

Rethinking our assumptions about the evolution of bird song and other sexually dimorphic signals

J. Jordan Price *

Department of Biology, St. Mary's College of Maryland, St. Mary's City, MD, USA

OPEN ACCESS

Edited by:

Michelle L. Hall,
University of Melbourne, Australia

Reviewed by:

Laszlo Zsolt Garamszegi,
Estación Biológica de
Doñana-Consejo Superior de
Investigaciones Científicas, Spain
Erik Enbody,
Tulane University, USA

*Correspondence:

J. Jordan Price,
Department of Biology, St. Mary's
College of Maryland, St. Mary's City,
18952 E. Fisher Rd., MD 20686, USA
jjprice@smcm.edu

Specialty section:

This article was submitted to
Behavioral and Evolutionary Ecology, a
section of the journal *Frontiers in
Ecology and Evolution*

Received: 03 February 2015

Accepted: 29 March 2015

Published: 14 April 2015

Citation:

Price JJ (2015) Rethinking our
assumptions about the evolution of
bird song and other sexually dimorphic
signals. *Front. Ecol. Evol.* 3:40.
doi: 10.3389/fevo.2015.00040

Bird song is often cited as a classic example of a sexually-selected ornament, in part because historically it has been considered a primarily male trait. Recent evidence that females also sing in many songbird species and that sexual dimorphism in song is often the result of losses in females rather than gains in males therefore appears to challenge our understanding of the evolution of bird song through sexual selection. Here I propose that these new findings do not necessarily contradict previous research, but rather they disagree with some of our assumptions about the evolution of sexual dimorphisms in general and female song in particular. These include misconceptions that current patterns of elaboration and diversity in each sex reflect past rates of change and that levels of sexual dimorphism necessarily reflect levels of sexual selection. Using New World blackbirds (Icteridae) as an example, I critically evaluate these past assumptions in light of new phylogenetic evidence. Understanding the mechanisms underlying such sexually dimorphic traits requires a clear understanding of their evolutionary histories. Only then can we begin to ask the right questions.

Keywords: ancestral, female song, phylogeny, sexual dichromatism, sexual dimorphism, sexual selection

Introduction

Male songbirds sing to attract mates and compete with rivals, and since Darwin these elaborate vocalizations have been widely acknowledged to have evolved through sexual selection (Darwin, 1859; Andersson, 1994). Research has long supported this premise by revealing aspects of male song production and complexity that are favored by females during mate choice and that benefit males during interactions with territorial neighbors (Marler and Slabbekoorn, 2004; Catchpole and Slater, 2008). Sexual dimorphism in song is generally assumed to be the outcome of sexual selection acting on males, whereas female singing has often been dismissed as anomalous (e.g., Beecher and Brenowitz, 2005; Byers and Kroodsma, 2009). Thus, alongside elaborate male plumage displays, male bird song has become a textbook example of a sexually-selected ornament.

Recent findings, however, appear to challenge this view. Female bird song is much more common than previously thought (Langmore, 1998; Riebel et al., 2005; Garamszegi et al., 2007; Price et al., 2009; Odom et al., 2014), especially among tropical species that defend year-round territories (Morton, 1996; Slater and Mann, 2004; Price, 2009). An extensive survey across songbirds has revealed the occurrence of female singing in over two thirds of surveyed species including 32 avian families (Odom et al., 2014). Earlier perceptions of bird song as a primarily male trait are now thought to reflect past geographical biases among researchers toward temperate passerine species, which are disproportionately well-studied and in which songs are produced almost exclusively by

males (Morton, 1996; Riebel, 2003). Even among tropical species, female singing might be widely underreported because many species with female song also have sexually monomorphic plumage and year-round territorial defense by both sexes, so female singers could be frequently mistaken for males (Price et al., 2008). Indeed, considering the higher avian biodiversity in the tropics, the occurrence of female song may be the rule rather than the exception among songbirds.

