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COMMENTARY

## A call to document female bird songs: Applications for diverse fields

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### ABSTRACT

Research on bird song has contributed to important advances in diverse biological fields from neurobiology to conservation biology. Bird song has traditionally been studied as an elaborate male trait, but female song is also widespread in both temperate and tropical species and likely evolved in the early ancestors of modern songbirds. However, female song is underrepresented in biological collections compared to male song, and we lack documentation of female songs for most songbird species. Better documentation of female bird song is necessary for an understanding of the prevalence, regulation, function, evolution, and conservation applications of avian vocalizations. Therefore, we call on all researchers to disseminate their observations of female bird song, and to spread the word among other researchers, students, field technicians, and citizen scientists that many female songbirds sing. To this end, we provide resources for disseminating recordings and written documentation of female song, including best practices for documentation, venues for archiving and publishing, and our citizen science project, the Female Bird Song Project. We especially appeal to researchers studying marked populations who can accurately assess sex-specific singing behavior. Documenting female song across many species and geographic regions is a major endeavor. By working collectively, we can make the greatest progress toward applying the resultant knowledge to a wide variety of fields.

**Keywords:** female bird song, natural history, documentation, natural sound archives, biological collections, citizen science

### Un llamado para documentar los cantos de las aves hembra: aplicaciones para diversos campos

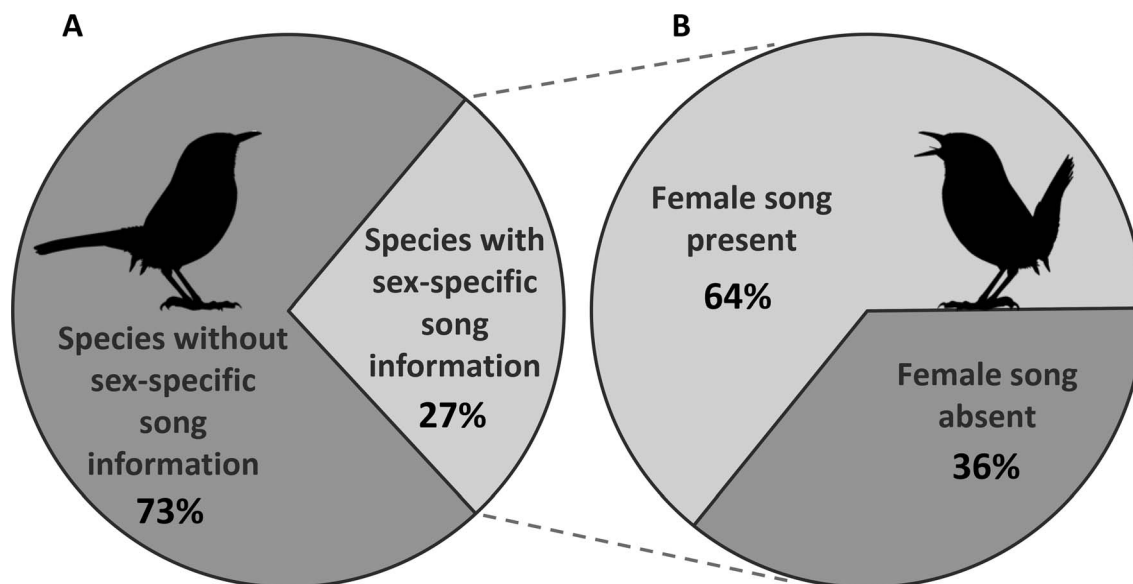
#### RESUMEN

La investigación del canto de las aves ha generado avances importantes en varios campos de la biología desde la neurobiología hasta la biología de la conservación. El canto de las aves ha sido tradicionalmente estudiado como un rasgo elaborado del macho, pero el canto de la hembra también está extendido en las especies templadas y tropicales y probablemente evolucionó en los primeros ancestros de las aves canoras modernas. Sin embargo, el canto de la hembra está sub-representado en las colecciones biológicas en comparación con el canto del macho y nos falta documentación del canto de la hembra para la mayoría de las especies de aves canoras. Se necesita documentar mejor el canto de la hembra para entender la prevalencia, regulación, función, evolución y aplicaciones a la conservación de las vocalizaciones de las aves. Por lo tanto, hacemos el llamado a todos los investigadores para que diseminen sus observaciones del canto de las hembras, y para que pasen la voz a otros investigadores, estudiantes, técnicos de campo y científicos ciudadanos de que muchas aves canoras hembra cantan. Con este fin, brindamos recursos para diseminar grabaciones y documentación escrita del canto de las hembras, incluyendo mejores prácticas para documentación, modos para archivar y publicar, y nuestro proyecto científico ciudadano: Proyecto del Canto de las Aves Hembra – [www.femalebirdsong.org](http://www.femalebirdsong.org). Hacemos un llamado especial a los investigadores con poblaciones marcadas quienes pueden evaluar con precisión el comportamiento del canto específico de cada sexo. Documentar los cantos de las hembras para muchas especies y regiones geográficas es un gran esfuerzo. Mediante el trabajo colectivo podemos hacer el mayor progreso hacia la aplicación del conocimiento resultante en una amplia variedad de campos.

**Palabras clave:** archivos de sonidos naturales, canto de ave hembra, ciencia ciudadana, colecciones biológicas, documentación, historia natural

Bird song is a complex behavior, the study of which has contributed to advances in a range of scientific fields, including neurobiology, avian physiology, behavioral ecology, evolutionary biology, and conservation biology

(Catchpole and Slater 2008). In the past, song has often been attributed primarily to male songbirds, but substantial research has emphasized that female bird song is widespread, can be structurally and functionally similar to



**FIGURE 1.** (A) Sex-specific information about song exists for only 27% of songbird species (Passeri); many of the remaining 73% of songbirds are monochromatic, tropical species in which female song is likely. (B) Of the species for which sex-specific song information is available, 64% have female song. Values from Webb et al. (2016). Silhouettes modified from Bob Comix (<http://www.supercoloring.com/silhouettes/wren>).

male song, and likely existed in the early ancestors of songbirds (Langmore 1998, Riebel et al. 2005, Odom et al. 2014, Hall and Langmore 2017). Thus, female bird song is biologically meaningful and has played a prominent role in the evolution of complex avian communication systems (Langmore 1998, Odom et al. 2014, Hall and Langmore 2017).

