

Differentiating the evolution of female song and male–female duets in the New World blackbirds: Can tropical natural history traits explain duet evolution?

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Female bird song and combined vocal duets of mated pairs are both frequently associated with tropical, monogamous, sedentary natural histories. Little is known, however, about what selects for duetting behavior versus female song. Female song likely preceded duet evolution and could drive apparent relationships between duets and these natural histories. We compared the evolution of female song and male–female duets in the New World blackbirds (Icteridae) by investigating patterns of gains and losses of both traits and their relationships with breeding latitude, mating system, nesting pattern, and migratory behavior. We found that duets evolved only in lineages in which female song was likely ancestral. Both female song and duets were correlated with tropical breeding, social monogamy, territorial nesting, and sedentary behavior when all taxa were included; however, correlations between duets and these natural history traits disappeared when comparisons were limited to taxa with female song. Also, likelihood values supported stronger relationships between the natural history traits and female song than between these traits and duets. Our results suggest that the natural histories thought to favor the evolution of duetting may in fact be associated with female song and that additional selection pressures are responsible for the evolution of duets.

KEY WORDS: Female bird song, Icteridae, selection pressure, vocal duets.

In the tropics and other environments with little seasonal change, many animals are able to reside and potentially breed throughout the year (Ricklefs 1969). While promoting extended longevity and long-term reproduction, such environments are also associated with heightened competition (Stutchbury and Morton 2001). High individual survival results in increased competition for mates and resources, which in turn may promote specific natural histories such as convergent sex roles and long-term, stable mating relationships (Emlen and Oring 1977; Stutchbury and Morton 2001). These natural histories may select for traits that help in defending resources and maintaining long-term monogamous relationships, such as conspicuous, sexually monochromatic plumage, and singing by both males and females (Amundsen 2000; Clutton-Brock 2009).

Female bird song and coordinated vocal duets between mated males and females are two traits whose evolution is associated with tropical natural histories (Farabaugh 1982; Langmore 1998; Hall 2004; Slater and Mann 2004). Research on the function of female song suggests that females sing to defend and compete for resources, attract or guard mates, and coordinate breeding activities (Langmore 1998). Likewise, birds are thought to duet to jointly defend territories, guard mates and paternity, and maintain contact and synchronize reproduction (Hall 2004; Dahlin and Benedict 2014). Therefore, female song and duets are expected to be prevalent in sedentary species that mate for multiple years and defend year-round territories (Hall 2004; Slater and Mann 2004). Indeed, both behaviors have been treated as functionally similar and attributed to many of the same selection pressures



(Langmore 1998; Hall 2004; Slater and Mann 2004; Dahlin and Benedict 2014).

Although many species exhibit both female solo song and coordinated male–female duets, these behaviors are not necessarily equivalent (Langmore 1998, 2002; Riebel et al. 2005). In many tropical bird species, for example, females perform complex solo songs similar to those of conspecific males that are not combined into duets (Brunton and Li 2006; Price et al. 2008; Geberzahn et al. 2009). In other species, males and females perform duets by combining vocalizations other than song (Benedict 2008). We should also note that female song and duets are not strictly a tropical phenomenon, but occur in many temperate species (Malacarne et al. 1991; Garamszegi et al. 2007; Benedict 2008) and may be related more to being nonmigratory than being tropical breeding (Logue and Hall 2014). Here we compare the evolutionary histories of female singing and duets in the New World blackbirds (family: Icteridae) to determine if both female songs and duets are associated with the same natural history traits or if these behaviors are favored by different selective factors.

Although our understanding of male–female duets has benefited from quite a number of functional studies and comparative analyses over the past few decades (Malacarne et al. 1991; Benedict 2008; Hall 2009; Dahlin and Benedict 2014; Logue and Hall 2014), female song has received less attention (Langmore 1998; Riebel 2003; Riebel et al. 2005). However, recent research reveals that female song is more common than previously thought in songbirds (Garamszegi et al. 2007; Price et al. 2009; Odom et al. 2014). In fact, female song probably evolved alongside male song in the early evolution of bird song (Odom et al. 2014). This has important implications for our understanding of duets because if female song evolved early in songbirds, then duets likely evolved after female song was already present. Duet evolution may be intrinsically dependent on the prior evolution of female song. However, most studies of duetting behavior have not concurrently examined the function and evolution of female solo song (e.g., Malacarne et al. 1991; Benedict 2008; Logue and Hall 2014).

