton and Zuk hypothesis requires significant heritability for both parasite resistance and song characteristics, I will discuss the genetic basis of these traits. Fifth, I will investigate the efficient parent hypothesis by analyzing the relationship between song and paternal effort, and also between parasites and paternal effort. Last, I will provide a summary of the evidence for the hypothetical relationship between the parasite load of the pair members, which is predicted by the contagion indicator hypothesis and the parasite avoidance hypothesis. After discussing the generality of these intraspecific roles, I will address the evolutionary consequences of the relationship between song and parasites. This discussion will be based on comparative studies that have tested for interspecific relationships between parasites and song traits in birds.

Because the immune system plays a pivotal role in defending animals against parasite attacks, an animal's ability to mount an efficient immune defense (so-called immunocompetence) will have consequences for parasite loads and signal elaboration (Norris and Evans 2000). Therefore, the relationship between sexual signaling and parasitism may be mediated by a trade-off between investment in sexual traits and immune defense. This view is reflected in studies of parasite-mediated bird song, because these studies tend to use both parasite-counts and measures of immune defense to assess the impact of parasitism. Accordingly, if song is to reflect parasite resistance of males, individuals with high quality songs should have fewer parasites or should be in better health status as mirrored by immunological variables. In the following discussions and analyses, I also adopted this view by combining evidence based on parasite-counts and measures of immune defense.

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### Meta-analysis

Meta-analytical techniques offer quantitative and objective methods to summarize a body of research by examining the magnitude and the generality of a predicted relationship (Hedges and Olkin 1985; Rosenthal 1991; Cooper and Hedges 1994). In such an approach, based on the standardized effect sizes of individual studies, an overall effects size may be calculated for the relationship in focus, and the general significance of the studied phenomenon can be tested while taking sample size into account. Hence, to extend verbal arguments with statistical approaches, I performed some simple meta-analyses on the available data to test for general patterns in the intraspecific association between parasitism and bird song. I estimated true effect sizes based on available studies testing the null hypothesis that males with higher parasite load or with inferior immune function have similar song attributes to males in better health status, which corresponds to the main prediction of hypotheses of parasite-mediated sexual selection. I used measures of immune function and parasite prevalence interchangeably, as was done in similar meta-analyses (e.g., Møller et al. 1999; Roberts et al. 2004). In this context, I assumed that an animal's ability to mount an effective immune defense (immunocompetence) reflects the ability of a host to prevent or control infection by pathogens and parasites (see also Norris and Evans 2000). However, I present analyses based on random effect sizes, which allows for a heterogeneous relationship between song and parasitism, for example, due to the combination of measures of parasite loads and immune defense.

For the meta-analysis, I collected results and included all published statistics (all two-tailed, nonparametric tests were treated as parametric). Different test statistics or significance levels were then transformed into effect size correlations. I then computed an overall effect size and tested if it was significantly different from zero. I distinguished between different song traits, and hence performed analyses with different subsets testing effects corresponding to specific song features. The categorization of song features

was based on assumptions about costs or constraints which might influence song (see also Vehrencamp 2000). If multiple tests were presented in a single study of the same biological hypothesis with the same song variable (e.g., in Saino et al. 1997b; Garamszegi et al. 2005b), an overall effect size was first calculated within that particular study (in this case the given sample size is the mean sample size). Hence, in any analysis, the effect sizes given for individual studies represent independent data points.

The use of a meta-analysis probably involves publication bias due to the unpublished negative results, and hence causes the presented tests to be conservative (e.g., Kotiaho 2002). However, I will rather focus on comparisons of effect sizes attributed to different song traits or to other factors. In these comparisons, publication bias may be assumed to appear randomly (e.g., the proportion of non-published and non-significant studies may be similar for each traits), and thus to not have confounding effects on the comparison in question. I included one non-passerine species, the tawny owl *Strix aluco*. The exclusion of this species from the analysis does not affect the results and the conclusions reported below.

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### The relationship between song traits and parasitism

Potential roles for song traits with different signal design

A key assumption of the majority of the hypotheses addressing the parasite-mediated selection of bird song is that there should be a negative relationship between parasite burden of a singing male and his song. If parasitism and the phenotypic expression of songs are associated with each other, the signaling processes mediated by parasites can be driven through two different mechanisms (Wedekind 1994a, b). First, following from the "handicap principle" (Zahavi 1975; Grafen 1990), signals of health might be reliable because the cost of production renders cheating impossible. Thus, the quality of songs of parasitized individuals would be affected by the physiological costs of infection. If the cost imposed by song production increases under parasite pressure, the potential exists for song to reveal the ability of a singer to bear the costs of both song production and immune defense via a handicap mechanism. As song is a flexible behavioral trait, it is reasonable to expect that it is sensitive to immediate conditional status mediated by parasites. Second, theoretically, cheap signals might directly reveal the identity of resistance genes under certain conditions (Wedekind 1994a). The model assumes that the signaling system has appropriate characteristics that allow signalers to provide detailed information about the genetics of various resistances. Wedekind suggested that odors of mammals may have such characteristics, since the chemical composition of body scents is complex, and their production is cheap. However, bird song may meet these criteria. Due to its multifaceted characteristics, bird song may potentially involve stable and condition-independent signals (Gil and Gahr 2002) that could indicate

individual quality, including parasite resistance. Therefore, healthy males might signal to what extent they are able to cope with infectious diseases even in the absence of current parasite pressure. If song and resistance genes are linked, inferior males would always produce poor quality songs, independent of immediate immune condition caused by the detrimental physiological effects of parasites. The hypotheses of parasite-mediated sexual selection predicting a relationship between parasites and sexual signals thus may not only work with heritable resistance and signal characteristics, but also with condition-independent signals that have a fixed genetic basis.

