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Evolution and life-history correlates of female song in the New World blackbirds

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Female song is much more prevalent in tropical than in temperate songbirds but, we know surprisingly little about the evolutionary origins of this striking latitudinal difference. Here I reconstruct the evolution of female song in the New World blackbird family (Icteridae) and compare historical changes in this trait to changes in several other life-history characters: social mating system, nesting pattern, and migratory behavior. Reconstructions using both parsimony and maximum likelihood methods show that female song has been lost repeatedly in this clade and that tropical ancestors with frequent female song almost invariably were monogamous, had dispersed nest sites, and were nonmigratory. Losses of female song were not consistently associated with changes in any single life-history characteristic across the family, but rather appear to have occurred for different reasons in different lineages, including the evolution of migration in the oriole genus (*Icterus*), the evolution of brood parasitism in the cowbirds (*Molothrus*), and the evolution of polygynous, colonial breeding in the oropendolas (*Psarocolius*, *Gymnostinops*) and caciques (*Cacicus*). These results support previous suggestions that the prevalence of female song in the tropics is largely explained by the life-history traits associated with tropical habitats. *Key words:* ancestral state reconstruction, comparative methods, duetting, female bird song, life history, phylogeny. *[Behav Ecol 20:967–977 (2009)]*

Birds in which both sexes produce complex song are much more common in the tropics than in temperate areas, where songs are produced primarily by males (Morton 1996; Stutchbury and Morton 2001; Slater and Mann 2004; Price et al. 2009). Tropical female song can take the form of precise, stereotyped duets, which have received much attention from researchers (reviewed by Farabaugh 1982; Hall 2004), or individually produced solo songs, which are less well studied and in fact may be underreported if singing females are frequently mistaken for males in these generally sexually monomorphic species (e.g., Illes and Yunes-Jiménez 2008; Price et al. 2008). Frequent female song, produced either individually or as part of a duet, could even be the rule rather than the exception in tropical songbirds (Morton 1996); yet, we know surprisingly little about the behavioral and ecological conditions associated with its evolution (Kroodsma et al. 1996; Langmore 2002; Slater and Mann 2004).

In those species that exhibit singing by both sexes, research to date suggests that females sing for many of the same reasons that songs occur in males (Langmore 1998, 2000; Hall 2004; Catchpole and Slater 2008). For example, studies of a variety of species indicate that females sing to deter same-sex rivals for resources or mates (Beletsky 1983; Sonnenschein and Reyer 1983; Cooney and Cockburn 1995; Levin 1996; Brunton et al. 2008; Illes and Yunes-Jiménez 2008; Mennill and Vehrencamp 2008). In some species, females may sing to attract mates (Langmore et al. 1996; Morton 1996; Eens and Pinxten 1998). Female song may also have a role in maintaining intrapair contact within territories (Logue 2007; Mennill and Vehrencamp 2008) and in coordinating breeding activities between long-term partners (Sonnenschein and Reyer 1983; Halkin 1997; Slater and Mann 2004).

These hypotheses for song function generally predict that female singing should occur most often in species with long-term male–female relationships and convergent sex roles, such as in monogamous songbirds that defend their territories year-round (Langmore 1998, 2000; Hall 2004; Slater and Mann 2004). Species with other life-history traits, such as polygynous or colonial taxa, should exhibit lower levels of competition among females for mates or resources, respectively, and migratory species presumably have male–female relationships that are less stable than those of sedentary pairs. Year-round territoriality, like female song, is relatively common in tropical environments (Stutchbury and Morton 2001, 2008), and this fact alone may largely explain the prevalence of female singers in the tropics. However, few previous studies have investigated the relationship between female singing and life history (Farabaugh 1982; Malacarne et al. 1991; Benedict 2008), and none have used rigorous phylogenetic comparative methods. Controlling for phylogeny is important when testing for such statistical associations between traits because just a few species-rich tropical clades with these characteristics could create a spurious correlation (Felsenstein 1985).

The New World blackbirds (family Icteridae; Clements 2007) provide an ideal model clade for investigating the relationship between female song and other aspects of life history. Many species in this group have been intensively studied, including both tropical and temperate taxa (Jaramillo and Burke 1999), and the phylogeny has been well resolved using both nuclear and mitochondrial DNA sequence data (Lanyon and Barker 2007). Different taxa can have substantially different rates of female song, from species that regularly duet or produce solo songs (*Dives dives*, Orians 1983; *Agelaius assimilis*, Whittingham et al. 1992, 1997) to taxa in which female song is relatively infrequent (*Icterus galbula*, Beletsky 1982) or not known to occur (*Sturnella neglecta*, Lanyon 1994). Furthermore, several other life-history patterns also exhibit wide variation within the family which could covary with female song. Mating behaviors range from social monogamy to some of the most extreme examples of polygyny known in birds (Robinson 1986; Webster 1992, 1994), and different species can nest as dispersed pairs, in dense colonies, or as obligate brood

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parasites (Jaramillo and Burke 1999). Although the territorial behaviors of many icterid taxa have not been studied in detail (Jaramillo and Burke 1999), probably most species with dispersed nests exhibit territorial defense by one or both of the sexes, whereas birds with clumped nests are either nonterritorial or defend only small areas around their nests (Searcy et al. 1999). Species also differ in their patterns of migration, from year-round residents to long-distance migrants (Jaramillo and Burke 1999).

A previous analysis of female song in this family showed that frequent female singing is significantly associated with tropical latitudes and that female song has been lost repeatedly in taxa with evolutionary shifts from tropical to temperate breeding ranges (Price et al. 2009). Some changes in song were not related to breeding latitude in that analysis, however, suggesting that female song evolution is influenced not by latitude itself, but rather by other aspects of life history that are associated with latitude. Here I reconstruct the evolution of social mating systems, nesting patterns, and migratory behaviors in the Icteridae to investigate whether historical changes in female singing behavior have been associated with changes in any of these other characteristics. From the hypothesis that female song is associated with longer term associations between mates and higher levels of competition between females for mates and resources, I predicted that female song should be relatively common in species that are monogamous, have dispersed rather than clumped nest sites, and are sedentary.

METHODS

Character scoring

Information about female singing behavior was obtained from Price et al. (2009), which compiled data from the literature for 65 of the approximately 101 named icterid species (Clements 2007). Only species with clear descriptions of singing behavior were included in the study, and all excluded taxa were tropical or southern temperate and were distributed across 15 genera (Price et al. 2009). I used the reported occurrence of female song relative to male song to score species as having 1) females that sing as frequently as males, 2) females that sing less frequently than males, or 3) females that are not known to sing. I ignored reported differences in the acoustic structure of male and female song because I could not quantify such differences using literature descriptions alone. Differentiating duetting species from solo singers was also difficult using literature descriptions because many icterid taxa combine their vocalizations haphazardly or only occasionally rather than performing highly stereotyped duets (e.g., Whittingham et al. 1997). I therefore included both duetting and solo-singing species in the first category above. Species in which females are reported to sing but not as often as males were included in the second category, and species in which females are reported to not sing or in which only male song has been described were included in the third. A previous comparative analysis by Price et al. (2009) scored female song in this family with just 2 character states by considering categories 2 and 3 above as one state. I treated female song here as a multistate character to help resolve some ancestral states that were ambiguous in that analysis, because multistate reconstruction can reveal details of history that a binary-state reconstruction would not (Kondo and Omland 2007).