Our research builds on two recent phylogenetic comparative analyses on the evolution of female song in the New World blackbirds (Price 2009; Price et al. 2009), a songbird family with many tropical and temperate representatives. Price et al. (2009) and Price (2009) showed that female song, either as solo song or combined with male songs as duets, is correlated with tropical latitudes and with a suite of natural history traits that tend to occur together in the tropics: social monogamy, dispersed nesting, and nonmigratory behavior. Female song evolved early in the evolutionary history of this group and has since been lost multiple times (Price et al. 2009). These evolutionary losses were associated with concurrent losses of any of the aforementioned natural history traits (Price 2009). The absence of female song in some species could have restricted the evolution of duets, creating a

perceived evolutionary relationship between duets and these natural history traits. Thus, natural history traits used to explain duet evolution could be responsible for the evolution of female song instead.

In this study, we explore the evolutionary connection between female song and male–female duets, and we investigate whether natural history traits associated with each can better explain one or the other. To understand how female song, duets, and other natural history traits are related in the New World blackbirds, we asked two questions: (1) have duets evolved primarily in lineages where female song is ancestral, and (2) can we determine which natural history traits are more strongly correlated with female song and which with duets? Answering these questions is important for accurately shaping future studies on the evolution of duets and identifying selection pressures that are responsible for the evolution of female singing and duetting.

Methods

SCORING FEMALE SONG, DUETS, AND NATURAL HISTORY TRAITS

We used character scoring for female song and breeding latitude from Price et al. (2009), and scores for mating system, nesting pattern, and migratory behavior from Price (2009). Price et al. (2009) and Price (2009) only included species for which unambiguous information about singing behavior could be found, resulting in inclusion of 65 species of the approximately 101 recognized icterid species in those studies (Clements et al. 2013). We therefore only included these same 65 species in our study. All excluded taxa were either tropical or southern temperate species, spanning 15 genera, but we do not think the exclusion of these taxa biased our results toward relationships associated with northern temperate taxa. Information on duets were gathered from a compilation of species accounts for the New World blackbirds (Jaramillo and Burke 1999) and field guides, articles, and other species accounts (see Price et al. 2009 for a detailed list of references by species). We searched for further information on duetting in several additional field guides and species accounts to verify that the current dataset was robust to the inclusion of instances of duetting for species for which we had female song information (Snyder 1966; Davis 1972; Edwards 1972; Meyer de Schauensee and Phelps 1978; Bond 1980; Hilty and Brown 1986; Raffaele 1989; Ridgely and Gwynne 1989; de la Peña and Rumboll 1998).

We defined duets as temporally coordinated or consistently overlapping vocalizations produced by a mated male and female, following definitions described by Langmore (2002) and Hall (2004). Any species whose accounts used the terms “duet” or “antiphonal” or described males and females as overlapping or combining their vocalizations were scored as duetting. All other species were scored as not duetting. Some icterids haphazardly

overlap their vocalizations, so our definition of duetting was intended to eliminate instances of overlapped vocalizations that may occur infrequently due to chance. Our definition also allowed for the inclusion of species that create duets using vocalizations other than songs. We defined songs as vocalizations used in defending resources or advertising for mates, following definitions described by Howell and Webb (1995) and Jaramillo and Burke (1999). Songs of many icterid species are performed in association with obvious visual displays and are distinct from other vocalizations, so presumably they were easy for authors to identify. We scored female song as present in a species if female singing rates are similar to male singing rates (including species with greater female song rates than male song rates, e.g., Price et al. 2008), following Price et al. (2009). This included species in which females use song as solos, as well as species that use song to create duets. Species in which female song is relatively infrequent or not thought to exist were scored as not having female song.

