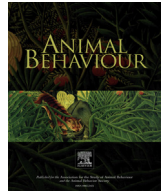




Contents lists available at ScienceDirect

Animal Behaviour

journal homepage: www.elsevier.com/locate/anbehav

Forum

Response to Kroodsma's critique of banded wren song performance research

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ARTICLE INFO

Article history:

Received 28 July 2016

Initial acceptance 23 September 2016

Final acceptance 1 November 2016

Available online xxx

MS. number: AF-16-00673

A critical review of a popular scientific theory, large or small, is something we applaud because, if well executed, it stimulates discussion and progresses science. However, such a review needs to be balanced, objective, informed and logical, especially if it concludes that a well-supported theory is flawed. Unfortunately, Kroodsma's current criticism (Kroodsma, 2017) of the birdsong performance literature suffers from the same weaknesses as his earlier criticism of song repertoire use in sexual selection (Byers & Kroodsma, 2009), despite the fact that he has been alerted to those mistakes (Collins, de Kort, Perez-Tris, & Telleria, 2011). Those weaknesses include outright errors and misrepresentations, highly selective citation of the literature and convoluted logic (sensu Podos, 2017). Here we would like to take this opportunity to redress the specific issues he raises with respect to our work on the banded wren, *Thryophilus pleurostictus*, and by doing so, illustrate how his criticism is flawed as a result of the above weaknesses, his restricted definition of 'song performance', and a misunderstanding of the song system of the banded wren.

Banded wren males possess song repertoires of approximately 25 distinct song types, which are largely shared with other males in their neighbourhood (Molles & Vehrencamp, 1999). The terminal trills of these song types vary in their trill note rate, frequency bandwidth and vocal deviation (maximal observed trill rates and maximal observed frequency bandwidths are inversely related in many songbirds, defining a negatively sloped upper limit line on a trill rate versus frequency bandwidth plot; the perpendicular

distance of a given trill from this line is its vocal deviation). Moreover, the trill notes themselves vary greatly in shape and complexity. Most of our research on this species has focused on the use of these song types in male–male territorial interactions (Burt & Vehrencamp, 2005; Hall, Illes, & Vehrencamp, 2006; Molles, 2006; Molles & Vehrencamp, 1999, 2001; Trillo & Vehrencamp, 2005; Vehrencamp, 2001; Vehrencamp, Ellis, Cropp, & Koltz, 2014; Vehrencamp, Hall, Bohman, Depeine, & Dalziell, 2007). We have shown that males negotiate their territorial boundaries primarily by varying short-term song type diversity and switching rate to indicate their propensity to approach, stand their ground or retreat from a territorial rival. Males also frequently song type-match each other during aggressive encounters. This primary role of song type choice does not rule out the possibility that subtle details of song structure also play a role and provide additional types of information about the sender, for both male and female receivers. The type-matching behaviour of countersinging males provides ample opportunities for receivers to compare their performances on the same song type, as proposed by Logue and Forstmeier (2008) for repertoire species.

The presence of signal component trade-offs (where two components of a signal are negatively correlated such that extreme values of one tends to inhibit extreme values of the other) sets up the potential for receivers to exert selective pressure on combinations that reveal useful information about the sender. This idea has been around for over two decades (Bradbury & Vehrencamp, 2011; Hebets & Papaj, 2005; Podos, 1997, 2017; Wells & Taigen, 1986). Whenever one observes a negative correlation between two signal components, it is worth testing this trade-off hypothesis (Podos's hypothesis 1) by looking to see whether receivers pay attention to alternative combinations of those components, and if so, whether individual variation in these combinations is associated with sender condition, context or reproductive success (Podos's hypothesis 2). The note structures of many birdsongs are obvious candidates for testing these hypotheses, because they are highly precise vocal utterances that have evolved under selective pressure from receiver responses in the contexts of territory defence and mate attraction (Collins, 2004; ten Cate, 2004). We examined

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several aspects of song performance in the banded wren, not limited to vocal deviation of trills as Kroodsma has restricted his critique to, but also the individual components of vocal deviation — trill rate and frequency bandwidth — along with trill note consistency, in multiple experimental and correlational studies. We have obtained consistent evidence that performance does matter in a repertoire species such as the banded wren.

