The evolution of song in female birds in Europe

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Bird song is usually regarded as an attribute of males. However, in some species, females may also produce songs even with comparable complexity to that of males. It has been suggested that female song may evolve due to similar selection pressures acting on males, but no study has yet investigated the evolution of female vocalization in a phylogenetic context, a gap that we intended to fill with this study. Based on standard descriptions in The Birds of Western Palearctic, we classified 233 European passerine species with respect to whether females are known to produce songs or not. We were more likely to find information on female song for species whose song is more studied than for less intensively studied species. When we traced information on female song on a phylogeny, we found that at least in 2 avian families, female song appeared to be the ancestral state, but such an ancestral state may be expected to be even deeper in the phylogenetic tree with increasing information on female song. In fact, we cannot exclude the possibility that the ancestor of European passerines had females capable of singing. In a preliminary comparative study based on the available data, we found some evidence that female song may have evolved under the influence of sexual selection as carotenoid-based dichromatism was positively related to female song among species. Our findings imply that due to publication bias, the evolutionary importance of female song is generally underestimated. *Key words:* bird song, calls, comparative study, female vocalization, repertoire size, sexual selection. *[Behav Ecol 18:86–96 (2007)]*

There is extreme variance in the complexity and temporal arrangement of male song in birds, which is generally thought to be the result of sexual selection (Catchpole and Slater 1995; Searcy and Yasukawa 1996; Searcy and Nowicki 2000). However, there is growing evidence that singing behavior is not restricted to males, as at least in some species females are also active vocally (Langmore 1998). Female song is usually described as less complex than male song (e.g., Hoelzel 1986; Kasumovic et al. 2003; Rogers 2005), but there are also examples of species where song parameters overlap between the sexes or where females sing songs as complex as males (e.g., Gahr and GarciaSegura 1996; Pavlova et al. 2005; Brunton and Li 2006).

Females may sing either in solo or duet, for broadly the same reasons as males (Langmore 1998; Hall 2004), most importantly to deter intrasexual competitors from territories or mates (Brown and Lemon 1979; Sonnenschein and Reyer 1983; Arcese et al. 1988; Hobson and Sealy 1990; Kriner and Schwabl 1991; Bensch and Hasselquist 1992; Cooney and Cockburn 1995; Langmore and Davies 1997; Langmore et al. 2002; Grafe et al. 2004; Rogers 2005; Seddon and Tobias 2006). However, females may also use song to maintain intra-pair contact and coordinate breeding activities (Ritchison 1983; Sonnenschein and Reyer 1983; Gilbert and Carroll 1999; de Silva et al. 2004), to attract mates (Langmore et al. 1996; Levin 1996; Morton 1996; Eens and Pinxten 1998), and to solicit copulations (Langmore et al. 1996, see also Cooney and Cockburn 1995). These studies emphasizing the biological relevance of female song generally imply that although female song seems to be rare, it is not a functionless by-product of extreme physiological conditions (Langmore 1998). As such, it should be sensitive to both sexual and natural selection, which should produce differences among species.

Female singing behavior varies between species (Riebel 2003; Riebel et al. 2005), which may have consequences for the evolution of associated neural structures (MacDougall-Shackleton and Ball 1999; Garamszegi et al. 2005). However, given that song production in females corresponds to certain social and ecological contexts (Langmore 1998), we can expect that interspecific variation in female song should be associated with intensity of natural and sexual selection. Such evolutionary roles could be identified in a phylogenetic context, although such studies remain rare if not absent. This is in striking contrast with the intense interspecific study of male songs (e.g., Read and Weary 1992; DeVoogd et al. 1993; Badyaev et al. 2002; Garamszegi and Møller 2004). Here we suggest that the scarcity of research on female song does not reflect its evolutionary importance. Although verbal arguments have suggested that the evolutionary role played by female song is underestimated (Riebel 2003; Riebel et al. 2005), according to our knowledge, no comparative study revealed the phylogenetic determination of female vocalization.

In this study, we reviewed species accounts from a secondary source (Cramp and Perrins 1985–1994) and collected data on the presence of female song in European passerines, which were then analyzed in a phylogenetic context. We tested the idea that female singing behavior might be ancestral (Riebel et al. 2005) and that absence not presence of song is a derived trait (i.e., that selection has driven females to give up singing in those extant passerine species where we do not observe female song any longer). We also make a preliminary effort to identify factors that may have contributed to the loss of female song in certain lineages. In general, we predicted that if female song is shaped by sexual selection, a trait reflecting the intensity of this selective force should be associated with the presence of female song. In particular, we predicted that if female song is used for mate guarding or mate attraction, female song should be present mainly in species in which there are considerable differences in male quality. These hypotheses were tested in a comparative phylogenetic framework, in which we related sexual dichromatism as a marker of sexual selection and variance in male quality to female song. We assumed that sexual dichromatism reflects differences in

male quality (Møller and Birkhead 1994; Bennett and Owens 2002) because in dichromatic species, male quality can vary from female-like plumage to elaborate male plumage (Svensson 1984), with a potentially stronger female competition for the males in latter category. Accordingly, we predicted that the relationship between dichromatism and female song will be positive. In our analyses, we controlled for differences in research effort because we predicted that the lack of information on female singing behavior may be an artifact of the paucity of specific studies designed to investigate the function and the evolution of female song.

METHODS

Estimating female song

We compiled information on female song from The Birds of the Western Palearctic (Cramp and Perrins 1985–1994). This handbook provides detailed information on behavioral and ecological traits including singing behavior. Even though each section was written by a different expert group of authors, they all follow a standard format and rely on the primary literature, which facilitates cross-species comparisons. We collected data for 233 passerine species, spanning 26 families and 84 genera. The gathered information for these species are given in the Appendix.

Descriptions on female song are usually very short and basically restricted to acknowledge whether females sing. Therefore, we were unable to collect quantitative information (e.g., repertoire size or song rate) on female song for a sufficient sample of birds allowing comparative studies of continuous traits. However, we could categorize female song in the following groups. Species for which it was clearly stated that females do not sing were considered as species with nonsinging females and were scored as "0." In many species, there was no information on female song, which were given an intermediate score of "1." Note, that having no report on female song may indicate truly that females do not sing, but it may also mean that females do sing in nature, but until now it went unnoticed. We gave a score of "2" to those species in which descriptions mentioned female song. We applied a broad-sense criterion, and we also accepted positive observations in captive animals as reported in our source as supporting evidence for female song. Similarly, we equally considered songs and subsongs (but not calls) as defined in the handbook. This categorization seems to be reliable as different observers arrive at similar categories even when using different sources, such as the German handbook edited by Glutz von Blotzheim (1985–1997) (association between scores when observers use the same sources: $\chi^2 = 12.26$, degrees of freedom [df] = 1,20, $P < 0.001$; when observers use different sources: $\chi^2 = 8.11$, df = 1,20, $P = 0.004$; see also Garamszegi et al. 2005).

