Birdsong performance studies: a contrary view

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Article history:
Received 5 February 2016
Initial acceptance 29 March 2016
Final acceptance 30 June 2016
Available online 18 January 2017
MS. number: AF-16-00107R

Keywords:
birdsong
chipping sparrow
performance
scepticism
sexual selection
swamp sparrow

Birdsong biologists interested in sexual selection and honest signalling have repeatedly reported confirmation, over more than a decade, of the biological significance of a scatterplot between trill rate and frequency bandwidth. This ‘performance hypothesis’ proposes that the closer a song plots to an upper bound on the graph, the more difficult the song is to sing, and the more difficult the song the higher quality the singer, so that song quality honestly reveals male quality. In reviewing the confirming literature, however, I can find no support for this performance hypothesis. I will argue here that the scatter in the graph for songbirds is better explained by social factors and song learning. When songbirds learn their songs from each other, multiple males in a neighbourhood will sing the same song type. The need to conform to the local dialect of song types guides a male to learn a typical example of each song type for that population, not to take a memorized song and diminish or exaggerate it in trill rate or frequency bandwidth to honestly demonstrate his relative prowess. When data in this scatterplot are coded both by song type and by male, it is the song type and the need to conform that explains the variability, not the quality of different males. There is no consistent, reliable information in the song performance measures that can be used to evaluate a singing male.

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Something in how a male songbird delivers his songs may convey something about his relative quality to those who listen, especially females, but identifying those somethings has proven challenging. In the study of birdsong repertoires and female choice, for example, it has been widely accepted that ‘Females of many songbird species show a preference for mating with males that have larger song repertoires’ (Nowicki, Hasselquist, Bensch, & Peters, 2000, page 2419), but in spite of a host of studies claiming to confirm the hypothesis, there is no strong evidence that males or females attend to the number of different songs that a male can sing (Byers & Kroodsma, 2009).

Another idea that has over the last decade gained much traction is the performance hypothesis developed by Podos, Peters, and Nowicki (2004) and Ballentine, Hyman, and Nowicki (2004), based on motor and performance constraints described by Podos (1996, 1997). Scatterplots of trill rates and frequency bandwidths show an inverse relationship: the more rapid the trill, the narrower the bandwidth (see Figs 4, 5 and 11 for examples). Blank areas with no data beyond an upper bound suggest a motor constraint; that is, the birds cannot produce those combinations of trill rates and bandwidths (but see Figs 4 and 6). The interesting hypothesis is that how close a song plots to the upper bound might reveal the difficulty of producing that song, so that songs near the upper bound honestly reveal a high-quality singer; both prospective mates and competing males might then use those high-performance songs to detect high-quality singers.

This hypothesis has ‘been adopted widely in tests of song function’ (Goodwin & Podos, 2015, page 1), is touted as ‘a premiere illustration of how performance constraints shape the evolution of mating displays [with] sexual selection favoring high performance trills’ (Wilson, Bitton, Podos, & Mennill, 2014, page 214), and has been repeatedly confirmed over the past decade. My careful scrutiny of those studies here, however, reveals that the hypothesis has become largely an assumption (‘generally assumed’; Cardoso, Atwell, Ketterson, & Price, 2007, page 901) and never truly tested (Prum, 2010, 2012); furthermore, given how song performance measures are distributed among song types and among males, the hypothesis becomes biologically implausible, if not impossible. Here I review the confirming studies, beginning with a most recent paper on chipping sparrows, Spizella passerina (Goodwin & Podos, 2014), because it reveals especially clearly the methods used to confirm the hypothesis. I then proceed to the studies of swamp sparrows, Melospiza georgiana, before briefly reviewing other species.

The problems that plague this birdsong performance literature are pervasive in sexual selection studies (Prum, 2010, 2012), including the study of birdsong repertoires (Byers & Kroodsma,
By discussing these problems in considerable detail here, I would hope that future studies could be more successful in avoiding these problems and do a better job of revealing truths about the natural world.

CHIPPING SPARROW

I begin by illustrating how a chipping sparrow acquires his song, because the roots of implausibility for the performance hypothesis lie in the biological basis for song learning. Then I show how those songs are used during aggressive interactions among males, especially in lek-like arenas during the dawn chorus. These two known biological features of chipping sparrows are not referenced by Goodwin and Podos (2014), but seriously undermine their conclusions.

The Biology of Song Learning by Chipping Sparrows

A young chipping sparrow acquires his song by copying the song of an adult next to whom he settles, as illustrated by Liu and Kroodsma (2006; Fig. 1). The adult’s song is copied whether the trill is delivered slowly (males 13 and 31, and males 20 and 22) or more rapidly (males 7 and 9, and males 24 and 35), during the social and aggressive interactions between the adult tutor and the youngster who is establishing his first territory. This conclusion is based on solid field evidence by colour banding 324 young chipping sparrows and following them during dispersal.

To further illustrate how a young male chipping sparrow learns rather precisely the song of his adult tutor, and especially the tutor’s trill rate, I recorded chipping sparrows during early May (2015) when they first returned from migration, before postlearning dispersal might occur. I used a Sound Devices 722 digital recorder and a stereo Telinga microphone to record 67 different males in two populations, one on a golf course in Lewiston, Michigan, U.S.A., the other in a city park in Northampton, Massachusetts, U.S.A. Birds were not banded, but I recorded most of the birds in rapid succession by moving directly from one singer to the next, so that the previous and next singer could be heard while recording a given male. If songs of suspected neighbours were identical, and I could not distinguish their songs in sonagrams, I conservatively assumed they were the same male and discarded one of the recordings from the data set. Using Raven Pro software, I measured trill rates and frequency bandwidths for three high-quality songs for each male, and used the median value in analyses (‘spectrogram window size’ in Raven: 110 for temporal measures, 2050 for frequency; lower and upper frequencies measured as -24 dB down from maximum power; I believe these methods match those routinely used in performance studies).

Among these 67 males, I found 14 pairs of adjacent males with essentially identical songs (see Fig. 2), as one would expect based on how chirping sparrows learn their songs. As is clear in Fig. 2, song types and trill rates are determined by where and from whom a male learns his song and cannot reflect any measure of his quality, in the performance sense of Ballentine et al. (2004) and Podos et al. (2004). A male with a trill rate of 25 is not ‘better’ than a male with a trill rate of 7; instead, he simply learned his song from a male having a trill rate of about 25, whereas the other bird learned his song from a male having a trill rate of about 7. One might argue, if pressed, that a young male could innately know his relative singing ability and then choose to settle next to an adult

Figure 1. Reprinted with permission from Figure 2 in Liu and Kroodsma (2006). ‘Yearling Chipping Sparrows imitate songs of an immediate neighbor, but the instability of territories results in only short-term song sharing among neighbors. (a) In May of 1996, 24 territorial males (numbered 1–24) were found in the Quabbin Cemetery, and a portion of each male’s song type (0.35 sec) is illustrated. Males 7 and 9 share similar song types, as do males 20 and 22. (b) In May of 1997, 26 territorial males were found in the cemetery, 16 returning adults (at least two years old) from the previous year and 10 birds breeding there for the first time. Males 7 and 9 both returned but are no longer neighbors, and male 22 did not return. Male 35 did not learn the song of his father (male 5) or his father’s close neighbors in 1996 or 1997, but instead appeared to learn from his immediate neighbor in 1997 (male 24). Male 31 also appeared to acquire his song from an immediate neighbor (male 13) in 1997, not from his father (male 10). Both 1997 yearlings (31 and 35) hatched late in the 1996 breeding season, and each most likely acquired his song during 1997, as a yearling’.  

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