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Review



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Animal behaviour

New insights from female bird song: towards an integrated approach to studying male and female communication roles

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Historically, bird song has been regarded as a sex-specific signalling trait; males sing to attract females and females drive the evolution of signal exaggeration by preferring males with ever more complex songs. This view provides no functional role for female song. Historic geographical research biases generalized pronounced sex differences of phylogenetically derived northern temperate zone songbirds to all songbirds. However, we now know that female song is common and that both sexes probably sang in the ancestor of modern songbirds. This calls for research on adaptive explanations and mechanisms regulating female song, and a reassessment of questions and approaches to identify selection pressures driving song elaboration in both sexes and subsequent loss of female song in some clades. In this short review and perspective we highlight newly emerging questions and propose a research framework to investigate female song and song sex differences across species. We encourage experimental tests of mechanism, ontogeny, and function integrated with comparative evolutionary analyses. Moreover, we discuss the wider implications of female bird song research for our understanding of male and female communication roles.

1. Female bird song is common and song in both sexes ancestral (the case for studying female bird song)

Bird song serves as a textbook example to illustrate stark sexual dimorphisms shaped by sexual selection: males sing to exclude same-sex competitors and attract females, which select for signal elaboration by preferring quality-linked exaggeration. However, this scenario provides little or no functional explanation for female bird song. Yet with increasing documentation across clades and biogeographic regions, female bird song can no longer be considered a rare exception. On the contrary, when contrasting the previous northern temperate zone-centred view with recent worldwide surveys, it becomes apparent that female song is phylogenetically widespread [1,2]. Moreover, concurrent phylogenetic reconstruction reveals male and female song as the most parsimonious ancestral state [1–3]. This challenges the notion that song dimorphisms resulted from uninterrupted divergent sexual selection on males. Instead, phylogenetic comparisons within and between taxa reveal patterns of sex differences (and absence thereof) suggesting that several evolutionary processes