Female song, however, is currently underrepresented, both in the literature and in biological (sound) collections. Investigating female song in conjunction with male song has great potential to advance both basic and applied research in the lab and in the field (Price 2015, Riebel 2016, Hall and Langmore 2017). For example, female song data could enable detailed comparative studies of neural song control or could allow sex-specific avian monitoring (Brenowitz 1997, Odom and Mennill 2010). In addition, to fully understand the evolution of complex song across songbird species, we need to investigate the selection pressures that have caused females to stop singing in some species while song has been maintained in both sexes in other species (Price 2015, Riebel et al. in press). First, however, we need more documentation of female bird song.

The goals of this commentary are to raise awareness of the fact that females of many bird species sing and to recruit researchers from diverse fields to play a crucial role in documenting female songs. We held a roundtable discussion on these topics at the 2016 North American Ornithological Conference in Washington, District of Columbia, USA, with a follow-up discussion at the 2017

Animal Behavior Society meeting in Toronto, Ontario, Canada (see Appendix Table 4 for a list of participants in each discussion). Here, we report the outcomes of these discussions by (1) briefly reviewing the history and current state of female bird song documentation, (2) describing how a range of fields will benefit from increased documentation of female bird song, (3) explaining existing needs in the field, and (4) outlining how individual researchers can improve awareness and documentation of female song, especially in collaboration with students, research assistants, and citizen scientists.

### The Deficit of Female Bird Song Documentation

Ornithologists generally recognize that some female birds sing (Catchpole and Slater 2008). However, many researchers are still largely unaware that female bird song is widespread, even in temperate species (e.g., Ritchison 1983, Halkin 1997, Garamszegi et al. 2007, Krieg and Getty 2016). A recent survey of all songbirds revealed that females sing in 64% of species in which the male sings (Figure 1; Webb et al. 2016). Furthermore, in 42% of passerine species (Passeriformes) found in the United States and Canada and in 43% of European songbirds (Passeri), females have been reported to have some amount of song (Benedict 2008, Garamszegi et al. 2007, Rodewald 2017). These numbers continue to grow as researchers watch closely for this behavior (e.g., Hahn et al. 2013, Campbell et al. 2016, Matthews et al. 2017). Also, many female nonpasserine species use complex vocal signals during breeding and in other contexts, suggesting

that interesting female vocal behavior may be pervasive across all birds (Benedict 2008, Geberzahn et al. 2009, Odom and Mennill 2010, Dahlin and Wright 2012).

Despite the pervasiveness of female song, we currently have a deficit of knowledge on this topic. First, for most species, we lack basic documentation of whether females sing. A recent study across all songbirds found that sufficient information does not exist for 3,500 of 4,814 species (73%) to determine whether females sing (e.g., no mention of the sex of the singer; Figure 1; Webb et al. 2016). Recent surveys suggest that the species that lack sex-specific song information are often monomorphic, tropical species in poorly studied or difficult-to-access regions, where female song is likely (Price et al. 2009, Odom et al. 2014, Webb et al. 2016). Second, there are few species for which we have detailed descriptions of female song structure and output as written articles, species accounts, or archived media (Langmore 1998, Riebel et al. 2005, Riebel et al. in press). In proportion to male songs, female songs are much less abundant in biological collections (Figure 2). When sex differences are known, it is important for researchers to document these differences in research articles and, especially, species accounts (Odom et al. 2014, Webb et al. 2016).

The deficit of female bird song research stems largely from a geographic bias that has resulted in a focus on male bird song (Kroodsma et al. 1996, Slater 2003, Beecher and Brenowitz 2005, Catchpole and Slater 2008). Although most bird species exist in the tropics, where song is common in both sexes, most research on bird song has been conducted in temperate regions, where male song is more abundant and evident than female song (Morton 1996, Slater and Mann 2004, Catchpole and Slater 2008, Fjeldså 2013). Nevertheless, as stated above, researchers have been accumulating evidence that females also sing in many temperate-breeding species and that female song is likely ancestral among all songbirds (Benedict 2008, Odom et al. 2014, Najar and Benedict 2015, Krieg and Getty 2016). Therefore, to fully document female song, we need to promote avian research in tropical locations and we need to look more closely at all avian species.

The geographic bias in bird song research also appears to have created a bias toward assuming that a singing bird is male (Figure 2). In 2 major collections, the Cornell Lab of Ornithology's Macaulay Library and xeno-canto, songs labeled as 'male' are much more abundant than songs labeled as 'female' (Figure 2A). Females sing less often than males in many temperate species, so numbers of female songs may be representative for temperate, dimorphic species, such as the Northern Cardinal (*Cardinalis cardinalis*; Figure 2B). However, for monomorphic species in which females sing, such as the House Wren (*Troglodytes aedon*) and European Robin (*Erithacus rubecula*), high proportions of male song suggest that