Despite these theoretical treatments of both costly and cheap signals of health, the possibility for different mechanisms for condition dependent and independent features of songs has rarely been considered (Buchanan et al. 1999; Garamszegi et al. 2004). Hence, the exact mechanistic link that generates a relationship between the expression of acoustic sexual characters and parasitism remains unclear. The predicted covariance between songs and infection status has received support in seven out of nine published intraspecific studies (Table 1). This summary shows that there are some song features that can be related to some parasites, or to some components of the immune system. However, studies seeking the relationship between parasites and secondary sexual characters, such as songs, have typically considered only a narrow range of sexual signals and parasites (Clayton 1991; Weatherhead et al. 1993). Avian song is known to be a multifaceted trait consisting of numerous structural parameters encoding different kinds of information (Gil and Gahr, 2002). Hence, the lack of significant relationship may arise simply because the relevant song trait was not measured in the particular study. Note that studies investigating a broad range of song features (e.g., Saino et al. 1997b) found that while some traits were related to immune function, others were not.

Knowing which song character is affected by pathogens is important, because this may shed light on the mechanism driving the association between song production, parasite resistance and parasite load. Based on constraints that determine signal reliability, different song parameters can be assigned to different signal types, reflecting signal design and the information being conveyed (Vehrencamp 2000). Due to the potentially different biological background of each song component, variation in different song traits may be caused by diverse selective pressures, with parasitism differentially affecting the evolution of different song components. Hence, multiple signals used in sexual contexts may reveal different information regarding parasite burden.

When I assigned song traits to some obvious categories, I found different patterns for different signal types in a meta-analysis of studies (Table 2). In general, performance-related traits seem to correlate with measures of parasitism more strongly than song features of other signal types. Therefore, the significant and positive main effect size for performance-related traits supports the most important prediction of parasite-mediated sexual selection. On the other hand, available data for other song signals do not provide

significant evidence for the covariation between song and parasites.

Acoustic traits that are energetically costly to produce may be expected to evolve as handicap signals of health status. Singing at high performance is thought to be a metabolically demanding activity (reviews in Lambrechts 1996; Vehrencamp 2000). Hence, individual quality differences in coping with energy demands may determine signal reliability in the context of parasite-mediated sexual selection on song traits. Performance-related traits such as song rate in the barn swallow *Hirundo rustica*, collared flycatcher *Ficedula albicollis* and the European starling *Sturnus vulgaris* (Møller 1991; Saino et al. 1997b; Duffy and Ball 2002; Garamszegi et al. 2004) and song flights in the sedge warbler *Acrocephalus schoenobaenus* (Buchanan et al. 1999) have all been found to be linked to parasitism. A statistical approach by meta-analysis revealed a significant effect size for the relationship between parasitism and those features of songs that are likely to be associated with energetic costs (Table 2). This may suggest that energetic constraints on acoustic trait expression and immune defense result in costly song attributes being reliable signals of parasitism. Only high quality, healthy males are able to maintain body condition and sing at high rates or at higher performance while under parasite pressure. This mechanism is consistent with the handicap principle (Zahavi 1975; Grafen 1990). However, recent laboratory studies suggest that energetic cost of singing is not pronounced, and the costs must be paid in another currency (Oberweger and Goller 2001; Ward et al. 2003; 2004). A potential handicap mechanism that mediates a relationship between sexual characters and parasites can act through circulating levels of testosterone (Folstad and Karter 1992; review in Roberts et al. 2004).

Other attributes of song seem to be intrinsic attributes of males (Vehrencamp 2000). Such signals, which are stabilized by physical ceilings instead of the direct cost of production are known as index signals (Maynard-Smith and Harper 1995; Zahavi and Zahavi 1997). Cheap traits may function as condition-independent signals of male resistance ability. Recent laboratory experiments suggest that the production of complex song does not necessarily involve metabolic costs (Oberweger and Goller 2001). In addition, it has been suggested that the neural costs of song, in terms of brain space needed for storing elaborate song, may not be of significant importance (Gil and Gahr 2002; Garamszegi et al. 2005a). Repertoire size, as a possible index signal of health (Vehrencamp 2000), has been given special attention in studies investigating song in relation to pathogens. Some studies have shown a correlation between repertoire size and parasitism (Buchanan et al. 1999), but other results found no effect in the expected direction (Weatherhead et al. 1993; Saino et al. 1997b; Garamszegi et al. 2004). In a meta-analysis of this mixed evidence, I found a weak and non-significant effect size for the relationship between song complexity and measures of parasite pressure (Table 2). I detected similarly tendency, when I focused strictly on studies that assessed (and reported) the

**Table 1** Predictions and evidences for the hypotheses of parasite-mediated sexual selection acting on bird song (H&Z: Hamilton and Zuk hypothesis; EP: efficient parent hypothesis; CI: contagion indicator hypothesis; PA: parasite avoidance hypothesis)

