ABSTRACT

Geographic and gender biases in the history of ornithology have led to missed opportunities, and in some cases, backwards understanding of key evolutionary and behavioral processes. In studies of elaborate coloration and song, female birds have historically been neglected. The main framework for thinking about the evolution of elaborate traits has been sexual selection, whereby competition for mates has led to elaborate coloration and long complex songs in males. Females have often been ignored or assumed not to change. Here we review current understanding of how these elaborate traits have evolved in temperate versus tropical areas. Ongoing research on orioles, other blackbirds, and all songbirds indicates that female song is much more common than previously thought. Social selection acting on both females and males throughout the year likely played an important role in the original evolution of bird song in both sexes. In many cases, the evolution of sexual dimorphism in both coloration and song is driven by the loss of elaboration in females, rather than the gain of elaboration in males. Accounting for both male and female display traits will lead to a clearer understanding of the evolution of coloration and song, which will also facilitate a more comprehensive understanding of the full scope of topics in avian ecology, evolution, behavior and conservation.

Keywords: female song, elaborate female coloration, sexual selection, social selection, tropical birds, temperate zone birds

LAY SUMMARY

- Historically, bird field research was concentrated in northern countries: most research on song and coloration focused on males.
- In the last 30 years, an increasing number of researchers have recognized that females in many species also have elaborate coloration and song, especially in the tropics.

- This paper reviews what we know about female song and female coloration in songbirds.
- We first examine how changes in female song and color have occurred across larger groups of species (evolutionary history).
- We also review how female color and song can be favored by sexual selection and social selection (current function).

INTRODUCTION - ELABORATE FEMALE SIGNALS

Elaborate song and coloration are some of the most striking features of the avian world. Most research on these topics has traditionally focused on males, especially those that breed in the temperate zone (Langmore et al. 1998, Odom et al. 2014). However, many of the best-known examples of elaborate coloration and vocalizations in birds are tropical birds in which both females and males have elaborate signals (see Dale et al. 2015, Odom et al. 2025). Examples include *Ramphastos sulfuratus* (Keel-billed Toucans), *Ara macao* (Scarlet Macaws), and *Cyanocorax luxuosus* (Green Jays), all of which have elaborately colored females.

In the context of elaborate vocalizations, a song of a *Cardinalis cardinalis* (Northern Cardinal) in North America could be produced by either a male or a female (Ritchison 1986). In Australia, the loud song of the *Psophodes olivaceus* (Eastern Whipbird) is not the song of one male bird, but rather a female-male duet (Rogers 2005). Similarly, in the Neotropics, many species of wrens, antbirds, and orioles produce duets that are some of the most noticeable songs of tropical rainforests (Mennill and Vehrencamp 2005, Seddon and Tobias 2006, Odom et al. 2016). However, the very definition of bird song for many years was explicitly male-focused: "long, complex vocalizations produced by males during the breeding season" (Bird Song, Catchpole and Slater, 1995). To understand elaborate signaling traits across birds, it is crucial to account for both male and female signals. Focusing on sexual selection acting on males is not

sufficient to understand the evolution of elaborate plumage and song (e.g., Price et al. 2009, Price 2015).

Instead, increasing evidence demonstrates that many elaborate advertisement traits may arise due to social selection (narrow sense; West-Eberhard 1979, Tobias et al. 2012). Social selection leads to elaborate traits when both females and males use signaling traits to compete for ecological resources outside of the mating context. When female birds use song or color to compete for territories or food in the non-breeding season, this provides some of the strongest evidence that such traits can arise and be maintained in contexts other than competition for mates (e.g., Murphy et al. 2009). Although a small number of previous studies in males have suggested possible evolutionary trade-offs between elaborate song and coloration (Badyaev et al. 2002, Tietze and Hahn 2024), the studies reviewed here support the widespread role of social selection in shaping both female coloration and female song.

Our review focuses especially on what we know about the *evolutionary history* of elaborate color and song. Most models of the evolution of elaborate traits assume that the common ancestor in a group lacked them (Omland and Hofmann 2006). Figure 1A shows a phylogeny of four closely related bird species. Focusing on the males to start with, three of the species have drab cryptic gray coloration. However, males in the species on the top have elaborate orange coloration. Given the phylogeny of these four species, parsimony indicates that the common ancestor of the group likely was gray, and that orange evolved recently in the ancestor of the species at the top (see Omland and Hofmann 2006).

In many traditional studies focused on males, female coloration would have either been ignored or assumed to remain unchanged (Omland and Hofmann 2006, Price 2015). The right side of Figure 1A depicts all four species with gray females; thus the common ancestor likely had gray females. Therefore, when males of the topmost species evolved elaborate orange

coloration, that lineage became sexually dichromatic. Importantly, we can only know that males evolving orange coloration led to dichromatism if we know that females did not change. Explicitly accounting for and scoring female coloration is crucial to understanding the evolution of sexual dichromatism even when females are not changing. In Figure 1A, male change is driving the evolution of dichromatism (Omland and Hofmann 2006).

Figure 1B demonstrates an alternative possibility: that the gain of sexual dichromatism could be caused by a loss of elaborate coloration in females. In this second hypothetical group, males of all species have elaborate orange coloration. Now, females of most species have elaborate orange coloration, but females of the topmost species have dull gray coloration. Again, it is more parsimonious that females of the topmost species lost orange (one change). Without knowing the phylogenetic relatives of the focal species, it is not possible to know whether sexual dichromatism resulted from a gain of elaborate coloration in males or the loss of elaborate coloration in females (Hofmann et al. 2008).

The implicit assumption that females are unchanging or passive has parallels to early behavioral studies of birds that often assumed females were behaviorally passive or unmoving (Gowaty 1997, 2003). For example, initial work on extra-pair copulations focused on the idea that males were forcing copulations on passive females (Morton et al. 1990, Westneat 1987). However, Stutchbury et al. (1994) demonstrated that female *Setophaga citrina* (Hooded Warblers) were leaving their territories to actively seek extra-pair copulations.

Knowing the phylogenetic history of these signaling traits is crucial to understand their evolution (Omland and Hofmann 2006, Price 2015). Until we know what evolutionary changes have occurred, it is impossible to understand why those changes have happened (see Tobias et al. 2012).

