



# Sex differences in song and plumage color do not evolve through sexual selection alone: new insights from recent research

J. Jordan Price<sup>1</sup>

Received: 3 November 2018 / Revised: 10 May 2019 / Accepted: 31 May 2019 / Published online: 15 June 2019  
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## Abstract

Recent studies show that traits long recognized as sexually selected ornaments, such as the bright plumage colors and melodious vocal displays of songbirds, have evolved in surprising ways. Male plumage colors are generally more elaborate and diverse than female colors, and in many species only males sing, so both of these dimorphisms are widely presumed to have evolved through sexual selection on males. Yet, in multiple widely divergent songbird clades, sexual differences in colors and songs have evolved through losses in females rather than gains in males. Indeed, changes in female phenotypes may be the principle driving factor affecting such sexual dimorphisms in most songbirds. Sexual dichromatism and song dimorphism also tend to be associated with life history traits other than mating system, such as seasonal migration or territorial behaviors. Altogether, these recent findings support the view that sexual dimorphism is an evolutionary byproduct of multiple, different selection pressures acting on each sex rather than just sexual selection on males. Researchers should therefore be cautious to avoid assuming that dimorphism itself is a character solely reflecting levels of sexual selection in species.

**Keywords** Female song · Ornament · Sexual dimorphism · Sexual selection · Sexual dichromatism

## Introduction

“Thus it is, as I believe, that when the males and females of any animal have the same general habits of life, but differ in structure, color, or ornament, such differences have been mainly caused by sexual selection” (Darwin 1859).

The elaborate songs and plumage colors of birds have long been considered textbook examples of sexually selected ornaments (Andersson 1994; Hill and McGraw 2006; Catchpole and Slater 2008). Darwin himself referred to these traits in outlining his theory of sexual selection, suggesting that “female birds, by selecting, during thousands of generations,

the most melodious or beautiful males, according to their standard of beauty, might produce a marked effect” (Darwin 1859). The striking color patterns and complex vocalizations of male songbirds, and concomitant differences between the sexes in these features, are thought to have evolved primarily through female choice and competition among males (Andersson 1994).

Males are often more elaborate and conspicuous than females in their colors and sounds, especially in northern temperate passerine species, which have been the focus of many studies to date (Marler and Slabbekoorn 2004; Hill and McGraw 2006). Females of these species are often relatively drab in comparison to males and rarely sing. Male songs and plumage colors also appear more diverse across taxa, whereas females are harder to distinguish, a fact well known to novice bird watchers who generally focus on males rather than females when learning to identify species (Sibley 2001). Given these patterns of elaboration and diversity, it is perhaps not surprising that past evolutionary changes in plumage and song are often assumed to have occurred primarily in males (Darwin 1859, 1871).

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Communicated by S. Kipper.

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This article is a contribution to the Topical Collection 27th International Ornithological Congress, Vancouver, Canada, 19 to 26 August 2018.

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✉ J. Jordan Price  
jjprice@smcm.edu

<sup>1</sup> Department of Biology, St. Mary’s College of Maryland, St. Mary’s City, MD 20686, USA

## Surprises in the evolution of sexual dichromatism

Yet, studies in recent decades seem to challenge these views. In one of the first phylogenetic comparative studies of plumage evolution, Irwin (1994) showed that variation in sexual dichromatism across the New World blackbird family (Icteridae) is largely explained by past evolutionary changes in females rather than in males. Reconstructions of ancestral character states using color data from both sexes revealed greater evolutionary lability in female colors than in male colors, with females of some species having bright or iridescent plumage like males, and females of other species having dull or brown plumage that is strikingly different from that of males.

