Sex and Asex: A clonal lexicon

Maria E. Orive
Department of Ecology and Evolutionary Biology
University of Kansas
1200 Sunnyside Ave.
Lawrence, KS 66045
morive@ku.edu

Stacy A. Krueger-Hadfield
Department of Biology
University of Alabama, Birmingham
1300 University Blvd.
Birmingham, AL 35294
sakh@uab.edu

Abstract

Organisms across the tree of life have complex life cycles that include both sexual and asexual reproduction or that are obligately asexual. These organisms include ecologically dominant species that structure many terrestrial and marine ecosystems, as well as many pathogens, pests, and invasive species. We must consider both the evolution and maintenance of these various reproductive modes and how these modes shape the genetic diversity, adaptive evolution, and ability to persist of the species that exhibit them. Thus, having a common framework is a key aspect of understanding the biodiversity that shapes our planet. In the 2019 AGA President's Symposium, *Sex and Asex: The genetics of complex life cycles*, researchers investigating a wide range of taxonomic models and using a variety of modes of investigation coalesced around a common theme – understanding not only how such complex life cycles may evolve, but how they are shaped by the evolutionary and ecological forces around them. In this introduction to the Special Issue from the symposium, we give an overview of some of the key ideas and areas of investigation (a *common clonal lexicon*, we might say) and introduce the breadth of work submitted by symposium participants.

Key words: sexual reproduction, asexual reproduction, clonal reproduction, partial clonality, evolution of sex

Sex and Asex – towards a common lexicon

The reproductive system (*sensu* Barrett 2011) is the main feature that determines the population structure of a given taxon. The prevailing mode of reproduction is thus a key life cycle component. Many organisms across the tree of life exhibit complex life cycle variation that often includes both sexual and asexual reproduction. Some organisms, such as *Daphnia*, sequentially switch between sexual and asexual forms. Others undergo both types of reproduction in the same life cycle stage, such as many plants, macroalgae, and marine invertebrates. And while many recently derived asexual lineages exist, bdelloid rotifers and a relatively small number of other taxa are unique in they seem to have secondarily lost all sexual reproduction long ago.

Entire symposia could be dedicated to simply defining sexual versus asexual reproduction. Indeed, biologists use the word *sex* to describe at least four different biological phenomena: these include the existence of separate sexes (or dioecy/dioicy); the fusion of two dissimilar gametes (or anisogamy); meiosis, which is a specialized form of cell division that leads to the production of reduced gametes; and genetic recombination itself (Orive 2020). Sex is also often thought of as two distinct processes: meiosis and syngamy (the joining of gametes, or fertilization). We will see that there are asexual forms of reproduction that have one, but not the other of these processes.

Similarly, there are a bewildering array of biological processes that fall under the definition of *asexual reproduction* (Table 1). These can be grouped in many different ways – for example, the distinction can be made between *agametic* forms of asexual reproduction (often referred to as vegetative reproduction in the plant literature, de Meeus et al. 2007), which only include somatic tissues, and *gametic* forms, which involve germline tissues (Hughes and Cancino 1985, Hughes 1989, de Meeus et al. 2007). Agametic modes of asexual reproduction are not completely distinct from one another and often grade into one another. For example, in considering clonal growth and fragmentation, there are many organisms that show clonal growth by iteration of modules (zooids in corals, seagrass shoots, etc.). In corals, for example, these new modules may arise through budding or partial fission. Modules may stay physiologically connected, but sometimes fragmentation occurs, leading to new, physically distinct individuals. Fission and budding are both forms of asexual and clonal reproduction that involve a separation of tissue into a *parent* and an *offspring.* The difference between these two modes can be a matter of degree, with forms of binary fission resulting in two physically distinct individuals that are (apparently) identical. Throughout, we will use the term *clonal* to refer to the types of asexual reproduction that result in genetically identical offspring.

There are also agametic forms of asexual reproduction that occur via the formation of specialized somatic tissues that give rise to the new (genetically identical) individual. One example is encapsulation, where there is the production of many encapsulated dormant bodies from somatic tissues that give rise to new organisms. This is seen in the production of gemmules by sponges. Another example is the formation of gemma or bulbils in plants, where there is growth of new plants from a callus of undifferentiated dispersible tissue or growth of specialized plantlets that are distinct from the parent and are capable of being dispersed (Tiffney and Niklas 1985).

Finally, *polyembryony*, which is defined as the production of more than one embryo from a single zygote, falls under the broad umbrella of agametic asexual reproduction, as it is the differentiation and division of the embryonic cells that leads to an increase in offspring number. This is seen across a wide range of organisms, from plants and certain bryozoans, to parasitic hymenopterans, red algae, and finally even in vertebrates, where the production of identical quadruplets from a single zygote in the nine-banded armadillo is a form of clonal iteration of the product of sexual reproduction (Loughry et al. 1998).