Our first indication that performance components affected male responses was obtained by Illes, Hall, and Vehrencamp (2006), building on the Ballentine, Hyman, and Nowicki (2004) study, in which songs modified to have faster (higher performance) or slower (lower performance) trill rates were simultaneously presented to territorial males. We found that most subjects initially approached the fast stimulus, but if they were exposed to a broader frequency bandwidth (lower vocal deviation or higher performance) trill, they subsequently spent less time close to the fast speaker. Kroodsma disparages the design, execution, analysis, results and conclusions of this study, and chides the many researchers who have cited the paper. We show below that each of his criticisms is either incorrect or misinformed.

First, Kroodsma states that the playback should have been conducted with blind observers. The experimental design consisted of a two speaker set-up each broadcasting a separate stimulus. The observers were not informed about which speaker broadcasted which stimulus. Nevertheless, as Kroodsma acknowledges for the Cramer and Price (2007) study, an acute observer might discern which was which by listening, and we would have had to deafen the observers to exclude this possibility.

Second, we are surprised that an experienced ornithologist expresses doubt about the possibility of tracking movements of birds in their tropical deciduous forest habitat (i.e. when he writes, 'Even though flagging is used to mark area boundaries, the task of monitoring the location of a moving bird in this habitat seems a high challenge to accomplish with much confidence'; Kroodsma, 2017, page e13). We always had three observers for these trials, and they were all well-trained, experienced field assistants with keen observational skills. The birds usually sang and called during the trials, further facilitating our ability to locate them.

Third, the pseudoreplication criticism is a red herring. Each subject's stimulus exemplars were uniquely prepared from different base songs, and we used a wide variety of song types and source males for the base songs, thus eliminating the possibility of pseudoreplication.

Fourth, Kroodsma argues that the degree artificiality of manipulated playback stimuli could account for subject responses. Our modification of trill rate involved increasing or decreasing the silent gap between trill notes to a similar degree, so both alternative stimuli had equivalently altered note-to-interval ratios. The two final stimuli differed in trill rate by approximately 25–30%, so the modification represented a modest 10–15% change, i.e. they were not extremely artificial or abnormal songs. Even an individual banded wren may increase its trill rate by up to 7% during playback experiments compared to dawn chorus singing (Vehrencamp, Yantachka, Hall, & de Kort, 2013). The paired stimuli did have the same number of trill notes, and thus different durations. No experiment can perfectly control for all song variables. Banded wren songs vary greatly in duration both within and between song types and within and between individuals. Vehrencamp et al. (2014) found that longer songs were associated with more escalated contests. So any potentially confounding effect of song duration in the Illes et al. (2006) study would be conservative, since the theoretically higher performance (faster trill) stimulus had the shorter song duration.

Fifth, we did examine the tendency for trill performance components to vary in a consistent way among song types within males

in the Vehrencamp et al. (2013) study, and we found largely consistent differences related to male age.