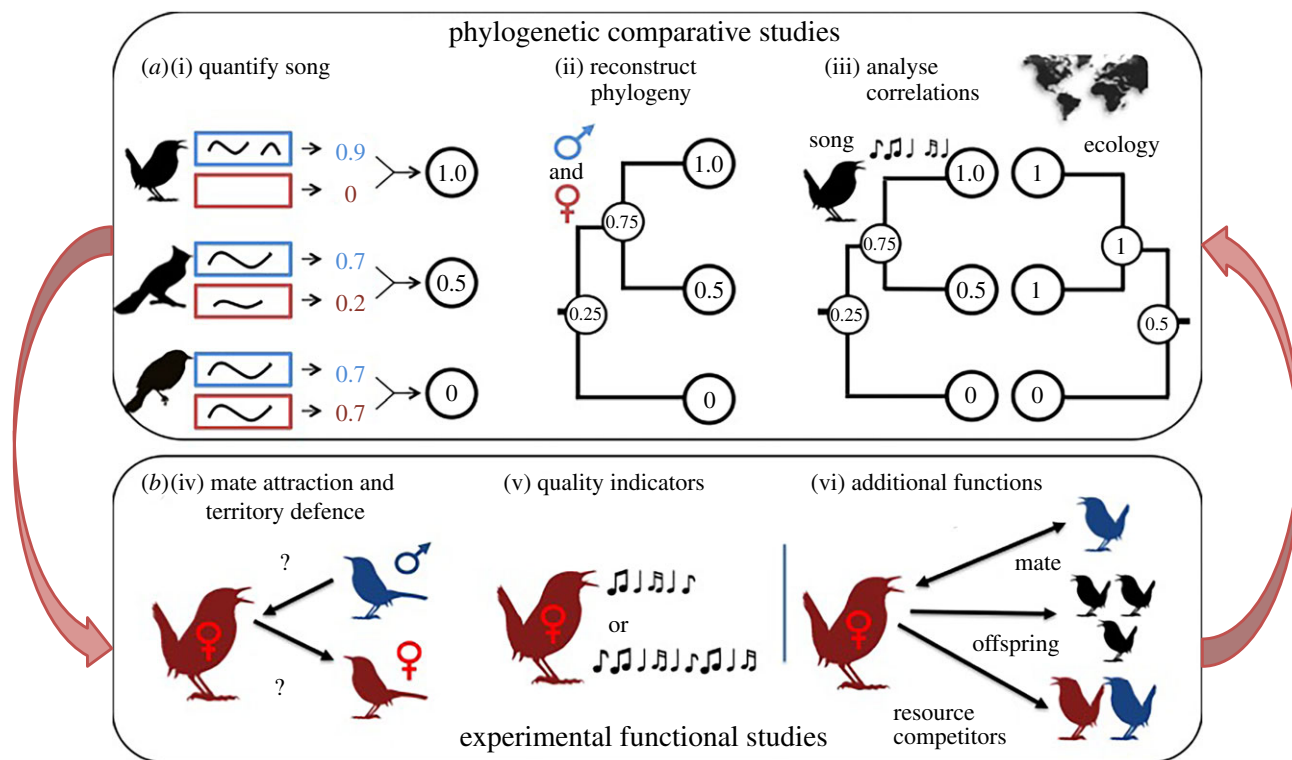


Figure 1. Investigating function and evolution of female bird song. (a) Phylogenetic comparative studies should (i) quantify song structure, (ii) reconstruct the extent of elaboration in females and males and (iii) compare elaboration with selection pressures. (b) Experimental studies should assess (iv) traditional mate attraction and territory defence functions, (v) potential quality indicators such as song complexity and repertoire size, and (vi) alternative functions, including communication with mates, offspring, or competitors for non-mate resources in both sexes across songbird species. Phylogenetic comparative (a) and experimental studies (b) should complement each other to iteratively refine hypotheses pertaining to female and male song function and evolution.

acted on both sexes, including repeated losses and re-gains in females [1,2,4]. A more diverse and dynamic evolutionary landscape underlying trait elaboration and sexual dimorphisms is unfolding that is supported by phylogenetic analyses in other signalling domains (e.g. colours in visual ornaments: [2,5]) and discoveries of single molecular switch mechanisms enabling fast losses and gains of sexual signalling traits in different animal taxa [6]. This new perspective that sexual dimorphisms can arise from both directional selection and repeated secondary trait loss raises new questions about which selection pressures contributed to the initial evolution, maintenance, or elaboration of song in both sexes in some species and the loss of female song in others [1,4].

With this brief review and perspective, we aim to stimulate discussion and coordinated research efforts to address these questions. We highlight the need for: improved documentation and quantification of sex differences in song, studies of the ontogeny and mechanism of female song learning and control, experiments to compare the current function(s) of female and male song, and analyses comparing the evolution of female and male song. Instead of a species-by-species re-run of male bird song research now focusing on females, future approaches should be integrative, simultaneously investigating male and female communication roles and interactions. This requires descriptive and experimental studies to catch up on documenting the natural history of female song, and testing a broader range of hypotheses, since traditional approaches rarely considered the impact of singing social partners on male song function. Sex-inclusive research on bird song also entails parallel testing of hypotheses in both sexes, enabling more consistent

interpretation of male and female behaviour than single-sex studies. For example, the use of song for territorial defence is almost by default considered ‘sexually selected’ in males, but socially selected in females (e.g. [7]), whereas we cannot detect obvious contextual differences in many cases (see §2d)—suggesting that either there is more sexually selected song in females or also more instances of socially selected song in males. Our aim is therefore to encourage observations and experimental tests of the function(s) and mechanisms regulating both male and female song and to integrate these findings with phylogenetically-controlled comparative analyses to understand factors driving the evolutionary origins, elaboration, and loss of song across all songbirds (figure 1).

2. Towards an integrative framework for studying female and male bird song

(a) Documenting female bird song

The foundation of integrative research on female and male song is detailed knowledge of its natural history (figure 2). Apart from duetting species [8,9], observational and experimental data on the presence, contexts, and correlates of song are rare for females [10] and females are highly under-represented in literature and sound collections. For only 27% of all songbird species is there sufficient information to even determine if female song is present or absent [2]. In the two largest collections of bird audio recordings only 0.03% (Macaulay Library) and 0.01% (Xeno-canto) of contributions are labelled ‘female’ [11]. In contrast, the most

