

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

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1 A critical review of a popular scientific theory, large or small, is something we applaud because,
2 if well executed, it stimulates discussion and progresses science. However, such a review needs
3 to be balanced, objective, informed and logical, especially if it concludes that a well-supported
4 theory is flawed. Unfortunately, Kroodsma's current criticism (Kroodsma, 2016) of the birdsong
5 performance literature suffers from the same weaknesses as his earlier criticism of song
6 repertoire use in sexual selection (Byers & Kroodsma, 2009), despite the fact that he has been
7 alerted to those mistakes (Collins, de Kort, Perez-Tris, & Telleria, 2011). Those weaknesses
8 include outright errors and misrepresentations, highly selective citation of the literature, and
9 convoluted logic (sensu Podos, 2016). Here we would like to take this opportunity to redress the
10 specific issues he raised with respect to our work on the banded wren (*Thryophilus pleurostictus*)
11 and by doing so, illustrate how his criticism is flawed as a result of the above weaknesses, his
12 restricted definition of "song performance", and a misunderstanding of the song system of the
13 banded wren.

14 Banded wren males possess song repertoires of approximately 25 distinct song types,
15 which are largely shared with other males in their neighborhood. The terminal trills of these song
16 types vary in their trill note rate, frequency bandwidth, and vocal deviation. (Maximal observed
17 trill rates and maximal observed frequency bandwidths are inversely related in many songbirds,
18 defining a negatively-sloped upper limit line on a trill-rate versus frequency bandwidth plot; the
19 perpendicular distance of a given trill from this line is its vocal deviation.) Moreover, the trill
20 notes themselves vary greatly in shape and complexity. Most of our research on this species has
21 focused on the use of these song types in male-male territorial interactions (Burt & Vehrencamp,
22 2005; Hall, Illes, & Vehrencamp, 2006; Molles, 2006; Molles & Vehrencamp, 1997, 2001; Trillo
23 & Vehrencamp, 2005; Vehrencamp, 2001; Vehrencamp, Ellis, Cropp, & Koltz, 2014;

24 Vehrencamp, Hall, Bohman, Depeine, & Dalziell, 2007). We have shown that males negotiate
25 their territorial boundaries primarily by varying short-term song-type diversity and switching rate
26 to indicate their propensity to approach, stand their ground, or retreat from a territorial rival.
27 Males also frequently song type-match each other during aggressive encounters. This primary
28 role of song type choice does not rule out the possibility that subtle details of song structure also
29 play a role and provide additional types of information about the sender, for both male and
30 female receivers. The type-matching behaviour of countersinging males provides ample
31 opportunities for receivers to compare their performances on the same song type, as proposed by
32 Logue & Forstmeier (2008) for repertoire species.

33 Trade-off coding (where two components of a signal are negatively correlated such that
34 extreme values of one tends to inhibit extreme values of the other) sets up the potential for
35 receivers to exert selective pressure on combinations that reveal useful information about the
36 sender. This idea has been around for over two decades (Bradbury & Vehrencamp, 2011; Heberts
37 & Papaj, 2005; Podos, 1997, 2016; Wells & Taigen, 1986). Whenever one observes a negative
38 correlation between two signal components, it is worth testing this trade-off hypothesis (Podos'
39 hypothesis #1) by looking to see whether receivers pay attention to alternative combinations of
40 those components, and if so, whether individual variation in these combinations is associated
41 with sender condition, context, or reproductive success (Podos' hypothesis #2). This is how
42 science proceeds: repeated testing of an hypothesis' predictions in a variety of species using a
43 variety of experimental approaches. The trills of many bird songs are an obvious candidate for
44 testing this hypothesis, because they are highly precise vocal utterances that have evolved under
45 selective pressure from receiver responses. We examined several aspects of performance in the
46 banded wren, not limited to vocal deviation as Kroodsma has restricted himself to here, but also

47 the individual components of vocal deviation, trill rate and frequency bandwidth, along with trill
48 note consistency, in multiple experimental and correlational studies. We have obtained consistent
49 evidence that performance does matter, even in a repertoire species.