The natural history traits included in our analysis were chosen based on their association with hypotheses pertaining to female song and duet function and evolution, and based on their potential to be readily observed and documented in most species in our study. Female song and male–female duets have been proposed to be prominent in tropical, monogamous species that defend their own territories year round (Langmore 1998; Stutchbury and Morton 2001; Hall 2004; Slater and Mann 2004). We scored breeding latitude, social mating system, nesting pattern (with dispersed nesting serving as a proxy for territoriality), and migratory behavior. Because the correlative analyses we performed required our characters to have only two states, we scored female song and these natural history traits as binary characters, as done by Price et al. (2009) and Price (2009). Including the same binary states and analyses as Price et al. (2009) and Price (2009) made our analysis of duet evolution comparable to these previous studies of female song evolution. Breeding latitudes were scored as either tropical or temperate, social mating systems were scored as either monogamous or nonmonogamous, nesting patterns were scored as either dispersed (solitary or spatially separated nesting) or nondispersed (colonial nesting or brood parasitic species), and migratory behaviors were scored as either sedentary (found in or around their breeding range year round) or migratory (seasonally relocating between distinct geographic ranges). We also created a composite natural history character, following Price (2009), in which species were scored as either monogamous, dispersed nesting, and sedentary or lacking any of these traits. Any species that did not possess all three of these traits were scored as not possessing the composite natural history. For detailed descriptions of these scoring methods, see Price et al. (2009) and Price (2009).

ANCESTRAL STATE RECONSTRUCTION AND CORRELATION ANALYSES

To better understand the evolutionary relationship between female song and duetting behavior across the New World blackbirds, we reconstructed the evolutionary history of duets and compared these to reconstructions of female song produced by Price et al. (2009). We used both unordered parsimony and Markov *k*-state one-parameter maximum-likelihood analyses performed in Mesquite version 2.75 (Maddison and Maddison 2011). Both models assume equal probabilities of gains and losses of a character. Parsimony analysis weights the contribution of each character state to a node equally, whereas maximum likelihood uses information provided by branch lengths to estimate the likelihood that a given character state existed at each node of the tree (Cunningham et al. 1998). We compared the ancestral patterns of change in female song and duets, paying particular attention to lineages that possessed both female song and duets and the apparent order of appearance of each trait.

We used concentrated changes tests (Maddison 1990) and Pagel's (1994) discrete likelihood correlation method to empirically test for correlated evolution between these two behaviors and each natural history trait. The concentrated changes test is a parsimony-based analysis that assesses the association of gains and losses of one character state with the presence or absence of another character state on a phylogenetic tree (Maddison 1990). The test is sensitive to the presence of equivocal ancestral states, so we conducted the test using all possible combinations of ACC-TRAN (favoring reversals over independent gains or losses) and DELTRAN (favoring independent gains or losses over reversals) for each trait, resulting in a range of *P*-values for each comparison. Pagel's (1994) method is a likelihood-based analysis that tests for an association between transitions in character states using branch lengths by comparing a correlated model of evolution to an uncorrelated (null) model of evolution. Each test was performed using 10,000 simulations.

Concentrated changes tests comparing female song to each of the four natural history traits were completed previously by Price et al. (2009) and Price (2009). Price et al. (2009) also compared female song to breeding latitude using Pagel's (1994) method. We performed additional comparisons using Pagel's (1994) method between female song and the remaining three traits. Correlations between character traits were assessed based on *P*-values from concentrated changes tests and Pagel's (1994) method. In addition, Pagel's (1994) method provides log likelihoods for the correlated and uncorrelated models. Comparing the magnitude of the log-likelihood differences of these two models allowed us to assess whether female song or duets were more strongly correlated to each natural history trait (larger likelihood differences indicate stronger correlation).