	<i>Acrocephalus schoenobaenus</i>	<i>Agelaius phoeniceus</i>	<i>Ficedula albicollis</i>	<i>Hirundo rustica</i>
Predicted relationships				
Song and parasites (H&Z, EP, CI)	Repertoire size, song flights, and blood parasites <sup>1</sup>	Negative evidence (repertoire size and parasite prevalence) <sup>2</sup>	Song rate and immune challenge <sup>3</sup>	Song rate, song duration, rattle peak amplitude frequency and mite and louse load, lymphocytes, sedimentation rate <sup>4-6</sup> Song rate and extra-pair paternity <sup>1,2</sup>
Song and listener's behavior (H&Z, EP, CI)	Repertoire size, song flights and pairing date <sup>7,8</sup>	Repertoire size, song switching and harem size, copulation solicitation, territory defense <sup>9-11</sup>	Song rate and territory retention, pairing success <sup>3</sup>	
Parasites and fitness (H&Z, CI)	Blood parasites and brood size <sup>1</sup>	Negative evidence (immune responses and reproductive success, survival) <sup>13</sup>	Trade-off between reproduction and immune response, serology, parasite prevalence <sup>14-17</sup>	Trade-off between reproduction and immune response, serology, parasite prevalence <sup>18-26</sup>
Heritability of song and parasite resistance (H&Z)	?	?	?	Heritable resistance <sup>28</sup>
Song and paternal effort (EP)	Repertoire size and food provision <sup>27</sup>	Repertoire size and food provision <sup>9</sup>	Negative evidence <sup>28</sup>	Negative evidence <sup>28</sup>
Parasites and paternal effort (EP)	Blood parasites and food provision <sup>1</sup>	?	Negative evidence <sup>28</sup>	Mite load and food provisioning <sup>29</sup>
Parasite load of pair members (CI, PA)	?	Negative evidence (haematzoa) <sup>30</sup>	?	?
Predicted relationships				
Song and parasites (H&Z, EP, CI)	<i>Strix aluco</i> call length, hoot frequency and blood parasites <sup>31,32</sup>	<i>Sturnus vulgaris</i> song rate, song-bout length and immune responses <sup>33</sup>	<i>Taeniopygia guttata</i> negative evidence (song rate and immune responses, serology) <sup>34</sup>	General patterns Certain song traits and certain parasites or components of the immune system
Song and listener's behavior (H&Z, EP, CI)	Hoot attributes and territory defense <sup>35</sup>	Repertoire size, song-bout length and female preference (territory defense) <sup>36-39</sup>	Song rate and mate preference, extra-pair copulation <sup>40,41</sup>	Well-established, but little is known about the role of parasite-mediated songs, no direct (experimental) evidence
Parasites and fitness (H&Z, CI)	Possible trade-off between reproduction and parasite load via food supply <sup>42</sup>	Conflicting evidence <sup>43-46</sup>	Trade-off between reproduction and immune response <sup>47</sup>	Parasites may affect life history, survival and reproductive success; trade off between immune-function and reproduction
Heritability of song and parasite resistance (H&Z)	Similar ectoparasite fauna of chicks and their fathers <sup>42</sup>	?	Song rate and the sizes of the song nuclei in the brain are heritable <sup>41,48</sup>	Few indirect evidence in other species, nothing is known about the genetic correlation between song and resistance
Song and paternal effort (EP)	Hoot frequency may signal paternal performance <sup>35</sup>	Negative evidence (repertoire size and incubation, food provisioning) <sup>49</sup>	?	In some species song may signal paternal quality, but little is known about the role of parasite-mediated songs
Parasites and paternal effort (EP)	?	?	Daily workload during paternal care and immune response <sup>47</sup>	Few evidence
Parasite load of pair members (CI, PA)	Similar ectoparasite faunas of pair members <sup>42</sup>	?	?	Few evidence

(1) Buchanan et al. 1999; (2) Weatherhead et al. 1993; (3) Garamszegi et al. 2004; (4) Saino et al. 2004; (5) Møller 1991; (6) Garamszegi et al. 2005b; (7) Buchanan and Catchpole 1997; (8) Catchpole 1980; (9) Yasukawa et al. 1980; (10) Yasukawa 1981; (11) Searcy and Yasukawa 1990; (12) Møller et al. 1998; (13) Westneat et al. 2003; (14) Cichon 2000; (15) Nordling et al. 1998; (16) Cichon et al. 2001; (17) Gustafsson et al. 1994; (18) Saino et al. 2001; (19) Møller 1990a; (20) Saino et al. 2001; (21) Saino et al. 1999; (22) Saino et al. 1998; (23) Saino et al. 1997a; (24) Lope and Møller 1993; (25) Møller 1993; (26) Møller 1990b; (27) Buchanan and Catchpole 2000; (28) L. Z. Garamszegi, unpublished data; (29) Møller 1994; (30) Weatherhead and Bennett 1991; (31) Redpath et al. 2000; (32) Appleby and Redpath 1997; (33) Duffy and Ball 2002; (34) Birkhead et al. 1998; (35) Galeotti 1998; (36) Mounjov and Lemon 1996; (37) Mounjov and Lemon 1991; (38) Gentner and Hulst 2000; (39) Eens et al. 1991; (40) Collins et al. 1994; (41) Houtman 1992; (42) Appleby et al. 1999; (43) Williams et al. 1999; (44) Likier et al. 2001; (45) Mazgajski and Kedra 1998; (46) Clark 1991; (47) Deerenberg et al. 1997; (48) Airey et al. 2000; (49) Mounjov and Lemon 1997.

relationships for repertoire size ( $r = 0.126$  [SE = 0.232],  $N = 94$  in four studies,  $P = 0.523$ ).

At this moment, few intraspecific data are available for the biological question at hand, thus the results of the formal meta-analysis should be interpreted with caution. If different roles were applicable for condition dependent and independent song traits, this would shed light on how resistance to parasitism and the effects of parasitism on immediate body condition contribute to signal expression. If handicap song traits are to indicate health and vigor through their cost of production, and index signals are to reflect intrinsic parasite resistance independently of immediate health status, this would imply a close match between signal design and the information being conveyed, and a role for multiple signals. Duffy and Ball (2002) suggested different functions for song rate and for song-bout length in the European starling, as these traits were correlated with different components of the immune system. Another study in the collared flycatcher showed that an immunological challenge affected song rate differentially to other song characteristics (Garamszegi et al. 2004). The possibility of similar multiple signaling mechanisms should be taken into account in future experiments.