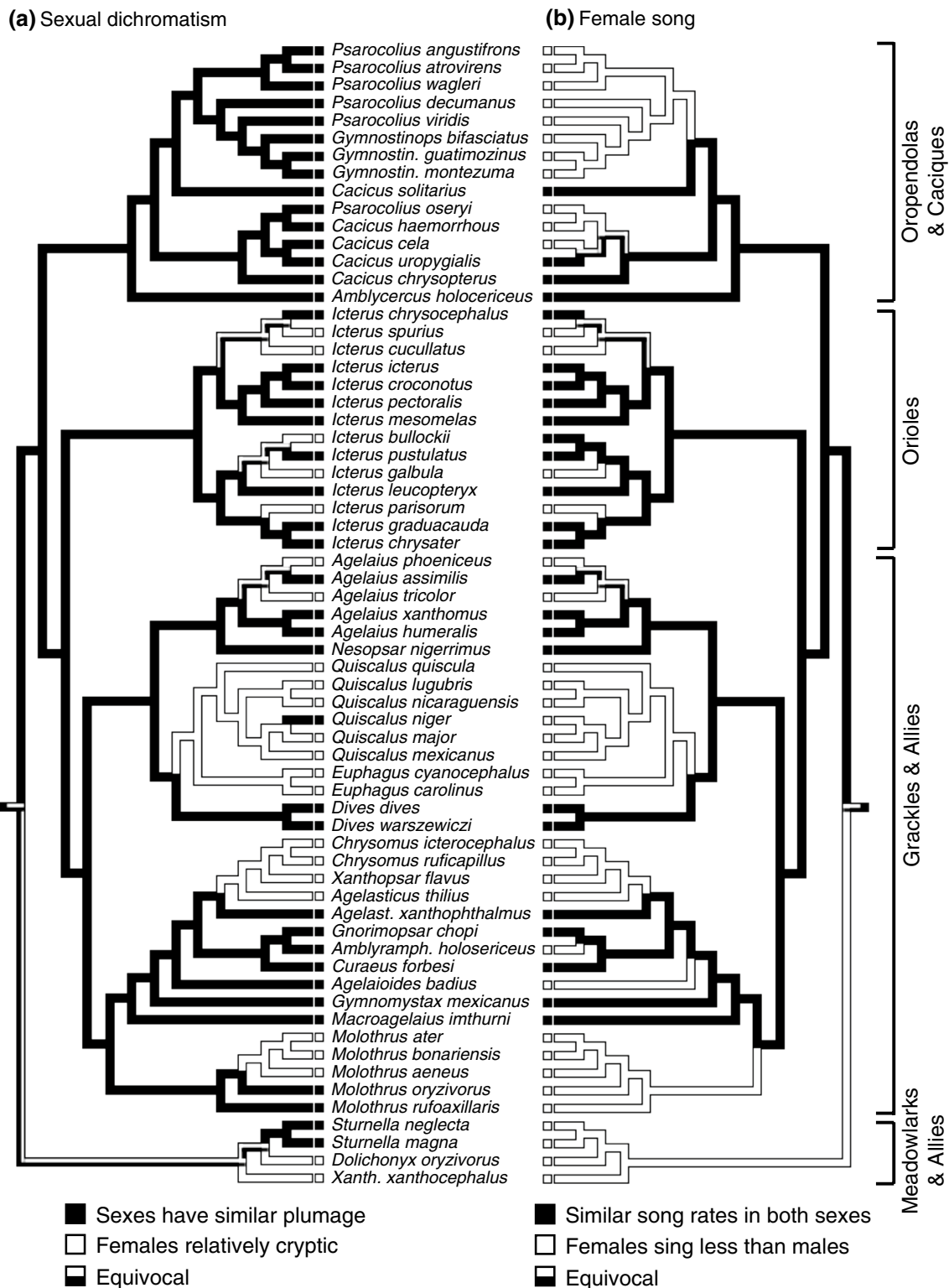
Irwin's (1994) paper was among a succession of innovative studies that used phylogenetic approaches to investigate avian plumage and behavioral evolution, following the popularization of these methods by Brooks and McLennan (1991), Harvey and Pagel (1991), and Martins (1996). These studies revealed that sexual dimorphisms can evolve through changes in either sex away from or toward a shared pattern, rather than just through changes in males (Wiens 2001; Badyaev and Hill 2003). Burns (1998), for example, showed that the evolution of sexual dichromatism in tanagers (Thraupidae) has involved more frequent plumage changes in females than in males (but also see Shultz and Burns 2017). Simpson et al. (2015) showed similar evolutionary patterns in New World warblers (Parulidae). Likewise, using quantitative spectrometer measurements of color rather than human visual scores, Hofmann et al. (2008) showed that sexual dichromatism in the New World orioles (genus *Icterus*) has evolved through losses of bright colors in females rather than gains of these colors by males. Males and females had similarly colorful plumage in the tropical common ancestor of the genus.