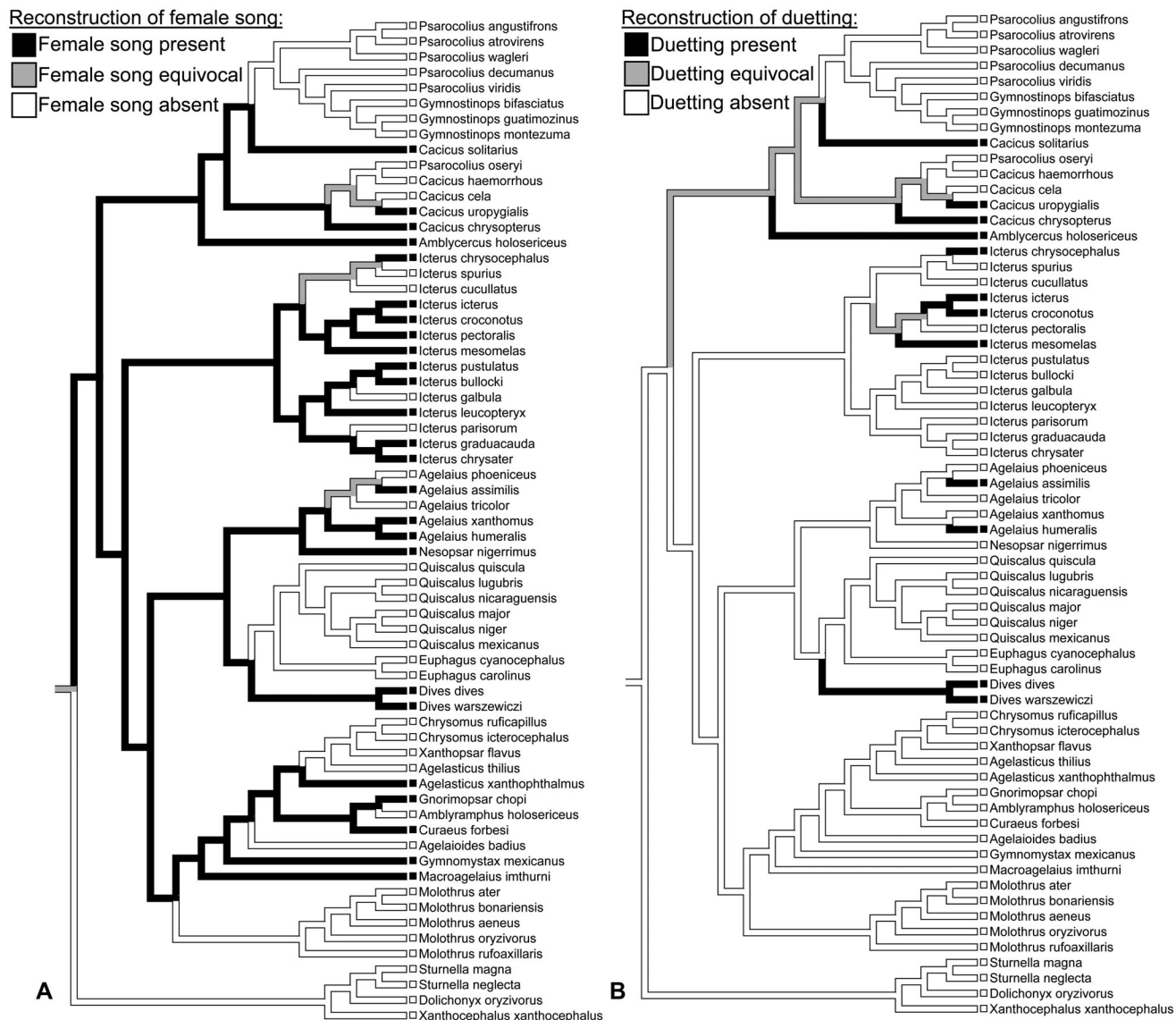


Figure 1. Parsimony reconstructions of (A) female song and (B) duetting in the New World blackbirds indicate duets evolved multiple times recently in lineages where female song was likely ancestral (this result was also strongly supported by maximum-likelihood reconstruction).