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### Measures of parasitism: parasite load vs. immunocompetence

Studies of parasite-mediated sexual selection are also often criticized for their limited focus in terms of parasites (Clayton 1991; Weatherhead et al. 1993). There is an obvious tendency for heterogeneity among studies with regards to which traits were used to reflect parasite pressure or immune condition (Table 2). Ectoparasite load, blood parasite prevalence, haematological variables, and immune responses have all been widely used as estimates of the impact that parasites have on individual hosts (Table 1). Counting parasites in the blood or on the feathers may provide direct information on how much an individual suffers from diseases. Hence, males with higher parasite load should have inferior songs, and this pattern has indeed found in some species, while not in others (Tables 1–2).

It has been claimed that the potential effect of a given parasite on fitness and the expression of secondary sexual characters of the host is expected to be small (Møller et al. 1999). This is because organisms may host many parasite species, but only a small fraction of them are debilitating, and the intensity of infection with different parasites is not strongly correlated. Therefore it may be relatively unlikely that prevalence data on a randomly chosen parasite species will show any association with song displays. Møller et al. (1999) showed that the relationship between parasitism and sexual traits are generally stronger in studies, which used immunological variables to reflect the general impact of parasites than in studies, which used parasite counts. Hence, the use of measures of general anti-parasite defense is superior to the use of data on the abundance of any particular parasite in studies investigating the role of secondary sexual characters in signaling parasitism. In spite of

this predicted superiority of measures of immune defense, studies relying on such measures provided mixed evidence for the relationship between song and anti-parasite defense (Tables 1–2).

We know very little about how the measures of immune function currently used by ecologists relate to real immunocompetence or parasite load. However, it may reflect, at least to some extent, how animals deal with real parasitic infection (Norris and Evans 2000). In addition, different immune responses may at least partly involve different and independent mechanisms. It has been suggested that there may be two possible components of variation in immune defense: general responsiveness and specificity of immune responsiveness (Schmid-Hempel and Ebert 2003). General responsiveness reflects the strength of an immune response irrespective of the particular parasite type, whereas specific responsiveness reflects the variation in the strength of immune responses against different pathogen types. Consequently, the potential relationship between song, parasites and immunocompetence might be very complex, because all components of the system could be interrelated (Fig. 1). In a single survey, the probability of measuring the effect of a selectively acting parasite species, the corresponding component of the immune function, and also the affected song trait is small. This phenomenon may raise special difficulties in the study of bird song in relation to parasitism. Notably, Saino et al. (1997b) found that only lymphocyte concentration was significantly associated with song rate, and several immunological measures were unrelated to different song features. Hence, measuring several song and parasite traits may help us to find the biologically relevant traits and their associations. However, in such a correlative study, a special care is needed to deal with Type I errors that are generated by the large number of tests performed. To detect the relevant relationship between various parasite and song traits (see Figure 1), multivariate statistical approaches should be developed. The identification of the specific parasitological and/or immunological factors that incur fitness costs to birds may provide some solution, in conjunction with the application of experimental approaches.

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### Observations vs. experiments

The hypothetical relationship between song and health is usually investigated using correlative approaches. Although covariance between male condition, immune function and parasitic infection may be a sign of the existence of physiological costs (Buchanan et al. 1999), this does not provide conclusive evidence for a direct cost of infection. Hence, the probable dual effect of parasites on songs mediated by intrinsic parasite resistance or by physiological cost cannot be assessed in correlative studies. However, experimental manipulation of an immune response could confirm the direct cost of infections determining song duration or elaboration (Buchanan et al. 1999; Redpath et al. 2000). For instance, an immune challenge experiment in the collared flycatcher suggested that