Because the biological meaning of having no information on female song (score 1) is confusing, we applied 2 approaches. First, we considered a minimal model, in which each "no report" was considered evidence for the lack of female song. Accordingly scores of 0 and 1 were pooled. Second, we considered a more reliable model, in which we used the original 3-state ordinal scores, and we considered that having no information on female song may not necessarily imply that females do not sing.

Research effort

The probability of having information on female song in a given species may depend on the intensity of studies targeting the species in general and its song in particular. Therefore, we estimated research effort at 2 levels and considered them in our comparative framework to control for their confounding effects. First, to assess the intensity of studies in general, we counted the number of papers published since 1972 on each species as cited in the Web of Science (http://www.isiknowledge.com). Second, to assess the intensity of studies focusing on the species' song in particular, we counted the number of words in the song-related sections (Song Display and Calls of Adults) in electronic version of The Birds of the Western Palearctic (Cramp and Perrins 1985–1994). We assumed that this measure reflects the intensity of research on song because the number of words in the song sections was smaller in species in which quantitative information is available for male song (e.g., listed in Read and Weary 1992; MacDougall-Shackleton 1997) than in species without available quantitative information on male song ($t_{231} = 6.215$, $P < 0.001$). Estimates of research effort were $\log_{10}$ transformed.

Sexual dichromatism

We scored the breeding plumage of all species as sexually monochromatic if males and females did not differ in coloration according to information provided by the descriptions in Cramp and Perrins (1985–1994) and otherwise as sexually dichromatic (with males bearing more colorful plumage than females). This procedure was repeated separately for carotenoid- and melanin-based coloration because they have fundamentally different signal content, and combining different colorations in a comparative analysis is not appropriate (Badyaev and Hill 2000). We distinguished carotenoid-based sexual monochromatism and dichromatism relying on colors that were yellow, orange, and red as caused by carotenoids (see Tella et al. 2004; Olson and Owens 2005 for similar criteria). For melanin-based coloration, we included all colors that were brown, black, or reddish brown as typical for coloration based on phaeo- and eu-melanin (see also Gray 1996; Tella et al. 2004; Olson and Owens 2005).

We are aware that our method of estimating plumage brightness based on human vision does not account for UV wavelengths that birds can perceive (Bennett et al. 1996; Andersson and Amundsen 1997; Cuthill et al. 2000). However, as Bennett et al. (1994) suggested "for heuristic purposes, it may be useful to express color patterns in subjective terms that humans can readily understand," especially if these are repeatable and standardized. If the modes of human sensual assessment are very different from those normal for the animals, a biological phenomenon could exist but fail to be detected by human appreciation. However, interspecific variation in plumage coloration visually assessed from handbooks and field guides have been repeatedly found to show biologically relevant patterns in relation to other variables (see Møller and Birkhead 1994; Bennett and Owens 2002).

Phylogenetic analyses

We considered the phylogenetic history of species when studying interspecific variation in the presence of female song. The composite phylogeny for birds used in the analyses was mainly based on Sibley and Ahlquist (1990), combined with information from other sources (Sheldon et al. 1992; Blondel et al. 1996; Badyaev 1997; Cibois and Pasquet 1999; Møller et al. 2001). We applied branch lengths (not shown here) from the tapestry tree of Sibley and Ahlquist (1990) for higher taxonomic levels. Within families, the distance between different genera was set to 3.4 $\Delta T_{50}H$ units and between species within genera to 1.1 $\Delta T_{50}H$ units. Using equal branch lengths, which is equivalent to an assumption of a punctuated model of evolution, gave very similar results. The phylogeny used in the comparative study is presented in Figure 2.

By allowing polytomies, we included all taxa in the phylogenetic tree for which we had coded female song as described above. We used unordered character states for the discrete categories, and we did not specify the direction of transitions. Characters were optimized over our phylogeny by using MacClade 4.03 based on Fitch parsimony (Maddison WP and Maddison DR 2001).

To test for the correlated evolution of female song and sexual dichromatism, we applied Pagel's discrete variable method available in the software Discrete (Pagel 1994). This method applies a continuous time Markov model to characterize evolutionary changes along each branch of a phylogenetic tree. Hypothesis testing in this program relies on likelihood ratio (LR) test statistic. This compares the log likelihood of the model for a null hypothesis (H_0) over the model for an alternative hypothesis (H_1), where the LR = -2 $\log_e(H_0/H_1)$. H_0 corresponds to hypothesis of independent evolution of traits, whereas H_1 refers to the hypothesis of correlated evolution of the 2 characters. Hence, the LR statistic, so-called omnibus test, compares the fit of the independent model with the fit of the dependent or correlated evolution of female song and sexual dichromatism. This test is asymptotically chi-square distributed with df = 4, and a Monte Carlo simulation procedure can be used to derive the null hypothesis distribution of significance. Because the phylogenetic framework available in Pagel's discrete model allows to test for the correlated evolution of 2 bivariate state variables, we used our 2-state category of female song (minimal model) without controlling for research effort. Note that by using the raw species data and by controlling for research effort, the 2-state and 3-state models give similar results (Table 1).

We also used Pagel's continuous model (Pagel 1997, 1999) to investigate whether there is a phylogenetic inertia in research effort. We did so because it may happen by accident that certain avian groups are more intensively studied than others, thus evidence for female song may be more likely in these groups. To address this question, we used a measure of phylogenetic correlation, lambda (λ), that varies between 0 (phylogenetic independence) and 1 (species' traits covary in direct proportion to their shared evolutionary history) (Freckleton et al. 2002). Relying on LR test statistics, we compared the log likelihood of an H_0 model with $\lambda = 1$ with the log likelihood of an alternative H_1 model in which the phylogenetic scaling parameter is permitted to take its maximum likelihood value. If the LR test is significant, it indicates that $\lambda < 1.0$ and that research effort is not seriously biased by phylogeny.

RESULTS

Among the 233 species, we found indication for the presence of song in females for 101 species. It was clearly stated that females do not produce song in 8 species only, whereas in 124 species, there was no information on female song. The categories of female song were dependent on research effort because we were more likely to find evidence for female song in more intensively studied species than in less studied species (no. of papers in Web of Science: $\chi^2 = 16.98$, $P > 0.001$, $N = 233$; no. of words in the song sections: $\chi^2 = 33.12$, $P < 0.001$, $N = 233$). Research effort is not seriously concentrated on specific avian taxa by chance (no. of papers in Web of Science: $\lambda = 0.216$ vs. $\lambda = 1.000$, $P < 0.001$; no. of words in the song sections: $\lambda = 0.516$ vs. $\lambda = 1.000$, $P < 0.001$); thus, phylogenetically biased research effort should not drive the phylogenetic distribution of female song data as reported below. The 2 independent estimates of research effort were significantly positively related to each other, indicating that they describe similar phenomena ($r = 0.458$, $N = 233$, $P < 0.001$). A multivariate analysis involving both measures of research effort revealed that research effort on song was a better predictor of any evidence of female song than research effort on the species in general (no. of papers in Web of Science: $\chi^2 = 3.12$, $P = 0.077$, $N = 233$; no. of words in the song sections: $\chi^2 = 21.51$, $P < 0.001$, $N = 233$; Figure 1). Therefore, we controlled for research effort on song in the below analyses of female song.