Our initial analyses suggested that all occurrences of duets were in taxa with female song (see below). Thus, to assess the potentially confounding effect of female song driving the apparent relationships between duets and the natural history traits, we also ran all correlation analyses between duets and each natural history correlate on a tree excluding all species except those with female song. This analysis allowed us to look for correlations between duets and each natural history trait within the subset of species in which female song already existed.

We conducted all reconstructions and correlational analyses on the same molecular phylogeny used by Price et al. (2009) and Price (2009). This tree was constructed using DNA sequence data from two mitochondrial and four nuclear loci and provides

strong support for the four major clades of Icteridae (Lanyon and Omland 1999; Lanyon and Barker 2007, also see Powell et al. 2014). We excluded species for particular trait comparisons if there was missing information for that trait for that species. All phylogenetic analyses were performed in Mesquite version 2.75 (Maddison and Maddison 2011), except the concentrated changes tests, which were performed in MacClade 4.0.8a (Maddison and Maddison 2003). To account for the multiple statistical tests caused by comparing female song and duets against each of the five natural history variables, we used a standard Bonferroni correction for five statistical comparisons. This resulted in a corrected cutoff for statistical significance of $P \leq 0.01$ (Westfall and Young 1993).

Table 1. Concentrated changes test results for female song and duets versus several natural history traits using all New World blackbird taxa included in the study. In addition, duets were compared to each natural history trait on a tree containing only species with female song.

Taxa	Vocalization type	Natural history trait	<i>P</i> -values*
All taxa	Female song	Breeding latitude	<0.01
All taxa	Duet	Breeding latitude	0.01 –0.02
Female song only	Duet	Breeding latitude	0.77
All taxa	Female song	Mating system	0.06–0.27
All taxa	Duet	Mating system	0.004 –0.03
Female song only	Duet	Mating system	1.00
All taxa	Female song	Nesting pattern	0.03 –0.25
All taxa	Duet	Nesting pattern	0.004 –0.06
Female song only	Duet	Nesting pattern	0.37
All taxa	Female song	Migration	0.003 –0.05
All taxa	Duet	Migration	0.01 –0.03
Female song only	Duet	Migration	0.88
All taxa	Female song	Composite	<0.01
All taxa	Duet	Composite	<0.01
Female song only	Duet	Composite	0.40

*Values in bold indicate statistically significant correlations at a *P*-value of 0.01.

Results

Twelve of the 65 species (18%) of New World blackbirds included in our study exhibited male–female duets. Most parsimonious reconstructions showed that duets were the result of multiple independent evolutionary gains (six gains if reversals are favored over independent gains [ACCTAN]; 10 gains if independent gains are favored over reversals [DELTRAN]; Fig. 1). Maximum-likelihood (Mk1) reconstruction agreed with parsimony reconstructions and most closely with the DELTRAN reconstruction, suggesting 10 independent gains of duetting (Fig. S1). Duetting was present in 34% of (12 out of 35) species with female song, and duets evolved only in lineages where female song was reconstructed as already existing (Fig. 1). Concentrated changes tests supported a very strong phylogenetic relationship between gains of duetting and the existence of female song ($P < 0.0001$ for all combinations of ACCTAN/DELTRAN). Pagel's (1994) discrete likelihood correlation method also supported a strong correlation between the evolution of female song and duets ($P < 0.0001$; log-likelihood difference = 12.30).

When all 65 taxa were compared, duets appeared to be related to all natural history traits (Fig. 2; Tables 1 and 2). Concentrated changes tests supported associations between gains of duetting and tropical breeding, social monogamy, dispersed nesting, sedentary behavior, and a composite of these last three traits (Table 1). Pagel's (1994) discrete likelihood correlation method also showed significant correlations between duets and mating system, migration, and the composite (Table 2). There was a moderate correlation between duets and breeding latitude ($P = 0.03$) and duets and nesting pattern ($P = 0.07$), but these

relationships were not significant with an adjusted *P*-value of 0.01 (Table 2).