Gametic forms of asexual reproduction include the various types of parthenogenesis. *Parthenogenesis*, or development from an unfertilized egg, can be clonal or aclonal. The term is widely used for animal asexual reproduction, but some forms produce offspring that have genetic variation and so are not strictly clonal (for a detailed review, see de Meeus et al. 2007). In some forms of parthenogenesis, sometimes termed *apomictic parthenogenesis*, meiosis is suppressed and the egg undergoes a single mitotic maturation division. This produces genetically identical offspring and is therefore a clonal form of reproduction. In contrast, in automictic forms of parthenogenesis, meiosis occurs along with a mechanism for restoring the diploid genome (for example, endomitosis, suppression of first or second meiotic division, fusing of pronuclei, or fusion of nuclei at first cleavage division). Thus, *automictic parthenogenesis* includes some sexual processes (recombination) and excludes others (syngamy) and is therefore not strictly clonal in the sense that it does not produce genetically identical progeny. Just to complicate things further, there are forms of automictic parthenogenesis where genetic recombination is suppressed, resulting in functional apomixis (Bell 1982), so that there, too, the distinction is not always a clean one. Confusingly, different terminology is used in plants and other non-animal taxa. The term *apomixis* (or *agamospermy*) is used for the production of seeds without fertilization, although in *pseudogamous apomixis*, pollen is necessary for the proper development of the endosperm (as opposed to *autonomous apomixis*, where pollen is not required). Further, apomictic embryos in angiosperms can be derived from maternal genetic material (termed *gametophytic apomixis*) or from somatic cells (*adventitious embryony*) (Whitton et al. 2008).

The products of clonal reproduction, or *ramets*, are often ecologically and demographically quite distinct from the products of sexual reproduction (new zygotes or *genets*). This is especially true for such types of clonal reproduction as fragmentation, fission, budding, and the formation of gemmae or bulbils. For example, consider the difference between the planktonic larvae of a coral, formed through sexual reproduction, with that of a new coral zooid, formed by budding or fission. The two types of offspring have different morphologies, dispersal capacities, and survival probabilities. On the other hand, there are types of clonal reproduction that produce individuals very similar to those produced by sexual reproduction. Clonal reproduction by some forms of parthenogenesis can give rise to offspring that are often morphologically indistinguishable from offspring produced sexually.

The different types of offspring possible in organisms with both sexual and asexual reproduction (*partial clonality*), and the fact that the products of clonal reproduction may remain physiologically connected (as in coral colonies) or separate (as in budding in hydra), create a need to carefully define what is meant by an *individual* (Buss 1985, 1987). The production of ramets may be considered either as a process of growth (an increase in the soma derived from the original zygote) or as a process of reproduction (formation of new individuals). Since physiologically separated individuals are to some degree independent (they survive or do not survive, etc.), clonal reproduction that produces physiologically distinct individuals is most often considered reproduction and not growth, although here, as with other definitions, the distinction is not always clear-cut. For example, a plant may put out stolons that are initially connected, but these connections may be lost via exogenous or endogenous means.

The difference between the genetic individual, or *genet*, and the physiologically distinct or demographic individual underlies many important ecological and evolutionary ideas. An example is in considering definitions of generation time. A common definition for generation time in a stationary population is the mean age of reproduction for individuals (Charlesworth 1980). For a population that is changing in size, definitions of generation time include the mean age at reproduction for a cohort of individuals or the mean age of the parents of a cohort of newborns for a population with a stable age (or stage) distribution. If only sexual reproduction is considered for resetting the generation, age is then the time since the parent was itself was produced sexually, giving a *meiotic generation time*, or a time from zygote to zygote, even if cycles of asexual or clonal reproduction exist (Orive 1993). However, it is also possible to consider the mean age at which new demographic individuals are produced, either sexually or clonally, where age would now indicate the time since the parent itself was produced sexually or clonally (see Orive 1993, Appendix A).

An important difference between gametic and agametic asexual reproduction potentially lies in the fate of mutations (Figure 1). In gametic forms of asexual reproduction, each offspring arises from one cell (ovum); therefore, any mutation will be found in all of the cells of the adult individual (Figure 1a). Future progeny of the individual will all carry the mutation, if they themselves are produced by parthenogenesis, versus only a half if produced by sexual reproduction (in diploids). Agametic offspring arise from a group of cells, with the total number of cells involved varying with the type of reproduction and species. The amount of representation in the adult soma for any mutations will therefore vary, as will the probability that future clonal and sexual offspring will carry the mutation (Figure 1b). The details of development, the manner in which cell lines segregate, and the potential role of within-individual selection between cell lineages will all play vital roles (Klekowski 1988, Otto and Orive 1995, Otto and Hastings 1998, Orive 2001). For example, recent empirical work in plants has found less apical meristem cellular division than expected (leading to fewer mutations) as well as mechanisms for an increased opportunity for within-individual selection via patterns of stem cell divisions that promote genetic heterogeneity when mutations do arise (Burian et al. 2016). Data consistent with this lower-than-expected mutation rate have been found in oak (Schmid-Siegert et al. 2017) and in Sitka spruce (although with a high per-generation mutation rate due to their very long generation times; Hanlon et al. 2019).