**Table 2** Meta-analyses of the intraspecific relationship between parasitism and bird song

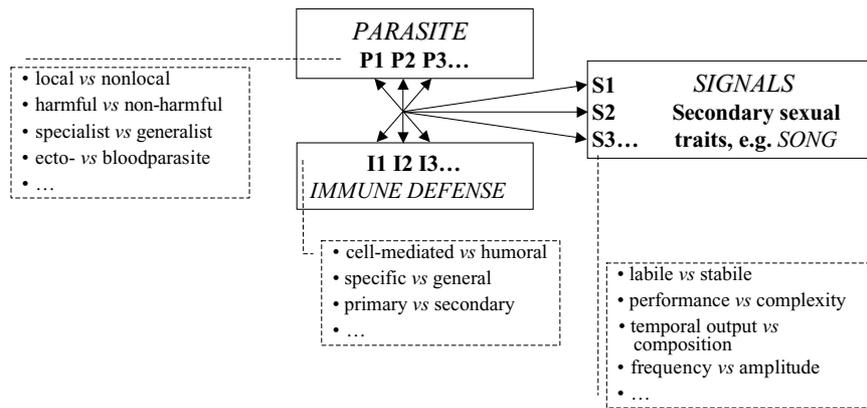
Species	Song trait	Data	Parasite	<i>N</i>	Effect size	Reference
<b>Performance-related song traits</b>						
<i>Acrocephalus schoenobaenus</i>	Song flight	obs	prev	15	0.328	Buchanan et al. (1999)
<i>Ficedula albicollis</i>	Song rate	exp	imm	27	0.463	Garamszegi et al. (2004)
<i>Hirundo rustica</i>	Song rate	exp	prev	61	0.560	Møller (1991)
	Song rate	obs	imm	41	0.081	Saino et al. (1997b)
	Song performance	obs	prev/imm	30	0.082	Garamszegi et al. (2005b)
<i>Strix aluco</i>	Call rate	obs	prev	20	0.030	Redpath et al. (2000)
<i>Sturnus vulgaris</i>	Song rate	obs	imm	15	0.514	Duffy and Ball (2002)
<i>Taeniopygia guttata</i>	Song rate	obs	imm	31	-0.125	Birkhead et al. (1998)
Combined				240	0.255 (SE = 0.117)	
					<i>P</i> = 0.026	
<b>Correlates of song complexity</b>						
<i>Acrocephalus schoenobaenus</i>	Repertoire size	obs	prev	15	0.578	Buchanan et al. (1999)
<i>Agelaius phoeniceus</i>	Repertoire size	obs	prev	22	-0.322	Weatherhead et al. (1993)
<i>Ficedula albicollis</i>	Repertoire size	exp	imm	27	-0.133	Garamszegi et al. (2004)
<i>Hirundo rustica</i>	PC1 <sup>a</sup>	obs	imm	31	0.043	Saino et al. (1997b)
	Repertoire size	obs	prev/imm	30	0.360	Garamszegi et al. (2005b)
<i>Sturnus vulgaris</i>	Song-bout length <sup>b</sup>	obs	imm	15	0.375	Duffy and Ball (2002)
Combined				140	0.141 (SE = 0.149)	
					<i>P</i> = 0.339	
<b>Traits reflecting song duration</b>						
<i>Ficedula albicollis</i>	Strophe length	exp	imm	27	-0.145	Garamszegi et al. (2004)
<i>Hirundo rustica</i>	Song length	obs	prev/imm	30	0.267	Garamszegi et al. (2005b)
<i>Strix aluco</i>	Call length	obs	prev	22	-0.220	Redpath et al. (2000)
	Call length	obs	prev	8	0.870	Appleby and Redpath (1997)
<i>Sturnus vulgaris</i>	Song-bout length	obs	imm	15	0.375	Duffy and Ball (2002)
Combined				102	0.225 (SE = 0.218)	
					<i>P</i> = 0.573	
<b>Frequency attributes</b>						
<i>Ficedula albicollis</i>	Frequency range	exp	imm	27	0.124	Garamszegi et al. (2004)
<i>Hirundo rustica</i>	Peak amplitude	obs	prev/imm	30	0.233	Garamszegi et al. (2005b)
	frequency <sup>c</sup>					
<i>Strix aluco</i>	Highest frequency	obs	prev	22	0.560	Redpath et al. (2000)
	Lowest frequency <sup>d</sup>	obs	prev	8	-0.730	Appleby and Redpath (1997)
Combined				87	0.123 (SE = 0.244)	
					<i>P</i> = 0.613	

The sign of an effect size indicates whether it is in the expected direction (+) or not (-). Data type reflects whether the given study used an observational (obs) or an experimental approach (exp). Parasite type can be either parasite prevalence data (prev) or a measure of specific immune function (imm). Random effect sizes are presented. <sup>a</sup>correlation for a principal component that involves high factor loadings for syllable repertoire size; <sup>b</sup>the given source (Duffy and Ball 2002) reports relationships for song length; however, based on the strong relationship between repertoire size and song-bout length (Eens 1997), in the given context song-bout length was used as a measure of song complexity; <sup>c</sup>combined effect for song and rattle peak amplitude frequency (when focusing on repertoire size strictly by the exclusion of table footnotes “a” and “b” from the analyses, the results are similar); <sup>d</sup>data extracted from a figure.

while song rate can operate as a reliable signal of health status due to direct physiological costs on male condition affecting song production, other song features may remain unchanged during parasite infection and may thus indicate intrinsic quality attributes of males, such as parasite resistance (Garamszegi et al. 2004).

In addition to manipulations that reduce immunocompetence, the immune function can also be stimulated exper-

imentally. For example, carotenoids are antioxidants and enhance the activity of the immune system (Møller et al. 2000a). It has been shown in the zebra finch that a manipulation of dietary carotenoid supply invokes parallel changes in cell-mediated immune function and sexual attractiveness in males (Blount et al. 2003). In addition, a medication experiment in blue tits *Parus caeruleus* revealed that intensity of infection by *Haemoproteus majoris* and the prevalence



**Fig. 1** The complexity of the associations between parasites, immune function, and song. When studying the relationship between song and parasitism, specific parasites or particular components of the immune system are related to some song traits. However, from other perspectives there may be many further possible interactions

among different components. In addition, different attributes of the signaling male may affect how it defends itself against different parasites and how it delivers songs. Thus, the probability of finding significant associations between randomly chosen variables is low.

of infection by *Leucocytozoon majoris* can be experimentally reduced, and the detrimental effects of natural levels of infection by these common parasite species can be controlled (Merino et al. 2000). Therefore, if song is to signal health and vigor, the enhancement of the immune function by carotenoid administration or medication may also result in improved song performance. This hypothesis remains to be tested.

An additional advantage of experimental approaches relative to observational studies is that they can control for other potentially confounding variables, such as age or territory quality, and can demonstrate causal relationships. Age may be of special importance, because recent works in the collared flycatcher and in the barn swallow have indicated that immune responsiveness may be age-dependent (Cichoń et al. 2003; Saino et al. 2003). In addition, bird song can also show consistent changes with age (e.g., Eens et al. 1992; Mountjoy and Lemon 1995; Hasselquist et al. 1996; Gil et al. 2001). If immune function, parasitism and secondary sexual characters can differ between age classes, any apparent relationship between sexual traits and parasite loads can be the result of systematic age effects (Thomas et al. 1995). Therefore, the apparent correlation between the expression of songs and parasitism may incorrectly suggest a causal relationship. Unpublished data in the great tit *Parus major* reveals the existence of such an interaction (T. Snoeijs et al. submitted manuscript), whereas another study in the barn swallow shows the opposite (Garamszegi et al. 2005b).

