Assortative mating, sexual selection and their consequences for gene flow in *Littorina*

Samuel Perini1,✉, Marina Rafajlović1, Anja M. Westram2, Kerstin Johannesson1, and Roger K. Butlin3

1 Department of Marine Sciences, University of Gothenburg, 40530 Gothenburg, Sweden  
2 IST Austria, Am Campus 1, 3400 Klosterneuburg, Austria  
3 Department of Animal and Plant Sciences, University of Sheffield, UK, S10 2TN

✉ Correspondence: [Samuel Perini <samuel.perini@gu.se>](mailto:samuel.perini@gu.se)

# TOADD

## Abstract

New species can form even though genes or migrants are being exchanged in the contact zone between two populations. Under a scenario where divergent populations are connected by gene flow, the establishment of complete reproductive isolation requires the joint action of multiple barriers to gene flow. One example where multiple barrier effects are coupled into one single trait (i.e. a multiple-effect trait) is when the trait that is the target of divergent natural selection does also mediate assortative mating. Theory suggests that this type of multiple-effect trait can have a strong contribution in the reduction of gene flow because it forms a direct link between divergent natural selection and assortative mating. Despite this clear expectation, there are only few cases where patterns of assortative mating have been described quantitatively and where their impact on gene flow has been determined. Two ecotypes of the coastal marine snail, *Littorina saxatilis*, occur in North Atlantic rocky-shore habitats dominated by either crab predation or wave action. They differ strongly in size and size-assortative mating has previously been documented and considered a significant contributor to reproductive isolation. Here, we analyse mating pattern with respect to size in intensively-sampled transects across boundaries between the habitats. We quantify the mating probability for a wide distribution of female to male size ratios by fitting models of the form often used in theoretical work on assortative mating. We show that the mating pattern is mostly conserved between ecotypes and it generates both assortment and sexual selection for small male size. What varies along the studied transects are the intensities of assortment and sexual selection as these are strictly dependent on the amount of size variance or the degree of size dimorphism. We then use simulations to predict the impact of assortative mating and sexual selection on the cline in size determined by divergent selection and on the barrier to gene exchange between ecotypes. The sexual components of isolation contribute to reproductive isolation between Crab and Wave ecotypes and the barrier to gene flow is mostly strengthen by stabilising sexual selection rather than assortment. Although the direction of sexual selection is the same between the two habitats and assortative mating seems to be ancestral to the ecotype formation, a multiple-effect trait such as size in *L. saxatilis* can be sufficient to maintain divergence between populations in the face of gene flow.

## Intro

Models of assortative mating typically assume that individuals mate with similar individuals with no difference in mating success. However, in natural populations where individuals mate assortatively, rare phenotypes undergo a mating disadvantage which can generate stabilising sexual selection (Kirkpatrick and Nuismer 2004).  
List of studies where different directions of sexual selection have been modelled (Servedio 2016).  
Sensory bias can be used as a case where sexual selection can take different selection and thus, either promote or impede complete reproductive isolation (Panhuis et al. 2001).

