Peer Community In Evolutionary Biology

On the evolutionary implications of being a social animal

Michael D Greenfield *based on peer reviews by* ***Rafael Lucas Rodriguez*** *and 1 anonymous reviewer*

Lluís Socias-Martínez, Louise Rachel Peckre (2023) Does sociality affect evolutionary speed? Zenodo, ver. 3, peer-reviewed and recommended by Peer Community in Evolutionary Biology. https://doi.org/10.5281/zenodo.10086186

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What does it mean to be highly social? Considering the so-called four 'pinnacles' of animal society (Wilson, 1975) – humans, cooperative breeding as found in some non-human mammals and birds, the social insects, and colonial marine invertebrates – having inter-individual relations extending beyond the sexual pair and the parent-offspring interaction is foremost. In many cases being social implies a high local population density, interaction with the same group of individuals over an extended time period, and an overlapping of generations. Additional features of social species may be a wide geographical range, perhaps associated with ecological and behavioral plasticity, the latter often facilitated by cultural transmission of traditions.

Narrowing our perspective to the domain of PCI Evolutionary Biology, we might continue our question by asking whether being social predisposes one to a special evolutionary path toward the future. Do social species evolve faster (or slower) than their more solitary relatives such that over time they are more unlike (or similar to) those relatives (anagenesis)? And are evolutionary changes in social species more or less likely to be accompanied by lineage splitting (cladogenesis) and ultimately speciation? The latter question is parallel to one first posed over 40 years ago (West-Eberhard, 1979; Lande, 1981) for sexually selected traits: Do strong mating preferences and conspicuous courtship signals generate speciation via the Fisherian process or ecological divergence? An extensive survey of birds had found little supporting evidence (Price, 1998), but a recent one that focused on plumage complexity in tanagers did reveal a relationship, albeit a weak one (Price-Waldman et al., 2020). Because sexual selection has been viewed as a part of the broader process of social selection (West-Eberhard, 1979), it is thus fitting to extend our surveys to the evolutionary implications of being social.

Unlike the inquiry for a sexual selection - evolutionary change connection, a social behavior counterpart has remained relatively untreated. Diverse logistical problems might account for this oversight. What objective proxies can be used for social behavior, and for the rate of evolutionary change within a lineage? How many

empirical studies have generated data from which appropriate proxies could be extracted? More intractable is the conundrum arising from the connectedness between socially- and sexually-selected traits. For example, the elevated population density found in highly social species can greatly increase the mating advantage enjoyed by an attractive male. If anagenesis is detected, did it result from social behavior or sexual selection? And if social behavior leads to a group structure in which male-male competition is reduced, would a modest rate of evolutionary change be support for the sexual selection - evolutionary speed connection or evidence opposing the sociality - evolution one?

Against the above odds, several biologists have begun to explore the notion that social behavior just might favor evolutionary speed in either anagenesis or cladogenesis. In a recent analysis relying on the comparative method, Lluís Socias-Martínez and Louise Rachel Peckre (2023) combed the scientific literature archives and identified those studies with specific data on the relationships between sexual selection or social behavior and evolutionary change, either anagenesis or cladogenesis. The authors were careful to employ fairly conservative criteria for including studies, and the number eventually retained was small. Nonetheless, some patterns emerge: Many more studies report anagenesis than cladogenesis, and many more report correlations with sexually-selected traits than with non-sexual social behavior ones. And, no study indicates a potential effect of social behavior on cladogenesis. Is this latter observation authentic or an artifact of a paucity of data? There are some a priori reasons why cladogenesis may seldom arise. Whereas highly social behavior could lead to fission encompassing mutually isolated population clusters within a species, social behavior may also engender counterbalancing plasticity that allows and even promotes inter-cluster migration and fusion. And briefly – and non-systematically, as the rate of lineage splitting would need to be measured – looking at one of the pinnacles of animal social behavior, the social insects, there is little indication that diversification has been accelerated. There are fewer than 3000 described species of termites, only ca. 16,000 ants, and the vast majority of bees and wasps are solitary.

Lluís Socias-Martínez and Louise Rachel Peckre provide us with a very detailed discussion of these and a myriad of other complications. I end with a common refrain, we need more consideration of the authors' interesting question, and much more data and analysis. One can thank Socias-Martínez and Peckre for pointing us in that direction.

References:

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Reviews

Evaluation round #2

DOI or URL of the preprint: https://doi.org/10.5281/zenodo.8397348
Version of the preprint: 2

Authors' reply, 08 November 2023

Dear Dr. Greenfield,

We want to thank you for your constructive criticism regarding our manuscript.

