Dear Dr. Greenfield, Dr. Rodriguez and anonymous reviewer,

We would like to thank you for your constructive criticism regarding our manuscript. The points the three of you raised sparked a wish to improve the manuscript regarding its content and structure. We think the present version fulfils such upgrading and would like to ask you to consider it again for publication. We have made several profound changes to address the issues of readability and flow, as well as including discussion around key literature and the role of methods in driving results:

First, we have reduced the introduction to focus on the relationship between sociality and evolutionary speed.

Second, after the general introduction, the two theoretical perspectives ("selectionist" and "populationist") are presented one after the other, and the possibility that both co-occur has been emphasized.

Third, the manuscript evaluates the empirical research as a whole instead of presenting it according to the perspective that motivated the study, as in the previous version. Regarding the empirical research reviewed, we have devoted most effort to expanding it with a significant increase from 32 to 89 studies included in Table 1. To structure the evidence, we proceeded first according to the time level observed (micro-, meso- and macroevolution), then by the evolutionary speed component (anagenesis, cladogenesis) and finally by the methodological approach used when the number of studies allowed it (e.g., experimental evolution, modelling, phylogenetics). This more fine-tuned way of analyzing the literature is visually summarized in a new figure (Figure 3), rendering a map to navigate the results.

Fourth, the new structure allows us to delve deeper into discussing the factors that might affect the results obtained and see the imbalances between different areas of research. For example, we could see that neither the evolutionary time level investigated, nor the methodology used are strong predictors of the support or lack of. On the contrary, the evolutionary speed component is with studies focusing on anagenesis yielding more support than those looking at cladogenesis.

Fifth, we have added several new aspects to the discussion. In light of the finer resolution yielded by the new structure, we have discussed more in detail the necessity for studies to investigate simultaneously selectionist and populationist perspectives. In addition, we discuss the possibility that the current framework focuses on a single winning phenotype in each social system while, in contrast, social selection could construct a community of the fittest phenotypes.

Finally, we have added a section detailing predictions on the strength of social selection and *Ne* changes arising from variation in social dimensions and components. This section is included in the discussion about previous limitations regarding how sociality was measured and has an accompanying figure (Figure 4). We believe such additions can act as an open door for future research in this domain.

A detailed answer to each criticism can be found below.

We look forward to your response.

Sincerely

Lluis Socias-Martínez, PhD

Michael D Greenfield, 27 May 2023 07:12

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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.

Social proxies: We have introduced a section regarding the relationship between social systems variation and strength of selection called "Predicting the effects of the different social systems' dimensions on evolutionary speed" (starting L559). The reviewed evidence shows amalgamations of several social dimensions into taxa-specific categories and focuses on single social dimensions' components while ignoring others. We believe that the inclusion of these predictions and the discussion around them might encourage future research with a more comprehensive approach that tests multiple hypotheses for the different social dimensions.
Evolution proxies: When enough evidence for a subsection existed we discussed the effects of different ways to measure evolutionary speed and introduced these findings in the summary at the beginning of each section (e.g., L.347). We also briefly address the problem of the proxies for evolutionary speed in the section "Separating the potential for evolutionary speed from its realization" (L.894-909).

2) Focus on the nuances of the selectionist and population approaches to the issue.

Within the theoretical background for each perspective, the different ideas contained and their relationships are emphasized. We have, for example, distilled the arguments in the "Selectionist perspective" (L142) and added a brief explanation of the concept of Ne in the "Populationist perspective" section (L290-299). Furthermore, throughout this version, we have tried to foster the dialogue between both perspectives by improving the structure of the text (both perspectives presented one after the other) and the analysis of the studies (now includes whether both perspectives were investigated simultaneously, Table 1, Figure 3). In addition, there is an emphasis made on the fact that these two perspectives are two sides of the same coin that should be studied in combination in a dedicated section in the discussion ("Selectionist and populationist perspectives have proceeded independently") (L787). Finally, the section "Predicting the effects of the different social systems' dimensions on evolutionary speed" (L559) and the accompagnying Figure 4 tailor the discussion on each perspective towards social variation, further expanding the possible nuances of each perspective.

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?

The present version includes targeted discussions regarding the effects of different methods used to conduct the studies on the results obtained throughout the "Empirical and theoretical evidence" section (starting L311). In addition, Figure 3 has been developed to navigate the evidence in light of the effects of the evolutionary speed component investigated, the selection/stochastic process and the time level while guiding the reader during the more in-depth analysis of the text.

4) The overall presentation should be more cogent, with attention paid to organization of the manuscript and general writing style.

The manuscript has been substantially edited to improve the chain of ideas and the evaluation of evidence.

Reviews

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.