I obtained information on other behavioral characteristics of icterid taxa from Jaramillo and Burke (1999). For each species, I scored 3 life-history characters that are easily observed and thus known for most taxa: social mating system, nesting pattern, and migratory behavior. Other potentially important characteristics, such as the contributions of each sex to parental care, were not included in this analysis because they are less well known in many tropical icterids (Jaramillo and Burke 1999; Searcy et al. 1999). For characters that vary across the geographic range of a species (e.g., partial migrants in which some parts of the range are migratory and others not), I scored the population in which most studies or observations of female song have been conducted (Price et al. 2009). Character scores for the 65 taxa included in the study are listed in the Appendix.

Social mating systems were scored as 1) monogamous, 2) polygynous, or 3) variable based on the predominant male–female associations in each species as described by Jaramillo and Burke (1999). Monogamous species are ones in which mating relationships typically (>95% of cases; Searcy et al. 1999) include just one male and one female during the breeding season, whereas polygynous taxa include males mating with more than one female concurrently. Species in which mating associations vary depending on habitat or local adult sex ratio (e.g., *Molothrus ater,* Jaramillo and Burke 1999) were scored as variable. In some taxa, social mating associations have been studied in detail using molecular data (e.g., Webster 1994; Searcy and Yasukawa 1995). For others, my scores were based on field observations compiled by Jaramillo and Burke (1999). I did not consider extrapair mating in these scores as this information was not available for most species.

Nesting pattern refers to the spatial dispersion of nesting females and was scored as 1) dispersed, 2) colonial, or 3) brood parasitic. I scored a species as dispersed if nests are never reported to be near each other, and I considered a species as colonial if females tend to be more clumped than required by the spatial distribution of the birds' preferred breeding habitat (following methods of Searcy et al. 1999). Obligate interspecific brood parasites (found only in the *Molothrus* genus) were assigned a separate character state because nest dispersion in these birds depends on the nesting behaviors of their hosts.

I scored each species as either 1) sedentary or 2) migratory based on whether birds are present year-round in their breeding ranges or are seasonally absent (Kondo and Omland 2007). Sedentary species include taxa that undergo local movements during the nonbreeding season as well as those that maintain permanent territories (Jaramillo and Burke 1999).

Phylogenetic comparative analyses

I reconstructed ancestral states for each character using the same molecular phylogeny used by Price et al. (2009). This tree is based on DNA sequence data from 2 mitochondrial and 4 nuclear loci, and it resolves relationships within and among the family's 4 major subclades: the oropendolas and caciques, the orioles, the grackles and allies, and the meadowlarks and allies (Lanyon and Barker 2007). I used 2 methods for each reconstruction: simple parsimony in MacClade (version 4.06; Maddison DR and Maddison WP 2003) and maximum likelihood in Mesquite (version 2.5; Maddison DR and Maddison WP 2008). The parsimony analysis assumed that all character states were equally weighted and unordered, and the maximum likelihood analysis used the Markov k-state 1-parameter model, which assumes equal rates of change between character states. Although parsimony is more widely used in such evolutionary reconstructions, maximum likelihood has some advantages over parsimony in that it uses information about phylogenetic branch lengths and indicates degrees of support (i.e., likelihood values) for potential ancestral states (Maddison DR and Maddison WP 2008).

In each reconstruction of female song, I refer to increases in female song rates relative to male song as "gains" and decreases in these rates as "losses." Quantifying female song relative to male song technically did not allow me to distinguish between character changes caused by increases in male singing and those caused by decreases in female singing. However, a previous comparison of male singing rates among icterid taxa that have substantially different rates of female song (in the oropendola–cacique clade; Price and Lanyon 2004) showed that male song outputs vary surprisingly little among species, suggesting that most changes have occurred in female singing rates.

I tested for an association between changes in female song and other behavioral characteristics using the concentrated changes test in MacClade (Maddison 1990). This parsimony-based method tests whether changes in a character are significantly concentrated on branches of a phylogeny with some other reconstructed character state, and it requires characters under comparison to have only 2 states each. I therefore converted female song and other life-history traits, as necessary, from multistate to binary parsimony reconstructions for these tests. For female song, I combined 2 of my scores, females that sing less frequently than males and those not known to sing, into one character state: "females sing less than males" (as done by Price et al. 2009). Combining scores in this way accounted for the possibility that infrequent female song in some species could have been mistakenly scored as absent (Garamszegi et al. 2007), and this approach also biased my analysis against identifying taxa as having female song because species were scored as having this trait only if females sing as frequently as males. For social mating systems, I created a "nonmonogamous" state by combining polygynous and variable taxa into one state to test the idea that losses of female song have been concentrated on branches of the phylogeny with nonmonogamous mating systems. Likewise, for nesting patterns, I created a "nondispersed" state by combining colonial and brood parasitic taxa to test whether losses of female song have been associated with the absence of dispersed nesting patterns in taxa. Migratory behavior was already scored as a binary character, which I used to test whether losses of female song have been associated with the loss of sedentary habits. I also tested the hypothesis that all three factors—monogamy, dispersed nesting, and sedentariness—are necessary for female song by first reconstructing life history as a composite character, in which every observed combination of mating, nesting, and migratory pattern was considered as a different character state (with 18 possible combinations), and then scoring branches on the phylogeny as either 1) monogamous, dispersed, and sedentary or 2) having any other life-history pattern. Finally, I compared all these life-history characteristics with breeding latitude, using latitude scores from Price et al. (2009), to test whether any individual or composite character states tend to be found in tropical or temperate taxa more often than expected by chance.

Every character had more than one possible reconstruction of ancestral states in parsimony reconstructions (see below), so for each comparison, I performed multiple concentrated changes tests using all possible combinations of DELTRAN (which favors independent gains/losses over reversals) and ACCTRAN (which favors reversals over independent gains/losses) assumptions for each character. Thus, each comparison generated a range of P values. I performed each test using 10 000 simulations.

RESULTS

Both parsimony and maximum likelihood multistate reconstructions of song evolution showed that female song rates have decreased repeatedly in comparison to male song in the New World blackbird family (Figure 1). Parsimony analysis resulted in 28 equally parsimonious reconstructions on the tree, all of which indicated that males and females had similar song rates in most ancestral taxa. This character state has been lost at least 12 separate times, with female song either becoming less frequent than male song or disappearing altogether. Maximum likelihood reconstructions provided strong support for similar male–female song rates in the ancestors of the oropendolas and caciques (likelihood = 0.74), the orioles (0.95), and the grackles and allies (0.91). Neither method supported any single character state for the ancestor of the meadowlarks and allies (all likelihood values <0.50). Parsimony also did not resolve the character state in the ancestor of the Icteridae, whereas maximum likelihood suggested that this ancestor had similar song rates in both sexes (likelihood = 0.69).

Parsimony and maximum likelihood methods indicated that ancestral taxa with frequent female song (i.e., ancestors of oropendolas and caciques, orioles, and grackles and allies) were also socially monogamous (Figure 2), had dispersed nests (Figure 3), and were sedentary (Figure 4). Likelihood values supporting these states ranged from 0.66 to 1.00. Polygynous mating has evolved from monogamous ancestors repeatedly in these clades, at least 6 times based on parsimony reconstructions (Figure 2). Likewise, colonial nesting evolved multiple times and brood parasitism evolved once, both from ancestors with dispersed nests (Figure 3), and migration evolved from sedentary ancestors at least 7 times independently using either method of reconstruction (Figure 4). Both methods also indicated that the ancestor of the meadowlarks and allies was polygynous (likelihood = 0.74) and had dispersed nests (1.00), but parsimony resolved this ancestor as migratory, whereas maximum likelihood suggested that it was sedentary (0.63). Neither method provided clear support for the social mating system of the ancestor of the Icteridae (likelihood of monogamy = 0.51, polygyny = 0.48; Figure 2), but both strongly indicated that this ancestor had dispersed nests (likelihood = 1.00; Figure 3). Maximum likelihood indicated that the ancestor of the family was sedentary (0.80), although this node was not resolved in parsimony reconstructions (Figure 4).

