Understanding Sex Differences in Form and Function of Bird Song: The Importance of Studying Song Learning Processes

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Birdsong is a culturally transmitted mating signal. Due to historical and geographical biases, song (learning) has been predominantly studied in the temperate zones, where female song is rare. Consequently, mechanisms and function of song learning have been almost exclusively studied in male birds and under the premise that inter- and intra-sexual selection favored larger repertoires and complex songs in males. However, female song is not rare outside the temperate zones and song in both sexes probably is the ancestral state in songbirds. Some song dimorphisms seen today might therefore be manifestations of secondary losses of female song. What selection pressures have favored such losses and other sexual dimorphisms in song? Combined mapping of phylogenetic and ecological correlates of sex differences in song structure and function might provide important clues to the evolution of male and female song. This requires parameterization of the degree of sexual dimorphism. Simple comparison of male-female song might not provide enough resolution, because the same magnitude of difference (e.g., repertoire overlap) could result from different processes: the sexes could differ in how well they learn ("copying fidelity") or from whom they learn ("model selection"). Different learning mechanisms might provide important pointers toward different selection pressures. Investigating sex-specific learning could therefore help to identify the social and ecological selection pressures contributing to sex differences in adult song. The study of female song learning in particular could be crucial to our understanding of (i) song function in males and females and (ii) the evolution of sex-specific song.

Keywords: vocal learning, females, oscines, signal evolution, cultural transmission, signal, plasticity

BOTH SEXES OF SONGBIRDS SING AND LEARN THEIR SONGS

What is in a name? Song in songbirds (*oscines*) is so ubiquitous and conspicuous that the songbirds, the most speciose avian clade (comprising almost half of the ∼10,000 extant species), were named after it. Song is typically learned early in life from conspecifics—what and how well young birds learn greatly affects the efficacy of their signals as adults (Catchpole and Slater, 2008; Lachlan et al., 2014; Peters et al., 2014). Song is currently the best-studied and probably most widely accepted animal example of a culturally transmitted mating signal (Slater and Ince, 1979; Mundinger, 1982; Podos and Warren, 2007; Riebel et al., 2015).

In most species song functions both as an armament and as an ornament, serving as a keep-away signal to same-sex competitors in the context of resource defense and as a signal to attract and stimulate mates for breeding (Catchpole and Slater, 2008). These functions tally with the canonical male sex role (Andersson, 1994): males can gain fitness by increased investment into sexual signaling to maximize the number of potential partners and exclude competitors. Male song indeed fulfils both functions (Kroodsma and Byers, 1991).

Social learning (typically from conspecifics) is crucial for the development of fully functional song. Ever since Thorpe's seminal studies on chaffinch song learning in the 1950s kick-started modern birdsong research by introducing spectrographic analyses (Slater, 2003; Riebel et al., 2015), the study of the function of birdsong and vocal learning have gone hand-in-hand. However, this inadvertently became a tale of male song learning only (Riebel, 2003; Riebel et al., 2005): due to historical and geographic research biases, songbirds were studied for many years predominantly in the Passerida of the temperate zones of Europe and North America, where female song is rare (Morton, 1996; Riebel et al., 2005; Odom et al., 2014). This led to the description of birdsong as a predominantly male trait, despite earlier reports of abundant female song in other biogeographic regions (Robinson, 1949; Morton, 1996). Only since the late 1990's has the mounting evidence of female song in other regions and clades resulted in a revision of this view: female song is now understood to be phylogenetically and geographically widespread (Robinson, 1949; Morton, 1996; Langmore, 1998; Riebel, 2003; Hall, 2004; Slater and Mann, 2004; Riebel et al., 2005; Garamszegi et al., 2007; Price, 2015). A recent phylogenetic analysis and ancestral state reconstruction even indicates song in both sexes as the most probable ancestral state (Odom et al., 2014). Current sex differences are thus likely the outcome of both secondary trait loss and selection pressures on sexually dimorphic song (Kraaijeveld, 2014; Odom et al., 2014; Price, 2015). This raises the question of why females stopped singing in some clades but not in others (Odom et al., 2014) and what selection pressures have led to varying degrees of sexual dimorphism (Price, 2015). One promising approach to tackle these questions that has already proven informative for some clades, is to map sex differences in song structure and function and their ecological correlates onto phylogenetic trees to identify common patterns of diversification and losses (Price, 2009; Odom et al., 2015). However, bird song is a mating signal with a twist: substantial phenotypic variation in this trait can arise from cultural transmission and the underlying social learning networks (Lachlan and Slater, 1999). This means that patterns of sex differences can be misleading if the underlying processes causing them are ignored. In the subsequent sections I shall first briefly highlight what we know about the relationships between song learning—both production learning by males and perception learning by females—and the functions of male song. From there I will move on to the question of how studying song production learning in females might provide important cues for hypothesis development regarding the function and evolution of sex differences in male and female song.

