Peer Community In
Evolutionary Biology

Evolutionary trajectories of social transitions: Higher social complexity is associated with lower effective population size and reduced efficacy of selection in termites

Trine Bilde *based on peer reviews by 2 anonymous reviewers*

Camille Roux, Alice Ha, Arthur Weyna, Morgan Lode, Jonathan Romiguier (2024) The impact of social complexity on the efficacy of natural selection in termites. bioRxiv, ver. 2, peer-reviewed and recommended by Peer Community in Evolutionary Biology.
https://doi.org/10.1101/2024.04.26.591327

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A comprehensive study by Roux et al 2024 investigates the impact of eusociality on the efficacy of natural selection in termites, with and additional focus on whether higher levels of social complexity are associated with lower effective population size (Ne) and relaxed purifying selection.

Eusociality is characterized by a division of reproductive labor, cooperative care of offspring, and overlapping generations, and has evolved independently across various animal taxa with the most complex social systems found in Hymenoptera (bees, wasps, ants) and termites. Because reproduction is limited to a few individuals, this leads to a reduced effective population size (Ne), which impacts genome evolution. Smaller Ne increases the influence of genetic drift, weakening the efficiency of natural selection and allowing the accumulation of weakly deleterious mutations. This phenomenon, known as the ”drift barrier,” alters the mutation-selection balance in eusocial organisms.

Studies in a range of social arthropods including ants, termites, crustaceans and spiders have shown an elevated ratio of nonsynonymous to synonymous substitutions (dN/dS), indicating relaxed purifying selection due to small Ne. In termite species with complex social structures, such as those with large colonies and high caste specialization, there are reports of higher dN/dS ratios compared to simpler social species. This suggests

that higher social complexity, reflected in traits like nesting strategies and developmental pathways, further reduces Ne and the effectiveness of natural selection.

The authors address these hypotheses by exploring the genomic impact of eusociality in termites (Isoptera) taking two approaches: First, they analyze transcriptome data from 66 Blattodea species and calculate the ratio of non-synonymous to synonymous mutations (dN/dS) as an indicator of natural selection efficiency and effective population size. They analyses reveal an increased dN/dS ratio in termites compared to other Blattodea species, reinforcing the notion that convergent evolution toward eusociality significantly reduces effective population size and weakens natural selection efficiency across the genome. Additionally, a comparison of 68 termite transcriptomes shows that this effect is more pronounced in species with higher social complexity. This is exciting as it advances our understanding of how increasing complexity in social organization decreases Ne and the efficiency of natural selection. The study substantiates the notion that social transitions follow evolutionary trajectories where lower and Ne and increasing drift have negative consequences for genome evolution (Ma et al 2024).

References:

Camille Roux, Alice Ha, Arthur Weyna, Morgan Lode, Jonathan Romiguier (2024) The impact of social complexity on the efficacy of natural selection in termites. bioRxiv, ver.2 peer-reviewed and recommended by PCI Evol Biol. https://doi.org/10.1101/2024.04.26.591327

Jilong Ma, Jesper Bechsgaard, Anne Aagaard, Palle Villesen, Trine Bilde, Mikkel Heide Schierup (2024) Sociality in spiders is an evolutionary dead-end.
bioRxiv 2024.04.22.590577. https://doi.org/10.1101/2024.04.22.590577

Reviews

Evaluation round #1

DOI or URL of the preprint: https://doi.org/10.1101/2024.04.26.591327
Version of the preprint: 1

Authors' reply, 16 September 2024

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Decision by Trine Bilde, posted 10 July 2024, validated 10 July 2024

revision

Dear Author

I apologize for the time it has taken to complete the evaluation of this reprint, this was due to illness.

I have received two reviews of the preprint, and both are positive about the study and find it very interesting. They have, however, also made several suggestions and recommendation, that I believe would improve the paper. Based on their comments, and my own reading, I invite a revision of the manuscript, which addresses these comments.

Both reviewers pointed out that elevated dN/dS ratios can also result from positive selection, and although the data support the prediction you make on effects of smaller Ne in eusocial species, the paper would benefit from mentioning the alternative explanation and discuss both options in more detail. Please see attached commnets.

The reviewers also recommended to include wider literature on this subject, and I also agree with this point. The reviewers have mentioned several studies that would add more nuance and relevant insight to the question of interest. In addition, there are several highly relevant comparative molecular evolution studies of social and solitary species, for example in social spiders (see https://pubmed.ncbi.nlm.nih.gov/28570031/ and https://academic.oup.com/mbe/article/36/6/1281/5420164) and in snapping shrimp (see https://academic.oup.com/mbe/article/38/4/1372/5991404). It would be very relevant to include these studies to better reflect other relevant work and study systems for this research area.

Please find the detailed comments and suggestions of the reviews attached.

