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Editorial: Advantages, limitations, and evolutionary constraints of asexual reproduction: An empirical approach

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Editorial on the Research Topic

Advantages, limitations, and evolutionary constraints of asexual reproduction: An empirical approach

Asexual proliferation is likely the primary mode of reproduction. It is ubiquitous in bacteria (Koch, 2002) and prevails in unicellular eukaryotes. It does not preclude genetic recombination, which in its simple form exists in procaryotes (Graumann and Premstaller, 2006), and in eukaryotes has evolved into the more complex process of meiosis. Asexual reproduction repeatedly evolved in all animal phyla (Knobil and Neill, 1998), but sex and recombination generally prevail (Otto, 2021). This fact points to the evolutionary importance of sex; however, a complete unifying theory of the various mechanisms behind the advantage of sexual vs. asexual proliferation is still in development (Maynard-Smith, 1978; Otto, 2021). Most interesting is why we don't see many animal systems combining the advantages of both modes of reproduction, such as cyclical parthenogenetic arthropods. While such rarity might seem counterintuitive to a simplistic understanding of natural selection, it is likely a result of evolutionary constraints (Kearney et al., 2022). Better insight into such complexity can be gained from studying the episodic development of asexual reproduction in different animal phyla.

Four papers included in the Research Topic "Advantages, Limitations, and Evolutionary Constraints of Asexual Reproduction: An Empirical Approach" demonstrate the diversity of patterns of asexual reproduction and suggest that it may evolve in parallel even within a single species. The empirical examples ranging from Cnidaria to insects and mollusks show both the diversity of the pathways driving asexual reproduction as well as the dependence of these pathways on the genetic architecture of an organism.

The study by Wang et al. explores the factors affecting reproduction in jellyfish. All Cnidaria can reproduce asexually (Ruppert et al., 2004), and this trait seems to be plesiomorphic for the entire group. In polyp strains of *Aurelia*, the authors identified six types of asexual reproduction. They showed experimentally that the type of reproduction, reproduction rates, and jellyfish blooming, depend on temperature and feeding; simultaneously, conspecific polyps from distant regions show different norms of reaction. The authors demonstrated a high plasticity of reproductive mode in the most primitive group of the studied metazoans, and its dependence on the environment and genetic architecture.

The organisms studied in three other papers belong to phyla where asexuality develops as a derived reproductive mode. Most insects reproduce sexually, with some exceptions (Gullan and Cranston, 2005). In mollusks, asexual reproduction does exist in some species only (Ponder and Lindberg, 2008).

In hymenopterans, females usually deposit unfertilized eggs producing haploid males, which then fertilize females and hence diploid recombinant females are emerging (Heimpel and De Boer, 2008). However, endoparasitic bacteria may trigger a switch of reproductive mode to true automixis (meiosis without fertilization; Mogie, 1986). Du et al. studied the diversity of reproductive modes in a parasitoid wasp. By combining cytological observations with the analysis of microsatellite genotypes, they showed that the reproduction of parthenogenetic females is apomictic, i.e., different from bacterial-induced parthenogenesis. The authors discuss whether apomixis may have any selective advantage. Indeed, although apomixis may accumulate deleterious mutations, it does not necessarily lead to the loss of heterozygosity and may be advantageous under certain conditions. This research demonstrates high diversity of pathways of shifting to parthenogenesis within a single species and is the first record of non-bacterial-induced apomixis in hymenopterans.

Kuhn et al. developed a computer simulation of heterozygosity loss during automixis and analyzed the occasional sexual production of queens in colonies of ants. The haploid males from a separate lineage fertilize the queens, which then produce sterile workers; reproduction of the queen lineage is thought to be strictly parthenogenetic *via* automixis. However, automixis causes a gradual loss of heterozygosity. The authors estimated the expected rates of heterozygosity loss and, alternatively, assumed that rare males produced by the queen may fertilize the females. The results suggest that 1–2% of progeny develop from fertilized eggs. This study is particularly important since it demonstrates that sexual reproduction might be easily missed during observations of natural populations, leading to wrongly concluding its absence. The same methodology can be applied to other parthenogenetic lineages, where sexual reproduction has not been recorded so far.

The paper of McElroy et al. is a case study of parthenogenesis, using transcriptome sequencing of RNA extracted from ovaries. The paper suggests that differences in gene expression follow patterns of spatial isolation between populations of aquatic snails, rather than reflecting differences between the lineages' reproductive modes. There are clusters of genes with expression patterns associated with asexual reproduction, involved in DNA synthesis and chromosome movement; genes related to the control of meiosis did not show expression differences related to reproductive mode. Only part of this gene cluster was consistently associated with reproductive mode, and the others separated sexual and asexual breeders from specific populations. These results are evident for a complex mechanism of switching between the reproductive

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modes, associated with the entire genetic architecture. Although the spontaneous production of parthenogens is not known for the studied organism, this study shows that it happened repeatedly in different geographic populations.

Overall, the studies included in this theme use a range of methodologies-ecological experiments, population genetic analysis, cytological observations, computer simulation, and the analysis of gene expression. And still, all send the reader the same important message: the mode of reproduction is a plastic feature, changing occasionally within the same species and even the same population, as a joint reaction to environmental influences and genetic architecture. There is hardly a universal mechanism determining the switch between the reproduction modes; diverting to asexual reproduction may be realized in different ways. Another message is that, despite rapidly developing methodologies, we understand too little about the true reasons for the reproductive mode variation, and can only state that this is a result of the joint effect of natural selection and evolutionary constraints. More studies are essential to search for general features of reproduction mode variation, persistent throughout the entire tree of life.

Author contributions

All authors listed have made a substantial, direct, and intellectual contribution to the work and approved it for publication.

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