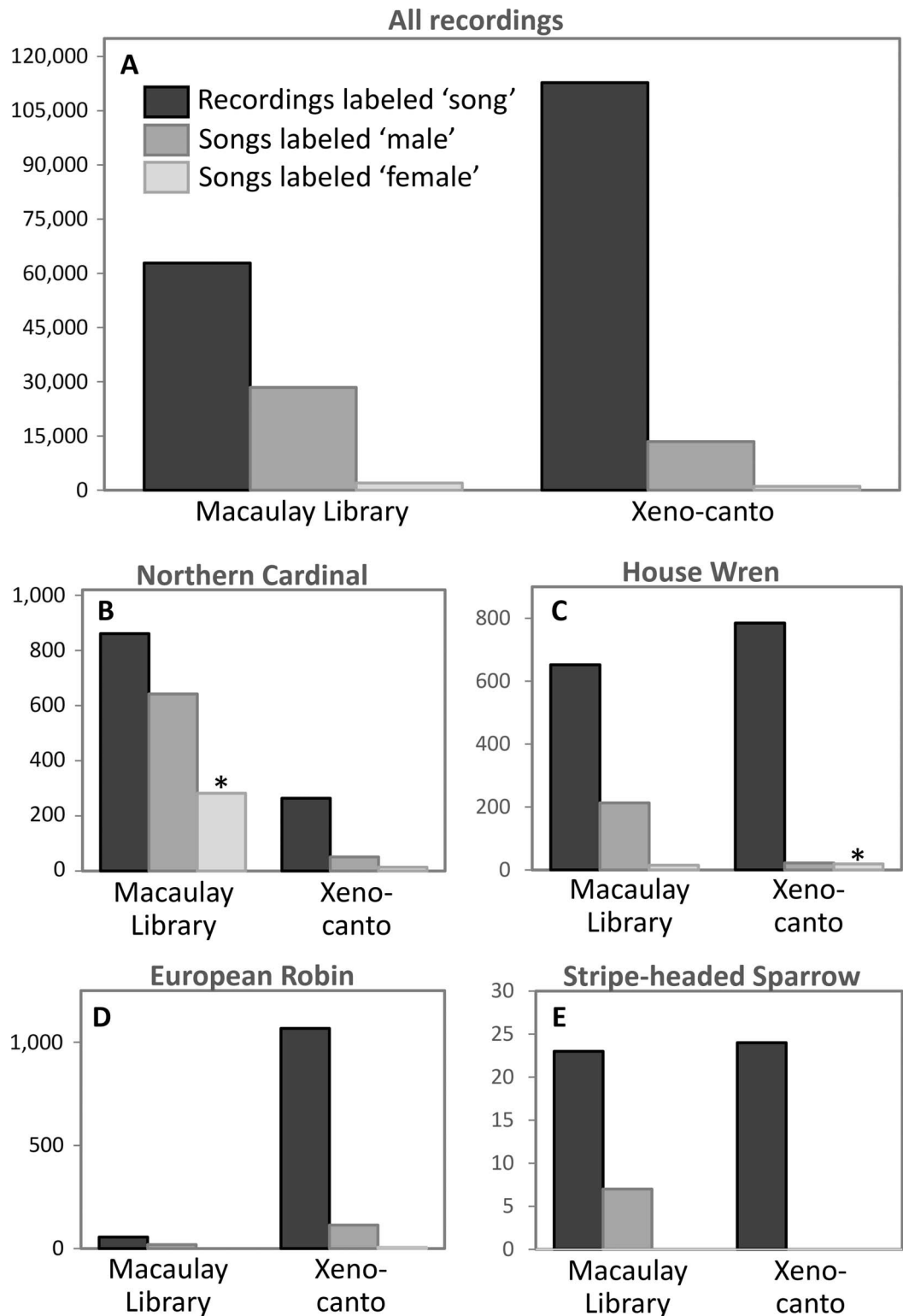
recordists label recordings as 'male' even when sex cannot be readily determined (Figures 2C and 2D). Particularly suggestive of bias, this trend exists even for the Stripe-headed Sparrow (*Peucaea ruficauda*), a tropical, monochromatic species in which song rates are known to be higher in females than males (Figure 2E; Illes and Yunes-Jimenez 2009). Hearteningly, most recordists label sex as 'unknown' for monochromatic species, as should be done when sex is uncertain or cannot be determined (Figure 2). Increased awareness of female song and closer observation of birds being recorded is needed to ensure accuracy of data pertaining to both sexes within media collections.

### Applications of Female Bird Song to a Variety of Fields

We see distinct advantages to knowing about sex-specific differences in bird song for a broad range of fields, including comparative physiology, neurobiology, behavioral ecology, evolution, and conservation biology. Information about female singing behavior will help us to address a wide range of field-specific questions, as outlined briefly below.

**Applications to neurobiology and physiology.** Compared with male bird song, we know little about the neurobiological and physiological mechanisms that control differences in female song (Riebel 2003, 2016, Riebel et al. in press). Therefore, there is ample room for research into the mechanistic, neurological, and hormonal regulation of female bird song production and development. Female song is particularly valuable for such studies because the extent of sexual song dimorphism varies across species and sometimes populations, offering a natural gradient of female-male dimorphism. Thus, detailed comparative studies could be designed to examine song control and development across species with varying amounts of female vs. male song. In addition, future research could compare female and male song control and regulation along multiple axes of singing behavior (i.e. song rate, structure, and context). Existing research indicates an underlying similarity in male and female song production mechanisms, but much work remains to be done to elucidate detailed sex-specific variation (Fortune et al. 2011, Christensen et al. 2017). Such studies will require documentation of female song so that researchers can appropriately choose study species and analyze results with respect to multiple song features. This research would expand our knowledge of how sex differences in morphology (Ballintijn and ten Cate 1997, Hardouin et al. 2014), neurobiology (Brenowitz et al. 1997, Riebel 2003, Gahr 2007, Fortune et al. 2011), and other mechanisms produce patterns of signal variation across all individuals in nature.