When relying on the minimal model, in which all species without information on female song were treated as species without female song, the most parsimonious tree of female song (Figure 2A) predicted that female song can be an ancestral state in at least 2 passerine families (Muscicapidae and Fringillidac). However, given the strong effect of research effort on female song categorization, we suspect that this

Table 1

Multivariate logistic models testing the relationship between female song and estimates of sexual dichromatism while holding research effort constant

Independent variables	Dependent variable: female song			
	χ^2	df	Slope ($\pm$SE)	P
Minimal model ($r^2 = 0.142$)	45.33	3		<0.001
No. of words in song sections	27.75	1	3.95 ($\pm$0.75)	<0.001
Melanin-based dichromatism	0.77	1	0.26 ($\pm$0.30)	0.382
Carotenoid-based dichromatism	3.90	1	0.72 ($\pm$0.36)	0.048
Realistic model ($r^2 = 0.115$)	43.78	3		<0.001
No. of words in song sections	30.37	1	3.40 ($\pm$0.62)	<0.001
Melanin-based dichromatism	0.50	1	0.20 ($\pm$0.28)	0.478
Carotenoid-based dichromatism	4.05	1	0.71 ($\pm$0.35)	0.044

In the minimal model, female song was used as a dichotomous variable, in which species without information on female song were considered to be species without female song. The realistic model corresponds to the situation when species without information on female song were distinguished from species without female song by using 3-state categories, with the former species placed in an intermediate category. $N = 233$.
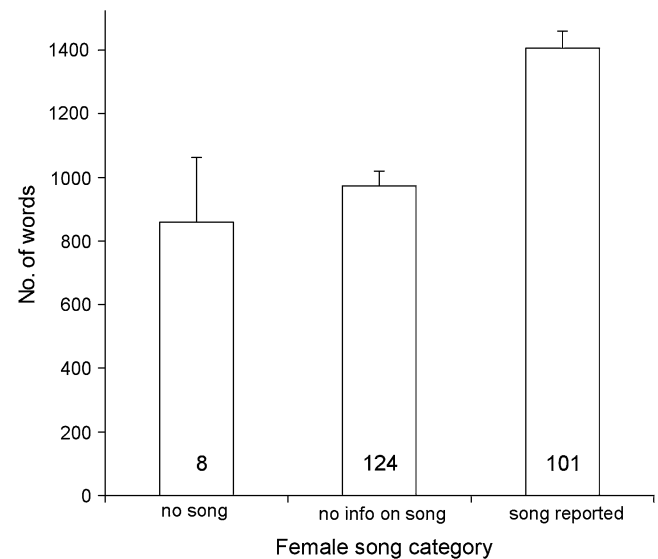

Figure 1
The relationship between research effort ($\pm$SE) and the categorization of female song when research effort was estimated based on the number of words in the songs sections of The Birds of the Western Palearctic (Cramp and Perrins 1985–1994).
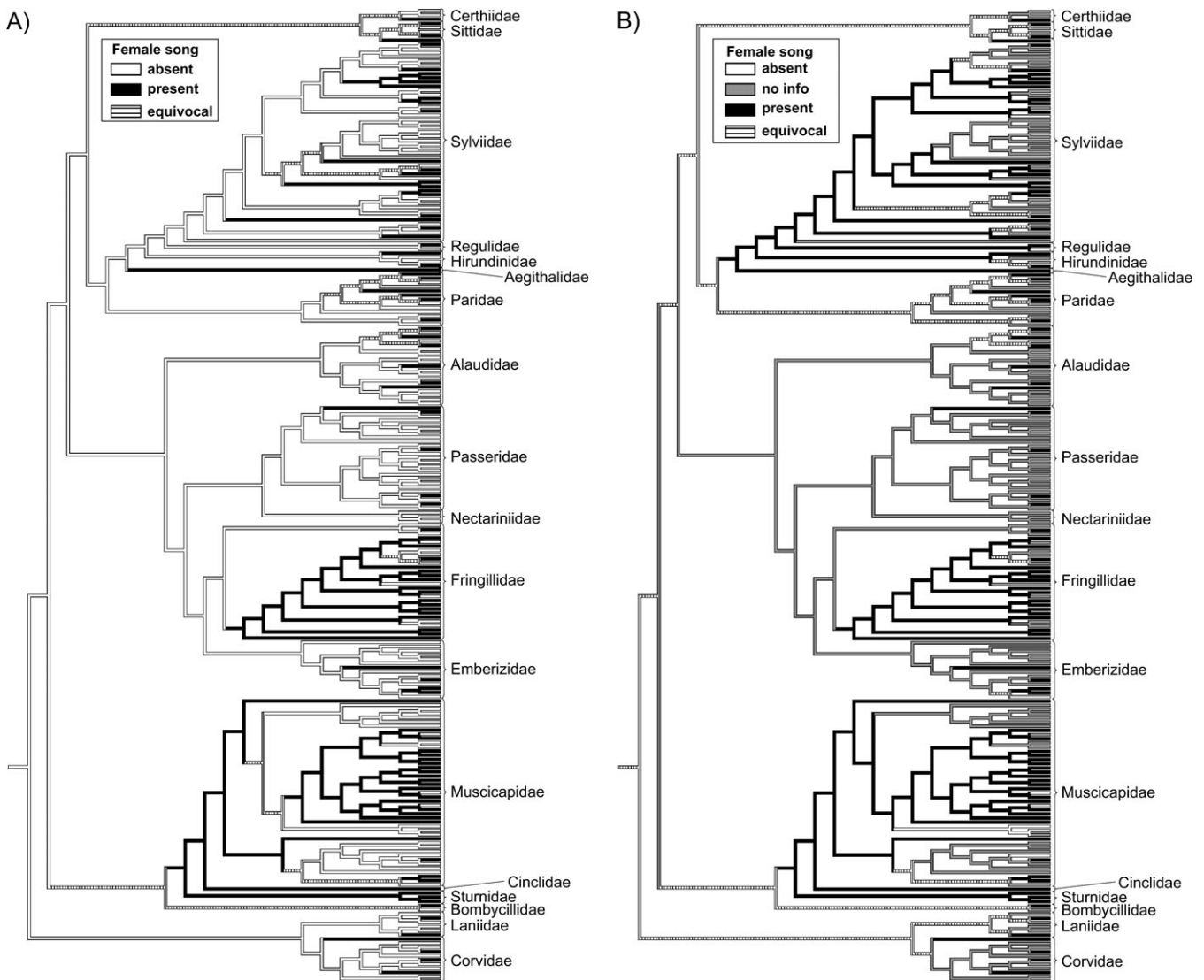
Figure 2
Phylogenetic distribution of female song in European passerines. (A) Minimal model, in which species without information on female song were treated as species without female song. (B) A more realistic model, in which species without information on female song were categorized into an intermediate group between species with evidence for the presence and absence of song.

minimal model is flawed by the fact that several little studied species with singing females were mistakenly categorized as species without female song in the minimal model. Therefore, we also created a more realistic model, which distinguished species without female song from species without information on female song by treating the latter category as an intermediate category. The most parsimonious tree of these categories revealed that the ancestral state of female song could be deeper in the phylogeny than suggested by the minimal model (Figure 2B). This phylogenetic model suggested that in addition to Muscicapidae and Fringillidae, female song could be the ancestral state in Sylvidae. In fact, we cannot reject the hypothesis that at the root of the tree, the ancestor of all European passerines had females that were able to sing.