Concentrated changes tests showed that female song is significantly associated with a monogamous, dispersed nesting, and sedentary life history when these traits are considered together as a composite character state ($P < 0.01$ in tests using all possible combinations of ACCTRAN and DELTRAN assumptions; Figure 5). Of the 21 species known to have this combination of life-history traits, only 1 (*Amblyramphus holosericeus*) lacks frequent female song and altogether only 4 species have frequent female song but lack all 3 of these traits (*Icterus bullockii*, *Agelaius xanthomus*, *Agelaius humeralis*, and *Dives warszewiczi*). When each life-history trait was considered separately, however, no single one was consistently associated with evolutionary changes in female song across the phylogeny. Of the 11 or more independent losses of female song (when reconstructed as a binary character; Figure 5A), at least 8 occurred in monogamous taxa, and concentrated changes tests showed that losses of female song have not been concentrated on branches of the phylogeny with nonmonogamous mating patterns (P values from 0.06 to 0.27 in all tests). Losses of female song were also not consistently associated with nesting pattern (P values from 0.03 to 0.25), with at least 4 losses occurring in dispersed nesting taxa. Losses of female song were significantly related to migration (P values from 0.003 to 0.05), with nearly all migratory species (18 of 19) having females that sing less often than males, if at all. However, at least 5 losses of female song have occurred in sedentary lineages, and females sing as frequently as males in only 56% (25 of 45) of sedentary species, so migration is clearly not the only factor influencing female song evolution. Female song appears to be associated with a suite of traits, the loss of any one of which may lead to the loss of female song.

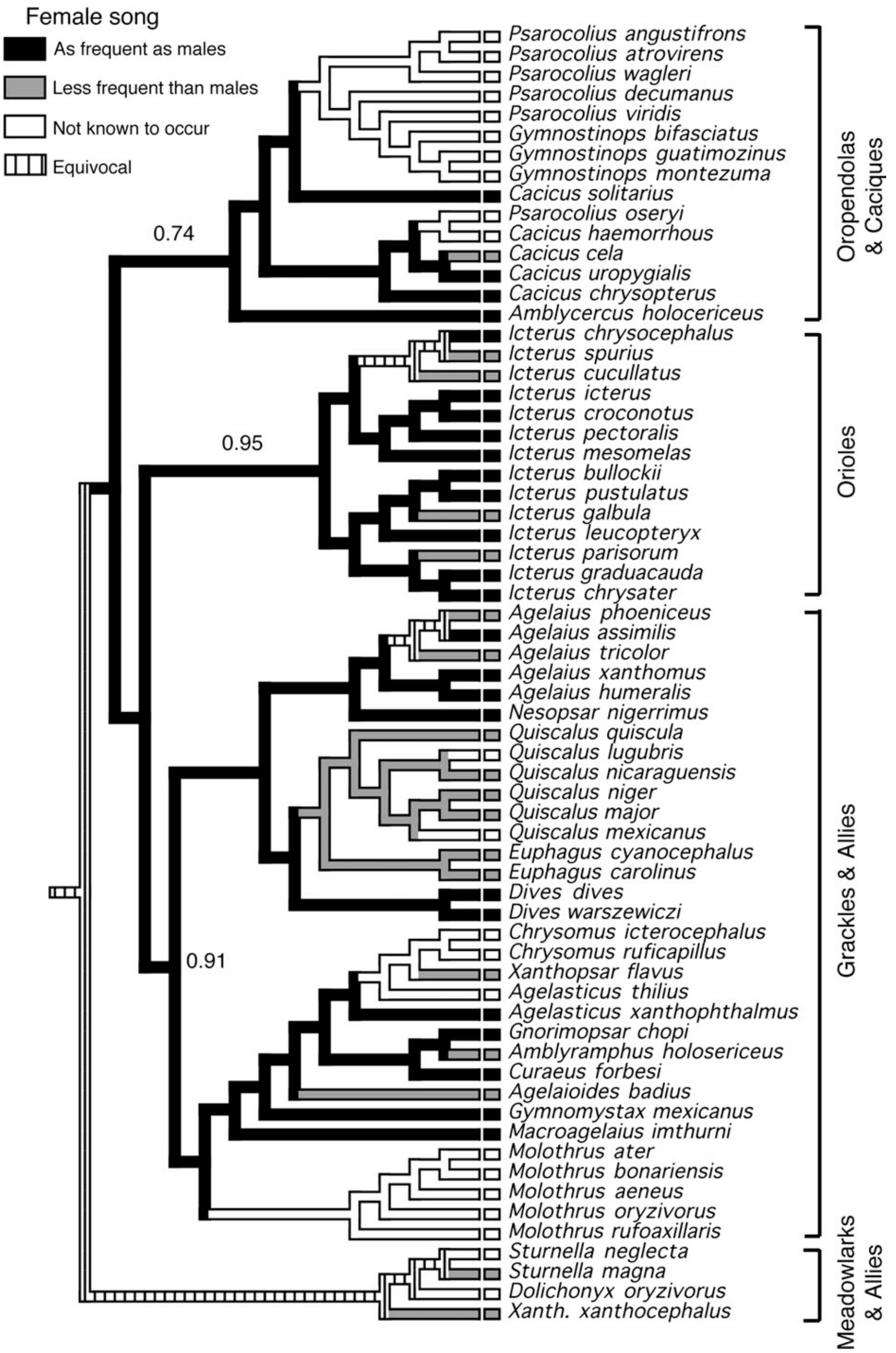

Figure 1
Ancestral state reconstruction of female song on a molecular phylogeny of the New World blackbird family. Female song rates were scored as a discrete, multistate character relative to male song and reconstructed using both unordered parsimony (shown here) and maximum likelihood. Both methods largely agreed in their support for ancestral states. Four major clades within the family are indicated on the right, and numbers at the base of each clade indicate maximum likelihood values supporting the ancestral states reconstructed using parsimony. No likelihood values are shown for ancestors of the meadowlarks and allies and for the family as a whole because these states were not resolved using parsimony.

Neither social mating system nor nesting pattern is significantly associated with breeding latitude in this family (P values from 0.08 to 0.21), with tropical breeding occurring in 63% (24 of 38) of monogamous species and 61% (20 of 33) of those with dispersed nesting patterns. In contrast, and not surprisingly, migration is strongly associated with temperate breeding ($P < 0.01$ in all tests), with all 19 migratory species breeding in northern or southern temperate habitats. Furthermore, largely because of this correlation between migration and latitude, species that are monogamous, dispersed nesting, and sedentary are significantly concentrated in the tropics ($P < 0.01$ in all tests). Only 2 taxa with this composite life-history pattern (*Cacicus chrysopterus* and *A. holosericeus*) were scored as having temperate breeding ranges by Price et al. (2009), and both occur in the southern hemisphere. Thus, differences in female singing rates between tropical and temperate habitats are largely explained by the evolution of migration.