Perhaps counterintuitively, studies have found relatively frequent past changes in female colors despite the fact that male colors appear more elaborate and diverse across species today. This was illustrated in a recent study of New World blackbird taxa (Price and Eaton 2014). Male colors are significantly more divergent among taxa than are female colors, yet female plumage colors have changed more dramatically in the evolutionary past. Similar patterns were found in Australasian fairy-wrens (Maluridae), in which Johnson et al. (2013) used a model-based approach to show that male plumage colors have diverged among species at relatively steady rates, while female coloration has changed rapidly in some lineages and little in others. Both blackbirds and fairy-wrens include a variety of strikingly colored males, with plumage that clearly play a role in male reproductive success (Searcy

and Yasukawa 1995; Rowley and Russell 1997; Jaramillo and Burke 1999). Nevertheless, within these and other passerine clades, female colors have changed more frequently and dramatically, repeatedly converging on similar cryptic color themes that make them appear as if they have not changed much at all (Burns 1998; Hofmann et al. 2008; Johnson et al. 2013; Price and Eaton 2014).

Sexual dichromatism is widely presumed to reflect relative levels of sexual selection, with polygynous species exhibiting higher levels of dichromatism than monogamous species. Researchers have even used sexual dichromatism as a proxy for sexual selection (e.g., Seddon et al. 2013). Yet few studies have found evidence for this relationship (Badyaev and Hill 2003; Dale et al. 2015; Dunn et al. 2015; Price 2015; Shultz and Burns 2017). In both the New World orioles and New World warblers, for instance, sexual dichromatism shows no relationship with mating system and instead is significantly associated with seasonal long-distance migration (Friedman et al. 2009; Simpson et al. 2015). Migration has evolved repeatedly in these two clades along with relatively dull female plumage from brightly colored female ancestors. Studies of other songbird groups have found associations between sexual dichromatism and a variety of life history factors other than mating system, including breeding latitude (Johnson et al. 2013) and nesting behaviors (Martin and Badyaev 1996; Soler and Moreno 2012; Drury and Burroughs 2016, but see Matysioková et al. 2017).

The life history correlates of sexual dichromatism can differ even within a single taxonomic family, as illustrated by the New World blackbirds. This diverse family includes three well-studied sister clades (Fig. 1): the grackles and allies, the New World orioles, and the oropendolas and caciques (Jaramillo and Burke 1999). In the grackles and allies, levels of dichromatism are significantly associated with social mating system, with polygynous taxa being more dichromatic than monogamous taxa (Irwin 1994; Price and Eaton 2014). In the orioles, in contrast, sexual dichromatism is not related to mating system but is significantly associated with migratory behavior (Friedman et al. 2009). And, finally, in the oropendolas and caciques, no one species is notably dichromatic, yet plumage colors in both males and females have diverged more rapidly among polygynous species than among monogamous species, strongly indicating that color patterns have changed under the influence of sexual selection (Price and Whalen 2009). Why dichromatism is associated with polygynous mating systems in the grackles and allies but not in the oropendolas and caciques is not well understood. But, clearly, the evolution of sexual dichromatism in birds is more complicated than we often assume.