**Applications to behavioral ecology and evolutionary biology.** The function and evolutionary patterns of female song are perhaps the best-investigated topics in female



**FIGURE 2.** (A) Female song recording numbers are low compared to those of male songs and the total numbers of song recordings in biological collections. In dichromatic species with female song, such as (B) Northern Cardinals (*Cardinalis cardinalis*), female song can be readily observed and recorded. In monochromatic species with female song, such as (C) House Wrens (*Troglodytes aedon*) and (D) European Robins (*Erithacus rubecula*), recordists often label recordings as male song, even though sex cannot be easily determined. This is true even for (E) Stripe-headed Sparrows (*Peucaea ruficauda*), a tropical, monochromatic species in which females sing more than males (Illes and Yunes-Jimenez 2009). An asterisk denotes samples that include research collections of known female songs.



bird song research, but we have still hardly scratched the surface of this field (Langmore 1998, Hall 2004, Slater and Mann 2004, Price 2015). Many questions surround what selective mechanisms are responsible for complex bird song in both sexes (Beecher and Brenowitz 2005, Byers and Kroodsma 2009, Tobias et al. 2012). Functional studies suggest that females may use song in similar contexts as males, such as mate attraction, as well as in broader contexts, such as coordinating mating activities or resource defense (Ritchison 1983, Langmore et al. 1996, Halkin 1997, Tobias et al. 2012). More experimental studies are needed, however, and researchers have only recently started examining vocal complexity in female birds (e.g., Pavlova et al. 2005, Brunton and Li 2006, Illes and Yunes-Jimenez 2009, Dalziell and Welbergen 2016, Riebel et al. in press). Connecting functional mechanisms to structural variation between male and female song for a diversity of species could produce large-scale insights into signal evolution (Hall and Langmore 2017). Comparative studies indicate that female bird song has been lost in certain major lineages of songbirds (Garamszegi et al. 2007, Price et al. 2009, Odom et al. 2014). Comparing the lineages in which both female and male songs are elaborate with lineages in which song has become reduced could provide new insights into what drives song complexity across songbirds (Price 2015). Future studies could apply genomic data and powerful phylogenetic analyses to investigate evolutionary origins, sex differences in trait expression, and the genetic underpinnings of observed evolutionary trends (Wirthlin et al. 2014, Wheatcroft and Qvarnström 2015, MacManes et al. 2017).

**Applications to conservation biology.** Song is a principal way in which birds are located, identified, and counted during point counts and other surveys. If singing females are counted as males during such surveys, then population size estimates and other monitoring outcomes are likely to be inaccurate (Emlen 1971, Reynolds et al. 1980, Hutto et al. 1986, Ralph et al. 1995). Improved documentation of female songs could provide reference audio files for field researchers to determine sex during surveys. In some species, female and male songs are distinct and frequent enough to allow estimates of population size for each sex based on their vocalizations. For example, the hoots of many owl species are sex-specific, and mated pairs of some species combine their calls into duets (e.g., Cavanagh and Ritchison 1987, Appleby et al. 1999, Grava et al. 2008, Odom and Mennill 2010). This sex-specificity could allow researchers to estimate the frequency of unpaired and paired individuals of both sexes across a population using acoustic surveys alone. In addition, studies of female bird song could help researchers to understand how urbanization and other anthropogenic factors might disrupt mating behavior. Many studies have examined how cities alter male songs,

but none that we know of have looked at female vocal behavior (Slabbekoorn and den Boer-Visser 2006, Ortega 2012). In species that use female vocal signals for mutual mate choice or pair coordination, studying anthropogenic effects on females as well as males could improve assessments of breeding impacts. Moreover, dialects also play a large role in mating decisions in songbirds, so understanding dialectal patterns of both sexes and how they affect mating will be important, especially for conservation involving translocations (Ryan 2006, Rowe and Bell 2007). Thus, to best implement techniques that evaluate pair and population health, researchers must first do the groundwork to locate and describe the vocalizations of both sexes.

### What Do We Need?

To achieve any of the above goals, our needs are still very basic. First, birders and researchers need to be aware that female birds regularly sing, and they need to take the time to evaluate the sex of singing birds. Second, we need documentation of female songs in the form of descriptions and recordings, with an emphasis on accurate and reliable sex-specific information (Table 1). Below we elaborate on each of these points. For some species or scenarios, it may be difficult to distinguish what constitutes ‘song,’ so we encourage the documentation and reporting of all interesting, elaborate vocalizations in females, as well as males.

**Awareness.** Female bird song is common in taxonomically diverse species across all geographic regions. We ask all our colleagues to keep this fact in mind, and to not assume that any singing bird is a male. Avian researchers regularly collect in-depth data about bird populations, and thereby create ideal opportunities to detect female song. Several recent field studies of female song have come from research groups that were not specifically studying communication behavior, but when they took the time to closely observe their study populations, they discovered that the females sang or had other female-specific vocalizations (Hahn et al. 2013, Matthews et al. 2017, K. Omland, J. Cooper, and R. Lachlan personal communication). Furthermore, we encourage researchers with captive birds to carefully monitor the vocalizations of known males and females as this can also lead to discoveries of sex-specific vocalizations, even in well-studied species (Baptista et al. 1993, Elie et al. 2010, Amy et al. 2015).

In addition to soliciting contributions from the academic community, we are working to raise awareness of female bird song among the general public, particularly citizen scientists (Benedict and Odom 2017). To this end, we and our colleagues have created a citizen science project and website, the Female Bird Song Project ([www.femalebirdsong.org](http://www.femalebirdsong.org); Table 2). This project is an international initiative based at Leiden University (Leiden, The

**TABLE 1.** Formats and outlets for documenting female bird song and elaborate female vocalizations.

Type of documentation	Important information to include	Outlet
Observations <sup>^</sup>	Sex <sup>§</sup> , how sex was determined, song or vocalization description, context, additional behaviors, media (photo, audio, or video)	eBird, iNaturalist
Recordings <sup>^</sup>	Sex <sup>§</sup> , how sex was determined, dictation of which vocalizations were made by the female, context, additional behaviors, visual media (photo or video), recording settings and conditions	Macaulay Library (via eBird upload), xeno-canto
Publications and written descriptions	A description of song structure, usage patterns, context, and variability, and references to archived audio or video	Journal articles and species accounts (Table 3)

<sup>^</sup> Use the phrase ‘Contributed for the female bird song project: femalebirdsong.org’ for contributions to be recognized as part of the Female Bird Song Project.