Furthermore, phylogenetic studies have shown that sexual differences in singing behavior are often the product of historical losses in females rather than gains in males (Price et al., 2009; Odom et al., 2014). In the New World blackbird family (Icteridae), for instance, evolutionary reconstructions show that both sexes sang at similar rates in ancestral taxa and that female song has since been lost multiple times independently across the clade, resulting in a large proportion of today's species in which songs are produced primarily by males (Price, 2009; Price et al., 2009). Female song probably also existed in the ancestor of all modern songbirds, suggesting that the absence or presence of female singing among many current taxa is the outcome of either past losses in females or the evolutionary maintenance of this behavior in both sexes (Odom et al., 2014).

Altogether, these findings call into question the long-standing assumption that sexual dimorphism in song is the outcome of sexual selection acting on males. But does this suggest that previous researchers, including Darwin himself, have been wrong about the evolution of male bird song through sexual selection? Here I contend that these new findings are surprising not because they contradict previous results but because they disagree with some of the assumptions we tend to make regarding the evolution of sexual dimorphisms in general and female song in particular, assumptions that may not be accurate. These include: (1) viewing sexual dimorphism as a discrete rather than continuously variable attribute, and thus underestimating its prevalence across taxa; (2) conflating evolutionary rates of change with levels of selection; (3) conflating current levels of elaboration and divergence in each sex with past evolutionary rates; (4) assuming that levels of sexual dimorphism necessarily reflect levels of sexual selection; and (5) viewing decreases in dimorphism, in song or in other traits, as evolutionary gains in one sex rather than losses of sex-specific developmental mechanisms.

These potential misconceptions may apply to other sexually-selected signals that can occur in both sexes, such as conspicuous plumage colors. The New World blackbirds have served as a model clade for investigating a variety of such sexual dimorphisms, including the evolution of male-female differences in color (Irwin, 1994; Hofmann et al., 2008; Friedman et al., 2009; Price and Eaton, 2014), size (Webster, 1992), and song (Price, 2009; Price et al., 2009; Odom et al., 2015). Here I focus on this avian group in particular to examine how our new understanding of the evolutionary history of bird song compares with that of other sexually dimorphic traits, especially sexual dichromatism, and how these patterns line up with our past assumptions.

Female Singing Should Not Indicate a Lack of Sexual Dimorphism in Song

Although female song is often treated as a discrete binary character in comparisons among species, with some species categorized as having female song and others not (e.g., Garamszegi et al., 2007; Price, 2009; Odom et al., 2014), evidence suggests that female singing can vary continuously across taxa in both expression and complexity. For example, the New World blackbird clade includes species in which female song has never been recorded (*Sturnella neglecta*), others in which females rarely sing (*Icterus galbula*), species in which both sexes regularly produce similar songs (*Agelaius assimilis*, *Icterus pustulatus*), and even species in which pairs combine their songs into highly coordinated duets (*Dives dives*) (Price et al., 2009; Odom et al., 2015). Thus, like sexual size dimorphism (Webster, 1992), sexual differences in song production in this family appear to fall along a broad continuum.

The treatment of female song as a discrete rather than continuous trait parallels approaches used in some previous comparative studies of sexual dichromatism in birds, in which species have been categorized as either dichromatic or monochromatic (e.g., Burns, 1998; Friedman et al., 2009; Soler and Moreno, 2012) despite observations that differences between the sexes can vary continuously. In fact, analyses of plumage reflectance data reveal that many differences in color are imperceptible to humans and that truly sexually monochromatic bird species are surprisingly rare (Eaton, 2005, 2007). The New World blackbirds again provide an example. Although many species in this clade are considered sexually monochromatic (Jaramillo and Burke, 1999), nearly all exhibit at least some sexual color differences based on thresholds of avian color discrimination, and across taxa the sexes vary from nearly indistinguishable to strikingly different along a continuous range (Hofmann et al., 2008; Price and Eaton, 2014).