Concerning Figure 3 and the analyses it represents, we would like to stress that our approach does not correspond to a meta-analysis. We reviewed as much evidence as we could find, but the evidence was not weighted, and no effect size was calculated according to the methods and data used in each study. The values 0, 0.5, 1, or -1 are labels we gave depending on our subjective evaluation of the presence or absence of support from the reviewed studies. In addition to the description in Figure 3, we have expanded the paragraph in the methods to state it clearly (see l.316-334). Regarding the use of connectors for the bibliographic search, we did not use any.

Regarding the discussion, we choose Peer Community, among other things, because it offers the space to develop discussion arguments that might not be addressed elsewhere. This said, we have taken advantage of your criticism and substantially edited the discussion. First, we have reordered the seven main points in a manner that improves the flow of ideas. Second, we have presented the structure of the discussion beforehand with the critical points raised as a way to help readers navigate it to their respective points of interest. Third, we have edited the content to reduce complexity and improve readability and interpretation.

Finally, we have edited the English extensively using paid correction engines.

Yours sincerely

Dr. Socias-Martínez and Dr. Peckre

Decision by Michael D Greenfield, posted 07 October 2023, validated 09 October 2023

Revision requested.

The revised version of 'Does sociality affect evolutionary speed?' is markedly improved, having addressed many of the issues raised in the review of the initial version. However, several problems remain and need to be corrected before I can recommend the preprint.

Figure 3 is an excellent summary of the results, but some details seem to be missing from its description. In particular, effect magnitude for a positive influence can be 1 or 0.5, but it is not clear how these different magnitudes were assessed using information from the original studies, which used different methods, sample sizes, etc. Similarly, more information on the key words, notably the connectors (i.e. and, or, not, etc) applied between key words, used in identifying relevant studies from the literature should be provided. This precision would be standard in any meta-analysis.

English language : Overall, the English is quite good, but there are still a great many errors : Lack of agreement between subject and verb, inappropriate words used, unusual spelling, etc. In some cases these errors will pose problems for readers whose first language is not English, and they need to be corrected. Please have the entire text checked competently.

Discussion. While the text from the beginning to line 498 is generally clear and of appropriate length, the discussion that follows is excessively long, and many parts are far too complicated as written. I advise a discussion that is reduced by at least 50%, that covers the main problems encountered in studying the sociality - evolutionary speed question in a concise and straightforward manner, and avoids lengthy attention to individual

studies. The current version of the discussion, with many convoluted arguments and run-on sentences, is likely to lose the attention of readers rather quickly. In your revision focus on cogent presentations that do not require boldface highlighting of terms in the text, a feature that is generally not found in the published literature.

Evaluation round #1

DOI or URL of the preprint: https://doi.org/10.5281/zenodo.7693687
Version of the preprint: 1

Authors' reply, 02 October 2023

Download author's reply

Decision by Michael D Greenfield, posted 27 May 2023, validated 30 May 2023

Revision requested.

It is clear from the reviews by the two referees, and from my own reading, that this manuscript concerns a novel and important topic in evolutionary biology and should eventually be published pending careful revisions. Both referees were enthusiastic about the topic but also pointed out several major problems that need to be addressed. I agree with their points and emphasize the following : 1) More attention should be paid to the objectivity of 'proxies' for evolution and (particularly) for sociality. 2) Focus on the nuances of the selectionist and population approaches to the issue. 3) It is not surprising that a uniform conclusion is not reached (sociality appears to be correlated with higher evolution rates ; or, alternatively, with lower rates or is uncorrelated), but can you infer the situations where such correlation holds and where it does not? 4) The overall presentation should be more cogent, with attention paid to organization of the manuscript and general writing style.

Reviewed by Rafael Lucas Rodriguez, 24 April 2023

This manuscript surveys tests of the hypotheses that sexual and social selection generate faster rates of evolutionary change and speciation. It provides a qualitative assessment of the state of the literature, and suggestions for how to make progress. I thought the ms provides useful discussion and points, but I would like to suggest refining some ideas and in some cases changing the approach.

1.
In the final tally, the ms reports that 67% of the studies surveyed provide support for the sexual selection hypothesis and 65% for the social selection hypothesis. I would like to note, as the ms points out, that studies have varied in the "quality" of the proxies used for strength of sexual or social selection. In my reading of some of these papers, I have noticed that studies with better proxies yield stronger support (see e.g., Figure 6 in Kraaijeveld et al. 2011 Biol Revs). I thought that it would be good to add some consideration of the quality (proximity to actual strength of sexual or social selection) of the proxies used across studies to the discussion in this ms.