Sixth, Kroodsma appears unable to consider that subjects that initially approached the fast stimulus would subsequently spend less time close to the speaker if the stimulus was a broad frequency bandwidth (low vocal deviation) song. Our conclusion for this result was that the subjects responded quickly to the more threatening stimulus, but were then more strongly repelled by the repeated playback of higher-performance trills. We (de Kort, Eldermire, Cramer, & Vehrencamp, 2009; Hall et al., 2006; Vehrencamp et al., 2007) and others (Collins, 2004; Searcy & Beecher, 2009) have written extensively about the difficulty of interpreting approach responses to alternative playback stimuli, and have recommended several solutions, such as presenting three alternative stimuli instead of two, monitoring other behavioural responses of receivers like singing and calling, and examining the sender's context and subsequent acts when delivering different song variants. The approach–negotiate–retreat sequence is typical of banded wren interactions (Vehrencamp et al., 2014). Rapid trill rate is an indicator of a highly motivated intruder (Vehrencamp et al., 2013), and a territory owner should respond to such a threat by approaching quickly (but not immediately attack). During close-range negotiation, repetitive delivery of the same song type indicates that a bird will no longer negotiate but will stand its ground (Molles, 2006; Vehrencamp et al., 2014). The Illes et al. study suggested that repetition of a broad bandwidth trill was especially threatening and caused the defending owner to back off after a shorter time. This repelling effect of broad-bandwidth songs was verified in a follow-up study by de Kort, Eldermire, Cramer et al. (2009), as discussed below. When birds back off, we know they are still interested in the stimulus because they keep singing, albeit from a distance. Thus Kroodsma's alternative explanation, that the birds were fleeing the slower, longer, low-performance songs, is inconsistent with the combined evidence from our other studies. Nuanced responses such as the one described in Illes et al. (2006) may be typical of two-speaker playback experiments to territorial male subjects (Reichert, 2011).

Finally, Kroodsma argues that we should have corrected all of the statistical tests in the entire results section with a Bonferroni multiple comparisons procedure. We think that a multiple comparison correction was not needed here. It is commonly acknowledged that the Bonferroni correction is far too harsh (i.e. Moran, 2003; Narum, 2006); the false discovery rate correction is superior in reducing type II errors, and we have done this correction in our papers where multiple variables were tested and presented in tables. In Illes et al. (2006), analyses were generated from three independent data sets that addressed completely different questions, thus they should not be combined as Kroodsma proposes. Some of the tests related to the playback experiment were presented to examine and dispel potential confounding effects. The remaining few tests addressed specific hypotheses and were not part of a multivariate fishing expedition to find the most significant variables. We presented power analyses and effect sizes for our tests, and these revealed stronger effects than the *P* values indicated.

As sceptical scientists in search of the truth, we set out to further examine the interesting results in Illes et al. (2006) with another playback experiment that manipulated only the frequency bandwidth of trills (de Kort, Eldermire, Cramer et al., 2009). Contrary to Kroodsma's claim, this study was conducted with observers blind to the bandwidth treatments, and the differences could not be detected by the observers. We separately presented three alternative bandwidth stimuli to subjects, and expressly quantified multiple measures of male response to address the significance of nuanced retreat responses. The results strongly confirmed the

earlier study: subjects avoided closely approaching high-performance stimuli but continued to sing and call from a distance; approached and negotiated with matching songs to the median-performance stimuli; and approached quickly but showed a lower vocal response to the low-performance stimuli (de Kort, Eldermire, Cramer et al., 2009).

Another pair of experiments explored male responses to songs of different trill note consistency (de Kort, Eldermire, Valderrama, Botero, & Vehrencamp, 2009). One experiment used natural songs of the same type and from the same male in his first year versus in his second or third year, when males sing more consistently. The second experiment compared songs of first-year birds to the same song manipulated to have greater trill note consistency. Both experiments found stronger responses to the more consistent song stimuli. We emphasize that our use of natural songs here, as recommended by Kroodsma, produced similar results to the experiment with manipulated songs. As mentioned earlier, we showed in Vehrencamp et al. (2013) that trill note consistency of all measured song types increased in males from their first to their second and third year, and then plateaued or decreased slightly for older birds. Male age is not only associated with territorial defence experience, which could be assessed during territorial encounters, but multiple lines of evidence also suggested that females avoided mating with or divorced first-year males and preferred older and more consistently singing males as extrapair partners (Cramer, Hall, de Kort, Lovette, & Vehrencamp, 2011).