Best regards

Trine Bilde

Reviewed by anonymous reviewer 2, 06 June 2024

Download the review

Reviewed by anonymous reviewer 1, 18 June 2024

Roux, Weyna, Lode and Romiguier present dN/dS estimations for termites, non-eusocial blattodeans and outgroups that support the hypothesis that eusociality reduces selection efficiency due to a reduction in effective population size. This effect is more pronounced when considering different levels of social complexity within termites. These results build on previous findings presented for Hymenoptera, thus reinforcing support for the hypothesis.

I found the manuscript enjoyable to read and very clear. The presented results are exciting and important. However, alas, a similar study has recently been published, most likely while this manuscript was in its final stages: Ewart et al. "Pervasive relaxed selection in termite genomes." Proceedings of the Royal Society B 291.2023 (2024).

The results from the current study support the findings from Ewart et al. while adding additional important findings on the effect of social complexity. I find it is, therefore, important that that paper should be cited and results compared, e.g. that transcriptomic results on larger species set confirm genomic analyses.....

Generally, I find this study important due to its similarity in findings for Hymenoptera, offering support for important convergent genomic mechanisms associated with the evolution of eusociality (as discussed in Mikhailova et al COIS 2023: 101136). Beside the aforementioned need to incorporate Ewart et al, I have only minor comments. These are mainly related to what the data prove and what they suggest, and how this is worded in the text:

1. Overall, although I agree that high dNdS is likely caused by low Ne due to social complexity, I would suggest toning down in some places that this is proven here. High dNdS can also be caused by adaptive evolution. There were no formal tests carried out for a relaxation of selection, just dN/dS. But the results do offer strong support.
2. What is the cause and effect of eusociality and low Ne - again I agree with the main assertions in this manuscript - but there are two examples where it could be argued that a low Ne preceded the evolution of eusociality: in solitary bees and in Cryptocercus. Using ants as an example where this was not the case is

difficult since it is difficult to find a suitable non-eusocial outgroup for ants.
This is discussed to some extent but then on lines 298ff the authors suggest eusociality is associated with decreases in Ne, rather than low Ne. The alternative scenarios and how they can be addressed in the future could be more openly addressed.

3. Also, please be careful when suggesting that low Ne is confirmed here, e.g. line 298. Theory predicts low Ne - and it certainly makes a lot of sense but the analyses here do not allow any direct inferences on Ne.

These are not major points and just need to be reworded to make it clear what is an interpretation and what is more directly measured by the data. For these reasons, I believe the title needs to be adapted accordingly, e.g. evolutionary rates support .... or something similar.

More detailed comments follow as they appear in the manuscript.

Intro:

- line 37: should be ”effective population size”
- lines 37-40: citations and examples missing
- line 56: dS is ”solely” driven by mutation rate - should be toned down to ”mainly” or ”predominantly” as other factors such as tRNA abundance, substituion bias play a role.

M&M:

- Blattodea dataset: were these alignments always single copy orthologues? And not always across all species?
- Social traits: Please provide a table showing how species were classified by social traits for both data sets
- line 133: Neo- and Basal Isoptera - please explain the distinction and why it is relevant
- line 134: worker type - please elaborate

Results & Discussion:

- line 157: ”we observe a notable lower efficiency of selection” - this is one example of point 1 above - you observe higher dnds ratios and this can be interpreted as.... There are more examples (e.g. line 167) but I won’t list them all
- line 165 and elsewhere: from here onwards the authors write ”Blattodae” instead of ”Blattodea”
- lines 185ff - refer to figure 2B in the text
- figure 1 caption: utilising ”identical” coding genes - what is meant here?
- figure 2: what do the two colours mean? Please use a legend. Should there not be two regression lines in plot 2A - one for termites, one for others?
- Table 1: caption is a bit short and lacking details
- line 201ff: this is a good point about pyhlogenetic corrections not being necessary for dnds. But what if the cause of the differences, i.e. Ne, is phylogenetic, for example if a reduction in Ne occurred in the common ancestor of all termites and Cryptocercus? This could be tested by comparing Termites+Cryptocercus to other groups as was done in table 1
- line 210f: I’m not sure if the dnds of Cryptocercus wrighti can be considered ”intermediate” - it is quite close to the mean for termites. Please provide a supplementary table of mean dnds values for all investigated species for each data set to make this clearer.
- line 219: this should be ALLOparental care
- Figure 4a: where is the dot for Cryptocercus in the left hand boxplot? It should be at around 0.125
- Social complexity: please also discuss the possible effect of indirect selection due to sterile workers in more socially complex species.
- line 287: the individual effect of worker type and nesting type is likely impossible to pull apart as they correlate. Therefore, the causes of indirect selection and Ne are also difficult to isolate. Please discuss.
- line 298: effective population size is not determined in this study.