<sup>§</sup> Complete fields requesting the sex of the singer. If uncertain, specify ‘unknown’ or ‘uncertain’ sex.

Netherlands) and the Cornell Lab of Ornithology (Ithaca, New York, USA), with collaborators across Europe, North America, and Australasia. The Female Bird Song Project asks birders, researchers, and wildlife recordists around the world to listen for instances of female bird song and to deposit observations and recordings of female songs in biological collections. The Female Bird Song Project website provides tools and resources for observers, including where to document female bird song, target species lists, best practices for notes, and tips for recognizing females.

**Documentation practices.** Documentation of female bird song may take several formats: (1) raw field observations of behavior, (2) audio and/or video recordings, and (3) written, published descriptions in journals or species accounts (Table 1). To fully benefit researchers working in multiple fields, these documentation types

should be widely available and clearly labeled as female bird song. We encourage all researchers to publish and archive female song data in indexed, searchable outlets that document structure, vocalization rates, context, and associated behaviors (Table 1). Whenever possible, written descriptions should be supported by archived photos, audio, and/or video files to preserve visual or acoustic features of the observed individual. All documentation should include metadata indicating the singer’s sex and how that was determined. If sex is uncertain, researchers should mark it ‘unknown,’ but include any information that may help others to determine the singer’s sex. Moreover, continuing to document male song alongside female song (e.g., recording or studying both in the same population) will be important for comprehensive evaluation of song in both sexes. Note that previous studies may have used recordings assumed to be from males, but that may have

**TABLE 2.** Resources for archiving female bird song online.

Resource	Web links	Tools and information provided
Female Bird Song Project	Website: femalebirdsong.org Facebook: <a href="https://www.facebook.com/femalebirdsong">facebook.com/femalebirdsong</a> Twitter: <a href="https://twitter.com/femalebirdsong">twitter.com/femalebirdsong</a>	Tools and information to increase awareness and documentation of female bird song; Upload instructions for eBird and xeno-canto; Target species lists, maps, and lists of contributors.
eBird and Macaulay Library	Websites: ebird.org; macaulaylibrary.org Facebook (official): <a href="https://www.facebook.com/ebird">facebook.com/ebird</a> ; <a href="https://www.facebook.com/macaulaylibrary">facebook.com/macaulaylibrary</a> eBird Facebook discussion group: <a href="https://www.facebook.com/groups/28873785455183">facebook.com/groups/28873785455183</a>	Linked tools for uploading observation checklists and media (media uploaded via eBird is contributed to the Macaulay Library); Online databases of sightings, photos, audio, and video; Information about uploading media, recording, and equipment; eBird Facebook forum for user questions and discussion.
iNaturalist	Website: inaturalist.org Facebook: <a href="https://www.facebook.com/inaturalist/">facebook.com/inaturalist/</a>	Upload tools for observations, photo, and sound; Database of animal observations and associated metadata; Discussion forums and contributor pages.
Xeno-canto	Website: xeno-canto.org Facebook (official): <a href="https://www.facebook.com/xenocanto">facebook.com/xenocanto</a> Facebook discussion group: <a href="https://www.facebook.com/groups/xenocanto">facebook.com/groups/xenocanto</a>	Tools and instructions for uploading audio recordings; Searchable collection of audio recordings; Maps of recording locations and recordist profiles; Information articles, discussion forums, and Facebook pages.

**TABLE 3.** Journals and outlets for publishing descriptions, natural history articles, or short communications of female bird song. A full list of ornithological journals can be found at Ornithology Exchange (<http://ornithologyexchange.org/journals/titles.html>).

Journal or venue	Article type
Acta Ornithologica	Short notes
American Midland Naturalist	Notes
Ardea	Short notes
Avian Research	Research (Short reports)
Birds of North America	Species accounts
British Birds	Articles
Canadian Field-Naturalist	Articles
Ecology	The Scientific Naturalist series (essays)
Emu	Short communications
Ibis	Short communications
Journal of Caribbean Ornithology	Research articles and notes
Journal of Field Ornithology	Original research articles
Journal of Ornithology	Short notes
Neotropical Birds	Species accounts
Notornis	Short notes
Ornithological Science	Short communications
Ornitologia Neotropical	Short communications
Ostrich	Short notes
Southwestern Naturalist	Notes
Wilson Journal of Ornithology	Short communications

been from females (Figure 2); therefore, recordings of known males will also be valuable. These practices will allow researchers to use song data with confidence well into the future.

### What Can You Do?

Documenting female songs from a wide geographic and taxonomic range of species will take time and will achieve the greatest success if many observers participate. Ornithologists can help by engaging fellow researchers, students, field technicians, and citizen scientists. Below we outline ways in which researchers can raise awareness and promote documentation.

**Spread the word.** Discuss female song with your colleagues, students, and employees. Encourage your students and technicians to watch for female song while they are in the field or lab. Teach them to include informed sex-specific information in their notes, when possible. When giving talks or engaging in outreach to the general public, mention that female birds sing. This is something of which not many people are aware, but can provide an interesting tidbit or goal for birders who are otherwise familiar with most species in their area. Such small gestures can make a large difference when they reach a wide audience.

**Share appropriate resources with citizen scientists, students, and technicians.** There are many online resources for both researchers and citizen scientists to document and archive female bird song (Table 2).

Disseminating these resources and knowledge about female song is a small but important step toward improving awareness and documentation. The Female Bird Song Project website provides a list of species in which female song has been documented and maps of where female song has been recorded. You can engage birders and recordists by pointing out species in which females sing. For this purpose, we include a list of species within the United States and Canada that are known to have female bird song (Appendix Table 5). This list is undoubtedly incomplete, but provides a starting point for interested wildlife enthusiasts.