Kroodsma's criticism of the language in the first sentence of the abstract of Vehrencamp et al. (2013) is totally unwarranted. We merely stated the general theoretical proposition being tested in our study, a standard protocol for scientific articles. The statement was fully justified given the large literature on performance constraints affecting sound production and the association of acoustic signal features with aspects of sender characteristics. Kroodsma does not appear to question the results, which showed that trill note consistency and frequency bandwidth increase with male age. We also discovered that trill note rate for a given song type increases during playback experiments in relation to the male's level of aggressive response, a result that has now been found in other species (Funghi, Cardoso, & Mota, 2015; Linhart, Jaska, Petruskova, Petrusek, & Fuchs, 2013). Thus this aspect of performance seems to provide cues to receivers about a rival's immediate aggressive motivation. We did not find any associations with male survival or our measure of body condition. Our results and interpretations were not biased by any desire to support or disprove the hypothesis, and in several instances we offered alternative hypotheses where appropriate.

Commenting further on this paper, Kroodsma (2017, page e14) writes (his italics): 'According to the scatterplot of trill rate and bandwidth for banded wrens (Fig. 11), relatively few songs are difficult to execute as defined in this performance context, because most songs fall far from the upper bound on the graph. Every male 'willingly' learns many 'low-performance', easy-to-execute songs in order to have particular song types in his repertoire, as if performance did not matter, as if there were no selection for difficult-to-execute songs as claimed in this paper'. Repertoire species such as the banded wren use contrasting song types to emphasize switching rates, short-term diversity and matching during territorial interactions (Molles, 2006; Vehrencamp et al., 2007, 2014). But Kroodsma has conveniently ignored another component of banded wren trills: their varied and complex note shapes as mentioned earlier. Trill note consistency is a third axis of performance in this species, and we showed in this paper (Vehrencamp et al., 2013, see supplementary online material) that consistency and vocal deviation trade off (are negatively correlated) within males and song types. Thus, song types far from the trill rate versus bandwidth

upper limit are not necessarily easy to execute, as they may have a complex shape that is difficult to repeat consistently.

Kroodsma concludes that we still await good answers to the question of what information listeners extract about singers from their songs beyond species identification. In fact, there is a growing body of data showing that aspects of vocal performance, including trill rate, vocal deviation, frequency excursion, trill note and song consistency and call rate/call duration trade-offs, do provide useful information to receivers in some species and are associated with reproductive benefits in many birds, mammals, anurans and crickets (e.g. Botero et al., 2009; Byers, Akresh, & King, 2015; Funghi et al., 2015; Linhart et al., 2013; Pasch, George, Campbell, & Phelps, 2011; Petruskova et al., 2014; Podos et al., 2016; Reichert & Gerhardt, 2012; Sprau, Roth, Amrhein, & Naguib, 2013; Wagner, Beckers, Tolle, & Basolo, 2012; Welch, Smith, & Gerhardt, 2014). Our studies have contributed to this body of knowledge, specifically by demonstrating the existence of cues to age and aggressive motivation, along with the strategic use of song type use patterns to indicate approach and retreat during territorial negotiations.

Acknowledgments

We thank Jeff Podos, Jack Bradbury, Dave Wilson and two anonymous referees for helpful feedback on earlier drafts of the manuscript. Our research was funded by the National Institutes of Health (R01-MH60461).