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

58 First, Kroodsma states that the playback should have been conducted with blind
59 observers. The experimental design consisted of a two speaker set-up each broadcasting a
60 separate stimulus. The observers were not informed about which speaker broadcasted which
61 stimulus. Nevertheless, as acknowledged for the Cramer & Price (2007) study, an acute observer
62 might discern which was which by listening and we would have had to deafen the observers to
63 exclude this possibility. Second, we are surprised that an experienced ornithologist expresses
64 doubt about the possibility of tracking movements of birds in their tropical deciduous forest
65 habitat. We always had three observers for these trials, and they were all extraordinarily adept
66 women with keen and experienced observational skills. The birds usually sang and called during
67 the trials, further revealing their location. Third, the pseudoreplication criticism is a red herring.
68 Each subject's stimulus exemplars were uniquely prepared from a different base song, and we
69 used a wide variety of song and trill types and source males for the base song, thus preventing

70 pseudoreplication. Fourth, our modification of trill rate involved increasing or decreasing the
71 silent gap between trill notes to a similar degree, so both alternative stimuli had an equivalently
72 altered note duration to silent interval ratio. The minimal difference in trill duration was unlikely
73 to be important, as individual birds naturally vary the number of notes in the trill as well as the
74 silent gap between notes. Moreover, the theoretically more intense signal had the shorter
75 duration, a conservative experimental design strategy. Fifth, we did examine the tendency for
76 trill performance components to vary in a consistent way among song types within males in the
77 Vehrencamp, Yantachka, Hall & De Kort (2013) study, and we found largely consistent
78 differences related to male age. Sixth, Kroodsma appears unable to consider that subjects that
79 initially approached the fast stimulus would subsequently spend less time close to the speaker if
80 the stimulus was a broad bandwidth (low vocal deviation) song. The only logical conclusion for
81 this result was that the subjects were more strongly repelled by the repeated playback of higher
82 performance trills. This repelling effect was subsequently verified by de Kort, Eldermire,
83 Cramer, & Vehrencamp (2009), as discussed below. The approach – negotiate – retreat sequence
84 is typical of banded wren interactions (Vehrencamp et al., 2014). We know that the birds are still
85 interested in the stimulus when they back off because they keep singing, albeit from a distance.
86 Nuanced responses may be typical of two-speaker playback to rival male subjects (Reichert,
87 2011). Seventh, Kroodsma asks how we know over what time frame songs should have an effect.
88 We had conducted numerous playback experiments on this species, with stimulus durations
89 ranging from 1-2 minutes and post playback periods ranging from 3-5 minutes, by which time all
90 subjects had usually left the area. We had also observed many natural interactions between males
91 lasting from about 2-10 min. In Vehrencamp et al. (2014) we quantified such interactions and
92 found that interactions from start to finish ranged from 26 to 828 sec with a median of 161 sec.

93 So the Illes et al. experimental protocol, with a playback period averaging 86 sec and a post
94 playback period equal to 180 sec, was well within the typical time frame of approach and
95 withdrawal for male-male encounters in the banded wren. Finally, Kroodsma argues that we
96 should have corrected all of the statistical tests in the entire results section with a Bonferroni
97 multiple comparisons procedure. It is commonly acknowledged that the Bonferroni correction is
98 far too harsh (i.e., Moran, 2003; Narum, 2006); the False Discovery Rate correction is superior in
99 reducing Type II errors, and we have done this correction in our papers where multiple variables
100 were tested and presented in tables. In the Illes et al. paper, our analyses were generated from
101 three independent datasets and addressed completely different questions, thus they should not be
102 combined as Kroodsma proposes. Some of the tests related to the playback experiment were
103 presented to examine and dispel potential confounding effects. The remaining few tests
104 addressed specific hypotheses and were not part of a multivariate fishing expedition to find the
105 most significant variables. We think that a multiple comparison correction was not needed here.
106 In addition, we presented power analyses and effect sizes for our tests, and these revealed
107 stronger effects than the p-values indicate. Our study therefore cannot be criticized on the basis
108 of unreasonable claims of unnatural stimuli, pseudoreplication, incompetent observers, and
109 faulty statistics.

110 As skeptical scientists in search of the truth, we set out to further examine the interesting
111 results in Illes et al. (2006) with another playback experiment that manipulated only the
112 frequency bandwidth of trills (de Kort, Eldermire, Cramer, & Vehrencamp, 2009). Contrary to
113 Kroodsma's claim, this study *was* conducted with observers blind to the bandwidth treatments,
114 and the differences could not be detected by the observers. We separately presented three
115 alternative bandwidth stimuli to subjects, and expressly quantified multiple measures of male

116 response to address the significance of nuanced retreat responses. The results strongly confirmed
117 the earlier study: subjects avoided high-performance stimuli but continued to sing and call from a
118 distance; approached and negotiated with matching songs to the median-performance stimuli;
119 and approached quickly but showed a lower vocal response to the low-performance stimuli.