PRODUCTION AND PERCEPTION LEARNING AND THE MATE ATTRACTION FUNCTION OF SONG

The mate attraction function of song is well supported by a large body of observational and experimental data from lab and field (Kroodsma and Byers, 1991; Andersson, 1994; Searcy and Yasukawa, 1996; Catchpole and Slater, 2008). There is now increasing evidence that female preferences, like male repertoires, are influenced by cultural transmission (Riebel, 2003). For the few species studied experimentally in this respect, the types of songs females experienced when young are generally preferred over unfamiliar songs in adulthood (Riebel, 2003). Learned preferences thus influence which songs within a population are attractive. This influence is not trivial, but guides mate choice (Riebel, 2003, 2009). In extremis, this can lead to preferences for song of another population within just one generation (Freeberg, 1996, 1998) or to preferences for the song of another subspecies (Clayton, 1990) or a preference for males that mimic the song of new host species in brood parasites (Payne et al., 2000). Song preferences affect mating patterns and gene recombination in the next generation, and for this reason learned mating preferences (for learned traits) are no longer seen as non-heritable phenotypic variation but to affect evolutionary dynamics in time and space (Verzijden et al., 2012). This is particularly true for birdsong, in which gene-culture co-evolution processes are driven by behavioral selection for learning the right types of song well (Lachlan and Feldman, 2003; Lachlan et al., 2013, 2014).

But from whom do females learn? Active song model choice has not been systematically studied in either sex (but for promising methods to approach these questions in wild birds see e.g., Lachlan and Slater, 2003; Templeton et al., 2010; Akcay et al., 2014). Experimental data from song tutoring studies in females show that memorization of preferred songs does not merely reflect availability or exposure frequency: female cowbirds, *Moluthrus ater*, that were raised with controlled exposure to songs preferred as adults those songs that during tutoring had been followed by adult females' "chatter" vocalizations (Freed-Brown and White, 2009). Group-housed young female zebra finches can develop song preferences for their male peers rather than adult tutors (Honarmand et al., 2015). How adult females react to specific variants of male song is thus dependent on their early song experiences (Riebel, 2003), and juvenile social and physical conditions (Holveck and Riebel, 2010; Riebel et al., 2010).

It is likely that in species where males and females sing, similar processes also affect the development of male song preferences. Despite increasing documentation of the potential mate attraction function of female song (Langmore, 1998; Hall, 2004), to the best of my knowledge male song preferences and song based male choice have not been studied, despite empirical evidence for a mate attraction function of female song (Langmore et al., 1996). Males, like females, might also be hormonally stimulated either directly by their partner's or even their own song (Kroodsma, 1976; Cheng, 2003). Interestingly, song can be positively reinforcing even in species with non-singing females,

such as zebra finches. Male zebra finches will work for song exposure in operant tasks and prefer to listen to songs of early tutors over unfamiliar songs (Riebel et al., 2002). If mechanisms that combine song memories and behavioral expression of preferences are in place even in species with non-singing females, searching for song preference learning in males might be well worth the while. Some of the methods used for female preference testing, such as phonotaxis paradigms, are likely to work in males as well, because males have been shown to be attracted to and approach playback of female song in species with singing females (Langmore et al., 1996).

PRODUCTION LEARNING AND THE RESOURCE DEFENCE FUNCTION OF SONG

The importance of song in the acquisition and defense of resources (territories, mates, nest sites) is undisputed for male song and male-female duets, and this might also be an important function of female solo song (Cain et al., 2015). But how important is it in this context to sing proper song? Song of male songbirds reared without adult models generally shows impoverished structure but nonetheless contains some species-specific signatures (Marler and Sherman, 1983). Such "isolate" song almost always functions less well (or not at all) in both inter-and intra-sexual contexts (Searcy et al., 1985). However, learning just any species-specific song might not suffice either: In species with clear regional variation, local songs generally elicit stronger territorial responses in playback paradigms where song is used to simulate an intruder (Podos and Warren, 2007; Catchpole and Slater, 2008). Even when learning from the local models only, learning these songs well can be of importance. In swamp sparrows, *Melospiza georgiana,* song variants that match the most typical regional variants in fine detail best, elicit stronger territorial reactions from territory owners—learning precision thus affects same-sex competition (Lachlan et al., 2014). Similarly, learning repertoires of many different songs might improve both a male's resource defense and mate attraction potential (Searcy, 1992; Beecher and Brenowitz, 2005). For male song, what is learned, from whom and how well can thus affect song function.