### Parasite-mediated songs and receivers

For a signaling mechanism to evolve, both sender and receiver must benefit from the receiver's action (Espmark et al. 2000). A second assumption of the hypotheses linking parasites to songs is that parasite-mediated sexual selection on song is that parasitism should determine the receiver's behavior via song. For example, it is relatively well-

established that certain song traits may be important for females when choosing social or extra-pair mates (Table 1). Nonetheless, care is needed in interpreting these findings as being direct indicators that song reflects parasitism. Strong evidence for parasite-mediated song performance affecting the behavior of signal receivers would be provided if preferred males simultaneously have superior song performance and health status. For example, Buchanan and co-workers (1999) demonstrated that repertoire size and song flighting in the sedge warbler may hold information on parasitism, since parasitized and nonparasitized males differed with regards with these traits. The authors' previous study using data for the same years (Buchanan and Catchpole 1997) revealed that these song features may be important in female choice, because males with larger repertoires and more song flights paired earlier. This may suggest that female sedge warblers can acquire parasite-free mates by preferring elaborate songs. If this were the case, nonparasitized males would be expected to enjoy higher pairing success, but pairing date was not affected by the presence of parasites (Buchanan et al. 1999). Therefore, it remains difficult to understand how features of song and parasite load affect female preference. Only a few efforts have been made to determine how health status and song displays affect the reaction of potential signal receivers. Male collared flycatchers that were more likely to be able to retain their nest boxes were in a superior state of health, and sang at higher rates (Garamszegi et al. 2004). The same study also showed correlatively that immunologically important song traits may determine mating success. These findings are consistent with the hypothesis that parasites may, through song, mediate both male–male competition and female choice.

An additional problem arising from available studies has been that although their correlative findings are consistent with the hypothesis that females adjust their choice according to song cues bearing information about health, alternative explanations for the observed patterns may remain. A stronger justification of the communicative functions of

song necessitates the design of adequate playback experiments, in which confounding effects can be controlled (Searcy and Yasukawa 1996; Searcy and Nowicki 2000). Currently, we know that song may reflect parasitism in at least five bird species (Table 1). Using the available information in designing playback experiments with particular species and particular song traits would increase our understanding on parasite-mediated acoustic communication in sexual selection.

From the receiver's perspective, it is often neglected that receivers of songs include not only females choosing mates, but also conspecific males that are repelled by the song (Searcy and Andersson 1986; Searcy and Nowicki 2000). Mating success is also affected by males' success in male–male competition for territories. Hence, it is difficult to determine correlatively whether earlier pairing is the product of female preference or of male–male competition (Searcy and Yasukawa 1996; Searcy and Nowicki 2000). Health status signaling may be important for male–male competition as well. Selection may be expected to favor males that are able to assess the health and vigor of their rivals, and song features that reflect immune quality may be used to assess the likelihood of success of a territorial challenge. If song contains information concerning the health or fitness of the singer, then competitors may be able to use song to judge which individuals are most likely to lose a dispute over a territory or mate. Alternatively, if a signal contains information about current health status, due to the risk of horizontal transmission of parasites, males may avoid fighting with less ornamented, ill individuals. To the best of my knowledge this mechanism has not been described in any species.

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### **The costs of parasitism: effect of parasites on host fitness**

The cost of parasitism has been well described in birds and reviewed elsewhere (e.g., Zuk and Stoehr 2002; Schmid-Hempel 2003). Increased parasite load, for example, may directly affect reproductive success, life history, dispersal and survival of avian hosts. In addition, trade-offs between reproductive effort and the cost of mounting an immune response have often been demonstrated, revealing a cost of parasitism. Pathogens have been shown to reduce the fitness of birds in those species that are investigated for the relationship between songs and parasites (Table 2). Some species, such as the barn swallow or the collared flycatcher, have been classic model systems for the study of sexual selection and reproduction in relation to parasitism and immune defense. On the other hand other species, such as the sedge warbler, have been less frequently investigated for the effects of parasites on host fitness, and in others, such as the European starlings the evidence is puzzling (Table 2). In tawny owls, there was an association between parasite load and food supply, suggesting that reproduction and immune system are likely to compete via energetic constraints due to food availability (Appleby et al. 1999). However, for the complete understanding of parasite-mediated sexual se-

lection on songs, the same parasite or component of the immune system should be demonstrated to be associated with acoustic displays, female preference and host fitness. This mechanistic link has been supported by correlative evidence, in the sedge warbler and in the barn swallow. In the sedge warbler, the same study of parasitic blood protozoans revealed that these parasites may affect song characteristics, and also reduce breeding success, as infected females had smaller brood size (Buchanan et al. 1999). In the barn swallow, haematophagous tropical fowl mites *Ornithonyssus bursa* decrease reproductive output in terms of clutch size, brood size and the number of fledglings (Møller 1990b), and also impair singing performance in terms of song rate (Møller 1991). In the collared flycatcher, immune challenge experiments indicated that elevated reproductive effort negatively affects the response of females to a mimicked parasite infection by sheep red blood cell injection (Cichoń et al. 2001), and the latter is known to decrease song rate in males (Garamszegi et al. 2004).