Sources of Bias

Historically, scientific publications on birds have been dominated by scientists in temperate regions, despite the presence of greater biodiversity in the tropics (Brown and Lomolino 1998, Soares et al. 2023). Female song is less common in temperate regions, which likely contributed to long-held assumptions that it is an uncommon or unimportant behavior (Riebel et al. 2005, Odom and Benedict 2018, Stutchbury and Morton 2023).

A recent broad literature review of organismal ecology papers found that only 18% of the bird-focused papers surveyed investigated species in the tropics (a consistent bias found across all examined taxa, including plants; Culumber et al. 2019). Many authors have called attention to this "neglect of the tropics", as understanding the diversity of tropical ecosystems is crucial for exploring foundational ecological concepts (Stroud and Feeley 2017). Furthermore, the comparative dearth of research is not for lack of qualified scientists in these regions, but rather reduced access to training opportunities, funding, and communication with the global scientific community. A group of 124 authors recently published a call for increased inclusion of ornithologists in the Neotropics, highlighting the value of their experience and perspectives in tropical research (Soares et al. 2023).

Female song has been historically understudied not only due to this geographic bias, but also due to a gender bias of the scientists conducting the studies. A literature review demonstrated that women were significantly more likely than men to be first authors of studies investigating female song, and that women are leading the field as it grows: 68% of first authors on female bird song papers were women, compared to 44% of first authors on general bird song papers (Haines et al. 2020). This study provided clear evidence of the importance of diverse perspectives in science for reducing implicit biases and expanding the breadth of knowledge of understudied topics. Although studying female animals provides invaluable insight into

evolution, conservation, and behavior, they remain less studied than male animals in a variety of fields, and several papers have provided suggestions for reducing sex bias in future investigations (Beery and Zucker 2011, Odom and Benedict 2018, Wu et al. 2025, Barros et al. 2026).

In both temperate and tropical species, scientific biases and plumage patterns may lead to misidentifying singing females as males. For example, female song in many tropical species can be missed due to sexual monomorphism, where males and females display similar plumage (Webb et al. 2016, Odom and Benedict 2018). In many species, yearling males retain immature plumage that is, in varying degrees, similar to female plumage, a phenomenon known as delayed plumage maturation (Lyon and Montgomerie 1986). In temperate species, female song may be missed if one or both sexes do not acquire their adult plumage patterns or coloration until after their first breeding period, which could lead to singing females being misidentified as yearling males (Hawkins et al. 2012).

Focus On Songbirds and New World Blackbirds

This review focuses on songbirds, because so much work has been done on elaborate vocalizations in this group, traditionally on males and increasingly more in females. We will also focus on previous work on the New World to make the review more concise and to ensure more analogous comparisons. We will use work on the New World blackbirds (Icteridae) as examples to illustrate these topics. This group has over 100 species with a mix of natural history traits: migratory and non-migratory, temperate breeding and tropical, varied mating systems, and a diversity of elaborate visual and vocal signals (Table 1, Jaramillo and Burke 1999). Several research groups have studied both coloration and song, both at the family level and within genera, especially the orioles (*Icterus*).

OVERALL UNDERSTANDING OF FEMALE SONG

As discussed above, evolution of elaborate bird song was historically framed as the result of sexual selection favoring male song for mate attraction and territory defense (Darwin 1871, Catchpole and Slater 2008). Several studies demonstrated that for species in which females were not known to sing, the addition of testosterone led to females producing song, which contributed to the paradigm that female song (if observed) was likely the result of shared genetic architecture with males or a hormonal aberration (Nottebohm 1980, Grisham and Arnold 1995, Byers and King 2000). Early studies likely misidentified singing females as males, especially when both sexes display similar plumage, or classified female vocalizations that would now be considered songs as more simple "calls" (Langmore 1998, Odom and Benedict 2018, Macdonald et al. 2019).

Phylogenetic Studies of Female Song

However, building on a growing number of studies reporting female song across a wide taxonomic range, a phylogenetic analysis of European songbird species found that female song was most likely the ancestral characteristic for at least two songbird families (Garamszegi et al. 2007). These authors were unable to reject the hypothesis that the common ancestor of all songbirds in the region may have had female song, contrasting the traditional assumptions for how this trait may have evolved (Garamszegi et al. 2007).

The hypothesis that elaborate song in both sexes represents the ancestral state was tested on a much broader scale across 34 different families (1,141 different species) by Odom et al. (2014). They found strong support that the common ancestor of all songbirds most likely had both male and female elaborate song, completely shifting the paradigm for how sexual

dimorphism in elaborate communication had evolved in songbirds. Rather than arising just in males due to sexual selection, bird song likely originated in both males and females as a result of social selection acting on both sexes. Furthermore, their study showed that 71% of the species investigated had female song, which demonstrated for the first time that female song is common, phylogenetically widespread, and not restricted to a few families or groups (Odom et al. 2014). Female song is likely even more prevalent than is currently documented, as we still lack knowledge of sex-specific vocalizations for the majority of songbird species around the world (Odom and Benedict 2018, Riebel et al. 2019, Austin et al. 2021).

The traditional view of male song evolving via sexual selection due to male-male aggressive competition for mates and/or mate attraction likely misses a large component of selection acting on bird song for both sexes. Song is also shaped through the pressures of social selection, where both males and females compete for access to resources throughout the annual cycle (Tobias et al. 2012, Odom et al. 2014). For example, female White-crowned Sparrows have been observed singing to chase off young male and female intruders in the winter (Baptista et al. 1993).