**Disseminate your findings.** Descriptions and recordings of female song can be shared in multiple ways, including (1) in public observation databases, such as eBird (<http://ebird.org/>) and iNaturalist (<https://www.inaturalist.org/>), (2) in media archives, such as the Macaulay Library (<https://www.macaulaylibrary.org/>) and xeno-canto (<http://www.xeno-canto.org/>), or (3) within published articles in journals or species accounts in books and edited volumes, such as the *Handbook of the Birds of the World* or the *Birds of North America* (<https://birdsna.org>; Tables 1–3). We strongly encourage all researchers who have observations and/or recordings of female songs to share them through any of the above outlets. For researchers who do not frequently use eBird or xeno-canto, the Female Bird Song Project website provides instructions for uploading to each and suggestions for the kinds of information to include (such as the sex of the singer and how sex was determined; Tables 1 and 2).

While fewer journals publish natural history notes or descriptive papers than in the past, such publications still have great value. Many bird-specific journals, especially those oriented toward fieldwork or with a regional focus, are excellent outlets for such documentation (Table 3). Scientific articles documenting female bird song in a species for the first time or quantifying differences between female and male song structure are generally simple to write and widely accessible, with appeal to researchers, students, and citizen scientists alike (e.g., Hall 2006, Logue et al. 2007, Koloff and Mennill 2013b, Campbell et al. 2016). Importantly, such detailed quantification of song can lay the groundwork for more extensive research in subsequent studies (e.g., Hall and Magrath 2007, Logue 2007, Koloff and Mennill 2013a, Odom et al. 2017). Accessible outlets for including female song descriptions in species accounts include the *Birds of North America* (<https://birdsna.org>) and *Neotropical Birds* (<https://neotropical.birds.cornell.edu>; Table 3). All ornithologists, including advanced students with knowledge of a particular species or family, can contribute to these publications (e.g., Cabe 1993, Yosef 1996, Koloff and Mennill 2011).



**Leverage global connections.** All researchers who document female bird song should be aware of geographic biases in our knowledge base. A good deal of song research is currently being conducted on species in temperate or subtropical zones within the U.S., Canada, Australia, New Zealand, and Europe. Research on and interest in female bird song is increasing in tropical and equatorial regions of the world, but more work is needed here as species diversity is high and female song is especially common in these regions (Slater and Mann 2004, Fjeldså 2013). It is currently unknown whether female song occurs in many African, Asian, and Pacific Island species, making documentation from these regions particularly valuable. Acknowledging the need for information from these areas and generating international interest are important steps. Actively establishing research programs or initiating collaborations with research groups, students, or citizen scientists in these regions could have tremendous and lasting impacts on documenting not only female bird song, but many aspects of avian biology across taxa.

## Conclusions

Increasing our knowledge of female bird song will advance avian research in a wide range of fields from neuroethology to conservation biology. Documenting female songs from a broad geographic and taxonomic range is a large task, with the potential for greatest success if researchers from all fields participate. Ornithologists can help by disseminating their observations and engaging researchers, students, field technicians, and citizen scientists. We encourage researchers to spread the word about female bird song, share applicable information and resources, and work with interested students and wildlife enthusiasts to listen for female song in established lab or field populations of marked, sexed individuals. Working collectively, we can best document the range of avian vocal diversity in both sexes for the broadest number of species. With these data we can then comprehensively address major questions about the regulation, function, evolution, and conservation applications of bird song.

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**Ethics statement:** No live birds were used in this study, only archived data.

**Author contributions:** The development of ideas, content, organization, and writing for this manuscript were shared by both coauthors.

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**APPENDIX TABLE 4.** List of participants and affiliations (at time of participation) in 2 discussions on female bird song.

2016 North American Ornithological Conference, female song roundtable	
Participant	Affiliation
Jennifer Ackerman	Independent author
Lauryn Benedict	University of Northern Colorado
Than Boves	Arkansas State University
Ioana Chiver	University of California, Los Angeles, Smithsonian Tropical Research Station
Becky Cramer	Smithsonian Migratory Bird Center
Alana Demko	University of Windsor
Stephen Ferguson	University of Memphis
Sharon Gill	Western Michigan University
Brendan Graham	University of Windsor
Emma Greig	Cornell Lab of Ornithology
Sylvia Halkin	Central Connecticut State University
Richard Hedley	University of California, Los Angeles
David Logue	University of Lethbridge
Alix Matthews	Arkansas State University
Shannon McNeil	Southern Sierra Research Station
Matt Medler	Cornell Lab of Ornithology, Macaulay Library
Dan Mennill	University of Windsor
Karan Odom	University of Maryland, Baltimore County
Kevin Omland	University of Maryland, Baltimore County
Jordan Price	St. Mary's College of Maryland
Dustin Reichard	Ohio Wesleyan University
Michael Rowley	University of Maryland, Baltimore County
Luis Sandoval	Universidad de Costa Rica
Evangeline Shank	University of Maryland, Baltimore County
Morgan Slevin	Arkansas State University
Diane Tracy	Southern Sierra Research Station
Mike Webster	Cornell Lab of Ornithology, Macaulay Library
2017 Animal Behavior Society meeting, female song discussion	
Participant	Affiliation
Lauryn Benedict	University of Northern Colorado
Christine Dahlin	University of Pittsburgh, Johnstown
Cara Krieg	Michigan State University
Karan Odom	University of Maryland, Baltimore County
Jordan Price	St. Mary's College of Maryland
Chris Templeton	Pacific University
Mike Webster	Cornell Lab of Ornithology, Macaulay Library

**APPENDIX TABLE 5.** List of North American passerine species with known female song. Data from the Birds of North America (Rodewald 2017). Updated from Benedict (2008).