Using the raw data, we created statistical models that included female song as a dependent variable and research effort on song and different measures of sexual dichromatism as independent variables. We found an association between the presence of female song and carotenoid-based sexual

dichromatism, but melanin-based sexual dichromatism was unrelated to female song (Table 1). When we considered the phylogenetic history of species and modeled the correlated evolution of traits by using Pagel's discrete method, we found significant evidence for female song coevolving with sexual dichromatism in carotenoid-based plumage (LR = 6.196, $P < 0.001$ after 100 simulations).

DISCUSSION

In this preliminary study of interspecific variation and evolution of song in female European passerines, we demonstrated that our knowledge about this phenomenon is seriously affected by the intensity of research on song. Despite this shortcoming, we were able to find some evidence for the recently proposed hypothesis that song in females may be a relatively ancestral state (Riebel et al. 2005). We found that, at least in 2 avian taxa, the presence of female song had been the ancestral state, whereas subsequent evolutionary transitions

may have led to that females lost or gave up singing in some species. We suspect that such evolutionary changes may have occurred during the very early phylogenetic history of European passerines. We also showed that these transitions may be favored by sexual selection because we found evidence for correlated evolution of carotenoid-based sexual dichromatism and female song. However, no significant relationship was found between melanin-based dichromatism and female song. Below, we speculate that our findings are in line with the hypothesis that female song may be shaped by similar selective factors as in males, with intrasexual competition and mate attraction playing important evolutionary roles (Langmore 1998).

Here we provided the first statistical evidence that our understanding about the importance of female singing behavior may be seriously affected by the little studied nature of the phenomenon. It is striking that in more than half of the studied species, we do not have information (or authors do not think that is important to acknowledge) as to whether females sing or not. In addition, quantitative information on female song is available only for a handful of species (e.g., Hoelzel 1986; Pavlova et al. 2005). However, species can be compared on the basis of the presence of female song, and even such a comparison provides biologically meaningful results. We find it surprising that female song is a neglected component of avian vocalization because clear-cut hypotheses suggest functions in mate attraction and intrasexual competition and thus predict evolutionary roles for female vocal traits (Langmore 1998). Such signaling mechanisms should have important consequences for intraspecific and interspecific variation in female song, similarly to patterns generally observed and investigated in males (Read and Weary 1990; Gil and Gahr 2002; Garamszegi and Møller 2004; Beecher and Brenowitz 2005).

Superimposing the information of female song on the phylogenetic history of European passerines, it seems likely that at least in some ancestral stages, female produced song (Figure 2). Even if we classify each species without information on female song as a species with nonsinging females, we were able to identify 2 families, in which the loss of female song may have been a secondary evolutionary step. Given the strong relationship between research effort and female song categories, we expect that in many species, in which we currently do not have information on female song, systematic research may reveal that females sing during mate attraction or mate guarding for example. These species that were thus mistakenly categorized in our minimal model may change the evolutionary picture summarized in Figure 2A but only toward a direction of more ancestral stage of female singing behavior. The effect of such miscategorization can be seen in the Sylvida group (Figure 2B). In this taxon, there is only one species, in which the used handbook reports no song in females. However, in most genera, there is at least one species where there is evidence for singing females implying that the discovery of female song may be expected in the less studied, sister species. Similarly, increasing information on female song can be expected to change the picture completely in the Passerida or in the Corvida group (Figure 2B). Such changes may result in song being an attribute of females at the root of the phylogeny, a pattern that is allowed by our more realistic model relying on 3-state ordinal scales. Note that a maximal model, which treats each species without information on female song as species with female song, would paint the entire phylogenetic tree in Figure 2 black that represents singing females. Although this would be an extreme situation, the reality must fall between the situations characterized by the minimal and maximal model.

The ancestral state of female singing is likely for several reasons. First, female song is prevalent in Australian birds (Robinson 1949), which are the ancestors of oscine passerines (Barker et al. 2002). Second, even females of some suboscine species can produce songs (Seutin 1987; Kasumovic et al. 2003; Seddon and Tobias 2006). Third, the majority of female birds studied so far are able to learn and discriminate songs as listeners (reviewed in Riebel 2003). Fourth, many experimental studies have shown that song production can be triggered even in nonsinger females with testosterone implants (e.g., Kern and King 1972; Kling and Stevenson 1977; Baker et al. 1987; Hausberger et al. 1995; De Ridder et al. 2002). These facts indirectly suggest that female song may have been more common in early phylogenetic stages, with females of some species being selected to stop singing, while they retained their sensitivity to neuroendocrine mechanisms and their ability to learn in others.

The selective factors that shape the evolution of female song remain to be identified. Here, we made an initial effort to test the hypothesis that female song can be favored by sexual selection as reflected by sexual dichromatism. Although we found some evidence that female song may be more likely in species with carotenoid-based sexual dichromatism, our results should be interpreted with caution due to the quality of available data. Additionally, the apparent relationship between female song and dichromatism may be driven by observer bias as in monochromatic species singing females may be more easily thought to be males than in dichromatic species (Arcese et al. 1988; Baptista et al. 1993; Langmore et al. 1996). However, such observer effects should result in associations for melanin-based dichromatism as well, which we failed to detect. Altogether, among the 124 species for which we found no information on female song, there were 67 dichromatic species (melanin-based and carotenoid-based combined), and this ratio (54%) is very similar to what we can observe in the group of species with singing females (59%). Therefore, detection bias toward more likely observation of dichromatic species to have singing females is unlikely to shape the observed positive relationship between carotenoid-based dichromatism and female singing. It seems that carotenoid-based dichromatism involves specific selection pressures for female song that are not associated with melanin coloration. For example, carotenoid-based plumage coloration is more dependent on physical condition and foraging abilities and less constrained developmentally than is melanin-based coloration, which may serve a basis for condition dependence (Gray 1996; Owens and Hartley 1998; Badyaev and Hill 2000). Therefore, selection for such condition-dependent signals in males can be accompanied by selection on song in females. This coevolution of sexual traits in the 2 sexes would be in accordance with the hypothesis that there may be more intense female mate guarding or territory defense when male mating value is highly variable but only if carotenoid-based sexual dichromatism reflects differences in male quality (see Introduction). However, alternative mechanisms remain applicable. Importantly, sexual dichromatism may also be a result of mutual sexual selection, if differences between sexes are due to the evolution female brightness (Jones and Hunter 1993; Irwin 1994). Taking the female's perspective into account, our results may also show that only those females are able to produce song that simultaneously develop less duller carotenoid-based colors relative to males. A strong negative relationship between song complexity and elaboration of carotenoid-based plumage coloration was documented in male cardueline finches, which may be the result of a trade-off between investment in 2 costly sexual traits (Badyaev et al. 2002). A similar trade-off between coloration and song that acts in females may shape a positive relationship between dichromatism and female song. In any case, given the preliminary nature of our study, the interspecific correlation between

the presence of female song and carotenoid-based dichromatism warrants further investigation, in which quantitative data on female song should be used in combination with control for several potentially confounding factors.