Changes in natural history traits can lead to changes in selection pressures on female signaling that may drive gains and losses of sexual dimorphism in song. In the two clades where female song has been reconstructed as the most likely ancestral state, Troglodytidae and the core Icteridae (excluding meadowlarks and allies), the current sexual dimorphism in song observed in many species is likely the result of a loss of female song (Price et al. 2009, Price 2015, Price et al. 2023). These findings match the scenario depicted in Figure 1B, where the evolutionary pattern is driven by female change. In both families, temperate-breeding migratory species are thought to have gained migration, having descended from a tropical-breeding, sedentary ancestor; previous work has found strong positive associations between this gain of migratory

192 behavior and the loss of female song (Price et al. 2009). The benefits of maintaining elaborate
193 female traits may be outweighed by the costs, especially when females may not benefit from
194 elaborate traits in temperate breeding migratory species with limited periods of territoriality.
195 Female song is more common in tropical-breeding species, but the association of
196 migration or temperate-breeding with the loss of elaborate female signaling is likely the
197 consequence of the loss of year-round territoriality. Within Icteridae, different lineages likely lost
198 female song as a result of multiple different shifts in natural history characteristics: the gain of
199 migration in the genus *Icterus*; the gain of brood parasitism in the genus *Molothrus*; and the gain
200 of polygynous, colonial breeding in the genera *Psarocolius*, *Gymnostinops*, and *Cacicus* (Price
201 2009). Migratory, parasitic, or colonial polygynous species do not maintain year-round
202 territories, suggesting that the loss of year-round territoriality may be one of the best supported
203 explanations for the loss of female song.
204 In addition, an analysis of over 1,300 songbird species found that more than any other
205 natural history characteristic, high incidences of female song were most strongly associated with
206 biparental care and year-round territoriality (Odom et al. 2025). This new research further
207 supports the argument that social selection may play a larger role than previously assumed in the
208 evolution and maintenance of female song. An earlier review by Slater and Mann (2004)
209 suggested that species that maintain long-term pair bonds (generally more tropical species),
210 likely have converging sex roles, leading to similar traits in both males and females.
211 Whittingham et al. (1992) found that male and female *Agelaius assimilis* (Red-shouldered
212 Blackbirds), non-migratory, tropical-breeding) participate more equally in territory defense and
213 have less sexual dimorphism in both song and plumage compared to their temperate-breeding
214 relative, *Agelaius phoeniceus* (Red-winged Blackbird). Furthermore, without strict seasonality,
215 males and females may rely on elaborate signaling to coordinate the timing of breeding efforts

(Slater and Mann 2004, see also Stutchbury and Morton 2023). Group coordination may also be important for maintaining female elaboration: a recently published analysis found strong associations between cooperative breeding and female song, even in species with reduced territoriality (Snyder et al. 2026).

The need for coordinated, long-term territory or resource defense is also thought to promote the evolution of coordinated vocal signaling like duetting, when males and females vocalize in overlapping or alternating patterns as a joint signal. In the family Icteridae, Odom et al. (2015) found that female song was an "evolutionary precursor" to duetting, as lineages with elaborate female song as the ancestral trait were more likely to subsequently also evolve duetting. Duetting is less common in migratory species (Logue and Hall 2014), and similar to solo female song, year-round territoriality is the best predictor for whether or not a species duets (Tobias et al. 2016, see also Stutchbury and Morton 2023). Additionally, some duetting species, primarily in tropical regions, have been shown to use their coordinated male and female songs as a more effective threat compared to solo song alone (Logue and Gammon 2004, Odom and Omland 2017, see also Langmore 1998).

Defending territories year-round may select for the maintenance of duetting even if solo female song is no longer selected for. For example, *Thryothorus ludovicianus* (Carolina Wren), one of the few species in Troglodytidae without elaborate female song, is a temperate, sedentary species in which both sexes defend territories across the full annual cycle. Despite having lost complex female song, female Carolina Wrens still use simple chatters to overlap with male songs, presumably for defending mates or territories (Price et al. 2023, Zapata and McEntee 2023). An analysis of the family Troglodytidae found strong associations between the degree of duet coordination or consistency and the length of the breeding season, providing additional support for the importance of long-term territory defense in the evolution of female vocal

240 signaling (Keenan et al. 2020). Interestingly, a review of songbirds in South Africa and Lesotho
241 found that year-round territoriality was more common in duetting species than in species with
242 solo female song (Mikula et al. 2020).

243 A recent review (Barros et al. 2024) found that the three most commonly reported
244 functions of female song were (in order): territory defense, intrapair communication, and
245 intrasexual competition or aggression (see also Langmore 1998). While there are certainly more
246 studies needed, all three of these functions have been reported in both temperate species (Arcese
247 et al. 1988, Halkin 1997) and tropical species (Logue and Gammon 2004, Demko and Mennill
248 2018), demonstrating that female song may be favored in a wide variety of contexts.

249 For species that have lost female song, the cause could be simply the result of a lack of
250 selection favoring this behavior, perhaps in the absence of year-round territoriality or pair bonds.
251 Alternatively, such a conspicuous signal as song may also be directly selected against if it
252 reduces female fitness (especially due to predation impacting survival and/or reproduction).
253 More research is needed to determine if female song may also carry an energetic cost, associated
254 with either the maintenance of neural/hormonal pathways or increased metabolic demand
255 (Garamszegi and Eens 2004, Garamszegi et al. 2006). Selection may operate differentially on
256 male and female signaling, particularly given the differential investment in reproduction between
257 the sexes, with females investing more energy and time in egg production, incubation, and
258 parental care. Parental cooperation has been shown to decrease in species with more intense
259 sexual selection on males (like polygynous species), leaving females responsible for most of
260 parental care (Burley and Johnson 2002, Remeš et al. 2015).

261 Many females have been observed to sing while incubating eggs or brooding chicks, and
262 whereas this behavior may play important functional roles, such as deterring competitors or
263 signaling to mates (Halkin 1997, Leonard 2008, Trnka et al. 2025), song on the nest is also likely

to attract predators or parasites and may carry significant costs. In *Malurus cyaneus* (Superb Fairy-wrens), females are more likely than males to sing on or close to the nest, and higher female song rates (but not male) significantly increased the risk of nest predation (Kleindorfer et al. 2016). The same pattern was observed for female song on the nest in a North American temperate species, *Mimus polyglottos* (Northern Mockingbird, Stracey et al. 2023). Interestingly, several studies have suggested that nest predation rates are often higher for songbirds in the tropics than those in temperate regions, so one might predict that song on the nest would be less common in the tropics (Martin 1996, Matysioková and Remeš 2022).

Recent Gains of Female Song

Case studies investigating recent *gains* of female song remain quite rare. One study of the Chaffinch genus *Fringilla* has found evidence that a gain of female song may evolve in species maintaining year-round territories (Cooper et al. 2023). Although the common ancestor of the family Fringillidae likely had female song (Garamszegi et al. 2007), several species and subspecies in the genus *Fringilla* on the Atlantic Islands recently shared a common ancestor with a mainland species without female song, *Fringilla coelebs* (Common Chaffinch, Cooper et al. 2023). These authors documented female song in four subspecies of the Common Chaffinch as well as the species *Fringilla teydea* (Tenerife Blue Chaffinch), which they hypothesized represents a recent evolutionary gain of this behavior. In contrast to their mainland relatives, these island females sing solo or in duets with males, and they are all found in "regions with low seasonality", where they defend territories year-round (Cooper et al. 2023).