DISCUSSION

Previous authors have suggested that the relative prevalence of female song in the tropics is explained by differences in the life-history traits found in tropical and temperate habitats (Morton 1996; Stutchbury and Morton 2001; Hall 2004; Slater and Mann 2004). In particular, female song is predicted to be relatively common in monogamous, sedentary songbirds, in which territorial pairs maintain year-round relationships and

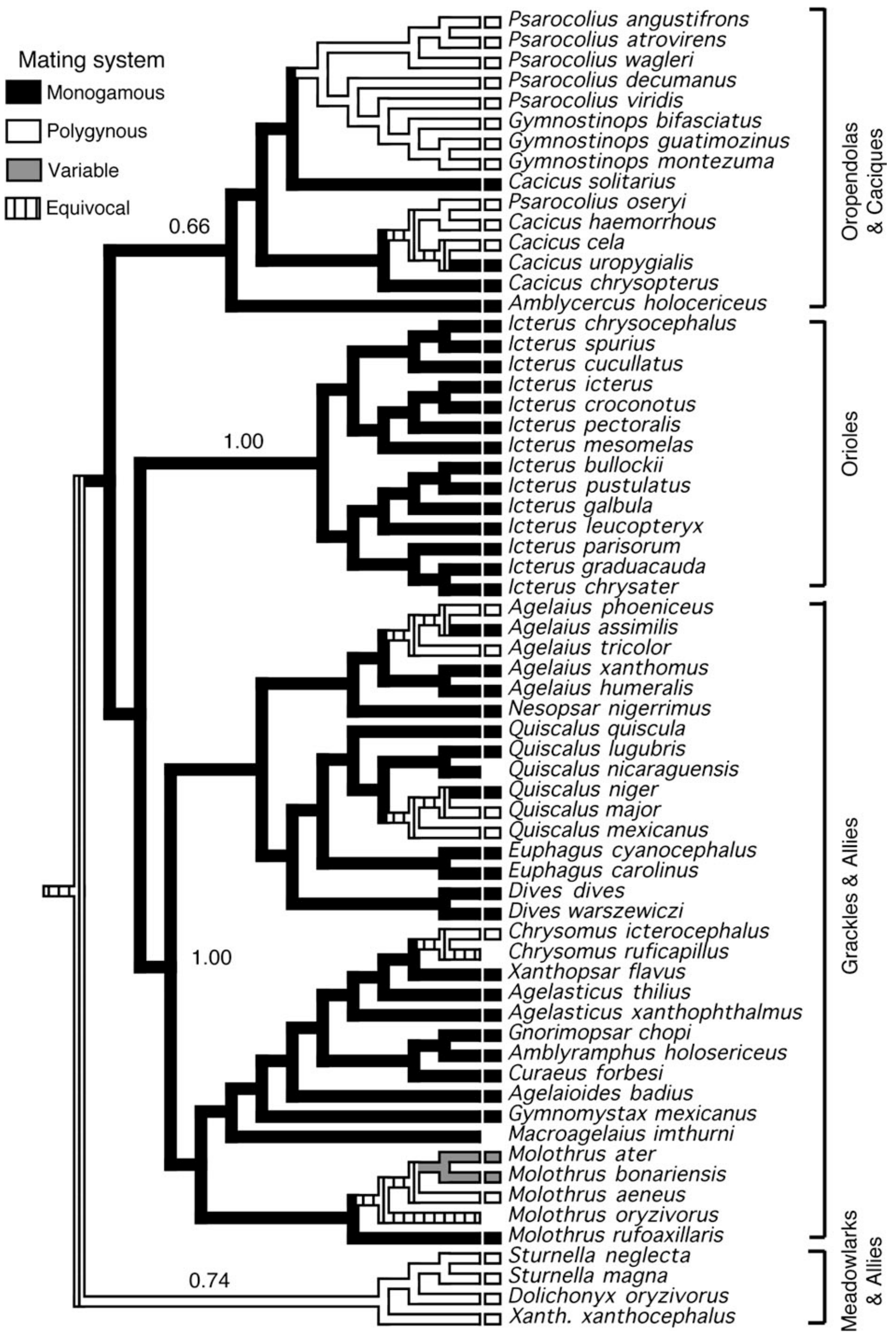

Figure 2
Reconstruction showing the evolution of social mating systems, with maximum likelihood values at the base of each major clade showing support for the character states reconstructed using parsimony. Three clades had monogamous ancestors, with polygyny evolving multiple times as a derived trait, whereas the ancestor of the meadowlarks and allies was polygynous. Neither reconstruction method indicated the mating system of the ancestor of the family.

there is increased competition among females for resources or mates (Farabaugh 1982; Langmore 1998, 2000; Hall 2004; Slater and Mann 2004). This study largely confirms those predictions by showing that female song in the Icteridae is found almost exclusively in species that are monogamous, dispersed nesting, and nonmigratory and further that this composite life-history pattern, with few exceptions, is found only in tropical taxa. To my knowledge, this is the first study to show a clear relationship between female singing and these life-history traits using phylogenetic methods, supporting several previous comparative studies that indicated similar relationships but did not control for phylogeny (Farabaugh 1982; Malacarne et al. 1991; Benedict 2008). By controlling for phylogeny in this study, I show that the observed relationships between female singing and life history are not explained by a few species-rich clades (Felsenstein 1985). Rather, female song co-occurs with a particular suite of life-history characteristics in multiple, independent lineages throughout the Icteridae.

Historical losses of female song in this family have been associated with changes in different life-history characteristics in different lineages (Figure 5). In the oriole clade, for instance, decreases in the occurrence of female song were clearly associated with the evolution of migration because all taxa in this clade are socially monogamous and exhibit dispersed nesting patterns. Conversely, losses of female song in the oropendolas and caciques were associated with the evolution of polygynous, colonial breeding systems because all taxa in this clade are sedentary. Female song also appears to have been lost with