## Methods

## Results

## Discussion

1. Assortment and how it varies along clines  
   Multiple factors can cause assortative mating such as mate availability and mating constraints (Crespi 1989). Can natural selection influence mate availability with different intensity across the wave-crab habitat boundary? and what about constraints due to different shell sizes?  
   Natural selection can also decrease the variance of the target trait over time and the level of this reduction does not have to be equal along the environmental cline. As the trait variance is reduced, more in one habitat than the other, the strength of assortment will follow the same pattern of reduction because assortment depends on the covariance of the female and male trait. Therefore, our inference of the strength of assortment is actually the likely result of a differential effect of natural selection on the size distribution of Crab and Wave populations. Specifically, natural selection seems to act more strongly in the crab habitat compared to the wave habitat.
2. Same for SS with comments about sexual dimorphism
3. Lack of ecotype effects  
   The evolution of a mating trait can be under sexual selection as females express preferences for certain trait values. These preferences can have originated because the male trait is an indicator of fitness (Fisherian runaway) but they can have also evolved independently from the male mating signal. A typical example of the latter situation is when a male trait arise and it is favoured by the female sensory bias (Basolo 1990; Panhuis et al. 2001).
4. Ancestral nature of mating pattern  
   The absence of a clear and different mating pattern between Crab and Wave populations suggests that assortment by size was not simply a by-product of local adaptation but rather it existed before the formation of ecotypes. Imagine a population of snails where females tend to be overall larger than males. The common mating pattern would be for a female to pair more likely with a smaller male. This ancestral mating bias due to sexual size dimorphism can generate stabilising sexual selection for smaller than average male size. If both environmental conditions and size variation allow for local adaptation, two distinct populations would form due to divergent natural selection on size and the combination of the ancestral mating bias and the recent size divergence would reduce mating probability between the two ecotypes while maintaining the same mating pattern. Conversely, we would have expected an obvious difference between Crab and Wave mating pattern if assortment originated as a by-product of ecological speciation.
5. Barrier effects from Marina’s simulations
6. Some speculation about impact on the origin of ecotypes  
   A previous individual-based model predicted that pre-existing mating preferences were responsible for the inhibition of ecotype formation (Sadedin et al. 2009). Yet, in our simulations we were able to predict that assortative mating and sexual selection contribute to the reduction in gene flow between Crab and Wave populations. However, the sexual barrier is not a primary isolating component underlying the origin of ecotypes but it has instead evolved after local adaptation exploiting the pre-existing bias based on size. This is something that was not possible to test with our data but it is a likely hypothesis given the lack of ecotype effects on the mating pattern, the resulting direction of sexual selection from sexual size dimorphism and the evidence for the ecological barrier to gene glow between Crab and Wave populations. Another assumption that we make is that differences in size are correlated with differences in the female preferences as assortment in *L. saxatilis* is considered to be under the phenotype matching or similarity-like rule. The correlation or coevolution between male sexually selected traits and female preferences is the first requirement for sexual selection being involved in speciation (Panhuis et al. 2001).
7. Broader comparison (i.e. beyond Littorina) on multiple-effect traits and on barrier effects of assortment in HZs (compare to Irwin and to (Jiggins and Mallet 2000), maybe Wolf, maybe Gay et al.).  
   Speciation by sexual selection and assortative mating has been simulated in many theoretical studies but how this evolutionary process unfolds in natural populations remains a challenging task. Models of speciation benefit from … A general agreement across the different models of assortative mating is that … (Kopp et al. 2018). Also, prezygotic barriers … (Irwin 2019). These predictions have been supported by a few empirical studies on model organisms … For the majority of natural populations identifying the individual component of isolation, the genetic basis and the traits involved does still represent an obstacle for the evidence of the role of assortment and sexual selection in speciation. For example, … (Panhuis et al. 2001). Multiple-effect traits can be particularly effective for the reduction of gene flow, especially when they serve as a transfer between divergent natural selection and assortative mating. However, the presence of such a trait does not imply the evolution of complete reproductive isolation because depending on the nature of the preference and its relationship with the mating signal, two distinct populations can either merge or stall while they keep exchanging migrants/genes. If the preference itself is not under direct divergent selection across the hybrid zone and is not associated with the mating signal, the strength of the sexual barrier is predicted to be weak and have a marginal contribution to population divergence with gene flow.

The underlying theory agrees on what is the most favourable scenario for the split of two species that are reproductively isolated and what is the scenario where speciation will be inhibited. There are examples in the wild of these two extremes but these are rarely encountered. Most of the biological cases will occur in between and they will also be influenced by a combination of components of isolation. For example, starting from a relatively simple scenario (Servedio 2016) … Moving onto hybrid zones (Irwin 2019) …

# References

Basolo, A. L. 1990. Female preference predates the evolution of the sword in swordtail fish. Science 250:808–810.

Crespi, B. J. 1989. Causes of assortative mating in arthropods. Animal Behaviour 38:980–1000.

Irwin, D. E. 2019. Assortative mating in hybrid zones is remarkably ineffective in promoting speciation. bioRxiv 637678.

Jiggins, C. D., and J. Mallet. 2000. Bimodal hybrid zones and speciation. Trends in Ecology & Evolution 15:250–255.

Kirkpatrick, M., and S. L. Nuismer. 2004. Sexual selection can constrain sympatric speciation. Proceedings of the Royal Society of London. Series B: Biological Sciences 271:687–693.

Kopp, M., M. R. Servedio, T. C. Mendelson, R. J. Safran, R. L. Rodrı́guez, M. E. Hauber, E. C. Scordato, L. B. Symes, C. N. Balakrishnan, D. M. Zonana, and others. 2018. Mechanisms of assortative mating in speciation with gene flow: Connecting theory and empirical research. The American Naturalist 191:1–20.

Panhuis, T. M., R. Butlin, M. Zuk, and T. Tregenza. 2001. Sexual selection and speciation. Trends in ecology & evolution 16:364–371.

Sadedin, S., J. Hollander, M. Panova, K. Johannesson, and S. Gavrilets. 2009. Case studies and mathematical models of ecological speciation. 3: Ecotype formation in a swedish snail. Molecular Ecology 18:4006–4023.

Servedio, M. R. 2016. Geography, assortative mating, and the effects of sexual selection on speciation with gene flow. Evolutionary Applications 9:91–102.