Thanks for raising this important criticism. We have tried to address it as follows: The presentation of the reviewed evidence has been made following a structure that presents different methods (see "Empirical and theoretical evidence" section starting L311, see also Figure 3). Within each part of this section, the support or lack thereof was evaluated in relation to the specific methods whenever enough variation in the studies existed. In many instances, the high variability between studies in the ways to measure sociality and evolutionary speed as well as the statistical procedures (e.g., controlling for philogeny), did not allow for any meaningful conclusion. Despite this, we think the current version might help interested readers to navigate the literature and the results with an awareness of the methodology being used and the possible impacts on the results obtained.

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.

This is an interesting point to which we have no clear answer. Nevertheless, we have tried to open the door for a more direct confrontation with this problem in the section "Predicting the effects of the different social systems' dimensions on evolutionary speed" (starting L559). For example, the bee/wasp example you provide reminded us of the discussions in primatology about what is more complex, a more hierarchical and predictable social structure or a more egalitarian society full of possible outcomes. We provided some predictions regarding this in the mentioned section (see Social structure). We think the discussion on other components might help establish the comparison of any two animal societies along multiple axes of social variation and their independent and synergistic effects on selection strength and Ne. Although we do not answer your concern directly, we think that including these predictions can help researchers evaluate whether social systems dimensions are good proxies for the strength of selection and the effects on Ne.

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.

As we see it, the selectionist perspective focuses on specific traits that "solve" the problems encountered in social competition contexts, and stronger selection might enhance the speed of spread of "new solutions". On the contrary, the populationist perspective deals with whole genomes evolving neutrally (in the absence of other forces). According to this dichotomy, we would expect specific characters or sets of characters, like cognitive skills or coloration patterns, to evolve in response to the processes described by the selectionists. Populationists' effects (drift), which might occur simultaneously, are more challenging to assess as these might affect any character but only be observable for those not under strong selection. We have tried to clarify this dichotomy throughout the selectionist and populationist sections (e.g., L142-310) and emphasized those studies that used genomics and population genetics methods to find a signal for drift.

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.

We think that tests using mathematical models are the first step from theory towards empirical research, although we are aware it is disputable. We have clearly stated now when we are discussing modelling literature to avoid any misunderstanding.

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 .

Regarding the first set of papers on sexual selection and speciation, we have discussed with some detail Kraaijeveld et al. (2011) and Janicke et al. (2018) regarding their methodology/proxies' effects. We have refrained from discussing the content of the other reviews as they delve into more mechanistic aspects that would demand space in an already long article while diverging the focus of the present work. Concerning the evidence on social selection, we have extensively expanded the discussion on them in the presentation of the evidence and in the discussion when specific limitations were evaluated.

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 .

We have added a paragraph regarding this issue in the discussion (L901-909).

Minor:

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

 Yes, added (L 143).

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

 This passage has been deleted, and the introduction to sexual selection effects on anagenesis and cladogenesis has been distilled to make the flow of ideas smoother. We have refrained from focusing on mate choice in the paragraph dealing with the mechanisms generating coevolution as it now explains both sexual and social contexts (L169-206).

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?

 We think it is because otherwise, the fitness advantage should quickly be on the side of characters that allow not reacting to a dishonest signal. However, we are aware that this could also be a coevolutionary arms race between cheaters and resistance to cheating. We decided not to enter this aspect despite its importance for understanding the evolution of signalling to avoid diverging the flow of ideas.

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

 Done, now it reads: "The cladogenetic effect of social selection results from different parts of a given metapopulation following divergent coevolutionary processes, thereby impeding gene flow and culminating eventually in reproductive isolation (Darwin, 1871; Fisher, 1930; West-Eberhard, 1979, 1983; Panhuis et al., 2001; Wilkinson & Birge, 2010; Boughman, 2016; Mendelson & Safran, 2021)." (L220)

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

We have deleted this section with the intention of keeping the ideas as simple as possible. We nevertheless will include a developed version of this paragraph in a future article.

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

 We had to read the Eberhard study several times to grasp the results considering the methods. We have included it as two different lines in Table 1. In the first line, which is classified as having no evidence of anagenesis arising from sexual selection, the results state: "Genera classified as having higher levels of intersexual competition do not evolve divergent genitalia more often." The second, classified as no support for sexual selection generating cladogenesis, reads: "The number of species having idiosyncratic genitalia does not differ among clades with a high or low level of intersexual competition."

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?

This paragraph has been deleted. A new paragraph that refines the previous one contains a more nuanced vision regarding a collection of subpopulations with possible different trajectories. We have added a section ("Amplification of social selection effects by environmental heterogeneity") where we further consider what environmental heterogeneities might make this sympatric speciation even more likely. (L255)

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

Thanks for this clarification. We meant that it is extensively used in sexual selection theory as it relies on mate choice. We have modified the sentence; it now reads: "Thus, if the environment varies, the "good genes" and "magic traits" perspectives (Servedio et al., 2011) can also apply to social selection contexts."(L270)

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.