Another example of a recent gain of female song was documented in a non-migratory population of *Junco hyemalis* (Dark-eyed Junco). In migratory juncos, female song has been reported as rare (Cardoso and Reichard 2016) or absent entirely (Nolan et al. 2002). However,

following the establishment of a year-round resident population in western California in the 1980s, three females in this population were documented singing during the early breeding period (Reichard et al. 2018).

Not all families where female song has been gained have found clear associations with shifts in natural history. The common ancestor of Parulidae, the New World warblers, was likely a migratory temperate-breeding species without female song: only 23% of extant species in this family have reports of female song (Najar and Benedict 2015). Thus, multiple distinct lineages of warblers likely represent relatively recent gains of this behavior. Unlike the previous studies examining the loss of female song (Price et al. 2009, Logue and Hall 2014), the gain of female song in New World warblers does not seem to be associated with any migratory condition or degree of plumage elaboration (Najar and Benedict 2015). Selection may act differently on the gain of female song in families in which ancestors did not have this trait, compared to in families where female song has recently been lost. Gains of female song would indeed be expected in cases where competition has become more intense, such that increased social selection (or sexual selection) would favor increased female elaboration (Tobias et al. 2012, Odom et al. 2014).

Male and Female Song Structure

As female song studies were becoming more frequent, many initially focused on categorizing female song as a simple binary character: present or absent. However, a growing number of studies are now focusing on quantifying female song elaboration in form and rate relative to male song (although "elaboration" or "complexity" have many operational definitions, see Benedict and Najar 2019, Rose et al. 2022). Often, studies of song form use acoustic characteristics such as duration, frequency, or syllable usage to determine how the structure of male and female songs compares. As discussed above, some have theorized that the natural

history characteristics of tropical breeding are more likely to support similarity between the sexes (Slater and Mann 2004, Stutchbury and Morton 2023). However, researchers have found species in both temperate and tropical regions with similar acoustic structure in the two sexes, which may suggest that male and female song experience similar selection pressures even without convergence of sex roles in both temperate regions (Hahn et al. 2013, Rose et al. 2018) and tropical regions (Graham et al. 2018, Rose et al. 2024, see also Odom et al. 2021). Even if a species has sexually dimorphic song, male and female songs may still be similarly elaborate (Yamaguchi 1998, Brunton and Li 2006).

Several temperate species have been found to have acoustically reduced (shorter duration, smaller frequency bandwidth, or lower elemental diversity) female song compared to males, potentially indicating relaxed selection on female song (Baptista et al. 1993, Wilkins et al. 2020, Krieg and Wade 2023, Moyer et al. 2022). Fewer studies have found reduced female song (compared to male song) in tropical species (Rogers 2005, Mennill and Vehrencamp 2005). For example, female *Icterus portoricensis* (Puerto Rican Oriole) sing significantly shorter songs than males, with a smaller range of frequencies. To our knowledge, no studies have found that female song was more acoustically elaborate than male song, although several have found that some males sing lower acoustic frequencies than females (Bradley and Mennill 2009, Dutour and Ridley 2020).

Female song structure may also be shaped by external constraints like habitat characteristics and morphology. For example, the female songs of *Thryophilus rufalbus* (Rufous-and-white Wrens) were more acoustically degraded than male songs in the same habitats, suggesting that acoustic transmission properties may influence the evolution of male and female song characteristics independently (Barker et al. 2009). Additionally, a recent analysis of the antbird family Thamnophilidae showed that female and male songs are similarly constrained by

body size and the degree of habitat exposure, which may lead to similar acoustic characteristics between the sexes (R. Beco, personal communication). Overall, more studies comparing acoustic characteristics of male and female song are still needed, especially in the tropics, to determine how factors such as habitat characteristics and vocal tract morphology may impact the evolution of song structure.

Male and Female Song Rate

Male and female songs have also been shown to differ in rate. Females sing less frequently than males in many temperate species (Arcese et al. 1988, Vondrasek 2006, Odom et al. 2026) and some tropical species (Mennill and Vehrencamp 2005, Templeton et al. 2011, Budka et al. 2023). Few species have shown similar male and female song rates (Cain and Langmore 2015). Interestingly, males and females may be temporally separated, with each sex singing more than the other at different times throughout the day. In a temperate species, *Cyanistes caeruleus* (Blue Tit), females were assumed to only sing rarely when observations were limited to the dawn chorus—the peak singing period for males. However, Sierro et al. (2022) found that female Blue Tits sang frequently throughout the day in "functionally similar contexts" to when males sang. This trend was also found in two tropical orioles, *Icterus icterus* (Venezuelan Troupial) and *Icterus portoricensis* (Puerto Rican Oriole), with female song rates higher than those of males during the day, but much lower than those of males during the dawn chorus (Odom et al. 2016, Moyer et al. 2025).

The sexes may also show different song rate patterns across the annual cycle, with one sex singing more than the other before breeding begins, but less often after laying (Magoolagan et al. 2019, Yelimlieş et al. 2025). Defending year-round territories may also be important for maintaining high female song rates: females of a sedentary subspecies of *Zonotrichia leucophrys*

nuttalli (White-crowned Sparrow) sang regularly throughout the nonbreeding season, whereas females of the migratory subspecies *Z. l. oriantha* only sang early in the breeding season, when territory competition was most intense (Baptista et al. 1993).

Only a few species, all exclusively tropical-breeding, are known to have consistently higher solo female song rates than males, especially *Icterus pustulatus* (Streak-backed Oriole) (Price et al. 2008, Illes and Yunes-Jimenez 2009; see also Kroodsma et al. 1987, Seeholzer and Gamarra 2020 for suboscine species). To our knowledge, no exclusively temperate-breeding species has ever been found to have consistently higher female song rates than male song rates. In general, sex-specific song rates remain understudied, and further research is needed to determine if there are any patterns in association with temperate or tropical breeding.