The form that this within-individual selection takes will have important consequences for the eventual fate of somatic mutations, depending, for example, on whether hard or soft selection is acting on the contribution of the multiple within-individual genotypes to whole organism reproduction (Slatkin 1984). In organisms such as plants, somatic mutations have been proposed as an additional source of genetic variation within a meiotic generation for natural selection to act upon, allowing long-lived plants a potential means to keep up with their often shorter-lived herbivores and pathogens (Whitham and Slobodchikoff 1981, Gill 1986, Sutherland and Watkinson 1986, Gill et al. 1995, Folse and Roughgarden 2011). A possible role in generating novel genetic diversity that can fuel adaptation is long-lived corals has also been proposed (van Oppen et al. 2011). For plants and other organisms with partial clonality, somatic mutations may also eventually be expressed in gametes for sexual reproduction, or in independent clonal offspring, adding to the genetic variation of the population as well as to the genetic variation within an individual (Orive 2001). Whether somatic mutations eventually add to population level variation is an open question. For example, in corals, there is evidence that more than one genotype in a colony can reproduce in some species (*Acropora hyacinthus*, Schweinsberg et al. 2014), while it appears that colony-specific mutations are not transferred to gametes in others (*Orbicella faveolata*, Barfield et al. 2016, but see also Olsen et al. 2019).

Clonal forms of asexual reproduction result in many important biological consequences. These can be broadly grouped into ecological or demographic consequences, and genetic consequences (although such a division is necessarily somewhat artificial). For organisms that are spatially dispersed in a heterogeneous environment, clonal reproduction allows a genet to take advantage of spatially dispersed resources and to survive localized mortality and predation (Cook 1983, Harper 1985). Ramets may die due to accidents, predation, or other reasons, but the genet may survive. Additionally, clonal organisms, like self-compatible monecious/monoicous organisms, have an advantage when dispersing to new areas (Baker 1955). If an individual finds itself in an unexploited patch, it has the ability to spread in the absence of a mate (but may suffer inbreeding depression under partial sexual reproduction; e.g., Reusch 2001, Somme et al. 2014). The phenomenon of *geographical parthenogenesis* (Vandel 1928, Gaggiotti 1994, Tilquin and Kokko 2016) predicts that asexuality is more likely to occur in habitats that are in some sense “marginal,” implying that some sorts of spatial structure may favor asexuality and at least allow the co-existence of sexual and asexual forms across a complex distribution of habitats (e.g., Peck et al. 1999). Both field studies (Dorken et al. 2001, aquatic plant; Karako et al. 2002, sea star; Tatarenkov et al. 2005, brown seaweed, Krueger-Hadfield et al. 2013, red seaweed) and laboratory experiments (Lagator et al. 2014, *Chlamydomonas*) point to empirical evidence for a relationship between the ability to persist in marginal, low quality, or novel habitats and clonal forms of reproduction.

Classically, the *frozen niche* hypothesis has been invoked to explain the association between clones and marginal environments (Vrijenhoek 1979), arguing that only certain genotypes can fare well in these environments. Clonal reproduction efficiently "freezes" part of the genetic variation that is generated by the ancestral (sexual) gene pool. In the case of heterozygote advantage, or overdominance, sexual reproduction leads to *segregational load*, in that heterozygous individuals produce both heterozygous offspring and less fit homozygous offspring. Clonal reproduction avoids segregational load, although how important a role this may play in natural populations is unknown (Haag and Roze 2007). Fixed heterozygosity is a predicted feature of clonal or partially clonal reproduction (Balloux et al. 2003), preserving allelic diversity within an individual (although this may be lost by mitotic recombination over the long term), while an overall loss of genetic diversity due to a decrease in effective population size (Orive 1993) and the loss of homozygous genotypes (Balloux et al. 2003) may also be expected. Recent work in aphids and algae have found evidence of increased heterozygosity in asexual populations (Halkett et al. 2005, Guillemin et al. 2008, Krueger-Hadfield et al. 2016). Furthermore, in truly clonal forms of asexual reproduction, offspring inherit an entire genome, and thus interactions across loci (epistatic interactions) are preserved. For phenotypic traits with multilocus inheritance, clonal offspring can thus inherit non-additive genetic variation, in addition to the additive genetic variation typically inherited under sexual reproduction in random mating populations. This additional source of inherited phenotypic variation can have important consequences under adaptation following environmental change (Orive et al. 2017).