2.
I appreciated the nuance the ms adds to the classification of social systems. But, along the lines of the above comment, this made me wonder whether the level of sociality (however defined) is as indicative of the strength of social selection as, say, a good proxy like sexual dichromatism is indicative of the strength of sexual selection. For instance, I would probably disagree with saying that social competition between honeybee queens is

stronger than between facultatively eusocial paper wasps. Perhaps here is an opportunity to devote some thought to suggesting what might be good proxies for the strength of social selection.

3.
I quite liked the classification of studies between selectionists and populationists—I hadn't come to think of the literature in those terms. However, while not denying what the ms says the populationists have done, it seems to me that the prediction for rates of evolutionary change is meant to deal with particular trait types rather than large genome sections (e.g., re: lines 365-393). For instance, classifying clades according to whether sexual selection on genitalia is possible (polyandrous clades) or not (monandrous clades) gives strong support to the prediction of greater divergence and extravagance in genitalia (Eberhard 1990 Am Sci 78, 134-141; Arnqvist 1998 Nature 393, 784-786). I thought that adding some such clarification to the ms would be good.

4.
I thought that the sections where the evidence for the hypotheses is assessed should better distinguish empirical studies from simulation studies. For example, in the section for "empirical evidence" starting in L216 it doesn't take long before simulations are included (L226). Maybe it is my bias as an empiricists, but theory has often concluded that X is impossible only to be proven wrong shortly after by observations; e.g., as with mate choice occurring at all. I would therefore suggest giving more weight to actual empirical evidence, and making a clearer separation of empirical studies from simulation studies.

5.
L216-223: I also thought this section should be expanded to discuss these studies more fully. Some of these papers provide the strongest evidence to date, and it seems to me that they deserve more discussion.
Similarly, I thought the passages in L404-407 and L 430-433 should also be expanded to discuss the results of these studies, rather than simply refer the reader to the table.

6.
Between the studies by Bush et al. 1977 and Marzluff & Dial 1991 (L422-on), I thought it would be useful to assess/discuss which had the better proxy for strength of social selection.

Minor:

7.
L126-127: with the concomittant differences in mate preferences, no?

8.
L135-160: I thought that introducing the term "mate choice" would help this passage clearer and smoother.

9.
L148-160, 344-356: is it necessary to assume high signal honesty regarding good genes for the hypothesis to lead to higher rates of evolutionary change and speciation?

10.
L168-169: and this can be initiated within-population ...

11.
L202-215: I thought this section should be expaned a bit to clarify what conditions might lead to sexual selection hindering speciation.

12.
L281-288: the Eberhard 2004 study is not about speciation.

13.
L340-341: I didn't follow the rationale for saying that these arguments require absence of gene flow; isn't the hypothesis that divergence in sexual ornaments and preferences can initiate reproductive isolation?

14.
L343: the hypothesis of magic traits arose from speciation theory, not sexual selection theory.

15.
L357-364: I didn't follow the ideas in this section. Is it an argument based on group selection/ecosystem-level selection? If so, I'd suggest omitting it. The references cited deal with within-population variation, not species diversity within communities.

16.
L416-417: I would not agree with this statement (re: it being generally acknowledged).

Reviewed by anonymous reviewer 1, 25 May 2023

How do social environments and social interactions influence the course of evolution? In this paper, the authors review different approaches to addressing this question and offer guidelines for future work that might help shed new light on social evolution based on gaps in existing literature. Specifically, they distinguish between a "selectionist" approach that focuses on how social interactions influence selection on traits, and a "populationist" approach that focuses on how social environments alter population structure (e.g., population size) in ways that quantitative genetics approaches tell us shape the course of evolution.

A strength of the paper is its link between evolutionary speed and social behavior, which is a fresh and interesting lens for understanding social evolution. I liked the way the authors distinguished between selection for traits and changes in effective population size as two pathways by which social living can shape evolutionary speed—this is a stimulating synthesis that I have not seen elsewhere. However, I found a number of issues prevent the paper from achieving its full potential. First and most critically, the writing lacks logical flow in many areas, which strongly negatively impacts that clarity of the paper. Many sections stretch on at great length, and topic sentences give no clear indication of what point each paragraph is making or how the paragraphs connect to each other to form a coherent message. Second, I liked aspects of the Figure and Table, but both need a bit of work to clearly deliver their message. Finally—and I recognize this might be a tall order—it would be nice to offer some clues about when and how sociality influences evolutionary speed. In the title the authors pose the question "does sociality affect evolutionary speed" and the answer offered by the paper appears to be "it depends." Given the breakdown into selectionist vs. populationist, cladogenesis vs. anagenesis, the many taxa reviewed in Table 1, it feels like the authors might have done much of the work needed to be able to offer a more impactful breakdown of the conditions under which sociality impacts evolutionary speed.