Who?	<ul style="list-style-type: none"> • male or female • age • status: - <i>high/low dominance</i> - <i>breeder</i> - <i>helper</i> 	<ul style="list-style-type: none"> • tutor:
When?	<ul style="list-style-type: none"> • time of day • season • context 	<ul style="list-style-type: none"> • juvenile or adult • pre- or postdispersal
What?	<ul style="list-style-type: none"> • song rate • song structure • total repertoire size 	<ul style="list-style-type: none"> • repertoire • timing • interaction rules
How?	<ul style="list-style-type: none"> • amplitude • tempo • matching • switching 	<ul style="list-style-type: none"> • memorization • motor practice (interactive: yes/no)
What for?	<ul style="list-style-type: none"> • correlations → hypothesis development → experimental tests (e.g. playback studies), see figure 1 	

Figure 2. Sex-inclusive song research should collect observational and experimental data in males and females. To stimulate balanced sampling schemes, the left column suggests a list of questions, columns 2 and 3 relevant factors and parameters.

recent literature-based estimate is that in 64% of songbird species females sing [2]. The current lack of documentation of female song in sound archives is probably partly due to both omission of sex-specific information and mislabelling of some singing females as males in monomorphic species if song is (erroneously) used to infer sex [11]. To avoid new biases, documenting female song ideally should include location, context and season and simultaneous documentation of male and female song [11–13].

(b) Metrics and analyses to compare female and male song

Studies comparing male and female songs require metrics and analyses that allow accurate assessment of song dimorphism (or lack thereof; see [14]) across the highly variable song structures and singing styles seen between species and the sexes. Past song comparisons often focused on repertoire size or a limited set of parameters only, but analyses should increase the array of metrics in which male and female songs may vary, such as spectral features (e.g. frequency and duration), syllable diversity or repertoires [15], and syntax [16,17]. Analyses that combine multiple structural features over the entire duration of a song or element (e.g. dynamic time warping, [18]) and subsequently capture the relative distances between individuals in trait space i.e. multi-dimensional methods that provide unit-free measures of distances among males and females (as already successfully used for evolutionary analyses of colour dimorphism [5]) seem most promising for multi-species comparisons

(e.g. [17,19]). However, more work is needed to develop methods that allow comparison of sex differences in structure and singing styles across species.

(c) Ontogeny and mechanisms regulating song

In songbirds, song development in nature usually involves social learning from conspecifics (generally referred to as song models or tutors), and adult sex differences can result from whom, what and when the sexes learn their songs (see figure 2 and for detailed discussion [20]). Both evolutionary and functional analyses can profit from understanding male and female vocal development and distinguishing between learned versus experience-independent song sex differences. Tutor choice and timing of the song learning process may affect territory establishment, song-based mate choice, and resulting population structure [21–23]. However, compared with male song, we know little about the development of female song. Male and female adult song could differ because during ontogeny the sexes differ in (i) what and how much they learn; (ii) from whom they learn (choosing sex-specific tutors could result in sex-specific song lineages); (iii) the duration of the sensitive phases; (iv) dispersal patterns (thus learning at different times or locations from different tutors); (v) motor practice (timing and amount of motor practice affects song stereotypy); or (vi) how sex-specific vocal tract anatomy affects song learning. Song sex differences are thus not necessarily proof of different learning abilities: some duetting species show pronounced sex-specific repertoires in the wild but learn either repertoire under laboratory conditions [24–26]. Field studies probably best

establish *from whom* males and females learn in their natural social networks (e.g. [27,28]) whereas experimental laboratory studies may provide greater resolution on the *what and when* of song learning, including lifelong plasticity (examples in [20,26]), which might then help to test functional hypotheses in the field, such as the role of improved song coordination over time in duetting [29,30]. Studies on song production learning should be complemented with studies on song preference learning, not only in females (for examples, see [20]) but also in males (e.g. using operant tests [31]), to ask whether learned preferences may also guide mate choice in males in species where female song functions in mate attraction.

Integrative and comparative studies of male and female song development could be highly informative for research on the neuromolecular bases of sexual differentiation and plasticity of the song system [32–35]. Until recently, the study of the neuroendocrinology of (male) song and sex differences focused on steroid hormones and was predominantly based on species from the most derived clade of the Passerida, which may not necessarily predict sex differences in the quantity and quality of song output in other clades and other biogeographic regions (for review see e.g. [32,34]). In Australian red-backed fairy wrens, *Malurus melanocephalus*, for example, males and females show clear sex differences in brain morphology and circulating androgen levels but sing equally prolific and complex song [19]. Likewise, the seasonal link between rising plasma testosterone and male song is not necessarily observed in females, or male birds of the tropics and subtropics [32], and physiological levels of testosterone seem poor predictors of variation in singing. Attention has now shifted towards species differences in steroid receptors and associated genomic responses in the song circuitry [33,34], which show surprisingly pronounced species differences [35]. Here, more integrative approaches including early-branching songbird lineages could help to identify the most likely ancestral states and ecological correlates of derived patterns and thus identify target species for physiological and neuromolecular research to update knowledge of the physiology of female song and the neuromolecular underpinning of sex-specific song development.