Long-term asexual reproduction is expected to lead to within-individual allelic sequence divergence resulting from the suppression of segregation (*Meselson effect*; Welch and Meselson 2000, Butlin 2002). A recent review of empirical studies that considered species with cryptic sex found inconsistent evidence for this type of allelic divergence (Hartfield 2016), although it is unclear whether this lack of divergence arises from gene conversion, mitotic recombination, or other genome-wide processes. A definitive determination of whether or not sexual reproduction is occurring in a lineage can be extremely difficult, with various molecular- and organismal-based approaches sometimes giving conflicting signals (Schurko et al. 2008). In this special issue, Jaron et al. (2021) characterize the genomic features in the published genomes of 26 parthenogenetic animal species, that represent at least 18 independent transitions to asexual reproduction. These included patterns for the accumulation of deleterious mutations and positive selection, intra-genomic (individual-level) heterozygosity, and the dynamics of transposable elements, as well as more unusual genomic features observed in individual parthenogenetic species. They show that no single genomic feature was replicated across the majority of these transitions, suggesting that many of these key genomic features are lineage specific rather than general features of the transition to asexual reproduction in animals.

Additionally, asexual reproduction can avoid the so-called *two-fold cost of sex* that arises from having male individuals (or male reproductive function) in a population instead of a population made up entirely of parthenogenetic females (Maynard Smith 1978). It is not clear, however, that agametic clonal reproduction brings the same two-fold advantage since offspring from agametic reproduction are often not readily comparable to offspring produced sexually. For example, offspring produced by budding are often considerably larger than sexually produced zygotes, so that each clonal offspring may have a greater energetic cost than a sexual offspring. Furthermore, pseudogamous apomicts still pay a cost of male function (e.g., producing pollen necessary to fertilize the endosperm). The exact two-fold advantage can only come about when the number of eggs (or the number of new offspring) produced by a female is the same regardless of whether they are produced sexually or not.

It is often thought that a major disadvantage of clonal reproduction is in the production of genetically homogeneous offspring in the face of heterogeneous selection regimes, either through spatial or temporal variation (Silander 1985, Hughes 1989). Another possible cost of agametic clonal reproduction is high *mutation load* due to a total deleterious mutation rate that is the sum of the rates across the many cells of the offspring (Kondrashov 1994), although this may be limited to organisms with obligate agametic clonal reproduction. This extra mutation load may, however, be greatly reduced or eliminated by within-individual somatic selection or other life history aspects (Otto and Orive 1995, Marriage and Orive 2012).

The Symposium

The last few decades have witnessed increasing amounts of theoretical and empirical work, including genetic and genomic studies, that approach an amazing breadth of questions regarding sexual and asexual reproduction. There has also been a growing appreciation of the importance of partial clonality, a characteristic of many taxa that are integral to global biogeochemical cycles and are foundational species in important ecosystems (e.g., corals or seagrasses, Schön et al. 2009). The balance between these two reproductive modes strongly influences the ecological success of a species (Halkett et al. 2005, Silvertown 2008) and the ability to track environmental change via phenotypic evolution (Orive 2017). In addition, many human pathogens and agricultural pests are clonal or partially clonal (e.g., aphids, malaria, phytophthora; de Meeus et al. 2007). The evolutionary trajectories of these taxa may have major consequences for ecosystem functioning and for human health and development. Thus, the lack of consensus and a generalized synthesis of our knowledge is troubling. In an effort to bring together a diverse suite of approaches and taxonomic models, the American Genetic Association Presidential Symposium in Portland, OR in 2019 focused on *Sex and Asex: The genetics of complex life cycles*.

In her 2019 AGA Key Distinguished lecture, published in this special issue, Otto (2021) described a major challenge facing asexual populations. With little to no recombination, selection at any one locus becomes much less effective because the fate of an allele is so strongly dependent on its genetic background. This *selective interference* provides a framework for understanding the various costs of asexual reproduction, including the loss of competing beneficial mutations (the Fisher-Muller or clonal interference hypothesis) and the loss of the best genotype in the presence of deleterious mutations (Muller's ratchet). This framework encompasses all forms of selection and helps account for the evolution and maintenance of sex, as well as the short-lived nature of many fully asexual lineages.