THE STUDY OF LEARNING MECHANISMS CAN HELP ELUCIDATE FUNCTION AND EVOLUTION OF FEMALE SONG

If song learning affects the efficacy of male songs in mate attraction and resource defense, this could hold for female song too where it fulfils these functions (examples in Langmore, 1998). But if learning song well is so important, why are there such pronounced sex differences in song (learning)? To date, we have no general explanation for the large interspecific variation in sex differences in song quantity and quality which spans the whole range from species with females that never sing (e.g., the zebra finch, Riebel, 2009) to species where females sing more often and more complex songs than males do (e.g., banded

wrens *Thryothorus pleurostictus,* Illes and Yunes-Jimenez, 2009). Moreover, sex differences in song go far beyond what might be needed to aid sex recognition (which can also be achieved with simple calls, see e.g., Mouterde et al., 2014; Kipper et al., 2015). Identical functions of song and sexual differentiation of song solely for sex recognition therefore seems a poor and unlikely general explanation for the vast differences in quantity, quality and context that can be found between male and female song (Langmore, 1998; Hall, 2004). It is here where the study of song learning mechanisms might provide important clues to understand the function and evolution of female song.

Identifying when and from whom females learn and whom they try to match e.g., whether they learn pre- or postdispersal, from kin from their natal area or from neighbors when establishing territories, from same- or opposite sex individuals, or their future mates provides important clues as to who might be the most important receivers of these songs. This in turn can help to develop testable hypothesis regarding the function of song. For example if song learning takes place only after dispersal and then only from territory neighbors then being able to song type match neighbors during territory defense is likely of (testable) higher relevance than for example kin recognition (in which case song learning should have taken place pre-dispersal and from relatives).

Knowing how females learn their songs should also enable the construction of more informative phylogenies. If song sex differences are scored solely by defining "maleness" of female song by looking at percentage shared song elements, ignoring learning, then we will obtain different trait values than when comparing repertoire size or learning accuracy. The hypothetical examples in **Table 1** are intended to illustrate this point: the first column shows schematic spectrograms representing a male and female song in a hypothetical songbird species. The two types of song are roughly of the same length and comparable complexity (both songs contain a 2-note syllable, a whistle note and a buzz note). The second and third column illustrate how male and female song is expected to look in the next generation under each of two different scenarios: (I) sex-specific model choice where males copy selectively from males and females selectively copy from females and (II) sex-specific copying fidelity where both sexes only partially copy their chosen models (some elements are missing, and there is some blending of the different model song types) but overall, one sex (here the male, in line with the classic view) imitates more components and does so more accurately. Below these song examples, I listed four parameters that are often used to score song sex differences. Notably, the two scores that take learning processes into account yield different patterns of scored sex differences than the two scores comparing males and females while ignoring model choice and copying fidelity. Analyses taking song learning into account would score no sex differences in amount and ability of learning under the sex-specific learning strategies in scenario I, but register a sex difference for the songs in scenario II. In contrast, analyses scoring sex differences by looking only at male-female repertoire sharing would arrive at the opposite conclusion: a maximum sex difference score under sex-specific model choice in scenario I and a less pronounced sex difference in scenario II (sex-specific

copying fidelity). Song parameter choice thus can affect both the direction and magnitude of sex differences.

This is of consequence for our attempts at constructing phylogenies: Evolutionary patterns often can only be discovered when traits are scored continuously rather than dichotomously (Dale et al., 2015; Price, 2015). The above examples illustrate that trait values can yield different results with regard to sex differences in song depending on whether learning processes are ignored or included. It is perhaps too early to speculate which of these measures is the most informative. For now, I hope to raise awareness for (a) that systematically scoring song differences between sexes with one method for all species must be premium for comparative studies and (b) that unraveling the song learning mechanisms and social model choice in combination with study of the interactions between sex-specific contexts and contents of song might provide important hints as to the function of evolution of these sex differences.

NOT ALL SEX DIFFERENCES IN SONG ARE INDICATIVE OF SEX DIFFERENCES IN SONG LEARNING CAPACITY

A final note of caution: sex differences can also be caused by other than social learning processes and not all sex differences in adult song necessarily reflect different learning strategies. Aspects of male and female physiology could differ such that even when both sexes learn the same songs (equally well) their songs sound different (Yamaguchi, 1998) because (1) sex differences in vocal tract anatomy affect vocal output (Ballintijn and ten Cate, 1997) and (2) seasonal and/or sex specific androgen levels could cause sex differences if females do not fully crystallize their song due to lower androgen levels. However, these questions as yet lack systematic study in songbirds (Gahr, 2014) and there are also observations of males and females that show no pronounced sex differences in song despite different steroid levels (Schwabl et al., 2015).