I've broken my comments into Issues, which I believe need to be addressed for this to be a rigorous paper, and Suggestions, which I offer as potential ways to improve the paper, but I don't see as necessary.

Issues

Throughout the paper, I find the logical flow of the writing to be very difficult to follow. The topic sentences

of paragraphs often don't give a clear picture of what content will appear in the paragraph, and how that content relates to the overall point made in that section of the paper. For instance, the whole sexual selection section reads to me like a long list of facts about sexual selection without an overarching point. Other sections proceed similarly—for instance, the social selection section reviews the work of West-Eberhard, but what point are the authors making by doing this? I urge the authors to work on ensuring that topic sentences a) introduce the content discussed later in the paragraph and b) link to other topic sentences to form a logical argument unfolding over the various sections of the paper. Similarly, at the start of a new section, it would be helpful if the authors introduced the role that the section plays in the overarching argument of the manuscript.

Table 1 – 1) The Perspective and Types of Selection columns are sometimes not legible. 2) there is a "Supported" column, but no column indicating what the prediction is from each of these hypotheses. Are they all predicted to increase evolutionary speed? Or just have any effect? 3) The table is never introduced or explained. What led the authors to choose this selection of papers? On line 546 there are some interesting percentages offered—this seems like exactly the sort of information that could be presented in a summary paragraph introducing the table. As it is now, I read the paper waiting for the moment that I was supposed to engage with the table, but the moment never came. 4) The table is often referenced in the context of making a point about the preponderance of evidence, e.g. (stating it's "contrasting" l. 286, or "overall positive" l. 649), but it is not very evident what the reader should see in the table to support these claims. Is there a way to present some of these quantitative insights from the table?

I'm not sure from Figure 1 if the categories under Social System are meant to be divided between the Selectionist and Populationists sides of the figure, but I don't think it's appropriate to do so. For instance, Mating Systems are expected to influence Ne. Also, as in Table 1, it's unclear what "Supported" means—does the "-" mean that increasing Ne slows cladogenesis, or that it has no effect on cladogenesis? Similarly, when the arrow by sexual selection has a + next to it, does this apply to directional sexual selection? Stabilizing selection is not expected to drive anagenesis or cladogenesis, right? I think in this figure, and perhaps throughout the paper, the authors should consider whether they are talking about the presence of selection per se or if they mean selection for novel or more / less exaggerated traits.

The introduction takes a very meandering course before arriving at the main topics of the paper. For instance, a great deal of time is spent on phylogenetic history and socioecological models, but these are not a central feature of the remainder of the paper. Meanwhile, other very central topics are not introduced at all, most notably the four dimensions of social systems outlined in the figure. The intro would make more sense if it focused more directly on sexual selection, population genetics, variation in social systems outlined in the Figure, and evolutionary speed.

I'm not sure what the "Empirical evidence" subsection of the "Sexual selection" section is achieving. This seems to be a bunch of articles recommended by the authors. This is an odd section of the paper to make such a recommendation, and I don't see how it falls under the category of empirical evidence.

The Social Structure box should include "Social relationships"

Suggestions

In the abstract, the authors state: "The current state of the art affords no conclusive answer on whether sociality promotes anagenesis and cladogenesis." This is a fine point to make, but given the extensive literature review performed here, I wonder if there is an opportunity to make a more impactful point by examining the contexts in which it does or does not influence evolutionary speed. It's not that surprising that the answer

to “does sociality affect evolutionary speed?” is “it depends.” But it would be very exciting to be able to say something about **how** sociality influences evolutionary speed, the contexts in which it does, and the contexts in which it does not. This is of course touched upon in the paper and a very challenging question, but I would love to see the authors be able to make some suggestions based upon their review of the literature.

The contrast between “selectionist” and “populationist” is an interesting framing for the paper, but I have some recommendations. I’d recommend an alternative framing, as people don’t like being put into boxes, and referring to “selectionists” and “populationists” suggests that scientists are categorizable into these two camps. Many may not ascribe to either, and others might see both approaches as useful. I think a simpler way would be to describe these as a social selection approach vs a population genetics approach—this labels the approach rather than the researchers, and also doesn’t require introducing new terms. Additionally, it wasn’t always clear to me whether the authors were thinking of these as two different biological processes or two different ways of studying social evolution. Could these be restated as biological processes (e.g., competition with conspecifics vs. changes in effective population size).

Evolvability – this term is a keyword and is mentioned in the introduction but is never defined and isn’t used much throughout the paper.

There were some language issues that affected the clarity of the manuscript, for instance on lines 49-50, 247-248, 275-276, 416-418, 464-465.

It is unusual to cite the proceedings of a dissertation defense in an academic paper.