Recent work in the evolution of complex life cycles has investigated which factors favor the maintenance of sexual or asexual reproduction, including which environmental or evolutionary conditions. Many of these have focused on the roles played by pathogens, predators, resource availability, and various geographic/environmental patterns (e.g., invasions). In this special issue, Brown et al. (2021) consider how the frequency of coercive males affect the frequency of sexually versus asexually produced progeny, and find evidence for reproductive polymorphism within populations of facultatively parthenogenetic Opiliones. In mayflies, Liegeois et al. (2021) find that the capacity for parthenogenesis may come at a cost for sexual reproduction, in the form of a trade-off between hatching success of parthenogenetic and sexual eggs. They argue that parthenogenesis may be selected nevertheless due to the mate limitation frequently faced by females in this ephemeral group of insects. Pathogens have been conclusively implicated in shaping patterns of sexual and asexual reproduction via Red Queen processes in many organisms, including the snail *Potamopyrgus antipodarum* (Gibson et al. 2018). This same system is considered here by Million et al. (2021), in a study considering SNP diversity, DNA content, and pathogen susceptibility in clonal lineages of *P. antipodarum*. They find high levels of diversity among the asexual snails, especially for DNA content, suggesting rapid genome evolution in these asexuals.

The relative roles of hybridization, asexuality, and speciation in the evolution of asexual species from sexual ancestors has been widely investigated across a range of organisms, including plant species in the genus *Boechera* and *Crepis* (Beck et al. 2011, Hersh et al. 2016), and in many vertebrates (e.g., loach fishes, Janko et al. 2012). In this issue, Rushworth et al. (2021) point out the importance of studying the common traits that are obligately correlated with asexuality in some taxa, including hybridization and polyploidy, and consider the fitness consequences of hybridization (reduced fitness due to interspecific reproductive isolation) as an important factor that may shape the evolution of asexuality in the genus *Boechera*.

Researchers have increasingly asked questions regarding how complex life cycles involving both sexual and asexual reproduction (i.e., partial clonality) influence evolutionary and ecological dynamics, including adaptation under changing environments, and questions of dispersal and clonal spread for invasive species. In this issue, Stoeckel et al. (2021) and Krueger-Hadfield et al. (2021) carry out a paired set of theoretical and empirical studies to consider how haplodiplontic life cycles (with somatic development in both haploid and diploid individuals) are affected by partial clonality. The relative sizes of the haploid and diploid genetic pools for population sampling and the degree of clonality arise as key parameters affecting genetic and genotypic diversity. Although only a handful of studies have genotyped both haploid and diploid stages, empirical data broadly support the theoretical predictions proposed by Stoeckel et al. (2021). Lozada-Gobilard et al. (2021) consider the importance of both reproductive mode (clonal versus nonclonal) and dispersal mechanism for shaping plant metacommunities occurring in island-like kettle-hole habitats. Ryan et al. (2021) offers an intriguing look at how reproductive plasticity, in the form of temperature-dependent fission, may help shape the historical distribution of clones and genetic diversity in the non-native range of an invasive sea anemone.

Investigations of the processes underlying sexual and asexual reproduction have led to important discoveries regarding aspects of soma/germline differentiation and the role of somatic mutations in generating both within- and between-individual genetic variation (Lopez and Palumbi, 2020). As part of this special issue, Collens and Katz (2021) argue for the role of genetic conflicts with mobile genetic elements in the evolution of the eukaryotic genome, with sex (meiosis) evolving within the context of the development of germline-soma distinctions in the last eukaryotic common ancestor, as a process that resets the germline genome by regulating or eliminating somatic genetic material.

And in the absence of sex, what happens to the rate of evolution in obligate asexuals? Does selective interference limit their evolutionary potential? Recent work has pointed to the possibility that other genomic processes such as amitosis (in *Tetrahymena*, Zhang et al., bioRxiv 794735) or gene conversion (in bdelloids, Welch and Meselson 2000) may play important roles in mitigating the possible long-term genomic consequences of strictly asexually or very rarely sexual reproduction. In this issue, Hartfield (2021) points out that under very rare sex, the coalescent history for pairs of alleles (and thus our ability to infer evolutionary history via sequence information) depends very strongly on the frequency of sex and on the rate of mitotic gene conversion, rather than on population size.

The 2019 AGA President's Symposium *Sex and Asex: The genetics of complex life cycles* scratched the surface of the taxonomic breadth of asexual and partially clonal organisms. We have only hinted at the wide expanse of experimental and theoretical questions that intrigue biologists interested in understanding the underpinnings of eukaryotic diversity. As Aanen et al. (2016) introduced in their own special issue on the underappreciated diversity of reproduction, it is when we dare to look that we see patterns shared broadly across taxa while others may be entirely unique. The collection of papers contributed to this special issue present a compelling argument that in order to understand the maintenance of biodiversity, we must continue to unravel the enigma of sexual reproduction and the myriad ways organisms reproduce.

Funding

This work was supported by the National Science Foundation (NSF DEB-1923495 to MEO), and by start-up funds from the University of Alabama at Birmingham and the Norma J. Lang Early Career Fellowship from the Phycological Society of America to SAKH.