At least, our results suggest that female song may be subject to evolutionary changes mediated by natural or/and sexual selection. Accordingly, evolutionary hypotheses in relation to female song make biological sense and could be tested in a comparative context. For example, female song may evolve in order to help species recognition. A counterintuitive observation in studies of hybridization is that hybrids are disproportionately common in avian taxa with the most extravagant divergence in external phenotype and hence supposedly easier to identify in a mate choice context (Panov 1989; Grant BR and Grant PR 1992; Arnold 1997). If female song acted as a premating isolation mechanism, one might justifiably assume that hybrids would be particularly rare in species with elaborate female song (Diamond and Terbough 1968). It would also be interesting to examine the relationship between female and male songs, which would allow us to understand whether songs of the 2 sexes are shaped by similar or sex-dependent selection pressures (see Ketterson et al. 2005;

Møller et al. 2005 for a similar discussion regarding the evolution of testosterone levels in males and females). Components of sexual selection (e.g., polygyny, extrapair paternity, and paternal care) would be potentially interesting determinants because female song has been suggested to evolve due to selection pressures similar to those that favor male song (Langmore 1998).

To summarize, supporting a recent suggestion formulated on theoretical grounds (Riebel et al. 2005), we demonstrated that song in females could be an ancestral condition, from which sexual selection may drive females of some species to give up singing. Our results emphasize the urgent need for studies focusing on female vocalization. By increasing the intensity of research targeting female song, we will be able to study the determinants of intraspecific variation of this interesting behavior. It may be interesting to investigate the costs and benefits of female song by inducing or eliminating song because if it is done in a phylogenetic context, this should result in patterns coherent with the present comparative findings. In addition, accumulated quantitative information at the interspecific level will allow more accurate species–species comparisons and thus the investigation of the evolution of female song.

APPENDIX

Scores for female song as estimated from The Birds of Western Palearctic ("0": evidence for no female song; "1": no information on female song and "2": evidence for female song), research effort as estimated by the number of words in the song sections and by the number of papers found in the Web of Science, and melanin- and carotenoid-based dichromatism

Species	Female song	No. of words	No. of papers	Melanin dichromatism	Carotenoid dichromatism
Acrocephalus agricola	2	806	1	0	0
Acrocephalus arundinaceus	2	2,175	141	0	0
Acrocephalus brevipennis	1	820	3	0	0
Acrocephalus dumetorum	2	1,780	4	0	0
Acrocephalus melanopogon	1	1,206	11	0	0
Acrocephalus paludicola	1	1,685	23	0	0
Acrocephalus palustris	2	2,051	25	0	0
Acrocephalus schoenobaenus	2	1,529	47	0	0
Acrocephalus scirpaceus	2	1,241	98	0	0
Acrocephalus stentoreus	1	1,527	2	0	0
Aegithalos caudatus	2	410	40	0	0
Alaemon alaudipes	2	1,028	7	1	0
Alauda arvensis	2	1,920	145	0	0
Ammomanes cincturus	1	989	1	0	0
Ammomanes deserti	1	888	5	0	0
Anthreptes metallicus	1	353	0	1	0
Anthreptes platurus	1	82	0	1	0
Anthus berthelotii	1	461	1	0	0
Anthus campestris	2	1,425	0	0	0
Anthus cervinus	1	2,006	1	0	1
Anthus gustavi	1	888	0	0	0
Anthus hodgsoni	1	1,728	2	0	0
Anthus novaeseelandiae	1	673	5	0	0
Anthus pratensis	1	1,547	39	0	0
Bombycilla garrulus	2	814	3	1	1
Bucanetes githagineus	1	656	2	0	1
Bucanetes mongolicus	1	317	0	0	1
Calandrella brachydactyla	1	1,687	6	1	0
Calandrella rufescens	1	1,524	8	0	0
Calcarius lapponicus	1	1,370	28	1	0
Carduelis cannabina	2	2,007	27	0	1
Carduelis carduelis	2	1,400	18	0	1
Carduelis chloris	2	1,369	88	1	1
Carduelis flammea	1	1,781	30	0	1
Carduelis flavirostris	1	1,584	6	0	1
Carduelis hornemanni	1	1,340	3	0	1
Carduelis spinus	2	2,082	36	1	1
Carpodacus erythrinus	2	1,737	17	0	1

Appendix, continued

Species	Female song	No. of words	No. of papers	Melanin dichromatism	Carotenoid dichromatism
Carpodacus rubicilla	2	1,170	0	0	1
Carpodacus synoicus	1	458	0	0	1
Carpospiza brachydactyla	1	889	2	0	0
Cercomela melanura	1	460	2	0	0
Cercotrichas galactotes	2	857	21	0	0
Certhia brachydactyla	1	1,749	17	0	0
Certhia familiaris	1	2,585	45	0	0
Cettia cetti	2	1,844	5	0	0
Chersophilus duponti	1	800	4	0	0
Cinclus cinclus	2	933	112	0	0
Cisticola juncidis	1	1,320	13	0	0
Coccothraustes coccothraustes	2	791	11	1	0
Corvus corax	1	1,244	137	0	0
Corvus frugilegus	1	1,034	57	0	0
Corvus monedula	2	896	62	0	0
Cyanopica cyanus	1	766	10	0	0
Delichon urbica	2	796	94	0	0
Emberiza aureola	1	967	2	1	1
Emberiza buchanani	1	661	0	1	0
Emberiza caesia	1	600	1	1	0
Emberiza cia	2	974	8	1	0
Emberiza cirlus	2	1,342	30	1	1
Emberiza citrinella	2	1,661	93	1	1
Emberiza hortulana	1	1,527	16	1	0
Emberiza melanocephala	1	853	38	1	1
Emberiza pallasi	1	612	0	1	0
Emberiza pusilla	1	1,042	3	0	0
Emberiza rustica	2	595	1	1	0
Emberiza schoeniclus	1	1,202	51	1	0
Eremalauda dunni	1	967	4	0	0
Eremophila alpestris	2	1,916	41	1	1
Eremophila bilopha	1	502	0	1	1
Eremopterix nigriceps	2	988	1	1	0
Erithacus rubecula	2	2,058	194	0	0
Ficedula albicollis	1	1,847	178	1	0
Ficedula hypoleuca	1	1,749	733	1	0
Ficedula parva	1	1,683	6	0	1
Ficedula semitorquata	1	995	0	1	0
Fringilla coelebs	2	1,318	168	1	0
Fringilla montifringilla	1	1,615	30	1	0
Fringilla teydea	1	378	3	1	0
Galerida cristata	2	2,113	13	0	0
Galerida theklae	1	1,583	6	0	0
Garrulus glandarius	2	1,113	45	0	0
Hippolais caligata	1	968	2	0	0
Hippolais icterina	2	1,517	13	0	0
Hippolais languida	1	997	0	0	0
Hippolais olivetorum	1	424	0	0	0
Hippolais polyglotta	2	1,371	8	0	0
Hirundo daurica	1	694	2	0	0
Hirundo rustica	1	843	587	1	0
Hypocolius ampelinus	1	623	0	1	0
Irania gutturalis	2	1,269	0	1	0
Lanius collurio	1	1,172	65	1	0
Lanius excubitor	2	1,191	36	0	0
Lanius isabellinus	1	445	1	1	0
Lanius minor	1	1,172	14	1	0
Lanius nubicus	1	602	2	1	0
Lanius senator	2	1,560	13	1	0
Locustella fluviatilis	1	1,928	5	0	0
Locustella lanceolata	1	1,033	1	0	0
Locustella luscinioides	2	2,081	12	0	0
Locustella naevia	2	2,390	8	0	0
Loxia curvirostra	2	1,837	47	0	1
Loxia leucoptera	2	1,712	16	0	1
Loxia pytyopsittacus	2	1,464	1	0	1
Loxia scotica	2	1,338	3	0	1
Lullula arborea	2	2,167	15	0	0
Luscinia calliope	2	1,110	0	1	0

