



# Peer Community In Evolutionary Biology

## Inbreeding compensates for reduced sexual selection in purging deleterious mutations

*Charles Baer* based on peer reviews by 3 anonymous reviewers

E. Noël, E. Fruitet, D. Lelaurin, N. Bonel, A. Ségard, V. Sarda, P. Jarne and P. David (2018) Sexual selection and inbreeding: two efficient ways to limit the accumulation of deleterious mutations. bioRxiv, ver. 3, peer-reviewed and recommended by Peer Community in Evolutionary Biology. <https://doi.org/10.1101/273367>

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Two evolutionary processes have been shown in theory to enhance the effects of natural selection in purging deleterious mutations from a population (here "natural" selection is defined as "selection other than sexual selection"). First, inbreeding, especially self-fertilization, facilitates the removal of deleterious recessive alleles, the effects of which are largely hidden from selection in heterozygotes when mating is random. Second, sexual selection can facilitate the removal of deleterious alleles of arbitrary dominance, with little or no demographic cost, provided that deleterious effects are greater in males than in females ("genetic capture"). Inbreeding (especially selfing) and sexual selection are often negatively correlated in nature. Empirical tests of the role of sexual selection in purging deleterious mutations have been inconsistent, potentially due to the positive relationship between sexual selection and intersexual genetic conflict. In their preprint, Noël *et al.* [1] report a cleverly designed, and impressively long-term, experimental evolution study designed to tease apart the relative contributions of selfing and sexual selection in purging deleterious mutations, using the self-compatible hermaphroditic snail *Physa acuta*. Hermaphroditism relieves at least some of the potential conflict between males and females because each individual expresses traits of each sex. The authors report a 50-generation (ten years!) evolution experiment with four experimental treatments: Control (C), in which snails reproduced by mass mating (allowing sexual selection) and the next generation was sampled randomly from offspring in proportion to maternal family size; Male-selection (M) in which snails reproduced by mass mating but maternal family size was held constant, removing the opportunity for fertility selection; Female fertility selection (F) in which snails mated monogamously but fertility selection was imposed, and selfing (S), in which snails reproduced by selfing every other generation, alternating with monogamy + fertility selection.

Juvenile survival was taken as the proxy for fitness and was measured for offspring of self-fertilization and of outcross matings. Each line type (C, M, F, S) was replicated twice. The results are enviably clear-cut: after 50 generations of evolution, outcross fitness dropped precipitously in the F treatment (monogamy+female fertility selection) and remained at ancestral levels in the other three treatments. Clearly, sexual selection in males is more efficient at purging deleterious alleles than is female fertility selection. Similarly, inbreeding depression was reduced in the S lines relative to the other treatments, indicating that, unsurprisingly, deleterious recessive mutations of large effect are purged under strong inbreeding. Outcross fitness in the S lines did not decline, in contrast to the F lines, which indicates that deleterious mutations are on average slightly recessive. Taken as a whole, this study by Noël et al. [1] provides a compelling empirical demonstration of the efficacy of both sexual selection and strong inbreeding as mechanisms of purging, and implicates sexual conflict as a potentially important factor in studies in which relaxation of sexual selection fails to result in purging.

### **References:**

[1] Noël, E., Fruitet, E., Lelaurin, D., Bonel, N., Segard, A., Sarda, V., Jarne, P., & David P. (2018). Sexual selection and inbreeding: two efficient ways to limit the accumulation of deleterious mutations. bioRxiv, 273367, ver. 3 recommended and peer-reviewed by PCI Evol Biol. doi: [10.1101/273367](<https://www.biorxiv.org/content/early/2018/08/07/273367.full.pdf>)

## **Reviews**

### **Evaluation round #2**

#### **Reviewed by anonymous reviewer 2, 26 June 2018**

The authors have provided a thoughtful and detailed response to the reviews, and I am satisfied with the revisions they have made to the manuscript.

Minor comments:

The symbol used to denote inbreeding depression in the figure 1 legend was formerly delta, and now seems to be an unusual symbol. Perhaps a symbol here is unnecessary, or "ID" could be used as in the Table 2 legend.

I recommend checking the in-text reference formatting for style and consistency.

### **Evaluation round #1**

DOI or URL of the preprint: <https://doi.org//273367>

Version of the preprint: 1

#### **Authors' reply, 19 June 2018**

[Download author's reply](#)

#### **Decision by Charles Baer, posted 19 June 2018**

##### **Revise**

Dear authors

The two reviewers have generally favorable opinions, but each makes substantive suggestions, which in my opinion the authors should address prior to sending a new version of the paper for recommendation.

In addition, the authors need to make the data available in a public format, either as supplemental material in the preprint or in a public data repository (e.g., Dryad).