Over the past few decades, interest in female song has dramatically improved the breadth of knowledge on the form, function, and evolutionary history of female song (Barros et al. 2024). However, for many species, we still lack detailed information on the specific fitness benefits that may maintain elaborate female song or the fitness costs that could lead to its eventual loss. More studies on female song form and function in both temperate and tropical species, as well as additional clade-level phylogenetic analyses of natural history correlates with female song, would provide more insight into how this elaborate trait may have evolved across passerines.

ICTERID CASE STUDIES ON FEMALE SONG

Research on the family Icteridae has led to many important insights into the phylogenetic history and functions of female song. Ancestral state reconstructions have found that female song most likely represents the ancestral characteristic for the New World orioles (genus *Icterus*; Price 2009, Price et al. 2009). All *Icterus* species in which sex-specific song has been investigated were found to have female song, although the degree of elaboration relative to male song varies

widely. For example, *I. pustulatus* (Streak-backed Oriole) is the only oriole (and one of the only songbirds) known to have consistently higher female song rates than male song rates across the annual cycle (Price et al. 2008). A small-scale study suggested high female song rates in *I. graduacauda* (Audubon's Orioles) (Flood 1990), and *I. bullockii* (Bullock's Orioles) have been reported to have higher female song rates than those of males during the nest-building stage (J. Lacson, personal observation, see also Miller 1931). Contrastingly, female *I. cucullatus* (Hooded Orioles) and female *I. galbula* (Baltimore Orioles) have reportedly rare songs (which for the Baltimore Oriole seem to be acoustically comparable to male song; Beletsky 1982, Pleasants and Albano 2020). However, this has yet to be studied in detail for either species.

Some species of orioles also duet: *I. icterus* (Venezuelan Troupial) males and females coordinate their singing into duets to defend territories year-round, with females singing more solo songs than males (Odom et al. 2016, 2019, Odom and Omland 2017). Another tropical oriole with well-documented duets is the *Icterus mesomelas* (Yellow-tailed Oriole) (Jaramillo and Burke 1999). However, male and female song (as well as duets) have only been investigated in detail for only a small number of species in this genus. This group presents an excellent opportunity for comparative analysis of female song, particularly given the diversity of natural history characteristics in the genus (Table 1). The presence or absence of female song is still not known for the majority of tropical oriole species.

Detailed Comparison of a Tropical-Breeding and a Temperate-Breeding Oriole

Building from previous studies on *Icterus* song, we compared male and female song in two different *Icterus* species, *Icterus spurius* (Orchard Oriole) and *Icterus portoricensis* (Puerto Rican Oriole) (Moyer et al. 2022, 2025, Moyer 2024). Although these papers only examined a single species from each breeding latitude, this is a phylogenetically informed comparison, as

Orchard Orioles are more closely related to Caribbean orioles than they are to any other temperate orioles, and the Orchard Oriole is the most closely related temperate-breeding oriole to the Puerto Rican Oriole (Sturge et al. 2009).

Orchard Orioles are migratory, temperate-breeding blackbirds, and the species is sexually dimorphic: adult males have chestnut feathers with black wings, tails, and heads, whereas adult females are olive-yellow with gray or dark olive wings and tails. Female Orchard Orioles were previously thought to have little to no song (Enstrom 1992, Scharf and Kren 2020, but see Scharf and Kren 2022). Contrastingly, Puerto Rican Orioles are non-migratory, tropical-breeding blackbirds endemic to the island of Puerto Rico. The species is sexually monomorphic, with both males and females displaying striking black and yellow feathers—one cannot distinguish the sexes based on plumage. There is good evidence that they maintain territories year-round (Moyer and Omland, pers. obs.). This species was previously documented to have female song, but it was not known to what degree females sing compared to males (Campbell et al. 2016).

We predicted that female song in Orchard Orioles would be under relaxed selection, since this species does not defend territories year-round, has the energetic constraints of migration, and has a shorter breeding season than Puerto Rican Orioles. On the other hand, female Puerto Rican Oriole song should be under more direct selection for defending year-round territories or coordinating breeding activities during their more lengthy breeding season. In Orchard Orioles, they found that female songs were shorter than male songs, and females sang nearly 95% less frequently than males (Moyer et al. 2022). Some Orchard Oriole females sang simple, short songs while others sang with more male-like durations and range of frequencies. Although some females sang during specific contexts, such as during a territorial dispute with a rival female, other females seemed to sing randomly or were never observed singing at all (Moyer et al. 2024; M. Moyer personal observation). Both males and females responded more strongly to male song

than to female song during playback experiments (Moyer et al. 2024). Furthermore, female syllable usage varied widely within and between individuals (Moreland et al. 2025).

This significant variation of Orchard Oriole female song in 1) acoustic structure, 2) production context, and 3) syllable syntax, suggests that female song in this species is under relaxed selection, as predicted, and that it does not serve a consistent function (Lahti et al. 2009, Reinhold 2011, Moyer et al. 2024, Moyer 2024, Moreland et al. 2025). The reduced female song in Orchard Orioles represents a partial loss of ancestral female song, which parallels the loss of elaborate female coloration in this species.

Surprisingly, Puerto Rican Orioles also showed significant acoustic differences between male and female songs, with the sexes differing significantly for seven of the eight variables measured, and female song rates lower than male song rates (Moyer et al. 2025). However, compared to Orchard Orioles, there is far more overlap in all acoustic characteristics of male and female Puerto Rican Oriole song, and both sexes showed similar variation in acoustic structure and syllable usage (Moyer et al. 2025). This suggests that song in this species is under similar selection pressures for both sexes.

Many studies have provided strong evidence for female song being selected for and serving important functions in both temperate and tropical species. However, we know of only one other case where researchers have investigated male and female song such closely related temperate and tropical congeners (Whittingham et al. 1992; see also Mennill 2001, Hagemeyer et al. 2012 for male song comparisons). Furthermore, this is one of the strongest examples of relaxed selection on female song. These studies on New World orioles demonstrate potential new avenues for studying bird song in both sexes, and this work provides valuable new insight into the functions and evolutionary history of this elaborate signaling behavior.