Appendix, continued

Species	Female song	No. of words	No. of papers	Melanin dichromatism	Carotenoid dichromatism
Luscinia luscinia	2	1,774	15	0	0
Luscinia megarhynchos	2	1,494	79	0	0
Luscinia svecica	2	2,108	43	1	0
Melanocorypha bimaculata	1	730	1	0	0
Melanocorypha calandra	1	1,440	2	0	0
Melanocorypha leucoptera	1	557	0	1	0
Melanocorypha yeltoniensis	1	836	0	1	0
Miliaria calandra	0	1,520	68	0	0
Monticola saxatilis	2	858	3	1	0
Monticola solitarius	2	1,283	2	1	0
Montifringilla nivalis	2	1,901	4	1	0
Motacilla alba	1	949	38	1	0
Motacilla cinerea	1	872	21	1	1
Motacilla citreola	1	519	4	1	1
Motacilla flava	1	1,329	27	1	1
Muscicapa striata	1	838	13	0	0
Nectarinia osea	1	660	22	1	1
Nucifraga caryocatactes	1	1,395	12	0	0
Oenanthe alboniger	0	389	0	1	0
Oenanthe deserti	2	1,066	0	1	0
Oenanthe finschii	2	1,117	1	1	0
Oenanthe hispanica	2	1,362	7	1	0
Oenanthe isabellina	2	1,470	2	1	0
Oenanthe leucopyga	2	1,302	1	1	0
Oenanthe leucura	2	1,113	11	1	0
Oenanthe lugens	2	903	1	1	0
Oenanthe moesta	2	889	0	1	0
Oenanthe monacha	0	293	0	1	0
Oenanthe oenanthe	2	1,697	72	1	0
Oenanthe pleschanka	2	1,700	5	1	0
Oenanthe xanthoprymna	2	1,436	0	1	0
Oriolus oriolus	2	1,778	10	1	1
Panurus biarmicus	1	679	23	1	0
Parus ater	2	1,144	67	0	0
Parus caeruleus	2	1,153	331	1	1
Parus cinctus	1	297	24	0	0
Parus cristatus	1	270	40	0	0
Parus cyanus	1	191	0	1	0
Parus lugubris	1	597	2	0	0
Parus major	2	1,811	1,231	1	1
Parus montanus	2	1,630	192	0	0
Parus palustris	2	1,131	94	0	0
Passer domesticus	1	747	661	1	0
Passer hispaniolensis	1	374	15	1	0
Passer iagoensis	1	116	0	1	0
Passer moabiticus	1	216	1	1	0
Passer montanus	1	613	68	0	0
Perisoreus infaustus	1	732	27	0	0
Petronia petronia	2	1,899	13	0	1
Petronia xanthocollis	1	472	11	0	1
Phoenicurus erythrogaster	1	230	0	1	0
Phoenicurus erythronotus	1	244	0	1	0
Phoenicurus moussieri	1	524	0	1	0
Phoenicurus ochruros	2	1,210	26	1	0
Phoenicurus phoenicurus	2	1,141	37	1	0
Phylloscopus bonelli	1	2,284	3	0	0
Phylloscopus borealis	1	1,480	1	0	0
Phylloscopus collybita	2	3,200	62	0	0
Phylloscopus inornatus	1	1,107	3	0	0
Phylloscopus sibilatrix	1	2,770	22	0	0
Phylloscopus trochiloides	2	2,098	9	0	0
Phylloscopus trochilus	2	3,392	126	0	0
Pica pica	2	1,321	238	0	0
Pinicola enucleator	2	1,358	8	0	1
Prinia gracilis	0	845	5	0	0
Prunella atrogularis	1	349	0	0	0
Prunella collaris	2	1,540	25	0	0
Prunella modularis	2	1,057	175	0	0
Prunella montanella	1	352	0	0	0

Appendix, continued

Species	Female song	No. of words	No. of papers	Melanin dichromatism	Carotenoid dichromatism
Prunella ocularis	1	244	0	0	0
Pycnonotus leucogenys	1	342	4	0	0
Pyrrhocorax graculus	1	781	20	0	0
Pyrrhocorax pyrrhocorax	1	670	56	0	0
Pyrrhula pyrrhula	2	1,229	31	0	1
Regulus ignicapillus	0	1,362	7	0	1
Regulus regulus	2	1,486	33	0	1
Remiz pendulinus	1	1,254	38	1	0
Rhamphocoris clotbey	1	630	1	1	0
Rhodopechys sanguinea	2	1,013	0	0	1
Riparia riparia	2	670	88	0	0
Saxicola dacotiae	0	191	4	1	0
Saxicola rubetra	0	650	18	1	0
Saxicola torquata	1	1,013	62	1	0
Scotocerca inquieta	2	906	1	0	0
Serinus canaria	2	872	117	0	1
Serinus citrinella	1	1,589	14	0	1
Serinus pusillus	2	972	1	0	1
Serinus serinus	2	1,304	32	0	1
Serinus syriacus	1	627	0	0	0
Sitta europaea	1	709	92	1	0
Sitta krueperi	1	339	0	1	0
Sitta neumayer	2	643	0	0	0
Sitta tephronota	2	383	0	0	0
Sturnus roseus	2	484	3	1	1
Sturnus unicolor	2	684	28	1	0
Sturnus vulgaris	2	2,427	1,187	1	1
Sylvia atricapilla	2	1,946	192	1	0
Sylvia borin	2	1,046	163	0	0
Sylvia cantillans	1	807	1	1	0
Sylvia communis	1	1,747	44	1	0
Sylvia conspicillata	1	957	1	1	0
Sylvia curruca	1	1,437	7	0	0
Sylvia deserticola	1	596	0	1	0
Sylvia hortensis	2	1,142	3	1	0
Sylvia leucomelaena	2	339	3	1	0
Sylvia melanocephala	1	1,141	11	1	0
Sylvia melanothorax	1	796	0	1	0
Sylvia mystacea	1	798	0	1	0
Sylvia nana	1	1,230	2	0	0
Sylvia nisoria	2	1,461	6	1	0
Sylvia rueppelli	1	712	0	1	0
Sylvia sarda	1	1,063	1	1	0
Sylvia undata	1	1,403	10	1	0
Tarsiger cyanurus	1	1,333	0	1	0
Tichodroma muraria	2	1,708	3	1	1
Troglodytes troglodytes	2	1,755	127	0	0
Turdoides altirostris	1	588	0	0	0
Turdoides squamiceps	2	929	30	0	0
Turdus iliacus	1	1,073	19	0	0
Turdus merula	2	2,079	265	1	1
Turdus philomelos	0	1,623	60	0	0
Turdus pilaris	1	1,163	46	0	0
Turdus ruficollis	1	912	1	1	0
Turdus torquatus	1	806	5	1	0
Turdus viscivorus	1	1,826	9	0	0
Zoothera dauma	1	1,126	2	0	0