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### **Heritability and genetics of parasite resistance and songs**

Pathogens tend to have shorter generation times than their hosts, and they can be rapidly selected to overcome host immune defenses. Parasites may maintain variability at loci that influence immunity in the host population. Such genetic variation may generate indirect selection on female mating preferences if females expressing a preference for males with higher resistance produce fitter offspring. Therefore, a critical assumption of the Hamilton-Zuk hypothesis is that parasite resistance and the expression of bird song, which are both targets of female choice, should be heritable and genetically correlated (Clayton 1991; Hillgarth and Wingfield 1997). These criteria are not required to be met by other models relying on direct fitness benefits to explain the parasite-mediated selection of song. Also, if the relationship between parasitism and songs is mediated by condition-dependent signal expression that reveals health and vigor, the heritability of traits is not necessarily maintained.

Heritable resistance to parasites is widespread among domestic animals and includes immunological, anatomical and physical mechanisms (Wakelin and Blackwell 1988; Wakelin 1996). Field-derived estimates of both genetic resistance to particular parasites and genetic determination of immunocompetence have indicated significant heritabilities (Glick 1983; Hillgarth 1990; Zuk et al. 1990; Cheng et al. 1991; Kean et al. 1994; Boulinier et al. 1997; Kurtz and Sauer 1999; Christe et al. 2000; Råberg et al. 2003). Among the species listed in Table 1, cross-fostering experiments with the barn swallows have suggested that genetic quality of the parent may affect the resistance of offspring to parasitism (Møller 1990a). In tawny owl chicks, the best predictor of parasite number was the parasite load of their fathers, but the parasites of chicks were not the parasites with which their fathers were heavily infested, which in turn could be due to inherited immunity (Appleby et al. 1999).

On the other hand, our knowledge about heritabilities of song traits is rather incomplete. Studies on particular song features have indicated that there may be considerable variation in heritabilities of different song traits (Hasselquist 1994; Brenowitz and Kroodsma 1996). It has been found in the zebra finch that attractive males have higher song rates and have sons with higher song rates (Houtman 1992), although song rate was unrelated to several measures of immune function (Birkhead et al. 1998). Additionally, in this species the neural basis of song production, as reflected by the size of the high vocal centre (HVC) determining song output, is the target of sexual selection and has significant heritability (Airey et al. 2000a). Only one breeding experiment has been able to show that differences in song learning are due to genetic differences (Mundinger 1995). Studies on crickets have confirmed that there is a positive genetic correlation between immune function and body size, which determines the characteristics of song in these animals (Ryder and Siva-Jothy 2000; Ryder and Siva-Jothy 2001). As yet there is no similar study in birds that shows a genetic correlation between song and parasitism. Thus, predictions regarding the heritability and genetic correlation of traits clearly merit further attention.

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### Songs, parasites and parental investment

For the efficient parent hypothesis to act via parasites it is required that parasite-mediated song should affect the parental effort of the male. It is often considered that bird song has the function to signal parental investment of the male (Yasukawa et al. 1980; Greig-Smith 1982; Hoi-Leitner et al. 1993; Welling et al. 1997; Buchanan and Catchpole 2000), but negative evidences have also been reported (Mountjoy and Lemon 1997; Rinden et al. 2000). In addition, it seems possible that female choice may in part be based on territory quality rather than song directly, but age may be a confounding factor as well (Buchanan and Catchpole 2000). From the parasite side it has been reported that increased parasite load may reduce parental investment of birds (e.g., Darolova et al. 1997; Buchanan et al. 1999; Ilmonen et al. 1999). Note that the relationship between infection status and feeding rate may appear in the opposite direction as well, if parents increase their parental investment at heavily parasitized nests in order to compensate the harmful effect of these parasites (Hurtrez-Boussès et al. 1998; Wesolowski 2001; Bouslama et al. 2002). The activation of the immune system by antigen injection can induce a drop in feeding rate (Råberg et al. 2000; Bonneaud et al. 2003), whereas enhanced parental effort at nestling care decreases antibody responsiveness (Deerenberg et al. 1997). These results imply that, as other components of reproduction, parental care is also traded against the maintenance of an efficient immune system, which suggests an important role for parasites. In a meta-analysis Møller et al. (1999) found a non-significant trend for a stronger relationship between parasites and sexual traits in species in which male provides paternal care. Based on this evidence we can assume that if song is affected by par-

asites, females choosing males with elaborate songs may gain a breeding partner that provide superior paternal care due to its superior health status. However, the conclusion that parasites directly mediate a link between song and parental investment may be immature. Again, it would be preferable to demonstrate the role of the same parasites or of component of the immune function on song and paternal care, but such an effort has rarely been made. Buchanan et al. (1999) analyzed variables on parasitism, song and paternal care in a single study, which indeed supported the efficient parent hypothesis. Møller (1994) demonstrated experimentally in the barn swallow that an infection with haematophagous mites reduces food-provisioning rate of parents. However, in a Spanish population there was no interaction between male provision rate and song characteristics (L. Z. Garamszegi et al. unpublished data), or between measures of immune status and food provisioning (P. Ninni unpublished data). As duration and frequency range of notes of the tawny owl were related to reproductive output and territory stability, it has been proposed that these traits may partially signal territory quality in terms of resources and better male parental performance (Galeotti 1998), but direct proof is lacking. Negative evidence was reported in the European starling. Males with large repertoire size—that strongly correlates with song-bout length (Eens 1997)—did not spend more time incubating nor did they make more feeding trips to the nestlings than did males with small repertoires (Mountjoy and Lemon 1997). Unpublished data in the collared flycatcher shows that an immune challenge does not affect male feeding rate during nestling care, and song rate does not covary with this measure of paternal care (L. Z. Garamszegi unpublished data). The lack of direct evidence from song studies for the efficient parent hypothesis may warrant further investigation.