References

- Ballentine, B., Hyman, J., & Nowicki, S. (2004). Vocal performance influences female response to male bird song: An experimental test. *Behavioral Ecology*, *15*, 163–168.
- Botero, C. A., Rossman, R. J., Caro, L. M., Stenzler, L. M., Lovette, I. J., de Kort, S. R., et al. (2009). Syllable type consistency is related to age, social status and reproductive success in the tropical mockingbird. *Animal Behaviour*, *77*, 701–706.
- Bradbury, J. W., & Vehrencamp, S. L. (2011). *Principles of animal communication* (2nd ed.). Sunderland, MA: Sinauer.
- Burt, J. M., & Vehrencamp, S. L. (2005). Dawn chorus as an interactive communication network. In P. K. McGregor (Ed.), *Animal communication networks* (pp. 320–343). Cambridge, U.K.: Cambridge University Press.
- Byers, B. E., Akresh, M. E., & King, D. I. (2015). A proxy of social mate choice in prairie warblers is correlated with consistent, rapid, low-pitched singing. *Behavioral Ecology and Sociobiology*, *69*, 1275–1286.
- Byers, B. E., & Kroodsma, D. E. (2009). Female mate choice and songbird song repertoires. *Animal Behaviour*, *77*, 13–22.
- ten Cate, C. (2004). Birdsong and evolution. In P. Marler, & H. Slabbekoorn (Eds.), *Nature's music: The science of birdsong* (pp. 296–317). San Diego, CA: Elsevier Academic Press.
- Collins, S. A. (2004). Vocal fighting and flirting: The functions of birdsong. In P. Marler, & H. Slabbekoorn (Eds.), *Nature's music: The science of birdsong* (pp. 39–79). San Diego, CA: Elsevier Academic Press.
- Collins, S. A., de Kort, S. R., Perez-Tris, J., & Telleria, J. L. (2011). Divergent sexual selection on birdsong: A reply to Byers. *Animal Behaviour*, *82*(5), e4–e7.
- Cramer, E. R. A., Hall, M. L., de Kort, S. R., Lovette, I. J., & Vehrencamp, S. L. (2011). Infrequent extra-pair paternity in the banded wren, a synchronously breeding tropical passerine. *Condor*, *113*, 637–645.
- Cramer, E. R. A., & Price, J. J. (2007). Red-winged blackbirds *Agelaius phoeniceus* respond differently to song types with different performance levels. *Journal of Avian Biology*, *38*, 122–127.
- Funghi, C., Cardoso, G. C., & Mota, P. G. (2015). Increased syllable rate during aggressive singing in a bird with complex and fast song. *Journal of Avian Biology*, *46*, 283–288.
- Hall, M. L., Illes, A., & Vehrencamp, S. L. (2006). Overlapping signals in banded wrens: Long-term effects of prior experience on males and females. *Behavioral Ecology*, *17*, 260–269.
- Hebets, E. A., & Papaj, D. R. (2005). Complex signal function: Developing a framework of testable hypotheses. *Behavioral Ecology and Sociobiology*, *57*, 197–214.
- Illes, A. E., Hall, M. L., & Vehrencamp, S. L. (2006). Vocal performance influences male receiver response in the banded wren. *Proceedings of the Royal Society B: Biological Sciences*, *273*, 1907–1912.
- de Kort, S. R., Eldermire, E. R. B., Cramer, E. R. A., & Vehrencamp, S. L. (2009). The deterrent effect of bird song in territory defence. *Behavioral Ecology*, *20*, 200–206.