120 Another pair of experiments explored male responses to songs of different trill note
121 consistency (de Kort, Eldermire, Valderrama, Botero, & Vehrencamp, 2009). One experiment
122 used natural songs of the same type and from the same male in his first year versus in his second
123 or third year, and the second experiment compared songs of first year birds to the same song
124 manipulated to have greater note consistency. Both experiments found stronger responses to the
125 more consistent song stimuli. As mentioned earlier, we showed in Vehrencamp et al. (2013) that
126 trill note consistency of all measured song types increased in males from their first to their
127 second and third year, and then plateaued or decreased slightly for older birds. Male age is not
128 only associated with territorial defense experience, which could be assessed during territorial
129 encounters, but multiple lines of evidence also suggested that females avoided mating with or
130 divorced first year males and preferred older and more consistently singing males as extra-pair
131 partners (Cramer, Hall, de Kort, Lovette, & Vehrencamp, 2011).

132 Kroodsma's criticism of the language in the first sentence of the abstract of (Vehrencamp
133 et al., 2013) is totally unwarranted. Abstract wording is necessarily brief. We merely stated the
134 general theoretical proposition being tested in our study, a standard protocol for scientific
135 articles. Kroodsma doesn't appear to question the results, which showed that trill note
136 consistency and frequency bandwidth increase with male age. We also discovered that trill note
137 rate for a given song type increases during playback experiments in relation to the male's level of
138 aggressive response, a result that has now been found in other species (Funghi, Cardoso, &

139 Mota, 2015; Linhart, Jaska, Petruskova, Petrusek, & Fuchs, 2013). Thus this aspect of
140 performance seems to provide cues to receivers about a rival's immediate aggressive motivation.
141 We did not find any associations with male survival or our measure of body condition. Our
142 results and interpretations were not biased by any desire to support or disprove the hypothesis,
143 and in several instances we offered alternative hypotheses where appropriate.

144 Commenting further on this paper, Kroodsma writes (his italics): “According to the
145 scatterplot of trill rate and bandwidth for banded wrens (Fig. 11), relatively few songs are
146 difficult to execute as defined in this performance context, because most songs fall far from the
147 upper bound on the graph. Every male ‘willingly’ learns many ‘low-performance’, easy-to-
148 execute songs in order to have particular song types in his repertoire, *as if performance did not*
149 *matter*, as if there were no selection for difficult-to-execute songs as claimed in this paper”.
150 Repertoire species such as the banded wren use contrasting song types to emphasize switching
151 rates, short-term diversity, and matching during territorial interactions. But Kroodsma has
152 conveniently ignored another component of banded wren trills: their varied and complex note
153 shapes as mentioned earlier. Trill note consistency is a third axis of performance in this species,
154 and we showed in this paper (Vehrencamp et al., 2013, see supplementary online material) that
155 consistency and vocal deviation trade-off (are negatively correlated) within male and song type.
156 Thus song types far from the trill rate vs. bandwidth upper limit are not necessarily easy to
157 execute, as they may have a complex shape that is difficult to repeat consistently.

158 Kroodsma surprisingly concludes that “we await good answers to the question... of what
159 information listeners extract about singers from their songs (beyond species identification)”. In
160 fact, there is a growing body of data showing that aspects of vocal performance, including trill
161 rate, vocal deviation, trill note and song consistency, and call rate/call duration trade-offs, do

162 provide useful information to receivers in some species and are associated with reproductive
163 benefits in many birds, mammals, anurans, and crickets (e.g., Botero, et al., 2009; Byers, Akresh,
164 & King, 2015; Funghi et al., 2015; Linhart et al., 2013; Pasch, George, Campbell, & Phelps,
165 2011; Petruskova et al., 2014; Reichert & Gerhardt, 2012; Sprau, Roth, Amrhein, & Naguib,
166 2013; Wagner, Beckers, Tolle, & Basolo, 2012; Welch, Smith, & Gerhardt, 2014). Our studies
167 have contributed to this body of knowledge, specifically by demonstrating the existence of cues
168 to age and aggressive motivation, along with the strategic use of song type use patterns to
169 indicate approach and retreat during territorial negotiations.