**Fig. 1** Ancestral state reconstructions of **a** sexual dichromatism and **b** female song, calculated using unordered parsimony on a molecular phylogeny of the New World blackbird family. Both are scored as binary characters, with sexual dichromatism scored based on whether the sexes have plumage that is similar or notably different, often with

relatively cryptic females (from Jaramillo and Burke 1999; Hofmann et al. 2008; Price and Eaton 2014), and with female song scored based on whether females sing as frequently as males or sing less frequently, if at all (from Price et al. 2009). Four major subclades within the family are indicated on the right

## Surprises in the evolution of singing behavior

Phylogenetic studies of bird song have revealed evolutionary patterns that are surprisingly similar to the evolution of sexual dichromatism (Price 2015). Both show relatively frequent changes in females, often in the same lineages (Fig. 1). A recent comparative study by Webb et al. (2016) found a significant positive correlation between the presence of female song and elaborate female plumage colors across songbirds, reflecting the evolution of reduced sexual dimorphisms in both of these traits. Songs and plumage colors are often viewed as different types of traits, one as a behavioral and the other as a morphological feature, yet both can involve anatomical differences between the sexes, whether in neuroanatomy (Gahr 2007) or in pigment or structural colors (Hill and McGraw 2006). Furthermore, although they are often treated as discrete binary characters, both actually vary continuously across taxa (Price 2015). The New World blackbird clade includes species in which female song has never been recorded (e.g., *Sturnella neglecta*), others in which females sing occasionally (*Icterus spurius*), still others in which both sexes sing at similar rates (*Agelaius assimilis*), and even species in which the sexes combine their songs into highly coordinated duets (*Dives dives*) (Price 2009; Odom et al. 2015). Color differences between males and females vary along a similar continuum, from strikingly different to virtually identical (Price and Eaton 2014). Both songs and colors are used as signals during mate choice and, when they do differ between the sexes, males are typically more conspicuous, elaborate, and diverse (Andersson 1994). Thus, both are widely presumed to have evolved through sexual selection on males (Darwin 1859, 1871).

As in sexual dichromatism, sexual differences in singing behavior have generally evolved through losses in females rather than gains in males (Price et al. 2009; Odom et al. 2014). Phylogenetic analyses of New World blackbird taxa show that both sexes sang in tropical ancestors and that female song has since been lost multiple times independently, resulting in current species in which primarily males sing (Fig. 1b; Price 2009; Price et al. 2009). Likewise, in a more extensive analysis of all songbirds, Odom et al. (2014) showed that females sang in ancestors and that the absence of female song in so many songbird species today is due to multiple evolutionary losses. Given that nearly all male songbirds sing (Catchpole and Slater 2008), these findings suggest that past changes in singing behavior have been more dramatic in females than in males.

Why has female song been lost in so many songbird lineages? Kleindorfer et al. (2016) showed that female

Superb Fairy-wrens (*Malurus cyaneus*) that sing near or inside their nests experience significantly higher rates of egg and nestling predation than do quieter females, whereas similar patterns were not found among males. Such sex-specific effects may be common in species in which the sexes contribute differently to parental care (Kleindorfer et al. 2016). As with the evolution of cryptic color patterns in females (Martin and Badyaev 1996; but see Cain et al. 2019), perhaps the evolution of not singing is an adaptation to avoid predation. Why this might be more important in some species than others deserves further investigation.

Studies show that female song is much more widespread than previously thought (Langmore 1998; Riebel 2003; Garamszegi et al. 2007; Odom et al. 2014; Riebel et al. 2019), especially among tropical songbirds (Stutchbury and Morton 2001; Slater and Mann 2004; Price et al. 2009). Approximately 71% of the species surveyed by Odom et al. (2014), across 32 deeply divergent avian families, exhibit female song. Previous views of bird song as a primarily male trait may be explained in part by the fact that most previous studies have focused on temperate songbird species, in which typically only males sing (Marler and Slabbekoorn 2004; Catchpole and Slater 2008). Moreover, considering the high levels of biodiversity in the tropics, and that many species with female song are also relatively sexually monomorphic in their plumage (Stutchbury and Morton 2001; Webb et al. 2016), female singers might frequently be assumed to be males, thus female song may be even more common than we currently realize (Odom and Benedict 2018).

