Peer Community In Evolutionary Biology

Inequality among the lexicons

Michael D Greenfield *based on peer reviews by 2 anonymous reviewers*

E. Harscouet-Commecy, N. Adenot, A. Thetiot, N. Bresciani, D. Oschadleus, R. Covas, F. Rybak, C. Doutrelant (2025) Colony size as the main driver of the evolution of song diversity and composition in weaverbirds. OSF, ver. 2, peer-reviewed and recommended by Peer Community in Evolutionary Biology. https://doi.org/10.31219/osf.io/z5bgy_v2

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It has now been over a century since the American linguist Edward Sapir observed that there are no 'primitive' languages, stating 'When it comes to linguistic form, Plato walks with the Macedonian swineherd, Confucius with the head-hunting savage of Assam' (Sapir 1921, p. 104). Nothing has been found among human groups since that would refute Sapir's insight. However, in interspecific comparisons among non-human animals, such equality is most definitely not the case, and scientists have asked what might account for some species being blessed with rich and complex communication while others seem to make do with a relatively undeveloped repertoire of signals. Many of the investigations have focused on acoustic communications, as these are more easily identified as signals, measured, and demarcated than substrate vibrations, odors and optical displays. But no consensus has emerged explaining the 'inequality among the lexicons'.

In the article 'Colony size as the main driver of the evolution of song diversity and composition in weaverbirds', Erwan Harscouet-Commecy and coauthors aimed to find definitive answers to the issue of interspecific differences in communication complexity. The article considers two aspects of communication complexity, basic diversity – essentially the number of different sounds made by a species – and 'composition', a higher level measure centered on acoustically recognizable 'types' of sounds. Sexual selection, social complexity, habitat and phylogeny are then examined as potential influences on communication. Weaverbirds, the monophyletic family Ploceidae, including 122 species in 15 genera in sub-Saharan Africa and tropical Asia, was an eminently appropriate choice for the study. The birds have diverse nesting and mating behavior and songs, and many have been investigated intensively. For their analyses, the authors were quite rigorous in evaluating the species' songs and in assessing the potential influences on song complexity. Unexpectedly, they did not find that heightened sexual selection led to complex songs, but they note that the proxy used for sexual selection – a polygynous as opposed to a monogamous mating system – may be inaccurate. Additionally, the strong pair bonding in monogamy may have actually selected for song complexity.

What the authors did find was a very clear influence of social complexity, measured by colony size, and a secondary influence of phylogeny. Questions do remain, such as the specific pathway – common genetic or

common cultural heritage – along which phylogeny influences song complexity. Another question one might raise is whether low song complexity in some species reflects reliance on other modalities of communication, e.g. plumage or movement displays. But at present, the article appears as a gold standard for investigating the complexity of communication among animal species.

References:

Sapir, E. 1921. Language: An Introduction to the Study of Speech. New York: Harcourt, Brace. ISBN 978-1-108-06378-4

E. Harscouet-Commecy, N. Adenot, A. Thetiot, N. Bresciani, D. Oschadleus, R. Covas, F. Rybak, C. Doutrelant (2024) Colony size as the main driver of the evolution of song diversity and composition in weaverbirds. OSF, ver.2 peer-reviewed and recommended by PCI Evol Biol https://doi.org/10.31219/osf.io/z5bgy_v2

Reviews

Evaluation round #1

DOI or URL of the preprint: https://doi.org/10.31219/osf.io/z5bgy
Version of the preprint: 2

Authors' reply, 18 March 2025

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Decision by Michael D Greenfield, posted 26 August 2024, validated 26 August 2024

Dear Dr. Harscouet-Commecy et al.,

I have now received two thorough reviews of your manuscript, and based on these evaluations and my own reading I am requesting that you revise the article accordingly. It is clear that you are addressing an important issue in evolutionary biology and behavior, that the manuscript is generally well-written, and that the information and analyses are strong. But the referees have each identified several general issues to address, in addition to minor points needing attention / correction, and I urge you to consider these general issues thoroughly in your revision. In your revision and accompanying response letter please identify your changes clearly, or jusfify why you are not making the recommended change.

I look forward to receiving your new version.

Michael Greenfield

Reviewed by anonymous reviewer 1, 22 August 2024

Title: Colony size as the main driver of the evolution of song diversity and composition in weaverbirds

Summary:

The authors have completed a study that first defines two measures of vocalizations in a group of birds, and employ phylogenetic comparative analyses to determine which potential species variables might affect vocalizations across species. The two variables the authors generated to describe vocal diversity are song diversity and song composition. The authors then determine if reproductive system, social system/size, and

phylogenetic history influence the differences across species. The authors find that social system and size affect both of the variables, however, the mating system does not significantly affect either of the two measures of vocalizations. The authors interpret these results as social system being of considerable influence on the evolution of vocalizations in the group of species they have studied.