Comparative methods also supported relationships between these same traits and female song (Fig. 2). Concentrated changes tests revealed highly significant relationships between losses of female song and temperate breeding and the loss of a composite monogamous, territorial, and sedentary natural history (Table 1; also see Price 2009; Price et al. 2009). In addition, concentrated changes tests provided some support for a relationship between female song and dispersed nesting and sedentary behavior, but did not support a relationship between female song and monogamy (Table 1; Price 2009). Pagel's (1994) discrete likelihood correlation method strongly supported correlated evolution of female song and all natural history traits examined (Table 2; Price et al. 2009). In fact, log-likelihood differences were over twice as large for female song compared to duets for nearly all natural history traits, indicating very strong support for correlated models of evolution between female song and these traits (Table 2). The one exception was migration, for which female song and duets had very similar log-likelihood differences (strengths of correlated evolution; Table 2).

However, when only the 35 species with female song were included, there was no longer any consistent relationship between duets and any of the natural history traits. Concentrated changes tests failed to find any relationship between gains of duets and tropical breeding, social monogamy, dispersed nesting, sedentary behavior, or a composite of these last three traits (Table 1). There was also no difference between correlated and uncorrelated models of evolution for duetting and breeding latitude, territoriality,

Table 2. Pagel's (1994) discrete likelihood correlation method results for female song and duets versus several natural history traits using all New World blackbird taxa included in the study. In addition, duets were compared to each natural history trait on a tree containing only species with female song.

Taxa	Vocalization type	Natural history trait	Log-likelihood: uncorrelated model	Log-likelihood: correlated model	Log-likelihood difference	P-value*
All taxa	Female song	Breeding latitude	-76.19	-62.74	13.45	<0.01
All taxa	Duet	Breeding latitude	-69.95	-65.93	4.02	0.03
Female song only	Duet	Breeding latitude	-21.38	-20.94	0.44	0.25
All taxa	Female song	Mating system	-65.06	-53.06	11.99	<0.01
All taxa	Duet	Mating system	-59.09	-53.97	5.13	0.01
Female song only	Duet	Mating system	-14.16	-14.07	0.09	<0.01
All taxa	Female song	Nesting pattern	-61.75	-54.51	7.23	<0.01
All taxa	Duet	Nesting pattern	-55.49	-53.49	2.00	0.07
Female song only	Duet	Nesting pattern	-22.74	-22.14	0.59	0.21
All taxa	Female song	Migration	-69.88	-64.56	5.32	<0.01
All taxa	Duet	Migration	-64.22	-58.71	5.51	0.01
Female song only	Duet	Migration	-19.25	-19.45	-0.20	0.92
All taxa	Female song	Composite	-69.92	-47.09	22.83	<0.01
All taxa	Duet	Composite	-64.09	-54.29	9.81	<0.01
Female song only	Duet	Composite	-24.22	-22.54	1.68	0.10

*Values in bold indicate statistically significant correlations at a P-value of 0.01.