REFERENCES

Andersson S, Amundsen T. 1997. Ultraviolet colour vision and ornamentation in bluethroats. Proc R Soc Lond B. 264:1587–1591.

Arcese P, Stoddard PK, Hiebert SM. 1988. The form and function of song in female song sparrows. Condor. 90:44–50.

Arnold ML. 1997. Natural hybridization and evolution. Oxford: Oxford University Press.

Badyaev AV. 1997. Altitudinal variation in sexual dimorphism: a new pattern and alternative hypotheses. Behav Ecol. 8:675–690.

Badyaev AV, Hill GE. 2000. Evolution of sexual dichromatism: contribution of carotenoid- versus melanin-based coloration. Biol J Linn Soc. 69:153–172.

Badyaev AV, Hill GE, Weckworth BV. 2002. Species divergence in sexually selected traits: increase in song elaboration is related to decrease in plumage ornamentation in finches. Evolution. 56:412–419.

Baker MC, Bjerke TK, Lampe HM, Espmark YO. 1987. Sexual response of female yellowhammers to differences in regional song dialects and repertoire sizes. Anim Behav. 35:395–401.

Baptista LF, Trail PW, Dewolfe BB, Morton ML. 1993. Singing and its functions in female white-crowned sparrows. Anim Behav. 46:511–524.

Barker FK, Barrowclough GF, Groth JG. 2002. A phylogenetic hypothesis for passerine birds: taxonomic and biogeographic implications of an analysis of nuclear DNA sequence data. Proc R Soc Lond B. 269:295–308.

Beecher MD, Brenowitz EA. 2005. Functional aspects of song learning in songbirds. Trends Ecol Evol. 20:143–149.

Bennett ATD, Cuthill IC, Norris K. 1994. Sexual selection and the mismeasure of color. Am Nat. 144:848–860.

Bennett ATD, Cuthill IC, Partridge JC, Maier EJ. 1996. Ultraviolet vision and mate choice in zebra finches. Nature. 380:433–435.

Bennett PM, Owens IPF. 2002. Evolutionary ecology of birds. Oxford: Oxford University Press.

Bensch S, Hasselquist D. 1992. Evidence for active female choice in a polygynous warbler. Anim Behav. 44:301–311.

Blondel J, Catzeflis F, Perret P. 1996. Molecular phylogeny and the historical biogeography of the warblers of the genus *Sylvia* (Aves). J Evol Biol. 9:871–891.

Brown RN, Lemon RE. 1979. Structure and evolution of song form in the wrens *Thryothorus sinaloa* and *T. felix*. Behav Ecol Sociobiol. 5:111–131.

Brunton DH, Li XL. 2006. The song structure and seasonal patterns of vocal behavior of male and female bellbirds (*Anthornis melanura*). J Ethol. 24:17–25.

Catchpole CK, Slater PJB. 1995. Bird song: biological themes and variations. Cambridge: Cambridge University Press.

Cibois A, Pasquet E. 1999. Molecular analysis of the phylogeny of 11 genera of the Corvidea. Ibis. 141:297–306.

Cooney R, Cockburn A. 1995. Territorial defense is the major function of female song in the superb fairy-wren, *Malurus cyaneus*. Anim Behav. 49:1635–1647.

Cramp S, Perrins CM. 1985–1994. The birds of the Western Palearctic. Oxford: Oxford University Press.

Cuthill IC, Partridge JC, Bennett ATD, Church SC, Hart NS, Hunt S. 2000. Ultraviolet vision in birds. Adv Study Behav. 29:159–214.

De Ridder E, Pinxten R, Mees V, Eens M. 2002. Short- and long-term effects of male-like concentrations of testosterone on female European starlings (*Sturnus vulgaris*). Auk. 119:487–497.

de Silva HG, Marantz CA, Perez-Villafana M. 2004. Song in female *Hylorchilus* wrens. Wilson Bull. 116:186–188.

DeVoogd TJ, Krebs JR, Healy SD, Purvis A. 1993. Relations between song repertoire size and the volume of brain nuclei related to song—comparative evolutionary analyses amongst oscine birds. Proc R Soc Lond B. 254:75–82.

Diamond J, Terbough JW. 1968. Dual singing by New Guinea birds. Auk. 85:62–82.

Eens M, Pinxten R. 1998. Female song for mate attraction: an overlooked phenomenon? Trends Ecol Evol. 13:322–323.

Freckleton RP, Harvey PH, Pagel M. 2002. Phylogenetic analysis and comparative data: a test and review of evidence. Am Nat. 160:712–726.

Gahr M, GarciaSegura LM. 1996. Testosterone-dependent increase of gap-junctions in HVC neurons of adult female canaries. Brain Res. 712:69–73.

Garamszegi LZ, Eens M, Erritzøe J, Møller AP. 2005. Sexually size dimorphic brains and song complexity in passerine birds. Behav Ecol. 16:335–345.

Garamszegi LZ, Møller AP. 2004. Extra-pair paternity and the evolution of bird song. Behav Ecol. 15:508–519.

Gil D, Gahr M. 2002. The honesty of bird song: multiple constraints for multiple traits. Trends Ecol Evol. 17:133–141.

Gilbert WM, Carroll AF. 1999. Singing in a mated female Wilson's warbler. Wilson Bull. 111:134–137.

Glutz von Blotzheim UN, Bauer KM. 1985–1997. Handbuch der Vögel Mitteleuropas Band. Wiebelsheim: Aula-Verlag.

Grafe TU, Bitz JH, Wink M. 2004. Song repertoire and duetting behaviour of the tropical boubou, *Laniarius aethiopicus*. Anim Behav. 68:181–191.

Grant BR, Grant PR. 1992. Hybridization of bird species. Science. 256:193–197.

Gray DA. 1996. Carotenoids and sexual dichromatism in North American passerine birds. Am Nat. 148:453–480.

Hall ML. 2004. A review of hypotheses for the functions of avian duetting. Behav Ecol Sociobiol. 55:415–430.

Hausberger M, Henry L, Richard MA. 1995. Testosterone-induced singing in female European starlings (*Sturnus vulgaris*). Ethology. 99:193–208.