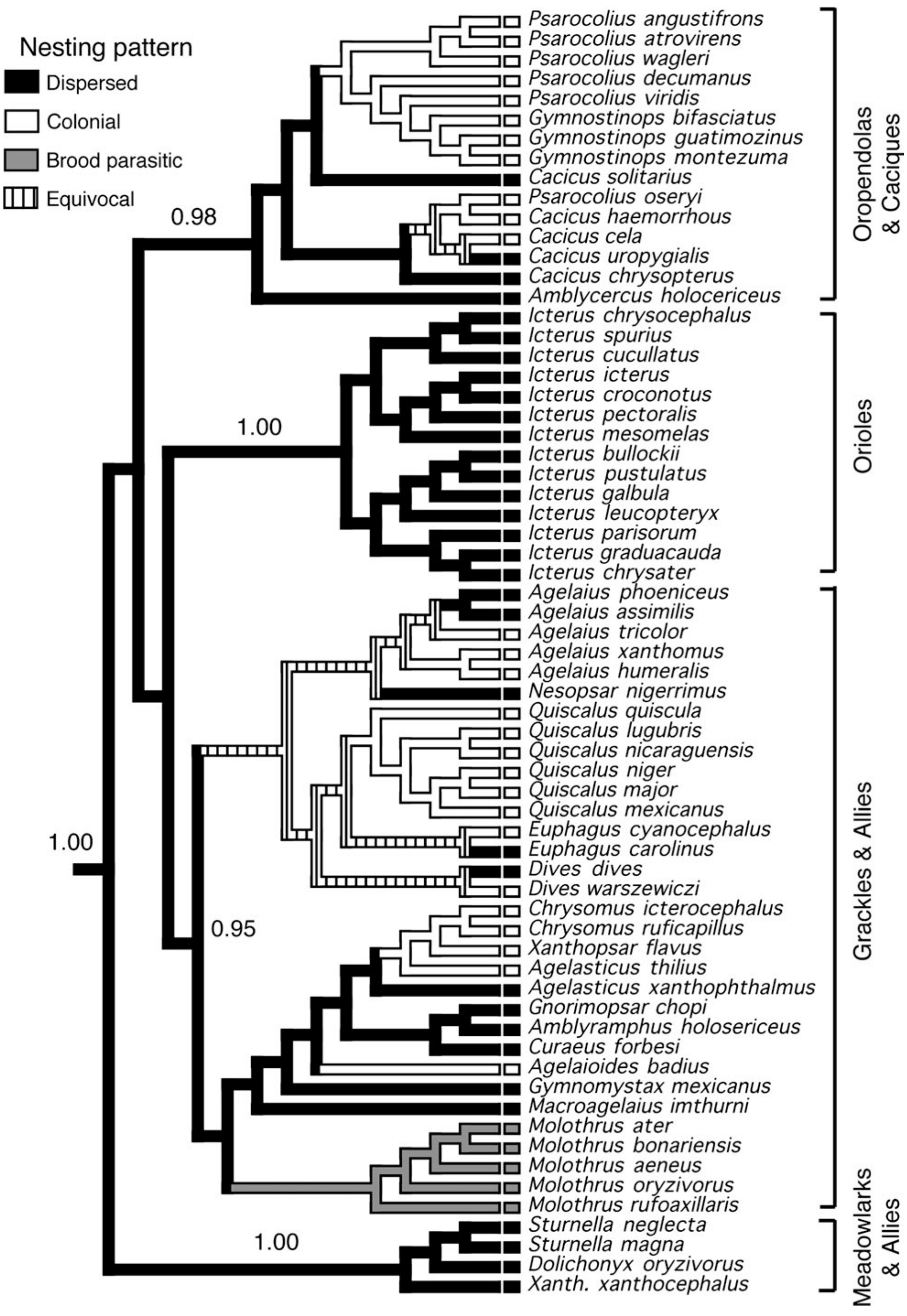

Figure 3
Reconstruction showing the evolution of nesting patterns, with maximum likelihood values at the base of each major clade showing support for the character states reconstructed using parsimony. Both methods indicate that the ancestors of all 4 clades and of the family as a whole had dispersed nests. Colonial nesting patterns evolved at least 5 times among the oropendolas and caciques and the grackles and allies, and obligate brood parasitism evolved once in the ancestor of the *Molothrus* genus.

the appearance of interspecific brood parasitism in the cowbirds (genus *Molothrus*) and with the loss of dispersed nesting in *Agelaioides badius*. Altogether, the evolutionary reconstructions presented here show that nearly all icterids with similar male–female song rates were also monogamous, dispersed nesting, and sedentary, and in all but one case (*A. holosericeus*), losses of female song were correlated with losses of this composite life-history pattern in one way or another. These results provide strong evidence that the differences we see in female song rates today are largely explained by ancestral changes in life history. Furthermore, although many changes in female singing occurred with changes in breeding latitude due to the evolution of migration (Price et al. 2009), such range shifts were clearly not the only factors affecting female song.

Nearly all icterid species with frequent female song are nonmigratory and have dispersed nest sites, suggesting that pairs stay in the same local areas year-round and are territorial. Nevertheless, female song might not necessarily be associated with year-round residence on territories, counter to some previous suggestions (Farabaugh 1982; Morton 1996; Langmore 1998, 2000; Hall 2004; Benedict 2008). Local movements during the nonbreeding season are thought to be a relatively common trait in nonmigratory icterids (Jaramillo and Burke 1999), though whether these movements are common in species with female song will need to be investigated. Furthermore, several icterid species with frequent female song do not exhibit strong territorial behaviors even during breeding (*D. warszewiczi*, Orians 1983; *A. xanthomus* and *A. humeralis*, Whittingham

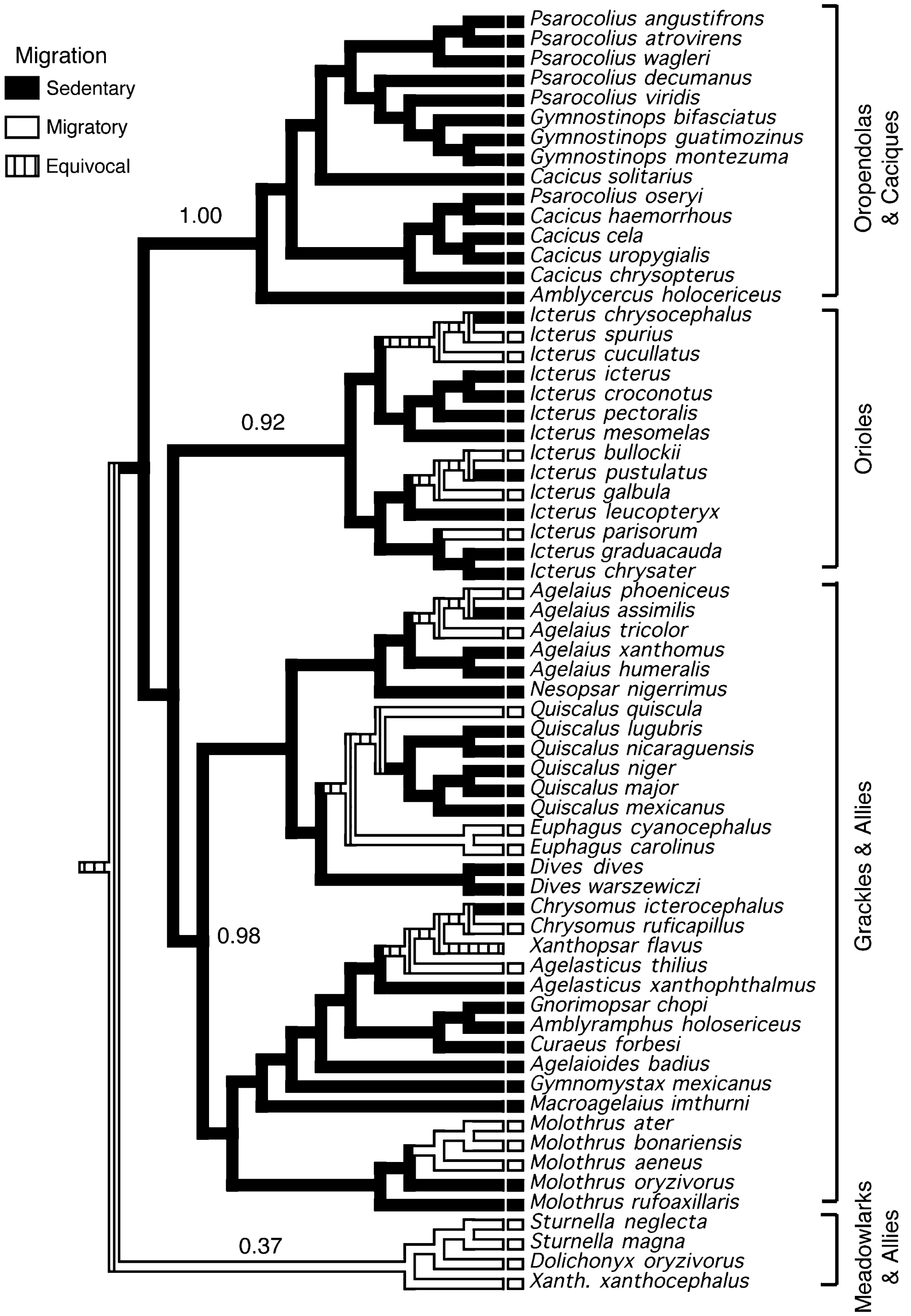

Figure 4
Reconstruction showing the evolution of migration, with maximum likelihood values at the base of each major clade showing support for the character states reconstructed using parsimony. Both methods indicate that the oropendolas and caciques, orioles, and grackles and allies had sedentary ancestors. Parsimony indicates that the ancestor of the meadowlarks and allies was migratory, whereas maximum likelihood suggests that it was sedentary (likelihood = 0.63).

et al. 1996). Thus, although year-round territoriality may be an important factor in the evolution of coordinated male–female duets, as suggested by Hall (2004) and Benedict (2008), such permanent territories may not be necessary for the appearance of female song in general.