Studies also show that song dimorphism has little direct relationship with mating system. Singing by both sexes does tend to occur in monogamous species, but generally only those species that are also non-migratory and defend year-round territories, a set of characteristics that is especially prevalent in the tropics (Slater and Mann 2004; Price et al. 2009). Indeed, this may largely explain why female singing is so much more common among tropical than temperate songbirds. The tropical ancestors of the New World blackbird family were apparently monogamous with year-round territories (Price 2009). Female song has been lost in some blackbird taxa along with the evolution of polygyny, but it has also been lost with the evolution of migration and with the evolution of colonial, non-territorial breeding (Price 2009). Female singing rates have changed for multiple reasons in different lineages. Thus, as with sexual dichromatism, levels of song dimorphism do not generally reflect levels of sexual selection.

The convergent sex roles seen in many tropical songbirds, in which both males and females jointly defend year-round territories, reach their most extreme form in species that combine their vocalizations into coordinated male–female duets (Langmore 1998; Hall 2009). Although not strictly

a tropical phenomenon (Garamszegi et al. 2007; Benedict 2008), female singing and duetting are nonetheless more common at tropical latitudes (Slater and Mann 2004). A variety of life history traits have been invoked to explain the existence of female song and duets (Langmore 1998; Hall 2009; Price 2009; Logue and Hall 2014; Baldassarre et al. 2016). Yet, female singing and male–female duetting are not equivalent, with one referring to song production by both sexes and the other including the additional step of male–female vocal coordination. Indeed, duetting behavior has evolved multiple times in New World blackbirds, but only in a small subset of the taxa in which both sexes sing (Odom et al. 2015). Furthermore, associations between duetting and various life history traits disappear when female song is controlled for, leaving the question of why duets evolved in these particular species unaddressed (Odom et al. 2015). Understanding the evolution of this striking example of behavioral coordination will undoubtedly be a major avenue of future research.

## Changing our perspectives

Why are recent findings about the evolution of color and song so surprising? Certainly the remarkable prevalence of female song reported by Odom et al. (2014) was unexpected given our previous disproportionate focus on northern temperate songbirds in which females rarely sing. But such geographic biases do not easily explain why we are so surprised to learn that evolutionary changes have occurred primarily in females rather than males. These patterns of female change do not necessarily disagree with the results of any previous studies. Rather, they disagree with some of our previous assumptions about how dimorphic traits tend to evolve (Price 2015).

For example, given the striking diversity of male plumage colors and vocal displays, in contrast to the relative lack of diversity in females, especially among temperate species (Sibley 2001; Catchpole and Slater 2008), it seems obvious that past changes have occurred primarily in males (Darwin 1859, 1871). Yet, recent studies suggest that these different patterns of diversity are explained by different sex-specific evolutionary modes, with males continuously diverging in their colors and songs (Price and Lanyon 2002; Price and Whalen 2009; Greig et al. 2013) and females exhibiting a more punctuated pattern of rapidly gaining or losing male-like traits (Price et al. 2009; Johnson et al. 2013; Price and Eaton 2014). Females of different species have repeatedly and convergently evolved similar traits, either through the evolution of similarly cryptic plumage or through the loss of song, which in effect has overwritten past changes. Apparently there are numerous ways for males to be visually or

vocally elaborate, but only a few ways for females to be cryptic or quiet.