Likewise, although female song occurs widely across songbird species (Odom et al., 2014), true sexual monomorphism in singing and in associated neuroanatomy might be relatively uncommon (MacDougall-Shackleton and Ball, 1999; Garamszegi et al., 2005). Even if female song is more widespread than we currently realize, it seems likely that most males and females differ in this trait in some way, such as in production rates or acoustic structure. These differences deserve further attention. Thus, like the occurrence of colorful pigments in female plumage, the occurrence of song in females should not necessarily imply a lack of sexual dimorphism in this behavior. Song may occur in both sexes but nevertheless may reflect selection pressures and patterns of evolutionary change that are sex-specific.

Rates of Evolutionary Change Do Not Necessarily Indicate Levels of Selection

Several studies have shown that male-female differences in singing behavior are often the product of historical changes in females rather than males (Price, 2009; Price et al., 2009; Odom et al., 2014). This again parallels studies of sexual dichromatism in

birds, which show that striking male-female color differences are often the outcome of past losses of conspicuous plumage colors in females rather than gains of these colors in males (Irwin, 1994; Burns, 1998; Wiens, 2001; Hofmann et al., 2008; Price and Eaton, 2014). Dramatic female changes have also occurred when dichromatism has decreased, with females evolving rapidly to look like males and males changing comparatively little over time (Johnson et al., 2013; Price and Eaton, 2014). Based on these patterns, one might assume that selection on females has been stronger than selection on males.

Yet, a lack of recent change in a trait should not necessarily indicate that it has not been favored by selection. Although selection is generally viewed as a driving force of evolutionary change, many adaptive phenotypic characters are under strong stabilizing selection and presumably have remained unchanged for long periods of evolutionary history (Price and Lanyon, 2002; McGlothlin et al., 2010). As an example, numerous studies show that the songs and conspicuous red epaulets of male red-winged blackbirds (*Agelaius phoeniceus*) are important sexually-selected signals that clearly influence male success (Searcy and Yasukawa, 1995). Nevertheless, phylogenetic analyses including other species in the *Agelaius* genus suggest that the buzzy songs, brightly colored epaulets, and glossy black plumage of males are ancestral traits that have changed relatively little since the common ancestor of this clade (Barker et al., 2008; Price et al., 2009; Price and Eaton, 2014). In contrast, female vocalizations and colors differ substantially among species (Jaramillo and Burke, 1999), some appearing very similar to males (*A. assimilis*, *A. xanthomus*, *A. humeralis*) and others strikingly different (*A. phoeniceus*, *A. tricolor*), reflecting significant past changes. Presumably, these rapid female changes have had no direct bearing on how male traits have been influenced by sexual selection.

Current Levels of Diversity Do Not Necessarily Reflect Past Rates of Change

Phylogenetic reconstructions of male and female plumage color evolution show that the sexes exhibit very different modes of change, with male colors diverging steadily over time and female colors changing periodically and relatively rapidly either away from or toward male patterns, resulting in respective increases or decreases in dichromatism (Johnson et al., 2013; Price and Eaton, 2014). These sex-specific evolutionary modes might reflect different mechanisms of selection, with male colors continuously changing through sexual selection (Prum, 1997; Price and Whalen, 2009) and female colors showing a more punctuated pattern of change through natural or social selection, perhaps based on levels of intra-sexual competition or the need for female crypsis near the nest (Martin and Badyaev, 1996; Amundsen, 2000; Soler and Moreno, 2012; Tobias et al., 2012).

Patterns of song variation reveal similar evolutionary differences between the sexes, with male song characteristics showing steady rates of divergence (Price and Lanyon, 2002, 2004) and females producing either male-like songs or very different vocalizations (Price et al., 2009; Odom et al., 2015). Indeed, among

many New World blackbird taxa, the evolution of song and color dimorphisms have occurred largely in parallel. All species with frequent female song also exhibit relatively low levels of dichromatism (Jaramillo and Burke, 1999; Price and Eaton, 2014). On the other hand, not all species that are dimorphic in song are likewise dimorphic in plumage, suggesting that the selective factors favoring male-female differences in these traits are not necessarily the same (also see Soma and Garamszegi, 2015).