Acknowledgments

The 2019 AGA President's Symposium would never have been possible without the tireless work and boundless energy of AGA Manager and Journal of Heredity Managing Editor Anjanette Baker, and we gratefully thank her for everything! In addition, preparation of this special issue occurred during the COVID-19 pandemic, and Special Issue Associate Editor M.E. Orive would like to express her deepest appreciation to all of the reviewers who worked so hard to keep the work going in the face of so many stressful situations, and to the authors of these papers, who persevered in the face of delays and difficulties. S.A. Krueger-Hadfield also would like to express her gratitude to M.E. Orive for her mentorship and collaboration on the clonal lexicon idea through many iterations. In addition, the authors thank S.P. Otto, whose thoughtful comments greatly improved the final version of this manuscript.

Table 1. Types of asexual reproduction

mode of reproduction	description	example organisms
agametic reproduction *(clonal)*	creation of new individuals from somatic tissues	
• clonal growth and fragmentation	characteristic of many modular organisms; in plants, can include formation of rhizomes, basal and root suckering, branch arching, and lianas	sponges, corals, algae, many plants
• fission	usually endogenous process involving division of parental organism	protozoa, annelids, turbellarian flatworms, anemones, some fungi
• budding	formation of new individuals from parental tissue due to growth and cellular differentiation; does not require division of parental individual	hydrae, some sponges, colonial hydroids, bryozoans, colonial ascidians, some fungi
• polyembryony	production of more than one embryo from a single zygote	plants, certain bryozoans, parasitic hymenopterans, vertebrates, red algae
• encapsulation	production of many encapsulated dormant bodies from somatic tissues which later give rise to new organisms	sponges (production of gemmules), algae
• gemma/bulbil	growth of new plants from a callus of undifferentiated dispersible tissue or growth of specialized plantlets that differ from the parent and are capable of being dispersed	plants
gametic reproduction	creation of new individuals from gametic tissues	
• parthenogenesis	development from an unfertilized egg	algae, plants, insects, rotifers, crustaceans, some vertebrates
apomictic parthenogenesis *(clonal)*	meiosis is suppressed and egg undergoes single mitotic maturation division; since no genetic recombination, this is a true clonal mechanism	
automictic parthenogenesis *(aclonal)*	meiosis occurs along with a mechanism for restoring the diploid genome	

References: Bell 1982, Hughes and Cancino 1985, Tiffney and Niklas 1985, Hughes 1989, de Meeus et al. 2007

References

Aanen, D., Beekman, M., and H. Kokko (2016). Weird sex: the underappreciated diversity of sexual reproduction. Phil. Trans. R. Soc. B. 371: 20160262

Baker HG. 1955. Self-compatibility and establishment after 'long-distance' dispersal. Evolution 9: 347–349.

Balloux, F., Lehmann, L. and de Meeus, T. (2003) The population genetics of clonal and partially clonal diploids. Genetics 164:1635-1644.

Barfield, S., G. V. Aglyamova, and M. V. Matz. (2016) Evolutionary origins of germline segregation in Metazoa: evidence for a germ stem cell lineage in the coral *Orbicella faveolata* (Cnidaria, Anthozoa). Proc. Biol. Sci. 283:20152128.

Barrett S.C.H. (2011) Why reproductive systems matter for the invasion biology of plants. In *Fifty Years of Invasion Ecology: The Legacy of Charles Elton* (Ed. Richardson DM), pp.195-210.

Beck, J.B., Alexander, P.J., Allphin, L., Al-Shehbaz, I.A., Rushworth, C., Bailey, C.D., and M.D. Windham (2011). Does hybridization drive the transition to asexuality in diploid Boechera? Evolution 66:985-995.

Bell, G. (1982) *The Masterpiece of Nature*. University of California Press, Berkeley.

Brown, T.A., Tsurusaki, N., and M. Burns (2021). Genomic determination of reproductive mode in facultatively parthenogenetic Opiliones. Journal of Heredity [special issue]

Burian, A., Barbier de Reuille, P., and Kuhlemeier, C. (2016) Patterns of stem cell divisions contribute to plant longevity. Current Biology 26:1385-1394.

Buss, L.W. (1985) The uniqueness of the individual revisited, in *Population Biology and Evolution of Clonal Organisms* (J.B.C. Jackson, L.W. Buss and R.E. Cook, eds.), pp. 467-505. Yale University Press, New Haven.

Buss, L.W. (1987) *The Evolution of Individuality*. Princeton University Press, Princeton.

Butlin, R. (2002) The costs and benefits of sex: new insights from old asexual lineages. Nature Reviews Genetics 3:311-317.

Charlesworth, B. (1980) *Evolution in Age-Structured Populations*. Cambridge University Press, Cambridge.