General Comments:

The authors have generated an especially interesting dataset to answer an important question in the evolution of communication and signal diversity. To test how communication changes across species, the authors employ appropriate comparative analyses and are thorough in their analysis. Most of the changes I have suggested are (hopefully) simple but I have two larger concerns I was hoping the authors might address. First, the authors break species down in to categories of colony size rather than use colony size as a numerical variable in the analysis. I was hoping the authors could provide an argument for the utility of examining colony size as a category rather than a numerical variable. While some weaver species have exceedingly large colonies, a log transformation of colony size might prevent overly strong influence of certain species in a comparative analysis.

Additionally, I would suggest the authors increase the depth of explanation of the song composition explanation in the methods. The authors have created a set of vocalization groups/types that may be present in multiple species, and having increased information about how these were defined, what the definitions are, and perhaps a visual example of 2-3 would be considerably helpful.

Specific Comments

Abstract: None

Introduction :

Lines 62-63: “unique elements that constitute a signal enables in addition to study signal composition.” The wording at the end of the sentence seems to have omitted a phrase or a clause. Please reword.

Lines 66-68: The authors argue that “similarities in signals across different evolutionary contexts have been insufficiently studied”. However, one example of similarity in signals is mimicry, and mimicry is a foundational field of study in ecology and evolution. I would suggest the authors revise the sentence.

Lines 87-89: The authors are describing signal composition, and to increase the clarity of the sentence they might add an example of describing signal composition. For instance, peak frequency or frequency modulation or a parameter that is especially salient for the current study.

Materials & Methods:

Lines 228-230: The syllable categories is an interesting measure but one question would be the sound correlation among syllables produced by different species.

Lines 238-239: For species where multiple individuals are measured, is song diversity averaged across individuals (after taking an average per individual if there are multiple songs recorded per individual)?

Lines 261-262: The authors state, “Accumulation curves could not be generated for song diversity, as syllables are redefined for each song”. While true, the authors might perform a simple PGLS to determine if the number of individuals recorded per species predicts overall species song diversity. Such an analysis would help confirm

that song diversity is not tracking sampling intensity in each species. Alternatively, the authors might down sample to the species with the smallest sampling intensity and determine if there is a relationship between their predictor variables and the dependent variable of song diversity.

Lines 265-267: Employing mating system as a proxy for sexual selection is a good idea, but one concern is the variation in polygamy. Is there considerable variation in the number of mates a focal individual might have across species. For instance, do some species maintain 2-3 mates per individual, whereas in others there might be 7-10 mates per individual?

Results:
Lines 354-356: The authors find that colony size affects increased song diversity. The colony size variable in this analysis has been compressed from the four levels in to two categories (as I understand it). If the authors were to instead repeat the analysis where you have 'colonial' vs 'noncolonial' categories do the results remain qualitatively identical? In other words, if the 'small' colony size was added to the rest of the colonial species.

Line 363: Remove the phrase "results showed that"

Discussion:
Line 423: The authors state that song in weaverbirds has hardly been studied, however, several studies have documented the acoustic properties and potential function of vocalizations in these species. Thus I would suggest the authors reword the sentence to say something along the lines of "The structure and diversity of functions has not been investigated across species".

Lines 484-488: The authors presented a plausible explanation of their results regarding sexual selection and song parameters in this section (and the paragraph overall). The authors mention that sexual selection might act on other aspects of song, such as the ability to repeat a note. Sexual selection might also push species towards producing notes/vocalizations at the performance limit given motor constraints. One study to consider citing here is https://royalsocietypublishing.org/doi/10.1098/rsbl.2008.0626.

Line 525: Slightly modify "play a role in the variance" to "play a role in explaining the variance"

Citations:
In line 113 the authors refer to a "Santos et al, 2023" but the methods list has a "dos Santos et al, 2023" study. Are these the same? Please check.

Figures & Tables:
The figures and tables in the main manuscript are well constructed and informative.

Supplementary material:
Was not able to access the supplementary material.

