



Forum Article

Birdsong ‘performance’ studies: a sad commentary



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Birdsong performance studies have embraced the significance of a scatterplot between trill rate and frequency bandwidth, using the distance that a given sound plots from an upper bound (i.e. ‘vocal deviation’) as a measure of how difficult it is to perform that sound; the relative difficulty of the performance then becomes a means by which to assess the quality of the song and the singer (review in Kroodsma, 2017). Those who promote this literature defend it by its wide acceptance: ‘... vocal deviation has been used widely as a composite index of vocal performance ...’ (Podos et al., 2016, page 204) and ‘Vocal deviation ... has indeed been adopted widely in tests of song function’ (Goodwin & Podos, 2015, page 1). ‘Studies of trilled vocalizations’, with their inherent “tradeoff” between syllable repetition rate and frequency bandwidth’, are hailed 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).

In reality, however, no available scientific data support these ideas. The considerable literature that has developed on this topic is instead a premiere illustration of how highly flawed methods have been used repeatedly to tell an intuitively appealing but unsupported story, all of which has until now escaped a critical evaluation.

The three responses to my Forum (Cardoso, 2017; Podos, 2017; Vehrencamp, de Kort, & Illes, 2017) do not refute the big-picture and methodological problems that I raise. Podos and Vehrencamp et al. distract from the big issues largely by addressing minor, secondary issues or nonissues altogether. Cardoso does not really

address the main problems I discuss, but instead offers advice on how to disentangle ideas and facts in performance-related research.

Below, I offer a few final thoughts on this topic.

OVERUSE OF THE WORD ‘PERFORMANCE’ OBFUSCATES—TWO EXAMPLES

As I described in my Forum (Kroodsma, 2017), using the non-neutral word ‘performance’ to describe measured vocal deviation serves to turn an assumption (that a sound with low vocal deviation is difficult to produce) into the conclusions that songs with low vocal deviation are ‘better’ and that birds with low vocal deviation therefore perform better and are higher-quality birds. I offer two examples of this kind of obfuscation from publications that were submitted after a draft of my Forum became widely available during December 2014.

Try reading Podos et al. (2016) without the hidden implications of the word ‘performance’, which occurs 139 times. Very quickly the paper has an entirely different feel; no longer is it on the cutting edge of sexual selection science, but instead it becomes a rather prosaic description of syllable complexity among songs, with no information on the relative difficulty of producing those syllables or whether the birds care. There is nothing wrong with a good description, which is what all of this performance research would have benefited from in the first place. A good description will last forever and would contribute more to our understanding of the natural world than all of the performance experiments I have critiqued.

Also try reading Cardoso and Atwell (2016) without the implications of the word ‘performance’. The title states that ‘Shared

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songs are of lower performance in the dark-eyed junco', *Junco hyemalis*, but without the word 'performance' to interfere, I am freer to ask questions about the nature of the shared songs. And I start to fret, for several reasons. Classifying the songs of more than 150 different males into more than 250 song types is a huge, highly subjective task. Also, the word 'shared' implies that different renditions of the same song type by different males are part of the same cultural tradition (i.e. males 'share' these songs because they have learned them from each other). But if the amount of sharing within a junco population drops to near zero at about 1 km (Figure 3 in Newman, Yeh, & Price, 2008), how can any songs between two sites 80 km distant be truly 'shared' (i.e. part of the same cultural tradition)? It is more likely that songs at these two distant locations are simply different dialects, which can have different trill rates and frequency bandwidths, i.e. different 'performances' (as in swamp sparrows, *Melospiza georgiana*, my Figures 6 and 8 in Kroodmsma, 2017). Any similarity between songs of the two locations would be by chance alone.

I then predicted one bias in Cardoso and Atwell's analyses, in that simpler syllables with fast trill rates would be more likely to be classified as shared, simply because less detail in the sonograms would be available for the human eye to classify them as 'unshared'. I predicted correctly, finding that the trill rates of songs classified as shared between these two locations (University of California at San Diego, 'UCSD'; Mount Laguna, 'ML') were significantly faster than trill rates of songs classified as unshared ($n_1 = 21$ shared songs, median = 10.6 syllables/s; $n_2 = 241$ unshared songs, median = 13.0 syllables/s; one-tailed t test: $t = 2.46$, $P = 0.007$ or $t = 2.64$, $P = 0.004$, depending on whether the 21 shared syllable rates come from the ML or UCSD data). By thoughtful reading and digging beneath the performance verbiage (the word 'performance' occurs almost once in each sentence), one finds no evidence that the (biased) classification of songs as shared or unshared across these two distant locations has any relevance to the birds themselves, much less to sexual selection or to any useful index of song performance.

FUTURE RESEARCH

I had an initial say in my Forum (Kroodmsma, 2017), although I had at first reached more broadly into the birdsong and sexual selection literature. The 'nutritional stress hypothesis' (Nowicki, Peters, & Podos, 1998), for example, also needs a full treatment. Someone wishing to tackle this topic could begin with Nowicki, Hasselquist, Bensch, and Peters (2000), one of the supporting pillars of this literature, in which the authors conclude that females can assess the quality of a male based on repertoire size, when only about 1% of the variation in repertoire size is statistically explained by a correlation with a proxy of physical condition. That notion was rebutted by Kroodmsma (2004) but perpetuated in Peters, Searcy, and Nowicki (2014), and cited over a hundred times in the literature as of January 2017 (Web of Science). I contend that the same kinds of faulty methods used in the vocal deviation literature have been used in the song repertoire literature (see review by Byers & Kroodmsma, 2009) and in the nutritional stress literature. The long-term damage by these studies to the scientific study of birdsong and sexual selection has been immense.

I agree with Cardoso and Podos in that there is much to learn in trying to understand what birds hear and how they might assess one another based on song. But which research programme can pursue these topics with sufficient objectivity, independence and credibility? One of the best clues is offered by the citations that authors choose to support and bolster their own work. With my Forum article in hand, Podos et al. (2016) continued to cite at face value almost all of the papers that I had reported as severely flawed, thus either implicitly or explicitly defending these works (see also

Goodwin & Podos, 2015; Podos, 2017). In contrast, Byers, Akresh, and King (2016), when studying 'Song and male quality in prairie warblers', *Setophaga discolor* (as quoted from their title), chose to frame their thoughts without reference to these papers. Authors choose the framework for their arguments and discussions but lose credibility when they rely on flawed research to reinforce their own work.

Science is the search for truths about the natural world, but when the chosen methods cannot reveal truths, science suffers, as does the credibility of all scientists in all disciplines, including climate science. Producing good science is a responsibility shared by all of us, by authors, referees, editors, among others. How this performance literature (and specifically the 'vocal deviation literature') has flourished for so long is disconcerting, and does not speak well for the gate-keepers of science.

The primary problem is described well by Gitzen (2007, page 748), who discusses how authors '... stretch available data, gloss over uncertainties in their evidence, and ignore contrary results ... [largely because] ... the personal rewards of ... [such behaviours] ... far outweigh risks ...'. Therein lies the key: only when the costs of producing faulty science outweigh the benefits will sound science prevail. In the performance literature I have reviewed, the benefits have until now far outpaced the costs.

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