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Cite this article: Akçay Ç, Beecher MD. 2015

Team of rivals in chipping sparrows? A comment on Goodwin & Podos. *Biol. Lett.* **11**:

20141043.

<http://dx.doi.org/10.1098/rsbl.2014.1043>

Received: 12 December 2014

Accepted: 1 March 2015

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The accompanying reply can be viewed at
<http://dx.doi.org/doi:10.1098/rsbl.2015.0319>.

Electronic supplementary material is available
at <http://dx.doi.org/10.1098/rsbl.2014.1043> or
via <http://rsbl.royalsocietypublishing.org>.

Animal behaviour

Team of rivals in chipping sparrows? A
comment on Goodwin & Podos

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Goodwin & Podos [1] (G&P hereafter) report an interesting study that claims to show male chipping sparrows form tactical defensive coalitions with their neighbours to fend off intruders. The most novel claim in the paper is that would-be allies make decisions to help or not depending on the relative trill rate of their neighbour's, the intruder's and their own song. Here, we offer a critique of the design, methods and analyses of the study and point out problems in each that we believe seriously undermine their conclusions about the supposed coalitions.

G&P first show that trill performance in chipping sparrows (as in many other songbirds [2]) is constrained by a trill rate—frequency bandwidth tradeoff (upper-bound regression shown in fig. 1 of G&P). Their subsequent analyses however, focus exclusively on trill rates. That trill rate is not a proper measure of trill performance constraint is nicely illustrated by the two sonograms in fig. 1 of G&P. Looking only at trill rate, the song in fig. 1*b* is 'superior' to the song in fig. 1*a* given the faster trill rate of the former. If, however, one takes into account both trill rate and frequency bandwidth and calculates each song's distance from the regression line (i.e. vocal deviation), the song in fig. 1*a* is actually superior (closer to the line) to the song in fig. 1*b*. Analyses on vocal deviation as predictor of 'coalitions' apparently did not yield significant effects (Sarah Goodwin, personal communication, 2014).

Secondly, none of the birds in the study was banded for individual identification. Instead the authors claim to identify birds from their songs. However, not all neighbours were recorded prior to or even during the experiment (Sarah Goodwin, personal communication, 2014). Moreover, prior work [2–4] on chipping sparrows has shown that (i) birds learn their songs from their neighbours, leading to song sharing, (ii) birds sing jointly at their shared boundary at dawn (when recordings were made) and (iii) territories in chipping sparrows are highly unstable, with frequent shifts and occasional poly-territoriality. Given these findings, identifying non-banded neighbours based solely on recordings would seem difficult at best. G&P do not give details on the basis of their identification in the paper or elsewhere, yet the argument put forward for the function of coalition formation depends critically on the supposed allies being neighbours.

A third problem is that the experiment is a within-subject design (asking whether males respond more aggressively to higher trill rates), but the analyses pertaining to the 'coalitions' are carried out as if all trials were independent. Two separate pseudo-replication issues are present. First, in their binomial and multinomial tests the authors count as independent data points two trials with the same subject and presumably the same 'ally'. Secondly, the authors use 15 stimulus tapes twice each, without accounting for this fact.

The final set of problems is with the sampling and statistics (electronic supplementary material, datasheet). First, the binomial test comparing trill rates of subjects and stimuli in 'coalition' trials is carried out assuming a chance level of 0.5, an even chance of subjects having lower or higher trill rates than the stimulus tape. Ignoring the pseudo-replication, the correct chance level in this binomial test can be shown to be two-thirds: in 32 out of 48 trials stimuli had

higher trill rates than subjects. With this chance level, the binomial test is not significant ($p = 0.23$ compared with the reported $p = 0.04$).

The authors also have a biased sample of subjects that have lower trill rates on average than the population at large. The average trill rate of the subjects is (mean \pm s.d.): 10.79 ± 3.19 Hz, whereas the average trill rate of 70 males recorded from the same population is 13.67 ± 4.83 Hz, a highly significant difference: unpaired $t_{92} = 2.72$, $p = 0.007$. This sampling bias is a critical flaw: much of the observed trill rate difference (5.23 Hz) between 'allies' and the subjects can be accounted for simply by this biased sampling which yields a significant difference between the subjects and population mean (2.88 Hz).

Despite the sampling bias, G&P assume a chance level of 0.5 in the binomial test comparing the trill rates of the subjects and the supposed allies. In principle, the correct chance level should be calculated as the ratio of potential allies (i.e. neighbours) with higher trill rates to those with lower trill rates relative to the recipients of defensive help. Because the neighbours were not banded and recorded, the actual chance level is unknown. The closest we can get is to compare the trill rates of subjects to the general population: the average trill rates of the eight subjects that 'received help' are lower than 74.3% of the trill rates in the population (i.e. almost three-quarters of any randomly selected males from the population would have a higher trill rate than these subjects). Taking 0.74 for chance level in the binomial test, and again ignoring pseudo-replication, one arrives at a

p -value of 0.13 (compared with reported value of 0.004). The true chance levels may be lower or higher than 0.74 but given the sampling bias and the lack of information on the actual chance levels, the results of this binomial test should not be taken as valid. The same problems with the chance levels also apply to the multinomial test.

To sum up, we believe the conclusion that chipping sparrows form coalitions with neighbours depending on relative song performance lacks empirical footing as of now although we definitely consider this question worth pursuing. In doing so, we urge researchers to consider the methodological concerns we have raised here, particularly the need to reliably identify (e.g. through banding) would-be allies and subjects and to measure the relevant traits that form the basis of the supposed strategies in all individuals. We also note that researchers need to give details of the actual behaviours involved in the presumed cooperation to permit distinguishing between competitive and cooperative strategies. Finally, we believe that studies of cooperative defence need also to show that the supposed defence does not involve an opportunistic attempt at a land-grab by showing that after the alliance event, the former boundaries between ally and resident remain intact.

Data accessibility. The data that were used in the analyses are available as electronic supplementary material to this paper.

Authors' contributions. Ç.A. and M.D.B. analysed the data and wrote the commentary.

Competing interest. The authors declare that they have no competing interests.

Funding. We received no funding for this study.

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