A surprising result of these sex-specific evolutionary modes is that male traits can appear significantly more elaborate and divergent among species than do female traits, despite the fact that females have changed more frequently and dramatically in the evolutionary past (Price and Eaton, 2014). While the males of different taxa have accumulated novel plumage features over time, for example, females have converged repeatedly on similarly cryptic color patterns, resulting in relatively dull female plumages that appear as if they have not changed much at all (Martin and Badyaev, 1996; Hofmann et al., 2008; Price and Eaton, 2014). In a similar way, male song features have evolved along multiple complex trajectories (Price and Lanyon, 2002, 2004), while losses of female song have produced outcomes that are largely the same across taxa (Price, 2009). Clearly, current levels of trait complexity and diversity are not good indicators of past rates of change.

Sexual Dimorphism Is Not Due to Sexual Selection Alone

Altogether, recent phylogenetic comparative studies provide strong evidence against the widely-held assumption that sexual dimorphism is driven by sexual selection alone. Even when levels of dimorphism correspond closely with social mating systems across taxa (Webster, 1992; Irwin, 1994; Dunn et al., 2001; Price and Eaton, 2014), male-female differences in any particular species are the product of different selective pressures acting on each sex and not simply strong selection on males (Badyaev and Hill, 2003; Cox and Calsbeek, 2009; Dunn et al., 2015). Indeed, dimorphisms in both song and plumage colors have been shown to be associated with an assortment of life history traits besides mating system, including breeding latitude, seasonal migration, nesting behavior, and territoriality (Martin and Badyaev, 1996; Friedman et al., 2009; Price, 2009; Soler and Moreno, 2012; Johnson et al., 2013; Odom et al., 2015). Nevertheless, the perception that levels of sexual dimorphism reflect levels of sexual selection remains pervasive, even among some researchers (e.g., Seddon et al., 2013; Bloch, 2015).

Levels of sexual dimorphism in a trait may have little direct relationship with the functions of that trait in attracting or competing for mates. Plumage features in a variety of passerine species are known to strongly influence male reproductive success but nonetheless differ little between the sexes (e.g., Hill et al., 1999; Doucet et al., 2005). Levels of dimorphism may also show little relationship with past rates of evolutionary change. In the oropendolas and caciques, for example, a clade within the New World blackbird family, plumage colors have evolved more

rapidly in polygynous than monogamous taxa, presumably due to sexual selection, yet none of these species are notably dichromatic (Price and Whalen, 2009).

Is Song Dimorphism the Result of Evolutionary Gains or Losses?

All autosomal genes spend half their evolutionary histories in males and half in females, on average and assuming equal sex ratios. Many genes have influences on the phenotype regardless of sex, whereas others have influences that are sex-specific and result in phenotypic attributes that are sexually dimorphic (Coyne et al., 2008). The evolution of such sex-specific genetic influences on the phenotype involves special selective mechanisms in which expression is favored in one sex and concurrently opposed in the other (Kimball and Ligon, 1999; Badyaev and Hill, 2003; Ketterson et al., 2005; Cox and Calsbeek, 2009). Secondary losses of sexual dimorphism in turn involve losses of these sex-specific molecular pathways, through changes in one or both sexes to match the other (Wiens, 2001).

By this logic, increases in dimorphism through losses of female singing behavior, as has occurred in many songbird lineages (Garamszegi et al., 2007; Price et al., 2009; Odom et al., 2014), involve the evolution of novel, sex-specific molecular pathways in females that secondarily influence the development of male-like traits. This is reflected in neurodevelopmental patterns, in which males and females initially develop equivalent neural song control systems which subsequently atrophy in the females of species that lack female song (Konishi and Akutagawa, 1985). Thus, from a developmental perspective, losses of female song and the neuroanatomical modifications associated with this change could be viewed as evolutionary gains. Contrariwise, decreases in song dimorphism through evolutionary gains of female song could be viewed as developmental losses, if the evolution of male-like singing in females involves the loss of female-specific neurodevelopmental pathways and behaviors.