OVERALL UNDERSTANDING OF ELABORATE FEMALE COLORATION

Research on elaborate female coloration has many parallels to female song, beginning with the historical neglect of female coloration. Studies of male ornamentation and female choice in the 1980s and 1990s (e.g., Andersson 1994) neglected female coloration and plumage ornaments. However, in the last 25 years, there has been increased recognition that studying female visual signals is crucial for a comprehensive understanding of avian coloration (Amundsen 2000, Dale et al. 2015). This research has included both phylogenetic studies of the extent and macroevolutionary patterns of female elaboration, and experimental and observational studies of the function of elaborate female signals in single species. Although most of this review focuses on elaborate plumage coloration, researchers have also conducted important work on plumage ornaments such as tail rackets (e.g., Murphy 2007) and bill coloration (Murphy et al. 2009).

Phylogenetic Studies of Female Coloration

At the broadest level, Dale et al. (2015) studied male and female elaboration across all Passeriformes and showed that female coloration was more elaborate in tropical species, a pattern potentially driven by several factors including longer-term pair bonds and year-round territoriality (see also Stutchbury and Morton 2023). Dale et al. (2015) point out that past studies often focused on male coloration in species with extreme sexual dimorphism, which leaves much of the elaborate coloration in songbirds unexplained. However, Dale et al. (2105) did not focus on the question of whether the common ancestor of all passerines had elaborate female coloration. Within songbirds (oscine passerines) there are many species-poor groups of Australasian songbird lineages that are successive sister groups to species-rich groups from the rest of the world (Barker et al. 2004). Many of these species-poor groups have female song (Odom et al. 2014), and many species in these groups have elaborate female coloration (e.g.,

480 many honeyeaters, Meliphagidae). Thus, it is possible that the common ancestor of songbirds
481 over 50 million years ago in Australasia had elaborate female coloration, but future detailed
482 work would be needed to code homologous characters suitable for ancestral state reconstruction.
483 Regardless of that specific answer, it seems clear that there are multiple examples of losses and
484 gains of elaborate female coloration across Passeriformes (e.g., Price 2019).
485 Early work on several New World songbird lineages provided initial indications that
486 many songbird lineages may have evolved dichromatism through the loss of elaborate female
487 coloration (see Figure 1B). Irwin (1994) used an unpublished molecular phylogeny of the
488 Icteridae to argue that changes in elaborate female coloration frequently caused changes in
489 dichromatism. Burns (1998) showed that many cases of gains or losses of sexual dichromatism
490 in tanagers (Thraupidae) were due to changes in female coloration.
491 Another line of research asked about rates of change of female color versus male color.
492 Price and Eaton (2014) used formal reflectance spectrophotometry to rigorously measure
493 coloration in New World blackbirds (Icteridae, especially grackles and allies). They showed that
494 female coloration changed much more than male coloration in several lineages. Their findings
495 included many examples of females gaining elaborate coloration, and some examples of females
496 losing elaborate coloration (see also Price 2019, Price et al. 2024).
497 Note that early work on this topic frequently spoke about the "brightness" of male versus
498 female coloration, and many ornithologists still reflexively refer to "bright" plumage. However,
499 rigorous use of formal color measurement made apparent the problem with that approach. In
500 reflectance spectrophotometry, "brightness" is defined as the total amount of light reflected by an
501 object. Researchers were surprised when females of some species came back as being brighter
502 than males. For example, the body of a male *Agelaius phoeniceus* (Red-winged Blackbird) is not
503 bright at all: black feathers generally reflect the least amount of light. In contrast, the cryptic

mottled tan/brown plumage of female red-wings reflects more light than the male's black plumage. Thus, females have higher brightness scores. As a result, most researchers have switched from talking about "bright plumage" to "elaborate plumage". Like in song studies, operational definitions of elaborate may vary but often refer to multiple contrasting colors, the presence of carotenoids or structural colors, or "male-like" patterns (Hofmann et al. 2008, Dale et al. 2015, Thibault et al. 2022). Conveniently, using the concept of elaborateness results in terminology that can be shared across studies of coloration and song.

Functions of Elaborate Female Color

Most of the proposed functions of elaborate female color are the same as those proposed for elaborate female song, including male mate choice, female-female aggression in the context of mating, and mate defense (Amundsen 2000, Tobias et al. 2012). Hernandez et al. (2021) reviewed evidence and conducted several meta-analyses testing several of these ideas. They demonstrated that 1) many studies showed evidence that female coloration scores were positively correlated with indices of condition, and 2) males exhibited preferences for females with higher color scores.

In addition, social selection may select for elaborate coloration via status signaling to defend resources outside of the mating context (Tobias et al. 2012). In many tropical orioles, for example, females and males have similar sex roles year round, so if males can benefit from status signaling with color, females are also likely to benefit. Murphy et al. (2009) studied *Icterus pustulatus* (Streak-backed Orioles) in Mexico and conducted an experiment with color-augmented taxidermic mounts. Female orioles responded more strongly to the color-augmented intruders than to the control group intruders, supporting a role for female color in status signaling.

The potential importance of social selection and status signaling outside of the mating context can be illustrated with the following scenario. Consider a female oriole early in the non-breeding season feeding on a cactus fruit near the boundary of the territory she shares with her mate. A male from a neighboring territory approaches and attempts to displace her from the fruit. However, she uses behavioral and color displays and successfully repels him. Sexual selection involves competing for mates with others of the *same sex*. In contrast, this scenario involving a female competing with a bird of the *opposite sex* far outside the breeding season helps make it clear that this is social selection (narrow sense) – selection for elaborate coloration in an ecological context far removed from obtaining mating opportunities (Tobias et al. 2012). Females signaling status while competing with males for resources, using coloration or other elaborate displays, could drive selection for female elaboration across the full range of avian taxa.

Price and Eaton (2014) also argued that gains of elaborate female color might reflect relaxed selection for cryptic female color. They pointed out that changes toward male-like color could be relatively easy and quick, given that the genetic and developmental mechanisms for elaborate coloration are already present in the males of many of the species they studied. The reverse is also true, because cryptic juvenile coloration is present in most orioles and many other songbirds (Jaramillo and Burke 1999). These contrasting scenarios emphasize that when considering the gain and loss of elaborate signaling traits, it is important to consider both the selection acting on traits in a social context (especially trait gains), and the selection acting on these elaborate traits in an ecological context (especially trait losses, see detailed discussion below).