Tyrannidae (Tyrant Flycatchers)	
1	Northern Beardless-Tyrannulet ( <i>Camptostoma imberbe</i> )
2	Olive-sided Flycatcher ( <i>Contopus cooperi</i> )
3	Western Wood-Pewee ( <i>Contopus sordidulus</i> )
4	Eastern Wood-Pewee ( <i>Contopus virens</i> )
5	Acadian Flycatcher ( <i>Empidonax virescens</i> )
6	Willow Flycatcher ( <i>Empidonax traillii</i> )
7	Least Flycatcher ( <i>Empidonax minimus</i> )
8	Buff-breasted Flycatcher ( <i>Empidonax fulvifrons</i> )
9	Black Phoebe ( <i>Sayornis nigricans</i> )
10	Eastern Phoebe ( <i>Sayornis phoebe</i> )
11	Say's Phoebe ( <i>Sayornis saya</i> )
12	Dusky-capped Flycatcher ( <i>Myiarchus tuberculifer</i> )
13	Ash-throated Flycatcher ( <i>Myiarchus cinerascens</i> )
14	Great Kiskadee ( <i>Pitangus sulphuratus</i> )
Laniidae (Shrikes)	
15	Loggerhead Shrike ( <i>Lanius ludovicianus</i> )
16	Northern Shrike ( <i>Lanius borealis</i> )
Vireonidae (Vireos)	
17	White-eyed Vireo ( <i>Vireo griseus</i> )
18	Bell's Vireo ( <i>Vireo bellii</i> )
19	Gray Vireo ( <i>Vireo vicinior</i> )
20	Warbling Vireo ( <i>Vireo gilvus</i> )
Corvidae (Jays, Magpies, and Crows)	
21	Gray Jay ( <i>Perisoreus canadensis</i> )
22	Steller's Jay ( <i>Cyanocitta stelleri</i> )
23	Florida Scrub-Jay ( <i>Aphelocoma coerulescens</i> )
24	Island Scrub-Jay ( <i>Aphelocoma insularis</i> )
25	California Scrub-Jay ( <i>Aphelocoma californica</i> )
26	Woodhouse's Scrub-Jay ( <i>Aphelocoma woodhouseii</i> )
27	Black-billed Magpie ( <i>Pica hudsonia</i> )
28	American Crow ( <i>Corvus brachyrhynchos</i> )
29	Hawaiian Crow ( <i>Corvus hawaiiensis</i> )
Monarchidae (Monarch Flycatchers)	
30	Kauai Elepaio ( <i>Chasiempis sclateri</i> )
31	Oahu Elepaio ( <i>Chasiempis ibidis</i> )
32	Hawaii Elepaio ( <i>Chasiempis sandwichensis</i> )
Alaudidae (Larks)	
33	Eurasian Skylark ( <i>Alauda arvensis</i> )
Hirundinidae (Swallows)	
34	Purple Martin ( <i>Progne subis</i> )
35	Bank Swallow ( <i>Riparia riparia</i> )
36	Barn Swallow ( <i>Hirundo rustica</i> )
Paridae (Titmice)	
37	Carolina Chickadee ( <i>Poecile carolinensis</i> )
38	Black-capped Chickadee ( <i>Poecile atricapillus</i> )
39	Boreal Chickadee ( <i>Poecile hudsonica</i> )
40	Gray-headed Chickadee ( <i>Poecile cinctus</i> )
41	Juniper Titmouse ( <i>Baeolophus ridgwayi</i> )
42	Tufted Titmouse ( <i>Baeolophus bicolor</i> )
43	Black-crested Titmouse ( <i>Baeolophus atricristatus</i> )
Sittidae (Nuthatches)	
44	Red-breasted Nuthatch ( <i>Sitta canadensis</i> )
45	Pygmy Nuthatch ( <i>Sitta pygmaea</i> )
46	Brown-headed Nuthatch ( <i>Sitta pusilla</i> )
Troglodytidae (Wrens)	
47	Canyon Wren ( <i>Catherpes mexicanus</i> )
48	House Wren ( <i>Troglodytes aedon</i> )
49	Winter Wren ( <i>Troglodytes hiemalis</i> )
50	Cactus Wren ( <i>Campylorhynchus brunneicapillus</i> )



APPENDIX TABLE 5. Continued.