We should expect such losses of dimorphism to be especially rapid given that much of the genetic and hormonal architecture for male-like song production is presumably already present in females (Lande, 1980; Kimball and Ligon, 1999; Ketterson et al., 2005). Increases in song dimorphism, in contrast, should occur more gradually since this involves the accumulation of novel traits in males or females, or both, through natural or sexual selection.

Evolutionary reconstructions of sexual dichromatism in both the New World blackbirds (Price and Eaton, 2014) and the distantly related Australian fairy wrens (Maluridae; Johnson et al., 2013) are largely consistent with these predictions. In both families, decreases in dichromatism have involved females rapidly

gaining male-like characteristics rather than the reverse, whereas increases in dichromatism have tended to occur more gradually and involve changes in either sex. It would be interesting to investigate such patterns in the evolution of male and female song.

A variety of selective mechanisms have been offered to explain the evolution of elaborate songs in females, including mutual mate choice, intra-sexual competition, and other forms of social selection (Langmore, 1998, 2000; Tobias et al., 2012). Yet, few of these hypotheses address why female songs tend to closely resemble those of conspecific males. The ideas presented here do not disagree with these hypotheses, but rather build on them by suggesting that selection for female song may occur especially rapidly since it favors genes and molecular pathways that may already exist. Understanding the mechanisms of past changes can help us to ask the right questions in understanding current traits.

Conclusions

Recent studies are prompting us to reconsider long-held assumptions about the evolution of male and female song. Rather than being anomalous, female singing is widespread among songbirds and indeed was probably present during the early evolution of bird song (Odom et al., 2014). Past geographic biases and other factors appear to have misled us toward the opposite perspective, that male-only song is the norm and that evolutionary changes in song have occurred primarily in males. Given our new perspective, we face exciting new challenges to understand the selective mechanisms underlying the diversity and evolutionary history of female song (Riebel et al., 2005; Price, 2009; Odom et al., 2015). Indeed, in many well-studied bird species, we should probably now be asking why females do not sing rather than why males do.

But these new findings should not necessarily alter our view of bird song as a model for studies of sexual selection. As hopefully conveyed here, past rates of female change and current levels of dimorphism may have little relevance to how male traits have been influenced by sexual selection. In fact, if anything, these new insights into our previous misconceptions are instructive and only further serve to illustrate what an effective research model bird song has become.

Acknowledgments

I thank Guest Associate Editors Michelle Hall and Naomi Langmore for the opportunity to contribute to this special issue. Dustin Reichard, Becky Cramer, Jordan Karubian, Erik Enbody, and László Garamszegi provided valuable comments on the manuscript.

References

- Amundsen, T. (2000). Why are female birds ornamented? *Trends Ecol. Evol.* 15, 149–155. doi: 10.1016/S0169-5347(99)01800-5
- Andersson, M. (1994). *Sexual Selection*. Princeton, NJ: Princeton University Press.
- Badyaev, A. V., and Hill, G. E. (2003). Avian sexual dichromatism in relation to phylogeny and ecology. *Annu. Rev. Ecol. Syst.* 34, 27–49. doi: 10.1146/annurev.ecolsys.34.011802.132441
- Barker, F. K., Vandergon, A. J., and Lanyon, S. M. (2008). Species status of the red-shouldered blackbird (*Agelaius assimilis*): implications for ecological,