We tried to criticize that the frameworks look at competition as if one single best phenotype could appear and be selected. Instead, a community of fit phenotypes, each with different strengths, could be selected in different subpopulations. Because of this, the cladogenetic effect would depend on overlaps in the fit phenotype communities rather than on a single best phenotype. We have moved these ideas into a section called: "Going beyond the focus on a single winning phenotype", now placed in the discussion. (L910)

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

*Agreed. The sentence now reads: "Since it has been proposed that small **Ne**s are associated with (Bush et al., 1977), or even necessary (Flegr, 2010), for speciation to occur, societies that result in small **Ne** should also induce higher cladogenetic speed." (L308)*

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 .

We agree that the first version might have appeared somewhat unrefined in its logical flow; this also reflected the state of maturation of these ideas (some of which were new to us). We have tried to improve the flow by changing the structure and, in some cases, removing non-vital arguments that distorted the main line of argument. For example, both perspectives are now presented one after the other to ease their comparison from a theoretical perspective. The empirical evidence has also been restructured to facilitate grasping our take on each point. We believe the writing and the organization have been improved to deliver a more coherent and focused message.

Table 1 – 1) The Perspective and Types of Selection columns are sometimes not legible.

Modified to be readable.

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?

We have introduced a column "Process" where we indicate, given the methods used in the study, what process was tested (Sexual selection, Non-sexual social, Neutral, or a combination of these). Then a column "Effect" indicates the observed effect, "1" being supportive (e.g., increase in selection strength leads to increase in evolutionary speed or decrease to a decrease), "0.5" both evidence and absence of evidence, "0" absence, "-1" contrary to the predictions and "np" not predicted by the framework. The dimensions and components tested are shown in "Dimension" and "Component" columns. In the "Results" the specific values tested (e.g., polyandry versus monogamy) can be found. We have developed a new figure (Fig. 3) that displays the results from Table 1 in a simplified way.

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.

In the introduction to the "Empirical and theoretical evidence" section, we detail how these studies were collected (L311-324). We then proceed to deal with an overview of findings regarding Table 1 and then to present the evidence with a defined structure corresponding first to the time level observed (micro-, meso- and macroevolution), then to the evolutionary speed component (anagenesis, cladogenesis) and finally to the methodological approach used when the number of studies allowed it (e.g., experimental evolution, modelling, phylogenetics). We believe the "Empirical and theoretical evidence" section is now deeply connected with table 1.

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?

Figure 3 was developed to answer this criticism. Thanks, it also helped us during the presentation of results and discussion.

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.

Agreed, this was not our intended message. Figure 1, now Figure 2, has been substantially edited and do not detail the different social systems' dimensions. A new figure, Figure 4, has been added to detail the predicted effects of the different social systems' dimensions on the strength of social selection and 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?

Current Figure 2 details the main findings from the reviewed literature as follows: The prediction is coded by the color of the link (red for a positive link: increase leads to an increase, blue for a negative link: increase leads to a decrease), then for each link "1" indicates that most tests reviewed (i.e., more than 50%) confirmed this link while "0" shows absence of support.

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.

This is an important distinction that we did not focus on explicitly. Despite this, we think that the presented rationale (West-Eberhard, 1979, 1983) *can work also on stabilizing selection as well. We have introduced a paragraph in this regard within the selectionist perspective section (L 207-218)*

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.

We have shifted the focus at the start by introducing social systems' dimensions and possible relationships on evolutionary speed. We have conserved a paragraph on the causes as a contrast to the consequences of social variation that have been less studied. We believe the introduction has been improved regarding the chain of ideas.

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.

Both sections for empirical evidence have been condensed into one that is now structured according to the level of analysis (time-level, evolutionary component and type of study).

The Social Structure box should include "Social relationships."

We have introduced social bonds in Figure 4 as well as discussed predictions about their effects on evolutionary speed (L691-705).

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.

*With the new analysis we were able to show some effects of the methodology albeit being a qualitative review we keep the insights as first evidence. In addition, the section "Predicting the effects of the different social systems' dimensions on evolutionary speed" (L 559), could be a first step towards more concrete answers to the "**how**" sociality affects evolutionary speed. In this section, we tried to offer some links between social variation and social selection strength as well as Ne effects on anagenesis and cladogenesis. At present, we feel unable to answer the question directly, but we feel comfortable in offering some steps towards it.*

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).

We agree that such labelling is reductionist and perhaps misleading when it refers to the authors. We have emphasized in the titles and throughout the text that these labels correspond to perspectives, not people and that both perspectives are the two sides of the same coin.

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

We have defined it as the "potential for evolutionary speed" when the term is used for the first time in the text (L102-103).

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.