(d) Song function

Different selection pressures are likely to be at work in species with monomorphic versus dimorphic song. If the sexes sound the same, their songs probably fulfil similar functions, best evidenced where partners can fill in for each other by singing both parts of a duet (so called pseudo-duetting, examples in [36]). In contrast, sex-specific songs suggest a functional advantage for signalling sexual identity (e.g. mate attraction or strong intra-sexual competition) or for sex-specific functions of song. However, since the field of female song function has seen little systematic study, we extrapolate from known male song functions to introduce new questions to further a male–female integrative approach.

Early studies on male song used elegant experiments to demonstrate that song functions primarily to defend territories and to attract females [37]. For example, replacing singing males with speakers delayed territory re-occupation [38] and increased female visitation rates to nest-boxes [39]. Numerous examples have since demonstrated how high

song output, complexity, or repertoire size advertises quality and resource holding potential to rivals and prospective mates, but these song functions have been predominantly studied in males [10]. Little is known about females that sing solo songs to defend territories ([10,40,41], but see [42]) and to attract mates in several polygynous and polyandrous species, where females must compete for male attention (e.g. [43,44]). Monogamous females may also use song for mate guarding [45] or for mate attraction [46]. Female song, like male song, can be an indicator trait, e.g. where female song complexity is correlated with age and experience [43,47], and song complexity and quantity predict breeding success [48,49]. However, experiments manipulating state, such as food supplementation [50] or early developmental conditions [51], which demonstrated condition-dependence of male song as an indicator of individual quality, are needed to test causal links for female song.

In many species, males sing year-round and increase song rates in response to (experimentally simulated) territorial intrusion [37]. Likewise, female song is common in species with year-round territories, including during non-breeding periods [52] or when solitary and unpaired [53], which raises the question of whether song also serves other functions in addition to mate attraction and territorial functions. Song in both sexes could mediate social dynamics in dense habitat where vision and low-amplitude calls would be insufficient for partner localization [54,55]. Female, like male song, may mediate competition with hetero-specifics for resources, including nest sites [56]. Both sexes of many species sometimes sing near the nest, potentially to coordinate parental investment and nest defence from predators (reviewed in [57]). Table 1 lists these hypotheses and how new playback experiments should test how males and females respond to the songs of their social partner or group members, whether they approach or match song types [58], and how this response is affected by context, location, season and song complexity. Furthermore, cost–benefit analyses may lead to interesting predictions regarding secondary losses of song, since costs of singing could differ for males and females [59,60].

To sum up, although experimental studies on the function of female song are rare in comparison with the substantial body of research on male birds of the north-temperate zones, and little is known about song function in the context of inter-sexual or female intra-sexual singing interactions, the studies conducted so far have revealed many different functions of female song. This suggests that song functions and communication roles typical of the highly seasonal northern temperate zones, with predominantly migratory songbird populations, may not extrapolate to other biogeographic regions with year-round residency and pairing, less seasonal breeding and other life-history differences.

(e) Comparative analyses

Across songbirds, there is considerably more variation in female than male song, ranging from species with no female song to species in which female song output or repertoire sizes are equivalent to or more extensive than in males (e.g. [41,61,62]). Phylogenetic comparative studies so far have examined the evolution of female song separately from male song (e.g. [1,4,63]). This was beneficial initially, when knowledge of female bird song was limited and its

Table 1. Hypothesized functions of bird song and experimental approaches for testing hypotheses in male and female birds simultaneously.