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### The risk of direct parasite transmission and song

The original parasite avoidance hypothesis did not require the expression of a trait to covary with parasite prevalence (Borgia and Collis 1989). If females, assess the parasite load of males directly, dark plumage may be useful when counting parasites. In this context visual traits may function well, but it is difficult to consider a selection for elaborate songs just to make ectoparasites easier to see.

A second assumption of the models that suggest an important role for direct parasite transmission, the parasite avoidance hypothesis and the contagion indicator hypothesis, is that the probability of being parasitized increases when mated with heavily infected males. A copulation may involve the risk of horizontal parasite transmission including sexually transmitted diseases (see references in Able 1996). In some species correlation between the parasite loads of pair members has been found that is an indication for the transmission of ectoparasites (Potti and Merino 1995; Hillgarth 1996; Appleby et al. 1999; Darolova et al. 2001). However, nothing is known about how song may function in the active contagion avoidance

behavior of females. It remains to be demonstrated in the same study that (i) males displaying song traits with high quality have fewer transmittable parasites; (ii) females show preference for these song attributes; and (iii) females mated to males producing high quality songs have smaller parasite load than females that are mated to males with songs of inferior quality. An experimental approach would have the potential to reveal that female preference for given song traits directly avoid the acquisition of parasites. For example, combined with the playback of songs with different qualitative attributes, the manipulation of ectoparasite load of males may allow experiments to test whether females use song cues to avoid parasite transmission.

As bird song plays an important role in intrasexual context, the contagion avoidance hypothesis may be at work in male–male competition. In a proposed alternative mechanism, males may avoid contesting with heavily infested rivals because of the risk of horizontal transmission of parasites. If this was true, an experimental approach should demonstrate that parasitized males are less frequently challenged by healthy individuals than non-parasitized males.

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### Evolutionary implications

In order for female choice to evolve, there must exist sufficient phenotypic variance among males to allow discrimination among potential mates, and this usually leads to directional selection (Møller and Pomiankowski 1993). Hence, mechanisms acting within species could have evolutionary consequences that are reflected by patterns observed among species. Song features that function to signal individual health within species may be expected to be related to parasitism across species as well. Consequently, in species experiencing high parasite pressure, sexual selection may have favored the expression of sexual signals because of the benefits of female mate preferences for healthy males. As discussed earlier, mate preferences for parasite-free males may evolve because of indirect fitness benefits through resistance genes (Hamilton-Zuk hypothesis), through direct benefits by avoidance of contagion (contagion indicator hypothesis) or through the acquisition of a mate with superior paternal quality (efficient parent hypothesis). Under a model of evolution determined by the costs that parasites impose on their hosts, species with high parasite pressure will develop more pronounced selection for signals of health, which leads to a positive interspecific correlation between pathogens and songs. Note that the parasite avoidance hypothesis does not require an intraspecific covariation between trait expression and parasite load. Thus, natural selection for mechanisms that help the detection of transmittable parasites cannot be expected to generate an interspecific relationship between parasites and songs. Contrary, the general validity of the other hypotheses of parasite-mediated sexual selection would require a positive interspecific relationship between the expression of songs and parasitism.

Although the comparison of song among species can be difficult (Krebs and Kroodsma 1980), comparative stud-

ies have provided supporting results regarding the role of parasites in the evolution of bird song (Hamilton and Zuk 1982; Møller et al. 2000b; Garamszegi et al. 2003), but negative evidence has been also reported (Read and Weary 1990). Although the positive interspecific relationship between song and parasite pressure is consistent with what the hypotheses of parasite-mediated sexual selection predict among species, other evolutionary mechanisms may be in effect (Garamszegi et al. 2003).

Notably, available comparative studies basically focused on song complexity. However, given the stronger effect size for the intraspecific relationship between song performance related traits and parasites (Table 2.), it would be interesting to see an interspecific analysis that tests for similar phylogenetic associations. If parasite-mediated sexual selection acting on song performance is truly a general phenomenon across birds, the costs of parasitism and song performance should drive a causal evolutionary linkage in which pathogens trigger sexual selection on songs due to female preference for healthy males.

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### Conclusions

In general, available intra- and interspecific examples indicate that bird song may function to signal health status. Several studies demonstrated a relationship between the expression of song and parasitism both within and among species. However, a significant amount of negative evidence is available, which makes generalization conservative.

The inconsistency of empirical results may, partly, be explained because signal design is related to the information being conveyed. Performance-related traits may be reliable indicators of immediate immune status, probably due to handicap mechanisms mediated by energetic constraints. Although song complexity may be an index signal of parasite resistance, a meta-analysis revealed no significant evidence for such a role. Since bird song is a multifaceted ornament consisting of components with potentially different biological determination and function, future experiments should attempt to uncover how different song traits signal information regarding parasite resistance and immediate health status.

Considering the communication between singers and receivers, for receivers of songs it might be beneficial to distinguish among males by acoustic cues reflecting health. Parasite-mediated sexual selection by songs thus may be expected to involve both female choice and male–male competition, but we basically lack supporting evidence. Therefore there is a need for further playback studies, which take the receiver's perspective into account.

Several hypotheses have been proposed to explain the association between parasitism and sexually selected characters, such as bird song. Therefore, males with superior immune status may provide parasite resistance genes for the offspring, display advanced parental abilities, harbor fewer transmittable parasites, and have a higher chance of winning territorial disputes. Although there are

obvious species-specific patterns, at present it is unclear which mechanism is of general importance. Of particular importance would be, a demonstration of the genetic association between parasite resistance and song quality. Such results would exclusively support the hypothesis proposing a role for indirect fitness benefits of females by parasite resistance genes, as was suggested by Hamilton and Zuk in their influential study (Hamilton and Zuk 1982).

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