A more important factor in the evolution and maintenance of female song may be the duration and stability of male–female associations in monogamous pairs. Males and females of sedentary species are likely to maintain longer and more stable relationships than migratory pairs that breed together for only part of the year, regardless of territorial behaviors. Moreover, female song may have a variety of functions for social communication other than just defense of resources or mates (Sonnenschein and Reyer 1983; Slater and Mann 2004; Mennill and Vehrencamp 2008). Detailed studies of the oriole clade (*Icterus*) could be a useful way to investigate these issues because all species in this group are monogamous and noncolonial (Jaramillo and Burke 1999), and changes in female song rates are so clearly associated with the evolution of migration. In addition, focusing on species that are exceptions to the general relationship shown in Figure 5, such as female singers that do not nest in dispersed locations and presumably are not territorial (*A. humeralis*, *A. xanthomus*, and *D. warszewiczi*), might provide further insights into the function of female song.

The evolutionary reconstructions presented here complement a variety of previous studies that have used phylogenetic methods to study behavioral evolution in the Icteridae. For

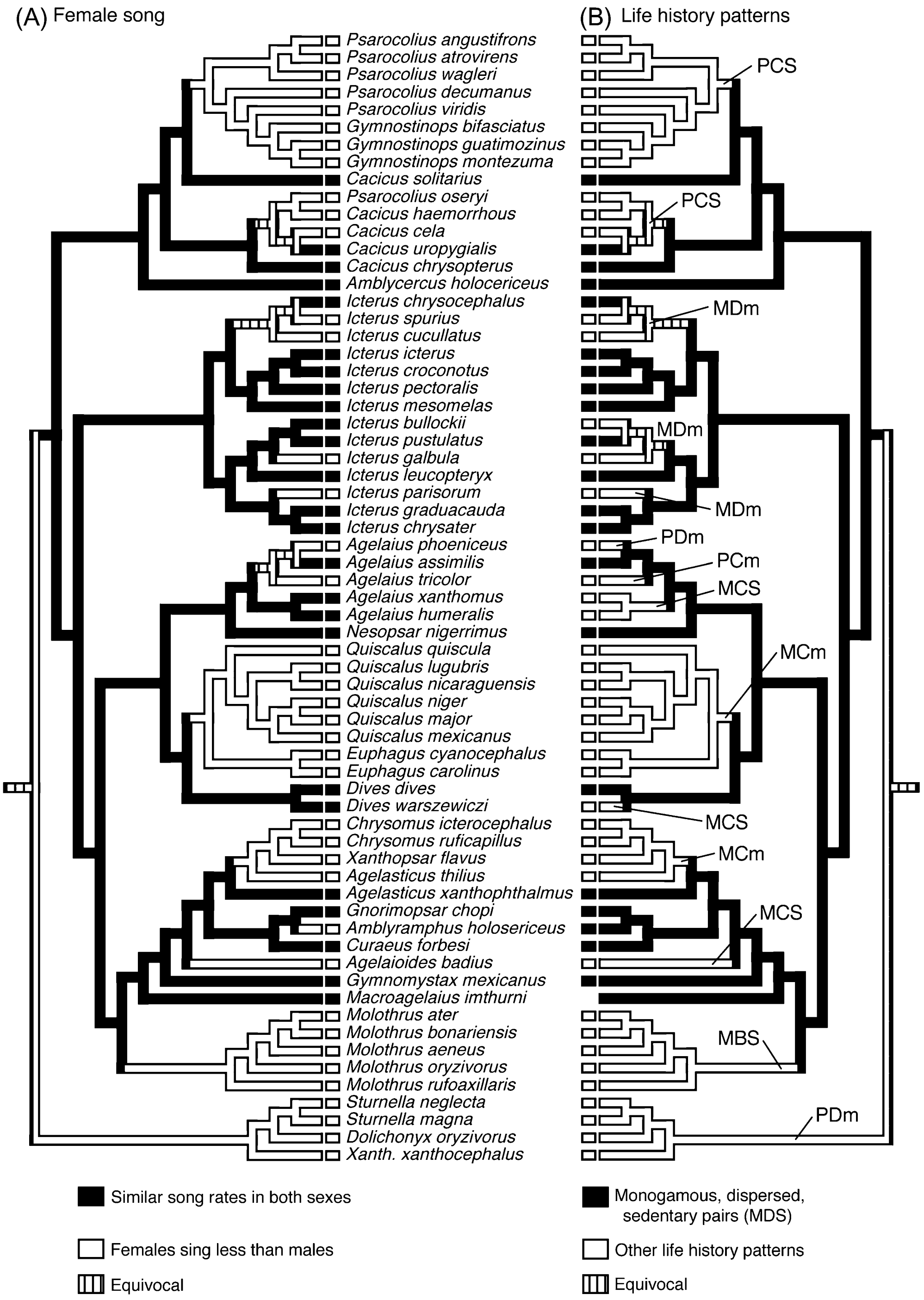

Figure 5
(A) Parsimony reconstruction of female song as a binary character, in which females that sing less frequently than males or are not known to sing were assigned the same character state (from Price et al. 2009). (B) Reconstruction of other life-history characteristics scored as a composite character, in which all observed combinations of mating system (M = monogamous or P = polygynous), nesting pattern (D = dispersed, C = colonial, or B = brood parasitic), and migratory status (S = sedentary or m = migratory) were mapped onto the tree as 10 individual character states. Lineages that nest as monogamous, dispersed, and sedentary (MDS) pairs are indicated on the tree, with transitions to other life-history patterns indicated by other 3-letter codes. Losses of female song were significantly concentrated on branches of the phylogeny in which this MDS life-history pattern was also lost (concentrated changes tests: $P < 0.01$).

example, Searcy et al. (1999) used parsimony reconstructions to show that ancestors of the oropendolas and caciques, orioles, and grackles and allies were monogamous and that ancestors of the meadowlarks and allies were polygynous, closely matching the results shown here. Searcy et al. (1999) also mapped territoriality and nesting patterns onto a phylogeny of the grackles and allies, showing that ancestors of this clade were territorial and had dispersed nest sites. My study provides further support for those general patterns by including additional icterid taxa and by using maximum likelihood methods. My results also extend the findings of Kondo and Omland (2007), who showed that migration has evolved in the oriole clade at least 5 times independently and over relatively short time periods. Mapping this character onto the entire family shows that migration has evolved rapidly in other lineages as well (e.g., *Agelaius* spp.; also see Barker et al. 2008) and, further, that these events were associated with rapid changes in the occurrence of female song. Finally, by reconstructing female song as a multistate rather than a binary character, I resolve some ambiguous findings of a previous binary reconstruction by Price et al. (2009), in which parsimony and maximum likelihood methods indicated different character states for some ancestors. Here, both methods indicated nearly identical evolutionary patterns throughout the family (Figure 1), providing much stronger support for the idea that female song has been repeatedly lost in the Icteridae.

Most previous research on bird song has focused on northern temperate passerines in which songs are produced primarily by males (Marler and Slabbekoorn 2004; Catchpole and Slater 2008), including temperate icterid species that are models for studying the evolution of male song by sexual selection (e.g., *Agelaius phoeniceus*, Searcy and Yasukawa 1995; *M. ater*, O'Loghlen and Rothstein 2003). Considering both sexes rather than just males, however, shows that selection has not worked on male songs alone. On the contrary, the results presented here show that both males and females sang in the ancestors of many taxa that now lack female song (also see Garamszegi et al. 2007). Male-biased song production in most temperate icterids is therefore not solely the product of selection for complex songs in males but has involved selection against such songs in females as well. These findings underscore the importance of considering evolutionary history in studies of sexual selection, and they should encourage future researchers to consider the histories of both sexes rather than just males in studies of avian song.