- morphological, and behavioral evolution in *Agelaius*. *Auk* 125, 87–94. doi: 10.1525/auk.2008.125.1.87
- Beecher, M. D., and Brenowitz, E. A. (2005). Functional aspects of song learning in songbirds. *Trends Ecol. Evol.* 30, 143–149. doi: 10.1016/j.tree.2005.01.004
- Bloch, N. I. (2015). Evolution of opsin expression in birds driven by sexual selection and habitat. *Proc. Biol. Sci.* 282:20142321. doi: 10.1098/rspb.2014.2321
- Burns, K. J. (1998). A phylogenetic perspective on the evolution of sexual dichromatism in tanagers (Thraupidae): the role of female versus male plumage. *Evolution* 52, 1219–1224. doi: 10.2307/2411252
- Byers, B. E., and Kroodsma, D. E. (2009). Female mate choice and songbird song repertoires. *Anim. Behav.* 77, 13–22. doi: 10.1016/j.anbehav.2008.10.003
- Catchpole, C. K., and Slater, P. J. B. (2008). *Bird Song, Biological Themes and Variations, 2nd Edn.* New York, NY: Cambridge University Press. doi: 10.1017/CBO9780511754791
- Cox, R., and Calsbeek, R. (2009). Sexually antagonistic selection, sexual dimorphism, and the resolution of intralocus sexual conflict. *Am. Nat.* 173, 176–187. doi: 10.1086/595841
- Coyne, J. A., Kay, E. H., and Pruett-Jones, S. (2008). The genetic basis of sexual dimorphism in birds. *Evolution* 62, 214–219. doi: 10.1111/j.1558-5646.2007.00254.x
- Darwin, C. (1859). *The Origin of Species*. London: J. Murray.
- Doucet, S. M., Mennill, D. J., Montgomerie, R., Boag, P. T., and Ratcliffe, L. M. (2005). Achromatic plumage reflectance predicts reproductive success in male black-capped chickadees. *Behav. Ecol.* 16, 218–222. doi: 10.1093/beheco/arl154
- Dunn, P. O., Armenta, J. K., and Whittingham, L. A. (2015). Natural and sexual selection act on different axes of variation in avian plumage color. *Sci. Adv.* 1:e1400155. doi: 10.1126/sciadv.1400155
- Dunn, P. O., Whittingham, L. A., and Pitcher, T. E. (2001). Mating systems, sperm competition, and the evolution of sexual dimorphism in birds. *Evolution* 55, 161–175. doi: 10.1111/j.0014-3820.2001.tb01281.x
- Eaton, M. D. (2005). Human vision fails to distinguish widespread sexual dichromatism among sexually “monochromatic” birds. *Proc. Nat. Acad. Sci. U.S.A.* 102, 10942–10946. doi: 10.1073/pnas.0501891102
- Eaton, M. D. (2007). Avian visual perspective on plumage coloration confirms rarity of sexually monochromatic passerines. *Auk* 124, 155–161. doi: 10.1642/0004-8038(2007)124[155:AVPOPC]2.0.CO;2
- Friedman, N. R., Hofmann, C. M., Kondo, B., and Omland, K. E. (2009). Correlated evolution of migration and sexual dichromatism in the New World orioles (*Icterus*). *Evolution* 63, 3269–3274. doi: 10.1111/j.1558-5646.2009.00792.x
- Garamszegi, L. Z., Eens, M., Erritzøe, J., and Møller, A. P. (2005). Sexually size dimorphic brains and song complexity in passerine birds. *Behav. Ecol.* 16, 335–345. doi: 10.1093/beheco/arl167
- Garamszegi, L. Z., Pavlova, D. Z., Eens, M., and Møller, A. P. (2007). The evolution of song in female birds in Europe. *Behav. Ecol.* 18, 86–96. doi: 10.1093/beheco/arl047
- Hill, J. A., Enstrom, D. A., Ketterson, E. D., Nolan, V. Jr., and Ziegenfus, C. (1999). Mate choice based on static versus dynamic secondary sexual traits in the dark-eyed junco. *Behav. Ecol.* 10, 91–96. doi: 10.1093/beheco/10.1.91
- Hofmann, C. M., Cronin, T. W., and Omland, K. E. (2008). Evolution of sexual dichromatism. 1. Convergent losses of elaborate female coloration in New World orioles (*Icterus* spp.). *Auk* 125, 778–789. doi: 10.1525/auk.2008.07112
- Irwin, R. E. (1994). The evolution of plumage dichromatism in the New World blackbirds: social selection on female brightness. *Am. Nat.* 144, 890–907. doi: 10.1086/285717
- Jaramillo, A., and Burke, P. (1999). *New World Blackbirds: The Icterids*. Princeton, NJ: Princeton University Press.
- Johnson, A. E., Price, J. J., and Pruett-Jones, S. (2013). Different modes of evolution in males and females generate dichromatism in fairy-wrens (Maluridae). *Ecol. Evol.* 3, 3030–3046. doi: 10.1002/ece3.686
- Ketterson, E. D., Nolan, V. Jr., and Sandell, M. (2005). Testosterone in females: mediator of adaptive traits, constraint on sexual dimorphism, or both? *Am. Nat.* 166, S85–S98. doi: 10.1086/444602
- Kimball, R. T., and Ligon, J. D. (1999). Evolution of avian plumage dichromatism from a proximate perspective. *Am. Nat.* 154, 182–193. doi: 10.1086/303228
- Konishi, M., and Akutagawa, E. (1985). Neuronal growth, atrophy and death in a sexually dimorphic song nucleus in the zebra finch brain. *Nature* 315, 145–147. doi: 10.1038/315145a0
- Lande, R. (1980). Sexual dimorphism, sexual selection, and adaptation in polygenic characters. *Evolution* 34, 292–305. doi: 10.2307/2407393