Moreover, physiological mechanisms and learning strategies can interact in multiple ways. And no learning strategy fits all: sex differences could come about because the sexes differ in different aspects of their learning strategies e.g., (1) one sex learns more or more accurately than the other (see **Table 1**), because (2) there are sex differences in the timing of the sensitive phase (Nelson et al., 1997; Yamaguchi, 1998) or (3) as a side effect of different habitat usage and/or dispersal patterns males and females are exposed to different models or (4) show differences in active model choice, meaning that they either pick different social models (see **Table 1**) or pick different song models from different tutors (Geberzahn and Gahr, 2013). The most conspicuous variant of the latter strategy would be true sex-specific lineages, where both sexes have specific vocalizations and learning takes place between same-sex individuals only (Price, 1998). This has been

TABLE 1 | Scoring song sex differences with and without taking learning processes into account yields different results.

	MODELS	TUTEES Sexes could differ in	
		I Model choice	II Copying fidelity
♂	A		
♀	B		
		↓	↓

		Measured sex differences	
SONG LEARNING			
% notes of tutee's song copied from tutor(s)		M = F	M > F
Total # of learned notes		M = F	M > F
SONG STRUCTURE (IGNORING LEARNING)			
Complexity (e.g., # different notes/total # notes)		M = F	F > M
"Maleness of song" (e.g., notes shared F/M)		0/4	2/5

Top panel: A and B represent a male (black) and female (orange) model song in a hypothetical songbird species. The songs are of comparable complexity: each has one 2-note syllable, one whistle note and one buzz note. With I) sex-specific model choice, male and female tutees end up with highly divergent songs (low "maleness" of female song) although both accurately learned from their respective model. In II) there is no sex-specific model choice and both sexes learned from more than one model but the male and female differ in how much they learned and how well ("copying fidelity"). In the example in the 3rd column, all notes in the male's song are accurate copies. In the female's song, comparison with the tutors' songs shows that not all notes are accurate copies and that there is also an improvised note type (in gray). Lower panel: This table illustrates how scored sex differences might differ depending on whether information on learning processes such as model choice or copying fidelity are included or not. For example, comparing each male and female with their respective model, yields no sex differences in amount and ability of learning in scenario I (Male M = Female F) but differences between males and females in how well they copied in scenario II (M > F). In contrast, an analysis scoring male-female note repertoire sharing, would arrive at the opposite conclusion: a maximum sex difference score in scenario I and less pronounced sex differences in scenario II. Song parameter choice thus can affect both the direction and magnitude of measured sex differences.

hypothesized for a number of species, but there has not yet been systematic study in a single species that was able to exclude all possible alternative explanations (for review and discussion see Riebel, 2003).

CONCLUSIONS AND OUTLOOK

To summarize and conclude: female songbirds in many species sing and learn which songs to sing. Females of both singing and non-singing species have been documented to also acquire their song preferences through social learning processes (Riebel, 2003). Learning and cultural transmission processes deeply impact the efficacy of the signal and both learned song and preferences are subjected to natural, social, inter- and intra-sexual selection processes. The timing of sensitive phases and mechanisms of model choice but also learning-unrelated behavior such as (sex-specific) dispersal patterns all impact song and eventually fitness. Ideally, the study of how developmental processes contribute to inter-individual variation in traits and preferences should go hand in hand with studies of song function. Questions we might want to ask in future studies investigating sex differences in song (and their costs and benefits) include:

1. Do males and females differ in the timing of song learning?
2. Are there sex differences in model choice (who is learning from whom)?
3. What is learned and how accurately, and does this depend on sex?

4. Is there evidence for sex-specific habitat usage and/or dispersal patterns that will lead to different model availability in males and females?

Identifying sex-specific learning strategies might provide important clues to the selection pressures on sexual differentiation of song. Asking why females in one species needn't learn precisely while in another exact copying (and from selected models) is important might lead us to the social factors selecting for particular learning strategies. There has been no systematic study of these questions in females yet, but systematic comparisons of how learning contributes to inter-individual variation in signaling and signal decoding will provide important steps toward unraveling the function(s) of intra-and inter-sexual song variation.

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The author confirms being the sole contributor of this work and approved it for publication.

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