possible functions of male and female song	suggested experimental approaches
Territorial defence	<ol style="list-style-type: none"> 1. Speaker replacement experiments. Test 'keep out' function of song by removing pair and comparing settlement time of male and female immigrants in relation to playback of male and/or female song (e.g. song presence/absence, songs versus calls, repertoires versus single song type). 2. Simulate intrusion (decoy or playback). Test whether female and/or male residents use increases in song rate or song complexity to defend their territory.
Distinguishing mate and resource defence	<ol style="list-style-type: none"> 1. Mate removal experiments. Compare song output of unpaired, monogamous and polygamous individuals; remove mate, document changes in song output. 2. Resource manipulation. Compare song output before and after adding or removing nest sites or supplementing food.
Mate attraction	<ol style="list-style-type: none"> 1. Speaker replacement experiments. Test mate attraction function of song by removing pair and comparing settlement time of male and female immigrants in relation to playback of male and/or female song (test if stimuli as above attract the opposite sex). 2. For cavity-nesting species in which either sex may establish the territory, playback experiments at nest boxes.
Mate stimulation	Laboratory playback experiments. Test male preferences for female song, and effects on male reproductive physiology and behaviour.
Advertising individual quality (e.g. to attract mate or defend territory)	<ol style="list-style-type: none"> 1. Food supplementation experiment. Test whether providing food when conditions are harsh leads to increases in song rate. 2. Manipulation of the early rearing environment (food, brood size, parasites). Test whether treatment(s) affects song learning outcomes/repertoire size.
Mediating social dynamics	<ol style="list-style-type: none"> 1. Playback experiments to test the 'What' and 'How' of adult song (figure 2), particularly interactive playback. 2. Network analyses (microphone arrays in the field, miniature backpack microphones in aviaries).

prevalence was unknown. Now that we understand that female song is widespread, it is important to study female and male song evolution simultaneously. Nevertheless, evolutionary patterns should also be examined for each sex independently within these studies to evaluate how losses and elaboration of song in each sex contribute to overall patterns of dimorphism, as has been done for other elaborate traits [4,5,64]. To this end, phylogenetic comparative studies can correlate ecological and natural history traits to losses and elaborations of song in each sex to identify their associated selection pressures [4]. This requires precisely quantified traits relevant to both sexes; ideally by quantifying and comparing song as a continuous, multi-dimensional trait (see §2b). Past analytical constraints limited phylogenetic comparative studies to correlations among binary character states, with song classified discretely, such as presence/absence or a few ordinal classifications (e.g. [1,63,65]). However, recent advances in phylogenetic comparative tools now allow comparisons of multiple continuous explanatory variables while controlling for phylogeny (e.g. [2,5,66]). Thus, the correlated evolution of complex traits, such as female and male song structure, can now be tested with increased precision. This will require incorporating a broad range of natural history and ecological traits that pertain to both sexes, ideally also measured continuously, representing sexual, social, and natural selection pressures (e.g. [5,7,66]), enabling us to evaluate hypotheses associated with initial gains or elaboration in both sexes, or loss of song in females.

Conclusions from these correlational phylogenetic analyses should in turn be tested via experimental studies on the function, costs, and benefits of female and male song. In this way, experimental studies can refine hypotheses supported by comparative studies and, in turn, inform the relevant questions for future phylogenetic comparative research (figure 1).

3. Conclusion—towards a sex-inclusive approach to animal communication

Historic and geographical research biases have led to gross underestimation of female bird song. Increasing documentation of female bird song shows it to be widespread, challenging us to revise the traditional male-focused framework and to investigate among-species diversity in sex-specific communication roles. Sex-inclusive research on animal signalling will expand our understanding of the natural history of song in both sexes and variation in the extent of acoustic dimorphism, facilitating experimental and comparative studies to identify factors driving the evolutionary dynamics of female and male bird song. Researching female as well as male song also considerably expands our understanding of social networks in bird song, from a sole focus on male–male networks, to include female–female networks and female–male networks where social dynamics may include both cooperation and conflict (e.g. long-term neighbours and breeding partners). Addressing open

questions regarding the different evolutionary scenarios and current selection pressures that led to or maintained so many different forms of sex differences (and their absence) requires concerted research effort into the mechanisms, function, and evolution of female and male bird song. Bird song research has already made many important contributions to the field of animal communication, and improving our knowledge of female bird song not only will rectify our currently incomplete understanding of the evolution and function of bird song, but also offers a tractable model system for improving our understanding of sex-specificity

of communication roles, complex social network dynamics, and trait loss and gains.

Data accessibility. This article has no additional data.

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