- Langmore, N. E. (1998). Functions of duet and solo songs of female birds. *Trends Ecol. Evol.* 13, 136–140. doi: 10.1016/S0169-5347(97)01241-X
- Langmore, N. E. (2000). “Why female birds sing” in *Animal Signals, Signaling and Signal Design in Animal Communication*, eds. Y. Epmark, T. Amundsen, and G. Rosenqvist (Trondheim: Tapir Academic Press), 317–327.
- MacDougall-Shackleton, S. A., and Ball, G. F. (1999). Comparative studies of sex differences in the song-control system of songbirds. *Trends Neurosci.* 22, 432–436. doi: 10.1016/S0166-2236(99)01434-4
- Marler, P., and Slabbekoorn, H. (2004). *Nature's Music, The Science of Birdsong*. San Diego, CA: Elsevier Academic Press.
- Martin, T. E., and Badyaev, A. V. (1996). Sexual dichromatism in birds: importance of nest predation and nest location for females versus males. *Evolution* 50, 2454–2460. doi: 10.2307/2410712
- McGlothlin, J. W., Whittaker, D. J., Schrock, S. E., Gerlach, N. M., Jawor, J. M., Snajdr, E. A., et al. (2010). Natural selection on testosterone production in a wild songbird population. *Am. Nat.* 175, 687–701. doi: 10.1086/652469
- Morton, E. S. (1996). “A comparison of vocal behavior among tropical and temperate passerine birds,” in *Ecology and Evolution of Acoustic Communication in Birds*, eds. D. E. Kroodsma and E. H. Miller (Ithaca, NY: Cornell University Press), 258–268.
- Odom, K. J., Hall, M. L., Riebel, K., Omland, K. E., and Langmore, N. E. (2014). Female song is widespread and ancestral in songbirds. *Nat. Commun.* 5, 3379. doi: 10.1038/ncomms4379
- Odom, K. J., Omland, K. E., and Price, J. J. (2015). Differentiating the evolution of female song and male-female duets in the New World blackbirds: can tropical natural history traits explain duet evolution? *Evolution* 69, 839–847. doi: 10.1111/evo.12588
- Price, J. J. (2009). Evolution and life history correlates of female song in the New World blackbirds. *Behav. Ecol.* 20, 967–977. doi: 10.1093/beheco/arp085
- Price, J. J., and Eaton, M. D. (2014). Reconstructing the evolution of sexual dichromatism: current color diversity does not reflect past rates of male and female change. *Evolution* 68, 2026–2037. doi: 10.1111/evo.12417
- Price, J. J., and Lanyon, S. M. (2002). Reconstructing the evolution of complex bird song in the oropendolas. *Evolution* 56, 1514–1529. doi: 10.1111/j.0014-3820.2002.tb01462.x
- Price, J. J., and Lanyon, S. M. (2004). Patterns of song evolution and sexual selection in the oropendolas and caciques. *Behav. Ecol.* 15, 485–497. doi: 10.1093/beheco/arl040
- Price, J. J., Lanyon, S. M., and Omland, K. E. (2009). Losses of female song with changes from tropical to temperate breeding in the New World blackbirds. *Proc. Biol. Sci.* 276, 1971–1980. doi: 10.1098/rspb.2008.1626
- Price, J. J., and Whalen, L. M. (2009). Plumage evolution in the oropendolas and caciques: different divergence rates in polygynous and monogamous taxa. *Evolution* 63, 2985–2998. doi: 10.1111/j.1558-5646.2009.00765.x
- Price, J. J., Yunes-Jimenez, L., Osorio-Beristain, M., Omland, K. E., and Murphy, T. G. (2008). Sex-role reversal in song? Females sing more frequently than males in the streak-backed oriole. *Condor* 110, 387–392. doi: 10.1525/cond.2008.8430
- Prum, R. O. (1997). Phylogenetic tests of alternative intersexual selection mechanisms: macroevolution of male traits in a polygynous clade (Aves: Pipridae). *Am. Nat.* 149, 668–692. doi: 10.1086/286014
- Riebel, K. (2003). The “mute” sex revisited: vocal production and perception learning in female songbirds. *Adv. Study Behav.* 33, 49–86. doi: 10.1016/S0065-3454(03)33002-5
- Riebel, K., Hall, M. L., and Langmore, N. E. (2005). Female songbirds still struggling to be heard. *Trends Ecol. Evol.* 20, 419–420. doi: 10.1016/j.tree.2005.04.024
- Searcy, W. A., and Yasukawa, K. (1995). *Polygyny and Sexual Selection in Red-Winged Blackbirds*. Princeton, NJ: Princeton University Press. doi: 10.1515/9781400863938
- Seddon, N., Botero, C. A., Tobias, J. A., Dunn, P. O., MacGregor, H. E. A., Rubenstein, D. R., et al. (2013). Sexual selection accelerates signal evolution during speciation in birds. *Proc. Biol. Sci.* 280, 20131065. doi: 10.1098/rspb.2013.1065
- Slater, P. J. B., and Mann, N. I. (2004). Why do the females of many bird species sing in the tropics? *J. Avian Biol.* 35, 289–294. doi: 10.1111/j.0908-8857.2004.03392.x
- Soler, J. J., and Moreno, J. (2012). Evolution of sexual dichromatism in relation to nesting habits in European passerines: a test of Wallace's hypothesis. *J. Evol. Biol.* 25, 1614–1622. doi: 10.1111/j.1420-9101.2012.02544.x