170

171 **Literature cited**

172 Ballentine, B., Hyman, J., & Nowicki, S. (2004). Vocal performance influences female response
173 to male bird song: an experimental test. *Behavioral Ecology*, *15*, 163-168.

174 Botero, C. A., Rossman, R. J., Caro, L. M., Stenzler, L. M., Lovette, I. J., de Kort, S. R &
175 Vehrencamp, S. L. (2009). Syllable type consistency is related to age, social status and
176 reproductive success in the tropical mockingbird. *Animal Behaviour*, *77*, 701–706.

177 Bradbury, J. W., & Vehrencamp, S. L. (2011). *Principles of Animal Communication* (2nd ed.).
178 Sunderland, MA: Sinauer Associates.

179 Burt, J. M., & Vehrencamp, S. L. (2005). Dawn chorus as an interactive communication
180 network. In P. K. McGregor (Ed.), *Animal Communication Networks* (pp. 320-343).

181 Cambridge: Cambridge University Press.

182 Byers, B. E., Akresh, M. E., & King, D. I. (2015). A proxy of social mate choice in prairie
183 warblers is correlated with consistent, rapid, low-pitched singing. *Behavioral Ecology*
184 *and Sociobiology*, *69*, 1275-1286.

- 185 Byers, B.E. and Kroodsma, D.E. (2009). Female mate choice and songbird song repertoires.
186 *Animal Behaviour*, 77, 13–22
- 187 Collins, S. A., de Kort, S. R., Perez-Tris, J. & Telleria, J. L. (2011) Divergent sexual selection on
188 birdsong, a reply to Byers. *Animal Behaviour* 82, e4—e7.
- 189 Cramer, E. R. A., Hall, M. L., de Kort, S. R., Lovette, I. J., & Vehrencamp, S. L. (2011).
190 Infrequent extra-pair paternity in the banded wren, a synchronously breeding tropical
191 passerine. *Condor*, 113, 637-645.
- 192 Cramer, E. R. A., & Price, J. J. (2007). Red-winged blackbirds *Agelaius phoeniceus* respond
193 differently to song types with different performance levels. *Journal of Avian Biology*, 38,
194 122-127.
- 195 de Kort, S. R., Eldermire, E. R. B., Cramer, E. R. A., & Vehrencamp, S. L. (2009). The deterrent
196 effect of bird song in territory defence. *Behavioral Ecology*, 20, 200-206.
- 197 de Kort, S. R., Eldermire, E. R. B., Valderrama, S., Botero, C. A., & Vehrencamp, S. L. (2009).
198 Trill consistency is an age-related assessment signal in banded wrens. *Proceedings of the*
199 *Royal Society B-Biological Sciences*, 276, 2315-2321.
- 200 Funghi, C., Cardoso, G. C., & Mota, P. G. (2015). Increased syllable rate during aggressive
201 singing in a bird with complex and fast song. *Journal of Avian Biology*, 46, 283-288.
- 202 Hall, M. L., Illes, A., & Vehrencamp, S. L. (2006). Overlapping signals in banded wrens: long-
203 term effects of prior experience on males and females. *Behavioral Ecology*, 17, 260-269.
- 204 Hebets, E. A., & Papaj, D. R. (2005). Complex signal function: developing a framework of
205 testable hypotheses. *Behavioral Ecology and Sociobiology*, 57, 197-214.
- 206 Illes, A. E., Hall, M. L., & Vehrencamp, S. L. (2006). Vocal performance influences male
207 receiver response in the banded wren. *Proceedings of the Royal Society B-Biological*