Reviewed by anonymous reviewer 2, 22 August 2024

Title and abstractDoes the title clearly reflect the content of the article? [XX] Yes, [ ] No (please explain), [ ] I don't know

Does the abstract present the main findings of the study? [XX] Yes, [ ] No (please explain), [ ] I don't know

IntroductionAre the research questions/hypotheses/predictions clearly presented? [XX] Yes, [ ] No (please explain), [ ] I don't know

Does the introduction build on relevant research in the field? [XX] Yes, [ ] No (please explain), [ ] I don't know

Materials and methodsAre the methods and analyses sufficiently detailed to allow replication by other researchers? [ ] Yes, [XX] No (please explain), [ ] I don't know –> see comments to authors regarding 'composition' and inter-observer reliability

Are the methods and statistical analyses appropriate and well described? [XX] Yes, [ ] No (please explain), [ ] I don't know

ResultsIn the case of negative results, is there a statistical power analysis (or an adequate Bayesian analysis or equivalence testing)? [ ] Yes, [ ] No (please explain), [XX] I don't know

Are the results described and interpreted correctly? [XX] Yes, [ ] No (please explain), [ ] I don't know

DiscussionHave the authors appropriately emphasized the strengths and limitations of their study/theory/methods/argument? [ ] Yes, [XX] No (please explain), [ ] I don't know –> see comments to authors regarding alternative explanation of song complexity potentially driving social complexity

Are the conclusions adequately supported by the results (without overstating the implications of the findings)? [ZZ] Yes, [ ] No (please explain), [ ] I don't know

Review of Manuscript:

This manuscript describes the complexity of song in weaverbirds and tests different factors that might explain that complexity. A strength of the study is that the authors tested multiple hypotheses – too many studies only test the Social Complexity Hypothesis to test whether larger groups or groups with more complicated social structures have larger signal repertoires. Another strength is that the authors looked at two metrics of song complexity – diversity and composition. The authors found that phylogenetic relationship and social complexity were strongly associated with song complexity, whereas sexual selection was not.

Although there is much to this manuscript that I like, I do have several concerns and comments. Two I see as really important to address. First, I was never completely clear on what 'composition' of the songs was – I have a general idea but am not sure. For sure, the authors need to define the term explicitly and early in the manuscript. The Kershenbaum et al. 2016 paper "Acoustic sequences in non-human animals: a review and prospectus" (Biol Rev 91 doi: 10.1111/brv.12160) seems relevant to this term. Second, the authors really need to report inter-observer reliability statistics for the coding of song elements (see lines 230-232). Also, it would be good to have inter-observer reliability statistics on the colony size differences variables they used (see lines 284-286) – I could see this potentially being a bit subjective.

I raise the additional comments here by line number and not in any order of importance.

Line 120-141. Is there any reason to believe that territory or home range densities might explain some of the variation in songs? This is one of the metrics of social complexity that is rarely studied – Terry Ord has published a couple studies on visual displays in lizards and how they relate to spatial variation and territory densities.

Line 177-181. Both of these definitions should come earlier in the paper, I think, and the one for 'composition' may need to be spelled out more thoroughly.

Line 201 and 205. I suggest "The song data were collected . . ." and "Sennheiser microphone (MKH70 with K6 power module) . . ."

Line 214-216. The average number of songs recorded per individual seems quite low and I wondered if this might result in problematic estimates of repertoire size / song diversity.

Line 219-220. On what data is the 1.5 sec criterion based? If two vocal elements are 1.4 sec apart from one another, that seems like a long time to me to consider them to be in the same song, but it is also quite possible I simply don't know the songs of these species well enough or don't understand the criterion used here correctly.

Line 237-239. How were specific individuals known in these multi-individual recordings given – I assume – individuals were not color marked?

Line 305-307. I am not sure I understand this sentence – maybe re-word?

Line 336-337. I suggest "received further statistical support . . ."

Line 344-346. How robust is this approach? If the authors compare "solitary" vs "grouped" do they get similar findings? What about if they compare "large" vs "all other" groups?

Line 357-358. I don't have the reference on hand, but Robin Dunbar has a 2012 paper (in the Philosophical Transactions theme issue on social complexity and communication) on the importance of social bonding to vocal complexity – perhaps that discussion / idea is relevant to the finding here?

Line 373-374. I am not sure I understand the figure – particularly Figure 1 b and its caption information. Do negative numbers indicate a negative effect – as in increased colony size is linked to a decrease in song diversity? That seems counter to the authors' interpretations and arguments.

Line 424-425. I suggest "proximity predicted both song diversity . . ." or "proximity was associated with both song diversity . . ."

Line 492. I suggest "no data currently exist . . ."

Line 495. Do the authors mean "interspecific" here rather than "intraspecific"?

Line 521-522. In comparative studies like this on the Social Complexity Hypothesis, it seems often difficult to determine whether social complexity might be driving vocal complexity (as the authors are arguing here) or whether vocal complexity that might evolve for other reasons might be making greater social complexity possible. I wondered if the phylogenetic signal detected here might actually be support for the latter interpretation. If the phylogenetic effect is considered 'strong', might this bolster an argument that increased song complexity (phylogenetically driven) is driving social complexity?