Collens, A. and L. Katz (2021). Opinion: Genetic conflict with mobile elements drives eukaryotic genome evolution, and perhaps also eukaryogenesis. Journal of Heredity [special issue]

Cook, R.E. (1983) Clonal plant populations. American Scientist 71:244-253.

deMeeus, T., Prugnolle, F., and Agnew, P. (2007) Asexual reproduction: Genetics and evolutionary aspects. Cellular and Molecular Life Sciences 64:1355-1372.

Dorken, M.E. and C.G. Eckert. 2001. Severely reduced sexual reproduction in northern populations of a clonal plant, *Decodon verticillatus* (Lythraceae). Journal of Ecology 89: 339-350.

Folse, H.J., and Roughgarden, J. (2011) Direct benefits of genetic mosaicism and intraorganismal selection: modeling coevolution between a long-lived tree and a short-lived herbivore. Evolution 66:1091-1113.

Gaggiotti, O.E. 1994. An ecological model for the maintenance of sex and geographic parthenogenesis. Journal of Theoretical Biology 167: 201-221.

Gibson, A.K., Delph, L.F., Vergara, D., and C.M. Lively (2018). Periodic, parasite-mediated selection for and against sex. American Naturalist 192:537-551.

Gill, D.E. (1986) Individual plants as genetic mosaics: ecology organisms versus evolutionary organisms, in *Plant Ecology* (M.J. Crawley, ed.), pp. 321-343, Blackwell Scientific Publications, Oxford.

Gill, D.E., Chao, L, Perkins, S.L., and Wolf, J.B. (1995) Genetic mosaicism in plants and clonal animals. Annual Review of Ecology and Systematics 26:423-444.

Guillemin, M.-L., Faugeron, S., Destombe, C., Viard, F., Correa, J.A. & Valero, M. (2008). Genetic variation in wild and cultivated populations of the haploid– diploid red alga *Gracilaria chilensis*: how farming practices favor asexual reproduction and heterozygosity. Evolution. 62:1500–19.

Haag, C.R. and D. Roze. (2007) Genetic load in sexual and asexual diploids: Segregation, dominance, and genetic drift. Genetics 176:1663-1678.

Halkett, F., Simon, J., and F. Balloux (2005). Tackling the population genetics of clonal and partially clonal organisms. Trends in Ecology & Evolution 20: 194–201.

Hanlon, V.C.T., Otto, S.P., and S.N. Aitken (2019). Somatic mutations substantially increase the per-generation mutation rate in the conifer *Picea sitchensis*. Evolution Letters 3:348-358.

Harper, J.L. (1985) Modules, branches, and the capture of resources, in *Population Biology and Evolution of Clonal Organisms* (J.B.C. Jackson, L.W. Buss and R.E. Cook, eds.), pp. 1-33. Yale University Press, New Haven.

Hartfield, M. (2016) Evolutionary genetic consequences of facultative sex and outcrossing. Journal of Evolutionary Biology 29:5-22.

Hartfield, M. (2021). Approximating the coalescent under facultative sex. Journal of Heredity [special issue]

Hersh, E., Grimm, J., and J. Whitton (2016). Attack of the clones: Reproductive interference between sexuals and asexuals in the *Crepis* agamic complex. Ecology and Evolution 6:6473-6483.

Hughes, R.N. and Cancino, J.M. (1985) An ecological overview of cloning in Metazoa, in *Population Biology and Evolution of Clonal Organisms* (J.B.C. Jackson, L.W. Buss and R.E. Cook, eds.), pp. 153-186. Yale University Press, New Haven.

Hughes, R.N. (1989) *A Functional Biology of Clonal Animals*, Chapman and Hall, London.

Janko, K., Kotusz, J., De Gelas, K., Slechtova, V., Opoldusova, Z., Drozd, P., Choleva, L., Popiolek, M., and M. Balaz (2012). Dynamic formation of asexual diploids and polyploid lineages: Multilocus analysis of *Cobitis* reveals the mechanisms maintaining the diversity of clones. PLOS One, https://doi.org/10.1371/journal.pone.0045384

Jaron, K.S., Bast, J., Ranallo-Benavidez, T.R., Robinson-Rechavi, M., and Schwander, T. Genomic features of asexual animals. Journal of Heredity, esaa031, https://doi.org/10.1093/jhered/esaa031

Karako, S., Achituv, Y., Perl-Treves, R. and D. Katcoff (2002). *Asterina burtoni* (Asteroidea: Echinodermata) in the Mediterranean and the Red Sea: Does asexual reproduction facilitate colonization? Marine Ecology Progress Series 234: 139-145.

Klekowski, E.J. (1988) *Mutation, Developmental Selection, and Plant Evolution*. Columbia University Press, New York.