- de Kort, S. R., Eldermire, E. R. B., Valderrama, S., Botero, C. A., & Vehrencamp, S. L. (2009). Trill consistency is an age-related assessment signal in banded wrens. *Proceedings of the Royal Society B: Biological Sciences*, 276, 2315–2321.
- Kroodsma, D. E. (2017). Birdsong performance studies: A contrary view. *Animal Behaviour*, 125, e1–e16.
- Linhart, P., Jaska, P., Petruskova, T., Petrussek, A., & Fuchs, R. (2013). Being angry, singing fast? Signalling of aggressive motivation by syllable rate in a songbird with slow song. *Behavioural Processes*, 100, 139–145.
- Logue, D. M., & Forstmeier, W. (2008). Constrained performance in a communication network: Implications for the function of song-type matching and for the evolution of multiple ornaments. *American Naturalist*, 172, 34–41.
- Molles, L. E. (2006). Singing complexity of the banded wren (*Thryothorus pleurostictus*): Do switching rate and song-type diversity send different messages? *Auk*, 123, 991–1003.
- Molles, L. E., & Vehrencamp, S. L. (1999). Repertoire size, repertoire overlap, and singing modes in the banded wren (*Thryothorus pleurostictus*). *Auk*, 116, 677–689.
- Molles, L. E., & Vehrencamp, S. L. (2001). Neighbour recognition by resident males in the banded wren, *Thryothorus pleurostictus*, a tropical songbird with high song type sharing. *Animal Behaviour*, 61, 119–127.
- Moran, M. D. (2003). Arguments for rejecting the sequential Bonferroni in ecological studies. *Oikos*, 100, 403–405.
- Narum, S. R. (2006). Beyond Bonferroni: Less conservative analysis for conservation genetics. *Conservation Genetics*, 7, 783–787.
- Pasch, B., George, A. S., Campbell, P., & Phelps, S. M. (2011). Androgen-dependent male vocal performance influences female preference in Neotropical singing mice. *Animal Behaviour*, 82, 177–183.
- Petruskova, T., Kinstova, A., Pisevcova, I., Mula Laguna, J., Cortezon, A., Brinke, T., et al. (2014). Variation in trill characteristics in tree pipit songs: Different trills for different use? *Ethology*, 120, 586–597.
- Podos, J. (1997). A performance constraint on the evolution of trilled vocalizations in a songbird family (Passeriformes: Emberizidae). *Evolution*, 51, 537–551.
- Podos, J. (2017). Birdsong performance studies: Reports of their death have been greatly exaggerated. *Animal Behaviour*, 125, e17–e24.
- Podos, J., Moseley, D. L., Goodwin, S. E., McClure, J., Taft, B. N., Strauss, A. V. H., et al. (2016). A fine-scale, broadly applicable index of vocal performance: Frequency excursion. *Animal Behaviour*, 116, 203–212.
- Reichert, M. S. (2011). Effects of multiple-speaker playbacks on aggressive calling behavior in the treefrog *Dendropsophus ebraccatus*. *Behavioral Ecology and Sociobiology*, 65, 1739–1751.
- Reichert, M. S., & Gerhardt, H. C. (2012). Trade-offs and upper limits to signal performance during close-range vocal competition in gray tree frogs *Hyla versicolor*. *American Naturalist*, 180, 425–437.
- Searcy, W. A., & Beecher, M. D. (2009). Song as an aggressive signal in songbirds. *Animal Behaviour*, 78, 1281–1292.
- Sprau, P., Roth, T., Amrhein, V., & Naguib, M. (2013). The predictive value of trill performance in a large repertoire songbird, the nightingale *Luscinia megarhynchos*. *Journal of Avian Biology*, 44, 567–574.
- Trillo, P. A., & Vehrencamp, S. L. (2005). Song types and their structural features are associated with specific contexts in the banded wren. *Animal Behaviour*, 70, 921–935.
- Vehrencamp, S. L. (2001). Is song-type matching a conventional signal of aggressive intentions? *Proceedings of the Royal Society B: Biological Sciences*, 268, 1637–1642.
- Vehrencamp, S. L., Ellis, J. M., Cropp, B. F., & Koltz, J. M. (2014). Negotiation of territorial boundaries in a songbird. *Behavioral Ecology*, 25, 1436–1450.
- Vehrencamp, S. L., Hall, M. L., Bohman, E. R., Depeine, C. D., & Dalziell, A. H. (2007). Song matching, overlapping, and switching in the banded wren: The sender's perspective. *Behavioral Ecology*, 18, 849–859.
- Vehrencamp, S. L., Yantachka, J., Hall, M. L., & de Kort, S. R. (2013). Trill performance components vary with age, season, and motivation in the banded wren. *Behavioral Ecology and Sociobiology*, 67, 409–419.
- Wagner, W. E., Jr., Beckers, O. M., Tolle, A. E., & Basolo, A. L. (2012). Tradeoffs limit the evolution of male traits that are attractive to females. *Proceedings of the Royal Society B: Biological Sciences*, 279, 2899–2906.
- Welch, A. M., Smith, M. J., & Gerhardt, H. C. (2014). A multivariate analysis of genetic variation in the advertisement call of the gray treefrog, *Hyla versicolor*. *Evolution*, 68, 1629–1639.
- Wells, K. D., & Taigen, T. L. (1986). The effect of social interactions on calling energetics in the gray treefrog (*Hyla versicolor*). *Behavioral Ecology and Sociobiology*, 19, 9–18.