ICTERID CASE STUDIES ON FEMALE COLORATION

The New World orioles (genus *Icterus*) show repeated loss of elaborate female coloration with shifts to migration and temperate zone breeding (Table 1, Friedman et al. 2009). Elaborate female coloration is present in nearly all tropical New World orioles. In most tropical oriole species, it is difficult or impossible to differentiate adult males and females in the field based on plumage coloration. Males of all oriole species (both tropical and temperate breeding) have patches of jet-black coloration, with most species also having large patches of yellow, orange or chestnut coloration. Females of most oriole species also have these striking patches of black and colored plumage.

However, females in the temperate breeding lineages have lost much of this contrasting coloration. The common ancestor of all orioles likely had elaborate coloration in both sexes (Hofmann et al. 2008). Elaborate female coloration has subsequently been lost repeatedly in the group, and across the genus, the loss of elaborate female color is strikingly correlated with the evolution of migration (Friedman et al. 2009). Examples of these losses are evident in the three temperate-breeding long-distance migratory species (*I. galbula,* Baltimore; *I. bullockii,* Bullock's; *I. spurius*, Orchard; Figure 2).

Note that there is one glaring exception to the tropical/temperate dichotomy in orioles– the tropical *I. oberi* (Montserrat Oriole) has also lost all hint of elaborate female coloration (Figure 2). We know of no ecological reason why the Montserrat Oriole is such an outlier–there is no evidence that they lack year-round territoriality, for example. However, there are several published examples of other taxa on small islands that have had changes in sexual dichromatism in unpredictable directions, perhaps due to random changes caused by founder events and/or small populations (Omland 1997, Kearns et al. 2020).

Of the temperate-breeding species, Orchard Orioles present the most dramatic case of

color loss, with adult females having no striking black or colored patches—the entire plumage consists of uniform olive-yellow coloration. It is noteworthy that this may be the oriole species that has lost the most male-like song features as well (Moyer et al. 2022). Therefore, there are likely increased costs and/or decreased benefits to elaborate female coloration in this lineage. An alternative or additional possibility would be that the Orchard Oriole lineage has experienced such selection pressures for longer. Although it is conceivable that increased predation in the temperate zone has selected for loss of color and song in Orchard Orioles, that seems unlikely to us. For example, many predator guilds that might select against elaborate colors—including snakes, mammals, and birds of prey—are present in both temperate and tropical ecosystems. Rather, it seems more likely that, given the limited role of females in territory defense in this species, and the very short amount of time that this species is territorial, the absence of a substantial benefit could be a crucial cause of the loss. In addition, predation during migration or on the winter grounds could select for loss of elaborate color in this and other migratory lineages (Simpson et al. 2015).

Note, however, that female song would not be lost because of predation during the non-breeding season. Female Orchard Orioles are not known to sing in the non-breeding season, and males seldom sing in the non-breeding season (K. Omland, personal observation). Therefore, lack of or reduced social benefit during the breeding season seems like the best explanation for the diminution of female song in Orchard Orioles. This observation suggests that a lack of benefit may also be a key driver for loss of female coloration in this species as well. Comparing the Orchard Oriole and its tropical relatives provides many opportunities to contrast the behavior, coloration and song of females in a tropical versus a temperate songbird.

SYNTHESIS - MULTIMODAL SIGNALING AND SOCIAL SELECTION

599 It is important to consider female song and elaborate female coloration in connection with each
600 other. Previous studies of multiple elaborate male traits have suggested that selection might favor
601 the elaboration of a single ornament or type of display. For example, Kusmierski et al. (1993)
602 studied this idea in male bowerbirds, involving the use of coloration versus bower characteristics
603 in female mate attraction. Sexual selection involving multiple male ornaments has also been
604 discussed with regard to multiple plumage ornaments (e.g., ducks, Omland 1996) or multiple
605 modes of male signaling (e.g., manakins, Ariznavarreta et al. 2025). Importantly, most of these
606 previous studies suggest that different types of signals or different signaling modalities evolve
607 independently.

608 In the context of this review, transference might predict trade-offs between elaborate
609 coloration and song (Badyaev et al. 2002, Tietze and Hahn 2024). Indeed, there are several
610 studies of multimodal signaling focused on the Estrildid finches that suggest that different female
611 traits (dance, plumage, song) can evolve independently (e.g., Soma and Garamszegi 2015,
612 Gomes et al. 2017).

613 However, in many cases, social selection likely drives the evolution of both female color
614 and female song in concert, and both forms of elaboration seem to experience similar selection
615 pressure (Webb et al. 2016). Species that have year-round territoriality, most often tropical
616 species, will experience stronger social selection compared to species that do not, and we find
617 that tropical species are more likely to have both elaborate female coloration and elaborate
618 female song. Webb et al. (2016) conducted a crucial large-scale comparative phylogenetic study
619 looking at female coloration and female song across 1,023 songbird species. They found a strong
620 correlation between female colorfulness and the presence of female song. They interpreted these
621 results to indicate that female song and elaborate female coloration have similar functions
622 (reinforcing signals), and that the two modes of elaborate signaling have evolved under similar

623 selection pressures.

624

625 **CONCLUSION - CONTINUED NEED FOR COMPARATIVE FEMALE SONG AND**

626 **COLORATION STUDIES**

627 In this review, we have examined both elaborate female song and elaborate female color.

628 Signaling in both visual and vocal traits can be studied in the context of similar costs and

629 benefits. Therefore, studying both female coloration and song in the same species or clades

630 presents excellent opportunities to advance our understanding of multimodal female signaling.

631 We note that in the last 25 years, Google Scholar lists over 1,500 publications on avian behavior

632 that have the term “female song” in the article, whereas roughly only 500 publications use the

633 terms “female color” or “female coloration”. Thus, research on female coloration has not

634 matched the ongoing intense interest in female song, indicating an important opportunity to

635 continue to investigate female advertisements and status signals.

636 There is increasing recognition in both the color and song research communities that

637 accounting for elaborate signaling in females is useful and necessary for understanding elaborate

638 traits across all birds and across all animals. Using phylogenetic approaches with rigorous

639 ancestral state reconstruction and phylogenetic comparative methods provides the crucial context

640 for understanding whether traits have changed in males, females, or both sexes. Furthermore,

641 comparing species with different characteristics based on their evolutionary relationships

642 provides unique opportunities, especially by highlighting cases where elaborate traits may have

643 recently been lost.