Hobson KA, Sealy SG. 1990. Female song in the yellow warbler. Condor. 92:259–261.

Hoelzel AR. 1986. Song characteristics and response to playback of male and female robins Erithacus rubecula. Ibis. 128:115–127.

Irwin RE. 1994. The evolution of plumage dichromatism in the new-world blackbirds—social selection on female brightness. Am Nat. 144:890–907.

Jones IL, Hunter FM. 1993. Mutual sexual selection in a monogamous seabird. Nature. 362:238–239.

Kasumovic MM, Ratcliffe LM, Boag PT. 2003. Song structure may differ between male and female least flycatchers. Wilson Bull. 115:241–245.

Kern MD, King JR. 1972. Testosterone-induced singing in female white-crowned sparrows. Condor. 74:204–209.

Ketterson ED, Nolan V, Jr, Sandell M. 2005. Testosterone in females: mediator of adaptive traits, constraint on sexual dimorphism, or both? Am Nat. 166:S85–S98.

Kling JW, Stevenson J. 1977. Development of song and reinforcing effects of song in female chaffinches. Anim Behav. 25:215–220.

Kriner E, Schwabl H. 1991. Control of winter song and territorial aggression of female robins "Erithacus rubecula" by testosterone. Ethology. 87:37–44.

Langmore NE. 1998. Functions of duet and solo songs of female birds. Trends Ecol Evol. 13:136–140.

Langmore NE, Cockrem JF, Candy EJ. 2002. Competition for male reproductive investment elevates testosterone levels in female dunnocks, *Prunella modularis*. Proc R Soc Lond B. 269:2473–2478.

Langmore NE, Davies NB. 1997. Female dunnocks use vocalizations to compete for males. Anim Behav. 53:881–890.

Langmore NE, Davies NB, Hatchwell BJ, Hartley IR. 1996. Female song attracts males in the alpine accentor *Prunella collaris*. Proc R Soc Lond B. 263:141–146.

Levin RN. 1996. Song behaviour and reproductive strategies in a duetting wren, *Thryothorus nigricapillus* 2. Playback experiments. Anim Behav. 52:1107–1117.

MacDougall-Shackleton SA. 1997. Sexual selection and the evolution of song repertoires. In: Nolan V, Ketterson ED, Thompson CF, editors. Current ornithology. New York: Plenum Press. p. 81–124.

MacDougall-Shackleton SA, Ball GF. 1999. Comparative studies of sex differences in the song-control system of songbirds. Trends Neurosci. 22:432–436.

Maddison WP, Maddison DR. 2001. MacClade version 4: analysis of phylogeny and character evolution. Sunderland (MA): Sinauer Associates.

Møller AP, Birkhead TR. 1994. The evolution of plumage brightness in birds is related to extrapair paternity. Evolution. 48:1089–1100.

Møller AP, Garamszegi LZ, Gil D, Hurtrez-Bousses S, Eens M. 2005. Correlated evolution of male and female testosterone profiles in birds and its consequences. Behav Ecol Sociobiol. 58:534–544.

Møller AP, Merino S, Brown CR, Robertson RJ. 2001. Immune defense and host sociality: a comparative study of swallows and martins. Am Nat. 158:136–145.

Morton ES. 1996. A comparison of vocal behavior among tropical and temperate passerine birds. In: Miller EH, editor. Ecology and evolution of acoustic communication in birds. New York: Cornell University Press. p. 258–268.

Olson VA, Owens IPF. 2005. Interspecific variation in the use of carotenoid-based coloration in birds: diet, life history and phylogeny. J Evol Biol. 18:1534–1546.

Owens IPF, Hartley IR. 1998. Sexual dimorphism in birds: why are there so many different forms of dimorphism? Proc R Soc Lond B. 265:397–407.

Pagel M. 1994. Detecting correlated evolution on phylogenies: a general method for the comparative analysis of discrete characters. Proc R Soc Lond B. 255:37–45.

Pagel M. 1997. Inferring evolutionary processes from phylogenies. Zool Scr 26:331–348.

Pagel M. 1999. Inferring the historical patterns of biological evolution. Nature. 401:877–884.

Panov EN. 1989. Natural hybridization and ethological isolation in birds. Moscow: Nauka Press.

Pavlova D, Pinxten R, Eens M. 2005. Female song in European Starlings: sex differences, complexity, and composition. Condor. 107:559–569.

Read AF, Weary DM. 1990. Sexual selection and the evolution of bird song: a test of the Hamilton-Zuk hypothesis. Behav Ecol Sociobiol. 26:47–56.

Read AF, Weary DM. 1992. The evolution of bird song: comparative analyses. Philos Trans R Soc Lond B. 338:165–187.

Riebel K. 2003. The 'mute' sex revisited: vocal production and perception learning in female songbirds. Adv Study Behav. 33:49–86.

Riebel K, Hall ML, Langmore NE. 2005. Female songbirds still struggling to be heard. Trends Ecol Evol 20:419–420.

Ritchison G. 1983. The function of singing in female black-headed Grosbeaks (*Pheucticus melanocephalus*): family-group maintenance. Auk. 100:105–116.

Robinson A. 1949. The biological significance of bird song in Australia. Emu. 48:291–231.

Rogers AC. 2005. Male and female song structure and singing behaviour in the duetting eastern whipbird, *Psophodes olivaceus*. Aust J Zool. 53:157–166.

Searcy WA, Nowicki S. 2000. Male-male competition and female choice in the evolution of vocal signaling. In: Espmark Y, Amundsen T, Rosenqvist T, editors. Animal signals: signaling and signal design in animal communication. Trondheim: Tapir Academic Press. p. 301–315.

Searcy WA, Yasukawa K. 1996. Song and female choice. In: Kroodsma DE, Miller EH, editors. Ecology and evolution of acoustic communication in birds. Ithaca (NY): Cornell University Press. p. 454–473.

Seddon N, Tobias JA. 2006. Duets defend mates in a suboscine passerine, the warbling antbird (*Hypocnemis cantator*). Behav Ecol. 17:73–83.

Seutin G. 1987. Female song in willow flycatchers (*Empidonax taillii*). Auk. 104:329–330.

Sheldon FH, Slikas B, Kinnarney M, Gill FB, Zhao E, Silverin B. 1992. DNA-DNA hybridization evidence of phylogenetic relationships among major lineages of *Parus*. Auk. 109:173–185.

Sibley CG, Ahlquist JE. 1990. Phylogeny and classification of birds: a study in molecular evolution. New Haven (CT): Yale University Press.

Sonnenschein E, Reyer HU. 1983. Mate-guarding and other functions of antiphonal duets in the slate-colored boubou (*Laniarius funebris*). Z Tierpsychol 63:112–140.

Svensson L. 1984. Identification guide to European passerines. 3rd ed. Stockholm: British Trust for Ornithology.

Tella JL, Figuerola J, Negro JJ, Blanco G, Rodríguez-Estrella R, Forero MG, Blázquez MC, Green AJ, Hiraldo F. 2004. Ecological, morphological and phylogenetic correlates of interspecific variation in plasma carotenoid concentration in birds. J Evol Biol. 17:156–164.