Cinclidae (Dippers)
51 American Dipper ( <i>Cinclus mexicanus</i> )
Regulidae (Kinglets)
52 Ruby-crowned Kinglet ( <i>Regulus calendula</i> )
Sylviidae (Old World Warblers)
53 Wrenit ( <i>Chamaea fasciata</i> )
Zosteropidae (White-eyes and allies)
54 Japanese White-eye ( <i>Zosterops japonicus</i> )
Muscicapidae (Old World Flycatchers)
55 White-rumped Shama ( <i>Copsychus malabaricus</i> )
56 Bluethroat ( <i>Luscinia svecica</i> )
57 Northern Wheatear ( <i>Oenanthe oenanthe</i> )
Turdidae (Thrushes and allies)
58 Eastern Bluebird ( <i>Sialia sialis</i> )
59 Townsend's Solitaire ( <i>Myadestes townsendi</i> )
60 Kamao ( <i>Myadestes myadestinus</i> )
61 Amaui ( <i>Myadestes woahensis</i> )
62 Olomao ( <i>Myadestes lanaiensis</i> )
63 Omao ( <i>Myadestes obscurus</i> )
64 Puaiohi ( <i>Myadestes palmeri</i> )
65 Bicknell's Thrush ( <i>Catharus bicknelli</i> )
66 Wood Thrush ( <i>Hylocichla mustelina</i> )
Mimidae (Mockingbirds, Thrashers, and allies)
67 Gray Catbird ( <i>Dumetella carolinensis</i> )
68 California Thrasher ( <i>Toxostoma redivivum</i> )
69 LeConte's Thrasher ( <i>Toxostoma lecontei</i> )
70 Northern Mockingbird ( <i>Mimus polyglottos</i> )
Sturnidae (Starlings and allies)
71 European Starling ( <i>Sturnus vulgaris</i> )
72 Common Myna ( <i>Acridotheres tristis</i> )
Ptilionotidae (Silky Flycatchers)
73 Phainopepla ( <i>Phainopepla nitens</i> )
Peucedramidae (Olive Warblers)
74 Olive Warbler ( <i>Peucedramus taeniatus</i> )
Passeridae (Old World Sparrows)
75 House Sparrow ( <i>Passer domesticus</i> )
Fringillidae (Finches, Crossbills, and allies)
76 Nihoa Finch ( <i>Telespiza ultima</i> )
77 Apapane ( <i>Himatione sanguinea</i> )
78 Iiwi ( <i>Drepanis coccinea</i> )
79 Hawaii Amakihi ( <i>Chlorodrepanis virens</i> )
80 Oahu Amakihi ( <i>Chlorodrepanis flava</i> )
81 Kauai Amakihi ( <i>Chlorodrepanis stejnegeri</i> )
82 Akekee ( <i>Loxops caeruleirostris</i> )
83 Hawaii Akepa ( <i>Loxops coccineus</i> )
84 Pine Grosbeak ( <i>Pinicola enucleator</i> )
85 Gray-crowned Rosy-Finch ( <i>Leucosticte tephrocotis</i> )
86 House Finch ( <i>Haemorhous mexicanus</i> )
87 Purple Finch ( <i>Haemorhous purpureus</i> )
88 Cassin's Finch ( <i>Haemorhous cassinii</i> )
89 Red Crossbill ( <i>Loxia curvirostra</i> )
90 White-winged Crossbill ( <i>Loxia leucoptera</i> )
91 Lawrence's Goldfinch ( <i>Spinus lawrencei</i> )
Calcariidae (Longspurs and Snow Buntings)
92 Smith's Longspur ( <i>Calcarius pictus</i> )
93 McCown's Longspur ( <i>Rhynchophanes mccownii</i> )
Passerellidae (New World Sparrows)
94 Spotted Towhee ( <i>Pipilo maculatus</i> )
95 Eastern Towhee ( <i>Pipilo erythrophthalmus</i> )
96 Lark Bunting ( <i>Calamospiza melanocorys</i> )
97 Savannah Sparrow ( <i>Passerculus sandwichensis</i> )
98 Grasshopper Sparrow ( <i>Ammodramus savannarum</i> )
99 Nelson's Sparrow ( <i>Ammodramus nelsoni</i> )

APPENDIX TABLE 5. Continued.

100 Seaside Sparrow ( <i>Ammodramus maritimus</i> )
101 Fox Sparrow ( <i>Passerella iliaca</i> )
102 Song Sparrow ( <i>Melospiza melodia</i> )
103 White-throated Sparrow ( <i>Zonotrichia albicollis</i> )
104 White-crowned Sparrow ( <i>Zonotrichia leucophrys</i> )
105 Dark-eyed Junco ( <i>Junco hyemalis</i> )
Icteridae (Troupials and allies)
106 Yellow-headed Blackbird ( <i>Xanthocephalus xanthocephalus</i> )
107 Eastern Meadowlark ( <i>Sturnella magna</i> )
108 Western Meadowlark ( <i>Sturnella neglecta</i> )
109 Orchard Oriole ( <i>Icterus spurius</i> )
110 Hooded Oriole ( <i>Icterus cucullatus</i> )
111 Bullock's Oriole ( <i>Icterus bullockii</i> )
112 Audubon's Oriole ( <i>Icterus graduacauda</i> )
113 Baltimore Oriole ( <i>Icterus galbula</i> )
114 Scott's Oriole ( <i>Icterus parisorum</i> )
115 Red-winged Blackbird ( <i>Agelaius phoeniceus</i> )
116 Tricolored Blackbird ( <i>Agelaius tricolor</i> )
117 Rusty Blackbird ( <i>Euphagus carolinus</i> )
118 Brewer's Blackbird ( <i>Euphagus cyanocephalus</i> )
119 Common Grackle ( <i>Quiscalus quiscula</i> )
120 Boat-tailed Grackle ( <i>Quiscalus major</i> )
121 Great-tailed Grackle ( <i>Quiscalus mexicanus</i> )
Parulidae (New World Warblers)
122 Ovenbird ( <i>Seiurus aurocapilla</i> )
123 Louisiana Waterthrush ( <i>Parkesia motacilla</i> )
124 Prothonotary Warbler ( <i>Protonotaria citrea</i> )
125 Common Yellowthroat ( <i>Geothlypis trichas</i> )
126 Hooded Warbler ( <i>Setophaga citrina</i> )
127 American Redstart ( <i>Setophaga ruticilla</i> )
128 Cerulean Warbler ( <i>Setophaga cerulea</i> )
129 Northern Parula ( <i>Setophaga americana</i> )
130 Bay-breasted Warbler ( <i>Setophaga castanea</i> )
131 Yellow Warbler ( <i>Setophaga petechia</i> )
132 Chestnut-sided Warbler ( <i>Setophaga pensylvanica</i> )
133 Black-throated Blue Warbler ( <i>Setophaga caerulescens</i> )
134 Prairie Warbler ( <i>Setophaga discolor</i> )
135 Canada Warbler ( <i>Cardellina canadensis</i> )
136 Wilson's Warbler ( <i>Cardellina pusilla</i> )
137 Painted Redstart ( <i>Myioborus pictus</i> )
Cardinalidae (Saltators, Cardinals, and allies)
138 Summer Tanager ( <i>Piranga rubra</i> )
139 Scarlet Tanager ( <i>Piranga olivacea</i> )
140 Western Tanager ( <i>Piranga ludoviciana</i> )
141 Northern Cardinal ( <i>Cardinalis cardinalis</i> )
142 Pyrrhuloxia ( <i>Cardinalis sinuatus</i> )
143 Rose-breasted Grosbeak ( <i>Pheucticus ludovicianus</i> )
144 Black-headed Grosbeak ( <i>Pheucticus melanocephalus</i> )