An especially interesting avenue for future research will be to compare aspects of female song other than just its occurrence relative to male song. Females can differ enormously in their levels of coordination with males, from exclusively solo singers (*Icterus pustulatus*, Price et al. 2008) to singers that occasionally coordinate their songs with males (*A. assimilis*, Whittingham et al. 1997) to pairs that regularly produce synchronized, antiphonal duets (*D. dives*, Orians 1983). The reasons for these differences among icterids are unknown, and it would be fascinating to compare these patterns to other detailed aspects of behavior, such as the extent of male–female relationships and the role of each sex in territoriality (Langmore 2002; Hall 2004; Slater and Mann 2004; Mann et al. 2009). Little is also known about the genetic, rather than social, mating systems of many songbird species, although it is suspected that rates of extrapair breeding differ between temperate and tropical environments (Stutchbury and Morton 2001, 2008; Macedo et al. 2008). Such patterns should have major influences on the interests of each sex during social interactions within and between pairs and consequently on the function of female song in these systems. Other life-history traits may also contribute to the evolution of female song, and future studies should address these issues through additional comparative analyses as well as detailed studies of individual species.

APPENDIX

Species	Female song[a]	Mating system[b]	Nest spacing[b]	Migration[b]
Agelaioides badius	Infrequent	Monogamous	Colonial	Resident
Agelaius assimilis	Duet with male	Monogamous	Dispersed	Resident
Agelaius humeralis	Duet with male	Monogamous	Colonial	Resident
Agelaius phoeniceus	Infrequent	Polygynous	Dispersed	Migratory
Agelaius tricolor	Infrequent	Polygynous	Colonial	Migratory
Agelaius xanthomus	Similar to male	Monogamous	Colonial	Resident
Agelasticus thilius	Rare or absent	Monogamous	Colonial	Migratory
Agelasticus xanthophthalmus	Similar to male	Monogamous	Dispersed	Resident
Amblycercus holosericeus	Duet with male	Monogamous	Dispersed	Resident
Amblyramphus holosericeus	Infrequent	Monogamous	Dispersed	Resident
Cacicus cela	Infrequent	Polygynous	Colonial	Resident
Cacicus chrysopterus	Duet with male	Monogamous	Dispersed	Resident
Cacicus haemorrhous	Rare or absent	Polygynous	Colonial	Resident
Cacicus solitarius	Duet with male	Monogamous	Dispersed	Resident
Cacicus uropygialis	Duet with male	Monogamous	Dispersed	Resident
Chrysomus icterocephalus	Rare or absent	Polygynous	Colonial	Resident
Chrysomus ruficapillus	Rare or absent	—	Colonial	Migratory
Curaeus forbesi	Similar to male	Monogamous	Dispersed	Resident
Dives dives	Duet with male	Monogamous	Dispersed	Resident
Dives warszewiczi	Duet with male	Monogamous	Colonial	Resident
Dolichonyx oryzivorus	Rare or absent	Polygynous	Dispersed	Migratory
Euphagus carolinus	Infrequent	Monogamous	Dispersed	Migratory
Euphagus cyanocephalus	Infrequent	Monogamous	Colonial	Migratory
Gnorimopsar chopi	Similar to male	Monogamous	Dispersed	Resident
Gymnomystax mexicanus	Similar to male	Monogamous	Dispersed	Resident
Gymnostinops bifasciatus	Rare or absent	Polygynous	Colonial	Resident
Gymnostinops guatimozinus	Rare or absent	Polygynous	Colonial	Resident
Gymnostinops montezuma	Rare or absent	Polygynous	Colonial	Resident
Icterus bullockii	Similar to male	Monogamous	Dispersed	Migratory
Icterus chrysater	Similar to male	Monogamous	Dispersed	Resident
Icterus chrysocephalus	Duet with male	Monogamous	Dispersed	Resident
Icterus croconotus	Similar to male	Monogamous	Dispersed	Resident
Icterus cucullatus	Infrequent	Monogamous	Dispersed	Migratory
Icterus galbula	Infrequent	Monogamous	Dispersed	Migratory
Icterus graduacauda	Similar to male	Monogamous	Dispersed	Resident
Icterus icterus	Similar to male	Monogamous	Dispersed	Resident
Icterus leucopteryx	Similar to male	Monogamous	Dispersed	Resident
Icterus mesomelas	Duet with male	Monogamous	Dispersed	Resident
Icterus parisorum	Infrequent	Monogamous	Dispersed	Migratory
Icterus pectoralis	Similar to male	Monogamous	Dispersed	Resident
Icterus pustulatus	Similar to male	Monogamous	Dispersed	Resident
Icterus spurius	Infrequent	Monogamous	Dispersed	Migratory
Macroagelaius imthurni	Similar to male	—	Dispersed	Resident
Molothrus aeneus	Rare or absent	Polygynous	Brood parasite	Migratory

Appendix, continued

Species	Female song[a]	Mating system[b]	Nest spacing[b]	Migration[b]
Molothrus ater	Rare or absent	Variable	Brood parasite	Migratory
Molothrus bonariensis	Rare or absent	Variable	Brood parasite	Migratory
Molothrus oryzivorus	Rare or absent	—	Brood parasite	Resident
Molothrus rufoaxillaris	Rare or absent	Monogamous	Brood parasite	Resident
Nesopsar nigerrimus	Similar to male	Monogamous	Dispersed	Resident
Psarocolius angustifrons	Rare or absent	Polygynous	Colonial	Resident
Psarocolius atrovirens	Rare or absent	Polygynous	Colonial	Resident
Psarocolius decumanus	Rare or absent	Polygynous	Colonial	Resident
Psarocolius oseryi	Rare or absent	Polygynous	Colonial	Resident
Psarocolius viridis	Rare or absent	Polygynous	Colonial	Resident
Psarocolius wagleri	Rare or absent	Polygynous	Colonial	Resident
Quiscalus lugubris	Rare or absent	Monogamous	Colonial	Resident
Quiscalus major	Infrequent	Polygynous	Colonial	Resident
Quiscalus mexicanus	Rare or absent	Polygynous	Colonial	Resident
Quiscalus nicaraguensis	Infrequent	—	Colonial	Resident
Quiscalus niger	Infrequent	Monogamous	Colonial	Resident
Quiscalus quiscula	Infrequent	Monogamous	Colonial	Migratory
Sturnella magna	Infrequent	Polygynous	Dispersed	Migratory
Sturnella neglecta	Rare or absent	Polygynous	Dispersed	Migratory
Xanthocephalus xanthocephalus	Infrequent	Polygynous	Dispersed	Migratory
Xanthopsar flavus	Infrequent	Monogamous	Colonial	—

[a] Information on female singing rates were obtained from Price et al. (2009).

[b] Data on social mating systems, nesting patterns, and migratory behaviors were obtained from Jaramillo and Burke (1999). Dashes indicate unknown character states.

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REFERENCES

Barker FK, Vandergon AJ, Lanyon SM. 2008. Species status of the red-shouldered blackbird (*Agelaius assimilis*): implications for ecological, morphological, and behavioral evolution in *Agelaius*. Auk. 125:87–94.

Beletsky LD. 1982. Vocalizations of female northern orioles. Condor. 84:445–447.