However, greater changes in females do not necessarily indicate that female traits have been under stronger selection. Numerous studies, for instance, have shown that the conspicuous red epaulets and buzzy songs of male Red-winged blackbirds (*Agelaius phoeniceus*) are important sexually selected signals that affect male reproductive success (Searcy and Yasukawa 1995). Nevertheless, phylogenetic analyses of the *Agelaius* genus show that these male traits have changed relatively little and that most changes in plumage colors and vocalizations have occurred in females (Fig. 1). Males across this genus are remarkably similar in their plumage colors and songs, whereas females differ substantially among species, with some appearing nearly identical to males (in *Agelaius assimilis*, *Agelaius xanthomus*, *Agelaius humeralis*) and others strikingly different (in *Agelaius phoeniceus*, *Agelaius tricolor*) (Jaramillo and Burke 1999; Price et al. 2009; Price and Eaton 2014). But this lack of change in males does not necessarily indicate a lack of selection. Although selection is generally viewed as driving evolutionary change, adaptive phenotypic characters can also be under strong stabilizing selection and remain unchanged for long periods of evolutionary history (Price and Lanyon 2002). Rapid female changes may have no direct bearing on how male traits are influenced by sexual selection (Johnson et al. 2013; Price 2015).

The evolution of sexual dimorphism, whether through gains or losses in males or females, involves the evolution of sex-specific mechanisms of genetic expression, favored in one sex but concurrently opposed in the other (Kimball and Ligon 1999; Wiens 2001; Kraaijeveld 2014). Unlike divergence among species, in which certain genes may be favored in some lineages and lost in others, divergence between males and females within a species involves autosomal genes that remain in both sexes but just differ in their influences (Kraaijeveld 2014). Given that all autosomal genes spend roughly half of their time in males and half in females, assuming equal sex ratios, genes cannot be lost in a species if they are expressed in one sex. Increases in sexual dimorphism likely involve the evolution of new sex-specific physiological pathways but not necessarily the evolution of new genes.

Following this logic, we should expect evolutionary losses of dimorphism to occur especially rapidly, given that the genetic and hormonal architecture for a trait expressed in one sex is presumably already present in the other (Kimball and Ligon 1999; Price 2015). This appears to be the case in both the New World blackbirds (Price and Eaton 2014) and Australasian fairy-wrens (Johnson et al. 2013), in which the evolution of bright male-like plumage colors in females has occurred relatively abruptly. This might also explain the apparently rapid evolution of female song in a

recently established non-migratory population of Dark-eyed Juncos (*Junco hyemalis*) in California (Reichard et al. 2018). This population originated from a larger migratory population during the 1980s. While female song is ancestral to all songbirds (Odom et al. 2014), it has not been recorded in the ancestral population of these juncos, presenting the intriguing possibility that female song has been rapidly regained (i.e., song dimorphism lost) within just a few decades.

## Conclusions and future directions

These and other new findings are prompting us to reconsider long-held assumptions about how avian plumage colors and songs evolve, which in turn presents exciting new challenges to our understanding of the underlying evolutionary mechanisms. Current trait diversity does not necessarily reflect past patterns of change, and current differences between the sexes do not necessarily indicate the influence of sexual selection alone. Sexual dimorphism is a product of different evolutionary mechanisms acting on each sex rather than just sexual selection acting on males.

Future research might disentangle these various selection pressures using an integrative approach that focuses on both sexes simultaneously (Price 2015; Webb et al. 2016; Riebel et al. 2019). Sex-inclusive studies should investigate the function and development of both female and male signals in individual species, allowing comparative analyses across species and between sexes to investigate the forces driving evolutionary change. Understanding the evolution of avian colors and songs will provide new insights into the evolution of sex differences in general.

Traits long-recognized as sexually selected ornaments, even referenced by Darwin (1859) himself in initially describing the process of sexual selection, are now known to have evolved in ways we did not expect. Yet, rather than contradicting past results, these new findings are important in that they reveal some of our own biases and preconceptions. Indeed, it makes one wonder what the study of avian evolution would look like if we had the opposite biases. What if the field of evolutionary biology had originated in a world where brightly colored, singing females were the norm? What if Darwin had grown up in the tropics rather than England? Would he have wondered why the females of so many temperate songbirds have such dull plumage colors? Would he have asked why females do not sing rather than why males do?

**Acknowledgments** I am grateful to Kristal Cain and Michelle Hall for inviting me to participate in their International Ornithologists' Union symposium on female ornamentation in birds. Support to attend the symposium was provided by a faculty development grant from St. Mary's College of Maryland.

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