Peer Community In Evolutionary Biology

Colour polymorphism does not increase diversification rates in lizards

Alejandro Gonzalez-Voyer *based on peer reviews by 2 anonymous reviewers*

Thomas de Solan, Barry Sinervo, Philippe Geniez, Patrice David, Pierre-André Crochet (2023) Color polymorphism and conspicuousness do not increase speciation rates in Lacertids. bioRxiv, ver. 2, peer-reviewed and recommended by Peer Community in Evolutionary Biology. https://doi.org/10.1101/2023.02.15.528678

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The striking differences in species richness among lineages in the Tree of Life have long attracted much research interest. In particular, researchers have asked whether certain traits are associated with greater diversification, with a particular focus on traits under sexual selection given their direct link to mating isolation.

Polymorphism, defined as the presence of co-occurring, heritable morphs within a population, has been proposed to influence diversification rates although the effect has been proposed as both promoting or alternatively impeding speciation. The effect of polymorphism may be positive, that is facilitating speciation if polymorphism allows to broaden the ecological niche, thus enabling range expansion, or enabling maintenance of populations in variable environments. Specialized ectomorphs have been observed in several species (e.g. Kusche et al. 2015, Lattanzio and Miles 2016, Whitney et al. 2018, Scali et al. 2016). Polymorphism may also facilitate speciation if a morph is lost during the colonization of a novel area or niche, resulting in rapid divergence of the remaining morphs and reproductive isolation from the ancestral population, known as the morph speciation hypothesis (West-Eberhard 1986, Corl et al. 2010). On the other hand, polymorphism may hamper speciation through disassortative maintaining by morph, which may maintain the polymorphism through the speciation process (Jamie and Meier 2020). An example of such a process is Heliconius numata where disassortative mate preferences based on color hampers ecological speciation (Chouteau et al. 2017). Previous evidence in birds and lizards suggests polymorphism favors diversification (Corl et al. 2010b, 2012, Hugall and Stuart-Fox 2012, Brock et al. 2021).

Here, de Solan et al. (2023) test the effect of polymorphism on diversification in Lacertidae, a family of lizards containing more than 300 species distributed across Europe, Africa and Asia. The group offers a good model system to test the effect of polymorphism on speciation as it contains several species with colour polymorphism, sometimes present in both sexes but restricted to males when present in the flank. Using

coloration data from the literature as well as photographs of live specimens for 295 species the authors tested whether the presence of polymorphism is associated with higher diversification rates.

While undertaking their project, another group independently tackled the same question (Brock et al. 2021), using the same model system but coming to very different conclusions. Therefore, de Solan et al. (2023) decided to also contrast their results with those of Brock et al. (2021) to determine the factors responsible for the contrasting results of both studies. The latter I consider one of the strengths of the work, given the careful re-analyses to determine the causes of the discrepancies between both studies. De Solan et al. (2023) found no association between the presence of polymorphism and diversification rates, even though they used different analytical approaches. Thus, this study is interesting as it provides results that do not support a positive effect of polymorphism on species richness. The use of a phylogeny with more limited species sampling (García-Porta et al. 2019) implied that the authors had to manually add 75 species, of which 17 were added to the tree based on information from previously published trees and 68 were added at random locations within the genus. To control for potential biases the authors repeated the analyses using a sample of trees with the imputed taxa, results were broadly concordant across the set of trees. The careful re-analysis contrasting Brock et al. (2021) and de Solan et al. (2023) results suggests the difference is mainly due to a difference in how species were coded as presenting polymorphism, which differed between the two studies, as well as a difference in the package version used to run the state-dependent diversification models. Interestingly non-parametric analyses yielded similar results across both datasets.

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Reviews

Evaluation round #1

DOI or URL of the preprint: https://doi.org/10.1101/2023.02.15.528678
Version of the preprint: 1

Authors' reply, 12 October 2023

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Decision by Alejandro Gonzalez-Voyer, posted 12 June 2023, validated 12 June 2023

Major Revision required

I have carefully read the pre-print titled Color polymorphism and conspicuousness do not increase speciation rates in Lacertids and obtained two expert reviews. I would first like to apologize for the exceptionally long time it has taken to provide a decision. The work was originally being handled by another recommender who decided to abandon the process as they were unable to secure any review. In total 30 invitations were sent out to secure two reviews. This is why the process was exceptionally long and I apologize for this. Nonetheless, you will see that both reviewers did an excellent job and provide very good suggestions to improve the work. I must agree with the comment that much greater clarity is required regarding the coding of the coloration, especially since you found this to be one of the reasons for the discrepancy between previously published resutls and your own. I tend to agree with the reviewer regarding the fact that coloration that is not in the same body region cannot be taken as polymorphism, as it could be argued that colors in different body regions could potentially play different roles in signalling or intra-sexual competition. Secondly, I also agree with the surprise expressed by one reviewer regarding the choice of phylogeny used. Nearly 30% of the species that you analysed were inserted into the tree based on taxonomic information, which is rather high. How many would need to be inserted in the other published phylogeny? If a smaller number why not use that one? Finally, a comment of my own has to do with sampling. In the Introduction you state the family is split into

two main clades, Gallotiinae, which contains a few and often insular species, and Lacertinae, which contains most lacertids. Then, in the last paragraph of the Introduction you state you used "the coloration data of all the species of this family, to address two questions". However, in the Methods you state that you removed strictly insular species. This suggests you have rather sub-sampled Gallotiinae and thus also that you don't really have a good representation of "all species from the family".

Reviewed by anonymous reviewer 1, 26 May 2023

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Reviewed by anonymous reviewer 2, 11 May 2023

In this manuscript, the authors investigate if increased rates of speciation can be associated with conspicuous body colouration and colour polymorphisms. Using the Lacertid lizards as their study system, they find that these traits are not related to speciation. They also show that these colouration patterns were gained and lost several times across the phylogeny, hinting at the evolutionary lability of colour traits.

Overall, the manuscript is well written. In particular, the hypotheses stated in the introduction are clear, and the diversification analysis was well described. The result found in this study showing a lack of an effect of colour polymorphisms on speciation rates is contradictory to findings in a similar recent study. The authors provide a thorough comparison of the methodology used in both studies, and discuss at length the reasons for the differing results. This is presented nicely in the supplementary methods and results. It is fairly uncommon to see this type of discussion and I think it is well thought out. The overall results are discussed within a broad context, for example the discussion of pre and post-zygotic isolation is interesting, but also importantly the discussion doesn't try to stretch the results too far.

I suggest some minor points that could be added or edited for clarity.

- Some photos or a figure showing the variation in colouration in the lacertid lizards would be nice, particularly showing an example of conspicuous colouration. This would also help to clarify lines 150-151, where a 'species was considered as having conspicuous coloration if…the side was not white'. In some other species and habitats, a bright white colour would be considered as conspicuous so there could be some extra explanation here.
- In the final paragraph of the introduction, it could be made clearer what type of data is being used (i.e. using photographs, genetic data, population level?).
- Some small typos on lines 51 (of as), 63 (loses), 65 (in a reproductive), 91 (macroevolutionary) and 340 (research).