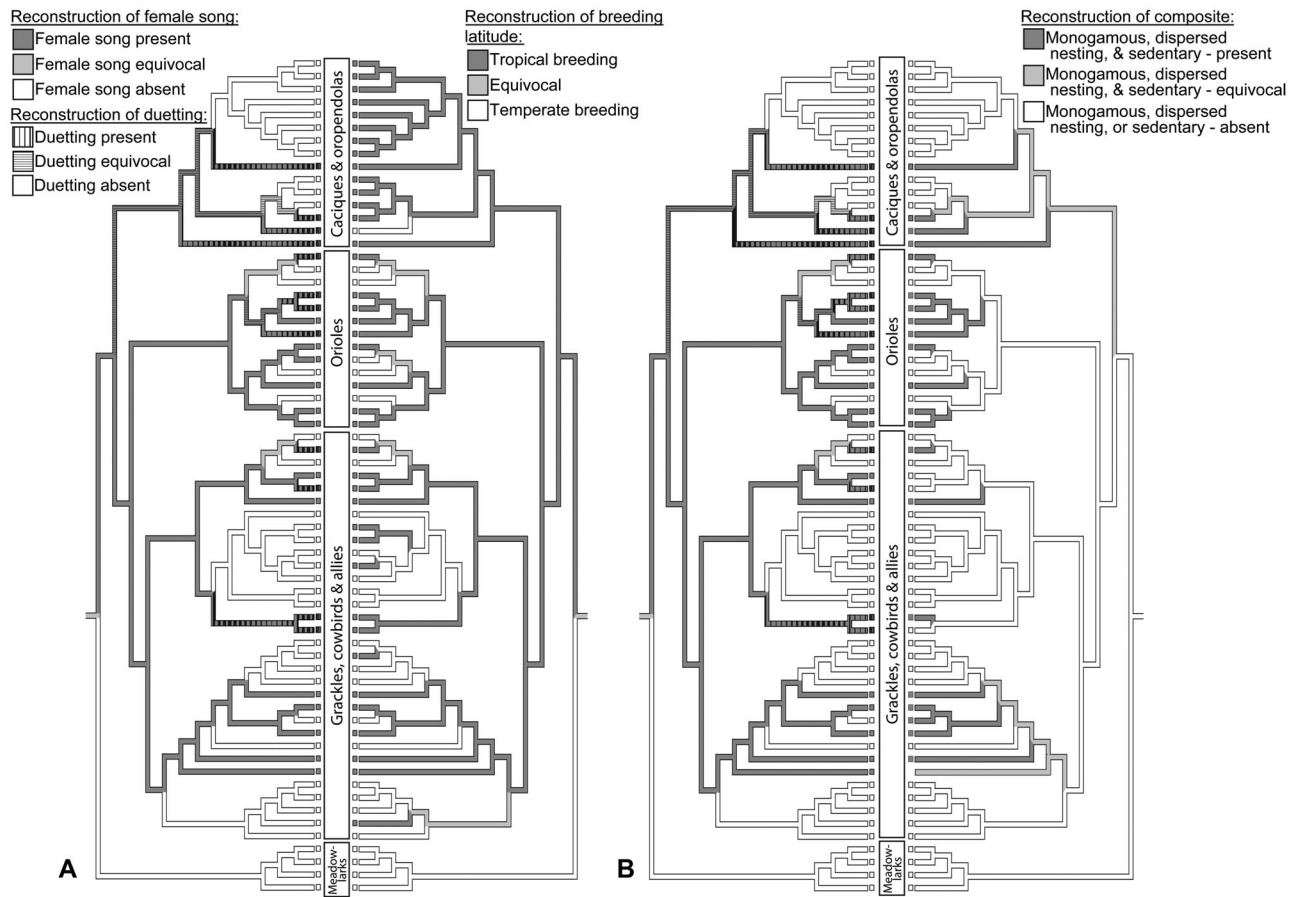


Figure 2. Parsimony reconstructions of duetting overlaid on female song (A and B—left trees) show that female song more closely matches parsimony reconstructions of tropical breeding (A—right tree) and a composite of monogamous, dispersed nesting, and sedentary natural histories (B—right tree).

migratory behavior, and the composite (Table 2). There was a significant correlation between monogamy and duetting among species with female song, but this relationship had a very small log-likelihood difference (0.09), indicating very little support for the correlated versus the null model (Table 2).

Discussion

Our comparison of female song and duetting revealed that duets in the New World blackbirds evolved in lineages where female song was common and likely ancestral, indicating that these two behaviors are not evolutionarily independent in this clade. Natural history traits hypothesized to be related to each were more strongly correlated with female song. In addition, when only taxa with female song were compared, relationships between duetting and these natural history traits disappeared. Thus, the apparent association between duets and these natural history traits may be a consequence of duetting behavior evolving in species with female song, which is strongly associated with these traits, rather than these traits themselves driving the evolution of duets.

A major difference we found between the evolution of female song and duets in the New World blackbirds is that duets have resulted from multiple, more recent evolutionary gains in comparison to female song. Similarly, recent research indicates that female song is ancestral to all songbirds (Odom et al. 2014). Female song was likely selected for early in the evolutionary history of songbirds for reasons promoting singing in both males and females. If duets have evolved more recently in all songbirds, something in addition to the selection pressures responsible for female song must have selected for males and females to combine their songs into duets.

