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Reply: Yes, Team of Rivals

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The main conclusions of our original report [1] were that male chipping sparrows form defensive coalitions in response to simulated territorial intrusion, and that coalition formation is predicted by relative structural properties of birds' songs. Akçay & Beecher (hereafter "A&B" [2]) critique our report on a number of fronts including study design, methods, analysis, and interpretation. We here address these critiques by clarifying points from the original report and by presenting new information and analyses.

A&B first question our focus on trill rate rather than vocal deviation as a predictor of coalitions. Vocal deviation is a composite index of performance based on trill rate and frequency bandwidth, and has indeed been adopted widely in tests of song function [3]. Yet the raw parameters themselves, trill rate and frequency bandwidth, are also proper indices of vocal performance because, in general, faster or wider bandwidth trills are harder to produce [3]. Our demonstration in chipping sparrow songs of a trade-off between maximal trill rate and frequency bandwidth [1] suggests that any of these parameters might signal vocal performance. Yet determining which are salient during vocal communication requires controlled perceptual tests that isolate the effect of each parameter, and variation therein, on birds' responses [1]. We now know that chipping sparrow males attend to trill rate, as birds' responses to playback in our original study [1, non-coalition trials] covaried with trill rates of both stimuli and subjects. By contrast it is unknown whether chipping sparrows perceive or attend to variations in frequency bandwidth or thus, by extension, vocal deviation.

A&B's other method and design critiques are readily countered. First, A&B question our reliance on song structure to identify individual chipping sparrows. Each male chipping

sparrow produces only a single song type, and these are individually distinct, thus allowing us to identify birds from their songs with confidence. This same “claim” has also been made and applied by others [4]; in Fig. S1 we offer a supplemental illustration and analysis that further confirm the individually-distinct nature of chipping sparrow songs.

Second, A&B worry about numerous aspects of chipping sparrow behavior — song sharing, dawn song at territory boundaries, territory instability, polyterritoriality, and “land-grabs” — that might have confounded our description of coalition behavior.

Neighboring birds do often share song types, but even similar song types are readily distinguished by structural features including trill rate (Fig S1). While birds sing jointly at territory boundaries at dawn, our playback trials were conducted (and coalitions observed) post-dawn, when more typical territorial behavior is observed. The instability of territories mentioned by A&B refers to the propensity of chipping sparrows to occasionally abandon territories over the course of the season. This has no bearing on coalition formation for our subjects, who remained on territory during the time frame of their trials. Polyterritorialty refers not to joint defense of the same territory, but rather to the rare behavior of single individuals defending multiple territories [5]. The relevance to coalitions here is not apparent to us. Allies did not seem to engage in "land-grabs"; although not indicated in our original report, we observed that soon after playback trials ceased, all allies flew back to their neighboring territories where they could be found on subsequent days.

A&B next offer two critiques about potential non-independence of data. The first critique, that all coalitions were not independent samples, is broadly overstated. The 9 coalitions occurred in 8 territorial males presented with 8 distinct song types -- all independent

samples. Moreover, coalitions for the one repeat beneficiary were initiated by different (and thus partly independent) trill rate variants. The second critique, about repeat use of stimulus “tapes”, is not only irrelevant to the topic of coalitions but is also incorrect, as the units in our analysis of trill rate effects were stimulus sets, not subjects.

The final set of critiques challenge our statistical analysis of two data patterns: (i) in every coalition observed (9 of 9), ally trill rates exceeded resident trill rates; and (ii) in 8 of 9 cases, trill rates of simulated intruders exceeded trill rates of residents. We had analyzed both patterns using binomial tests, and A&B offer that our assumptions of 0.5 chance levels (made *a priori* as we had no expectations of bias) could be recalibrated. For the first test (allies x residents), A&B's proposed recalibration uses population-wide data, following their blanket assertion that "neighbors were not...recorded". Although not stated in our original report, we did in fact record complete neighborhoods for 3 of our later subjects, and for these birds the recalibrated chance level (% neighbors with trill rates exceeding those of corresponding beneficiaries) is 0.49. If we merge these precisely observed values with the population-based chance level estimate of 0.74 for the remaining 6 birds, as recommended by A&B [2], a significant effect is retained (recalibrated chance level = (0.49 * 0.333) + (0.74 * 0.666) = 0.656, weighted Binomial Test p = 0.033). For the second test (simulated intruders x residents), we concur with A&B's proposed recalibration and corresponding p-value adjustment.

To conclude, we stand by our original methods, design, and analyses, with the one caveat that relationships among intruder, resident, and ally trill rates were not as statistically robust as estimated by our original, uncalibrated binomial test values. Nevertheless, available data still support our original interpretation: chipping sparrows

form teams of rivals in response to simulated territorial intrusion, and those teams of rivals are predicted by song structure. Open questions about coalition formation in chipping sparrows will be best resolved not through further parsing of available data, but in follow-up studies that use targeted experimental designs and larger sample sizes.

References

1. Goodwin, S.E., Podos, J. 2014 Team of rivals: alliance formation in territorial songbirds is predicted by vocal signal structure. *Biol. Lett.* **10**, 20131083. (doi:10.1098/rsbl.2013.1083).

2. Akçay, C. & Beecher, M.D. 2015 Team of Rivals? *Biol. Lett.* in press.

3. Podos, J., Lahti, D.C. & Moseley, D.L. 2009 Vocal performance and sensorimotor learning in songbirds. *Adv. Study Behav*. **40**, 159-195. (doi:10.1016/S0065-3454(09)40005-6).

4. Liu, W.C., & Kroodsma, D.E. 2007. Dawn and daytime singing behavior of chipping sparrows (*Spizella passerina*). Auk **124**: 44-52.

5. Liu W.C. 2004 The effect of neighbours and females on dawn and daytime singing behaviours by 83 male chipping sparrows. Animal Behaviour 68, 39-44.