- 208 *Sciences*, 273, 1907-1912.
- 209 Kroodsma, D. E. (2016). Birdsong performance studies: a contrary view. *Animal Behaviour*.
- 210 Linhart, P., Jaska, P., Petruskova, T., Petrusek, A., & Fuchs, R. (2013). Being angry, singing
211 fast? Signalling of aggressive motivation by syllable rate in a songbird with slow song.
212 *Behavioural Processes*, 100, 139-145.
- 213 Logue, D. M., & Forstmeier, W. (2008). Constrained performance in a communication network:
214 Implications for the function of song-type matching and for the evolution of multiple
215 ornaments. *American Naturalist*, 172, 34-41.
- 216 Molles, L. E. (2006). Singing complexity of the banded wren (*Thryothorus pleurostictus*): Do
217 switching rate and song-type diversity send different messages? *Auk*, 123, 991-1003.
- 218 Molles L. E. & Vehrencamp, S. L. (1999). Repertoire size, repertoire overlap, and singing modes
219 in the Banded Wren (*Thryothorus pleurostictus*). *Auk*, 116, 677-689.
- 220 Molles, L. E., & Vehrencamp, S. L. (2001). Neighbour recognition by resident males in the
221 banded wren, *Thryothorus pleurostictus*, a tropical songbird with high song type sharing.
222 *Animal Behaviour*, 61, 119-127.
- 223 Moran, M.D. (2003) Arguments for rejecting the sequential Bonferonni in ecological studies.
224 *Oikos*, 100, 403-405.
- 225 Narum, S.R. (2006) Beyond Bonferonni: Less conservative analysis for conservation genetics.
226 *Conservation Genetics*, 7, 783-787.
- 227 Pasch, B., George, A. S., Campbell, P., & Phelps, S. M. (2011). Androgen-dependent male vocal
228 performance influences female preference in Neotropical singing mice. *Animal*
229 *Behaviour*, 82, 177-183.
- 230 Petruskova, T., Kinstova, A., Pisvejcova, I., Mula Laguna, J., Cortezon, A., Brinke, T., &

- 231 Petrusek, A. (2014). Variation in trill characteristics in tree pipit songs: Different trills for
232 different use? *Ethology*, *120*, 586-597.
- 233 Podos, J. (1997). A performance constraint on the evolution of trilled vocalizations in a songbird
234 family (Passeriformes: Emberizidae). *Evolution*, *51*, 537-551.
- 235 Podos, J. (2016). Birdsong performance studies: Reports of their death have been greatly
236 exaggerated. *Animal Behaviour*.
- 237 Reichert, M. S. (2011). Effects of multiple-speaker playbacks on aggressive calling behavior in
238 the treefrog *Dendropsophus ebraccatus*. *Behavioral Ecology and Sociobiology*, *65*, 1739-
239 1751.
- 240 Reichert, M. S., & Gerhardt, H. C. (2012). Trade-offs and upper limits to signal performance
241 during close-range vocal competition in gray tree frogs *Hyla versicolor*. *American*
242 *Naturalist*, *180*, 425-437.
- 243 Sprau, P., Roth, T., Amrhein, V., & Naguib, M. (2013). The predictive value of trill performance
244 in a large repertoire songbird, the nightingale *Luscinia megarhynchos*. *Journal of Avian*
245 *Biology*, *44*, 567-574.
- 246 Trillo, P. A., & Vehrencamp, S. L. (2005). Song types and their structural features are associated
247 with specific contexts in the banded wren. *Animal Behaviour*, *70*, 921-935.
- 248 Vehrencamp, S. L. (2001). Is song-type matching a conventional signal of aggressive intentions?
249 *Proceedings of the Royal Society of London Series B-Biological Sciences*, *268*, 1637-
250 1642.
- 251 Vehrencamp, S. L., Ellis, J. M., Cropp, B. F., & Koltz, J. M. (2014). Negotiation of territorial
252 boundaries in a songbird. *Behavioral Ecology*, *25*, 1436-1450.
- 253 Vehrencamp, S. L., Hall, M. L., Bohman, E. R., Depeine, C. D., & Dalziell, A. H. (2007). Song

- 254 matching, overlapping, and switching in the banded wren: the sender's perspective.
255 *Behavioral Ecology*, 18, 849-859.
- 256 Vehrencamp, S. L., Yantachka, J., Hall, M. L., & de Kort, S. R. (2013). Trill performance
257 components vary with age, season, and motivation in the banded wren. *Behavioral*
258 *Ecology and Sociobiology*, 67, 409-419.
- 259 Wagner, W. E., Jr., Beckers, O. M., Tolle, A. E., & Basolo, A. L. (2012). Tradeoffs limit the
260 evolution of male traits that are attractive to females. *Proceedings of the Royal Society B-*
261 *Biological Sciences*, 279, 2899-2906.
- 262 Welch, A. M., Smith, M. J., & Gerhardt, H. C. (2014). A multivariate analysis of genetic
263 variation in the advertisement call of the gray treefrog, *Hyla versicolor*. *Evolution*, 68,
264 1629-1639.
- 265 Wells, K. D., & Taigen, T. L. (1986). The effect of social interactions on calling energetics in the
266 gray treefrog (*Hyla versicolor*). *Behavioral Ecology and Sociobiology*, 19, 9-18.
- 267