Selective forces responsible for the evolution of duets beyond female song could include a change in the strength of an already existing selection pressure or a previously unconsidered selection pressure. Because female song is a likely precursor for duets in many species, a change in a natural history trait related to female song could drive the evolution of duets. For example, if a species with female solo song that is already tropical breeding, sedentary, and dispersed nesting becomes strongly territorial or territorial for a larger portion of the year, it is possible that this species might

be more likely to evolve duets. Alternatively, duets could evolve due to entirely different selection pressures. When we removed all species without female song from our analyses, we no longer saw the strong correlation between these natural history traits and duets. We should note that removing all species without female song decreased the number of species in these analyses by half, so we also probably experienced reduced power for these analyses. Nevertheless, loss of any one of the composite natural history traits is associated with loss of female song (Fig. 2; Price 2009) and therefore the ability to evolve song duets. This relationship could be all that reinforces the apparent correlation between duets and these natural history traits.

Several recent studies have examined the association of duets with natural history traits and found duetting to be correlated with monogamous, year-round territorial, sedentary natural histories (Malacarne et al. 1991; Benedict 2008; Logue and Hall 2014). None of these studies, however, directly examined duet evolution in combination with female song. The question of what is driving the evolution of duets in species with female song needs comparative analyses that incorporate female song, duets, and a variety of natural history traits. Studies that examine the extent of female song and duetting compared to natural history traits may be able to detect more nuanced patterns relating the evolution of duets to the evolution of female song. We also need studies on phylogenetically and geographically diverse taxa. In the New World blackbirds only a small subset of species duet, and females and males use songs rather than other vocalizations to create duets. Species in other taxonomic groups are known to use vocalizations other than song to produce duets (Benedict 2008) and duets are more common in other groups of songbirds, such as the neotropical wrens (Mann et al. 2009). Analyses that compare patterns of gains and losses of female song and duets across a diversity of lineages will help continue to resolve the evolution of female song versus duets across songbirds.

Because female song may be a precursor to duets in many tropical species, it is important that functional studies of duets also incorporate female song into their project designs. Similar to the way female song could be influencing our perception of duet evolution, duets and solos could have very similar functions. Many functional duet studies compare duets to male and female solo songs (e.g., Hall 2000; Rogers et al. 2007; Dahlin and Wright 2012). It is important that functional duet studies continue to incorporate solos to evaluate whether particular functions are specific to duets. Moreover, functional studies that explicitly compare female song and duets may be especially valuable for evaluating differences between these two behaviors.

The evolutionary relationship between female song and duets has implications beyond songbirds. Many suboscine and non-passerine (nonsongbird) species also duet (e.g., Seddon and Tobias 2006; Odom and Mennill 2010), not to mention

many primates, anurans, and insects (Marler and Mitani 1988; Bailey 2003; Kelley 2004). The selection pressures and sequence of events underlying the evolution of female vocalizations versus duets might vary among taxa. Thinking about how and why female vocalizations originated in the first place and then how and why males and females came to combine their songs into duets is a thought process that could benefit research on the evolution of duets in all taxa (e.g., Bailey 2003).

CONCLUSIONS

Our results indicate that female song is an evolutionary precursor for duets in the New World blackbirds. Because female song likely evolved first, its evolution could be driving associations with natural history traits traditionally separately associated with the evolution of duets. Studies on the function and evolution of duets should incorporate female song to prevent deductions about the function and evolution of duets that are really driven by female song. Phylogenetic comparisons and detailed species-specific studies that take into account the evolution of both female song and duets will have the best chances of teasing apart evolutionary causes of complex, coordinated duets.

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DATA ARCHIVING

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Supporting Information

Additional Supporting Information may be found in the online version of this article at the publisher's website:

Figure S1. Maximum-likelihood (Mk1) reconstruction of duetting in the New World blackbirds (Icteridae).