- Soma, M., and Garamszegi, L. Z. (2015). Evolution of courtship display in Estrildid finches: dance in relation to female song and plumage ornamentation. *Front. Ecol. Evol.* 3:4. doi: 10.3389/fevo.2015.00004
- Tobias, J. A., Montgomerie, R., and Lyon, B. E. (2012). The evolution of female ornaments and weaponry: social selection, sexual selection and ecological competition. *Phil. Trans. R. Soc. B Biol. Sci.* 367, 2274–2293. doi: 10.1098/rstb.2011.0280
- Webster, M. S. (1992). Sexual dimorphism, mating system and body size in New World blackbirds (Icterinae). *Evolution* 46, 1621–1641. doi: 10.2307/2410020
- Wiens, J. J. (2001). Widespread loss of sexually selected traits: how the peacock lost its spots. *Trends Ecol. Evol.* 16, 517–523. doi: 10.1016/S0169-5347(01)02217-0

Conflict of Interest Statement: The author declares that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

Copyright © 2015 Price. This is an open-access article distributed under the terms of the Creative Commons Attribution License (CC BY). The use, distribution or reproduction in other forums is permitted, provided the original author(s) or licensor are credited and that the original publication in this journal is cited, in accordance with accepted academic practice. No use, distribution or reproduction is permitted which does not comply with these terms.