Beletsky LD. 1983. Aggressive and pair bond maintenance songs of female red-winged blackbirds (*Agelaius phoeniceus*). Z Tierpsychol. 62:47–54.

Benedict L. 2008. Occurrence and life history correlates of vocal duetting in North American passerines. J Avian Biol. 39:57–65.

Brunton DH, Evans B, Cope T, Ji W. 2008. A test of the dear enemy hypothesis in female New Zealand bellbirds (*Anthornis melanura*): female neighbors as threats. Behav Ecol. 19:791–798.

Catchpole CK, Slater PJB. 2008. Bird song: biological themes and variations. 2nd ed. New York: Cambridge University Press.

Clements JF. 2007. The Clements checklist of birds of the world. 6th ed. Ithaca (NY): Cornell University Press.

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.

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

Farabaugh SM. 1982. The ecological and social significance of duetting. In: Kroodsma DE, Miller EH, editors. Acoustic communication in birds. New York: Academic Press. p. 85–124.

Felsenstein J. 1985. Phylogenies and the comparative method. Am Nat. 125:1–15.

Garamszegi LZ, Pavlova DZ, Eens M, Moller AP. 2007. The evolution of song in female birds in Europe. Behav Ecol. 18:86–96.

Halkin SL. 1997. Nest-vicinity song exchanges may coordinate biparental care of northern cardinals. Anim Behav. 54: 189–198.

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

Illes AE, Yunes-Jiménez L. 2008. A female songbird out-sings male conspecifics during simulated territorial intrusions. Proc R Soc Lond B Biol Sci. 276:981–986.

Jaramillo A, Burke P. 1999. New World blackbirds, the icterids. Princeton (NJ): Princeton University Press.

Kondo B, Omland KE. 2007. Ancestral state reconstruction of migration: multistate analysis reveals rapid changes in New World orioles (*Icterus* spp.). Auk. 124:410–419.

Kroodsma DE, Viellard JME, Stiles FG. 1996. Study of bird song in the Neotropics: urgency and opportunity. In: Kroodsma DE, Miller EH, editors. Ecology and evolution of acoustic communication in birds. Ithaca (NY): Cornell University Press. p. 269–281.

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

Langmore NE. 2000. Why female birds sing. In: Epmark Y, Amundsen T, Rosenqvist G, editors. Animal signals, signaling and signal design in animal communication. Trondheim (Norway): Tapir Academic Press. p. 317–327.

Langmore NE. 2002. Vocal duetting: definitions, discoveries and directions. Trends Ecol Evol. 17:451–452.

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

Lanyon SM, Barker FK. 2007. Exploring patterns of morphological evolution in the New World blackbirds. In: 125th Meeting of the American Ornithologists' Union, 2007 August 9. Laramie (WY): American Ornithologists' Union, University of Wyoming.

Lanyon WE. 1994. Western meadowlark (*Sturnella neglecta*). In: Poole A, editor. The birds of North America online. Ithaca (NY): Cornell Lab of Ornithology.

Levin RN. 1996. Song behaviour and reproductive strategies in a duetting wren, *Thryothorus nigricapillus* I: removal experiments and II: playback experiments. Anim Behav. 52:1093–1117.

Logue DM. 2007. Duetting in space: a radio-telemetry study of the black-bellied wren. Proc R Soc Lond B Biol Sci. 274:3005–3010.

Macedo RH, Karubian J, Webster MS. 2008. Extrapair paternity and sexual selection in socially monogamous birds: are tropical birds different? Auk. 125:769–777.

Maddison DR, Maddison WP. 2003. MacClade 4. Sunderland (MA): Sinauer Associates, Inc.

Maddison DR, Maddison WP. 2008. Mesquite: a modular system for evolutionary analysis [Internet]. Version 2.5. Available from: http://mesquiteproject.org.

Maddison WP. 1990. A method for testing the correlated evolution of two binary characters: are gains or losses concentrated on certain branches of a phylogenetic tree? Evolution. 44:539–557.

Malacarne G, Cucco M, Camanni S. 1991. Coordinated visual displays and vocal duetting in different ecological situations among Western Palearctic non-passerine birds. Ethol Ecol Evol. 3:207–219.

Mann NI, Dingess KA, Barker FK, Graves JA, Slater PJB. 2009. A comparative study of song form and duetting in Neotropical *Thryothorus* wrens. Behaviour. 146:1–43.

Marler P, Slabbekoorn H. 2004. Nature's music, the science of birdsong. San Diego (CA): Elsevier Academic Press.

Mennill DJ, Vehrencamp SL. 2008. Context-dependent functions of avian duets revealed by microphone-array recordings and multispeaker playback. Curr Biol. 18:1314–1319.

Morton ES. 1996. A comparison of vocal behavior among tropical and temperate passerine birds. In: Kroodsma DE, Miller EH, editors. Ecology and evolution of acoustic communication in birds. Ithaca (NY): Cornell University Press. p. 258–268.

O'Loghlen AL, Rothstein SI. 2003. Female preference for the songs of older males and the maintenance of dialects in brown-headed cowbirds (*Molothrus ater*). Behav Ecol Sociobiol. 53:102–109.

Orians GH. 1983. Notes on the behavior of the melodious blackbird (*Dives dives*). Condor. 85:453–460.

Price JJ, Lanyon SM. 2004. Patterns of song evolution and sexual selection in the oropendolas and caciques. Behav Ecol. 15: 485–497.

Price JJ, Lanyon SM, Omland KE. 2009. Losses of female song with changes from tropical to temperate breeding in the New World blackbirds. Proc R Soc Lond B Biol Sci. 276:1971–1980.

Price JJ, Yunes-Jiménez L, Osorio-Beristain M, Omland KE Murphy TG. 2008. Sex-role reversal in song? Females sing more frequently than males in the streak-backed oriole. Condor. 110:387–392.

Robinson SK. 1986. The evolution of social behavior and mating systems in the blackbirds (Icterinae). In: Rubenstein PI, Wrangham RA, editors. Ecological aspects of social evolution. Princeton (NJ): Princeton University Press. p. 175–200.

Searcy WA, Yasukawa K. 1995. Polygyny and sexual selection in red-winged blackbirds. Princeton (NJ): Princeton University Press.

Searcy WA, Yasukawa K, Lanyon S. 1999. Evolution of polygyny in the ancestors of red-winged blackbirds. Auk. 116:5–19.

Slater PJB, Mann NI. 2004. Why do the females of many bird species sing in the tropics? J Avian Biol. 35:289–294.

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

Stutchbury BJM, Morton ES. 2001. Behavioral ecology of tropical songbirds. San Diego (CA): Academic Press.

Stutchbury BJM, Morton ES. 2008. Recent advances in the behavioral ecology of tropical birds. Wilson J Ornithol. 120:26–37.

Webster MS. 1992. Sexual dimorphism, mating system and body size in New World blackbirds (Icterinae). Evolution. 46: 1621–1641.

Webster MS. 1994. Female-defense polygyny in a Neotropical bird: the Montezuma oropendola. Anim Behav. 48:779–794.

Whittingham LA, Kirkconnell A, Ratcliffe LM. 1992. Differences in song and sexual dimorphism between Cuban and North American red-winged blackbirds (*Agelaius phoeniceus*). Auk. 109:928–933.

Whittingham LA, Kirkconnell A, Ratcliffe LM. 1996. Breeding behavior, social organization and morphology of red-shouldered (*Agelaius assimilis*) and tawny-shouldered (*A. humeralis*) blackbirds. Condor. 98:832–836.

Whittingham LA, Kirkconnell A, Ratcliffe LM. 1997. The context and function of duet and solo songs in the red-shouldered blackbird. Wilson Bull. 109:279–289.