644 Across songbirds, there are likely many other cases of recent losses of elaborate female

645 color and/or female song, especially in temperate lineages, that will lead to further insights in the

646 evolution of elaborate female traits. We hypothesize that there will also be examples of recent

losses in tropical lineages that have evolved colonial polygyny or brood parasitism, where social selection may not favor female signaling in the absence of territoriality (Price 2009). Given the strong evidence that the evolution of dimorphism in male and female signaling traits is driven by loss of these traits in females, future studies should seek to investigate such additional examples of female signaling being lost or reduced. Of course, cases of recent gains of elaborate female traits also provide important opportunities, although they may be fewer.

As we emphasized at the beginning of this review, many of the most conspicuous signals in birds include both male and female traits. Only by considering both female and male signals can we fully understand the extent, history, mechanisms, and functions of elaborate advertisement traits across all birds.

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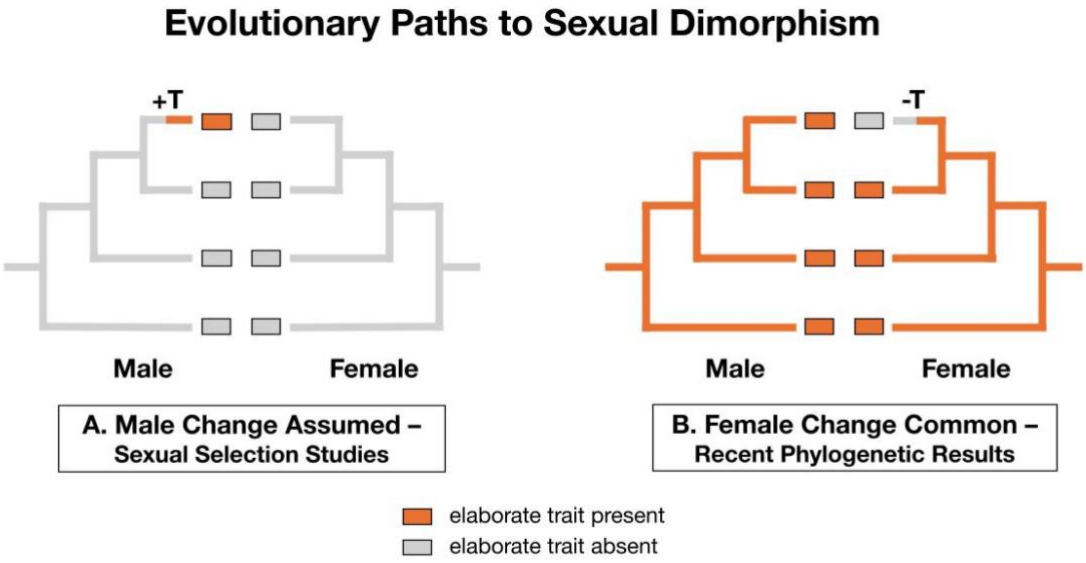

Figure 1. Phylogenetic perspective on the gain and loss of elaborate advertisement traits. Figure 1A depicts the scenario implicitly assumed by most classic sexual selection studies: males gaining an elaborate trait leading to sexual dimorphism. Figure 1B shows a different scenario, with females losing an elaborate trait leading to sexual dimorphism. +T indicates a gain and -T indicates a loss of elaborate advertisement traits. (Based on Omland and Hofmann 2006).

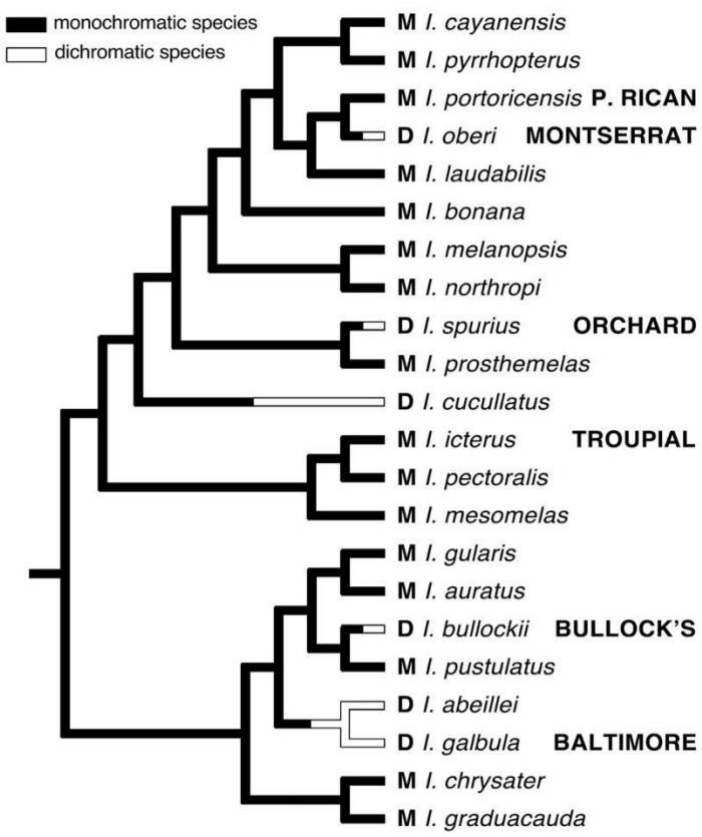

Figure 2. Ancestral state reconstruction of female color in New World orioles (*Icterus*) (based on throat color, simplified figure based on Hofmann et al. 2008). The common ancestor is reconstructed as monochromatic, and elaborate female color is shown being lost five times (four of those in migratory species). English common names are shown for species highlighted in the text. (NOTE: *I. northropi* was incorrectly coded as dichromatic by Hofmann et al. 2008).

Table 1: Comparison of natural history traits typical of tropical versus temperate breeding migratory songbirds. Based especially on studies of New World orioles (*Icterus*), but likely applies to many other songbird lineages. See also Stutchbury and Morton (2023).

Natural History Trait	**Tropical**	**Temperate**
Migration	Sedentary	Migratory
Territoriality	Year-round	Few months
Pairing	Year-round (long-term)	Few months
Song	Similar between sexes	Female diminished
Coloration	Elaborate in both sexes	Elaborate males/cryptic females