### **Reviewed by anonymous reviewer 2, 07 March 2018**

Both sexual selection and inbreeding can purge genetic load, but the relative impact of these processes has not previously been investigated, to my knowledge. Noel et al. experimentally evolved populations of simultaneous hermaphrodites under conditions that limited selection on male or female function, and the level of inbreeding. By using a hermaphroditic organism they avoided the confounding effect of sexual conflict that have caused problems in related experiments. They find evidence that sexual selection through the male function prevents the accumulation of genetic load, but that regular inbreeding can provide a similar benefit. These results provide a useful confirmation of the hypothesis that sexual selection purges deleterious genetic variation, and have interesting implications for the evolution of mating systems.

The authors report on a well-controlled and labor-intensive experiment, and describe their hypotheses and findings clearly, with appropriate statistical analyses. The Discussion is thoughtful and well-organized. As such, I only have minor comments.

1. The authors note that juvenile survival and inbreeding depression in the control populations did not change between the two experimental time points, suggesting that the initial population was at equilibrium, which is useful in interpreting the changes observed in other groups of lines. It is not clear whether the authors have any data on juvenile survival and inbreeding depression from the start of the experiment (time zero); if so this would be a valuable addition.
2. To some extent the manuscript presents inbreeding and sexual selection as mutually-exclusive possibilities. The authors discuss the idea that alternating episodes of sexual selection and inbreeding could be highly effective in eliminating genetic load. Another way that these processes might both operate is if there is selection among gametes within selfing individuals. This might occur in plants, where genes are expressed in pollen. There is even reason to believe that a form of sexual selection among cells within yeast tetrads can purge mutations (e.g., Tazzyman et al. 2012, JEB). The authors could consider briefly noting these possibilities in the Discussion.
3. Some formatting corrections seem to be necessary in the figures and tables. In Figure 2 there are groups labeled "A1" and "A2", which I assume should be "S1" and "S2". In Tables 1 and 2 the P-values given in scientific notation seem to be missing multiplication symbols, e.g., " $3 \cdot 10^{-16}$ ".

### **Reviewed by anonymous reviewer 1, 07 March 2018**

This manuscript reports the temporal change in juvenile viability of several lines of a hermaphroditic snail differing in terms of sexual selection and inbreeding, with the overarching goal of testing the role of sexual selection vs. inbreeding in eliminating deleterious mutations, a question that has rarely been addressed. Overall this is a really nice study, with a careful experimental design and intriguing, original results.

My only relatively major suggestion is to try and provide more explicit theoretical expectations regarding the effects of sexual selection vs. inbreeding, in particular which types of mutations they are likely to purge most effectively. The prediction is clear for inbreeding (recessive mutations), but less so for sexual selection. For example, I think two extreme, caricatural situations may produce the same observed results: (1) inbreeding and sexual selection purge the same single pool of mutations (~all mutations), such that juvenile survival stays the same in treatments C, M and S or (2) inbreeding and sexual selection purge different, non-overlapping pools of mutations that each contribute equivalently to the genetic load, with the same outcome in terms of relative juvenile survival (=identical for C, M and S, all lines having purged half of the load). These two contrasting situations would however differ in terms of the absolute value of the load, which should be higher in situation (2) where only half of the load is purged in lines C, M or S vs. (1), where pretty much all the load is purged in these lines. A comparison with a fifth treatment, selfing + outcrossing with mass-mating

instead of monogamy, would have helped separating the two (note: I am saying this as a criticism of the experimental design, which is impressive enough as it is). I think it can be useful to be able to pinpoint which types of deleterious mutations can be purged by each process, as this would have consequences e.g. to discuss the benefits of mixed mating, but I may be wrong and I would very much appreciate the thoughts of the authors on this point. Obviously the authors are aware of the possibility that the two processes target different types of mutations (e.g. lines 392-418), and address part of this question via the study on recessive mutations/inbreeding depression, but it would be very helpful to introduce this possibility as soon as the introduction.

On a related note, the authors mostly distinguish two types of deleterious mutations (highly recessive vs. partially recessive, although they hint at other architectures for the load in the discussion); however, a number of sexually-selected traits are likely to be quantitative characters, for which mutations are not unconditionally deleterious. Instead, their effect on fitness depends, among other things, on the genotype at other loci controlling the character. Do the author have any expectations on how polymorphism at QTL may be impacted by sexual selection and inbreeding?

My frustration of not being able to single out easily the expectations may come from the fact that I am not a specialist of sexual selection, but that may be true of many future readers of the manuscript, and I think it would be helpful if the authors can improve this aspect.

A few minor additional comments:

Lines 123-124: this sentence ("occurs both to gain mates and among stored sperm...") is not clear

Line 229: inbreeding depression is a measure of the effects of inbreeding on fitness. I would therefore replace "sensitivity to inbreeding depression" (which makes no sense) with either "levels of inbreeding depression" or "sensitivity to inbreeding"

Line 230: I would re-order the sentence to read "was detected between G20 and G50 on average over all lines" (otherwise one may interpret the sentence as no differences among lines)

Figure 2: replace "A1" and "A2" with "S1" and "S2"

Note: I could not find the information that the data are available on an open online repository. This should be added, as I understand this is mandatory for a recommendation in PCI