Kondrashov, A.S. (1994) Mutation load under vegetative reproduction and cytoplasmic inheritance. Genetics 137:311-318.

Krueger-Hadfield SA, JE Kübler and SR Dudgeon (2013) Reproductive effort in the red alga, Mastocarpus papillatus. Journal of Phycology 49: 271-281

Krueger-Hadfield SA, NM Kollars, JE Byers, TW Greig, M Hamman, D Murray, CJ Murren, AE Strand, R Terada, F Weinberger and EE Sotka. (2016) Invasion of novel habitats uncouples haplo-diplontic life cycles. Molecular Ecology 25: 3801-3816.

Krueger-Hadfield, S., Guillemin, M.-L., Destombe, C., Valero, M. and S. Stoeckel (2021). Exploring the genetic consequences of clonality in haplodiplontic taxa. Journal of Heredity [special issue]

Lagator, M., Morgan, A., Neve, P. and N. Colegrave. 2014. Role of sex and migration in adaptation to sink environments. Evolution 68(8): 2296-2305.

Liegeois, M., Sartori, M. and T. Schwander (2021). Extremely widespread parthenogenesis and a trade-off between alternative forms of reproduction in mayflies (Ephemeroptera). Journal of Heredity, esaa027, https://doi.org/10.1093/jhered/esaa027

Loughry, W. J., P. A. Prodohl, C. M. McDonough, and J. C. Avise (1998) Polyembryony in armadillos, American Scientist 86:274–279.

Lopez, E.H. and S.R. Palumbi (2020). Somatic mutations and genome stability in clonal coral colonies. Molecular Biology and Evolution 37:828-838.

Lozada-Gobilard, S., Schwarzer, C., Dyer, R., Tiedemann, R., and J. Joshi (2021). Genetic diversity and connectivity in plant species differing in clonality and dispersal mechanisms in wetland island habitats. Journal of Heredity [special issue]

Marriage, T.N., and Orive, M.E. (2012) Mutation-selection balance and mixed mating with asexual reproduction. Journal of Theoretical Biology 308:25-35.

Maynard Smith, J. (1978) *The Evolution of Sex*. Cambridge University Press, Cambridge.

Million, K.M., Bhattacharya, A., Dinges, Z.M., Montgomery, S., Smith, E., and C.M. Lively (2021). DNA content variation and SNP diversity within a single population of asexual snails. Journal of Heredity, esaa048, https://doi.org/10.1093/jhered/esaa048

Olsen KC, Moscoso JA, Levitan DR (2019) Somatic mutation is a function of clone size and depth in Orbicella reef-building corals. Bio Bull 236: 1-12

Orive, M.E. (1993) Effective population size in organisms with complex life histories. Theoretical Population Biology 44:316-340.

Orive, M.E. (2001) Somatic mutations in organisms with complex life histories. Theoretical Population Biology 59:235-249.

Orive, M.E., Barfield, M., Fernandez, C., and Holt, R.D. (2017) Effects of clonal reproduction on evolutionary lag and evolutionary rescue. American Naturalist 190:469-490.

Orive, M.E. (2020) The evolution of sex, in *The Theory of Evolution* (S.M. Scheiner and D.P. Mindell, eds.), pp. 273-295, University of Chicago Press.

Otto, S.P., and Orive, M.E. (1995) Evolutionary consequences of mutation and selection within an individual. Genetics 141:1173-1187.

Otto, S.P., and Hastings, I.M. (1998) Mutation and selection within the individual. Genetica 102/103:507-524.

Otto, S.P. (2021) Selective interference and the evolution of sex. Journal of Heredity, esaa026, https://doi.org/10.1093/jhered/esaa026

Peck, J.R., Yearsley, J., and G. Barreau (1999). The maintenance of sexual reproduction in a structured population. Proceedings of the Royal Society B: Biological Sciences 266: 1857–1863.

Reusch, T.B.H. (2001) Fitness-consequences of geitonogamous selfing in a clonal marine angiosperm (*Zostera marina*). Journal of Evolutionary Biology 14:129–138

Rushworth, C.A. and T. Mitchell-Olds (2021). The evolution of sex is tempered by costly hybridization in *Boechera* (rock cress). Journal of Heredity, esaa041, https://doi.org/10.1093/jhered/esaa041

Ryan, W., Aida, J., and S. Kruegar-Hadfield (2021). The contribution of clonality to population genetic structure in the sea anemone *Diadumene lineata*. Journal of Heredity [special issue]

Schmid-Siegert, E., Sarkar, N., Iseli, C., Calderon, S., Gouhier-Darimont, C., Chrast, J., Cattaneo, P., Schutz, F., Farinelli, L., Pagni, M., Schneider, M., Voumard, J., Jaboyedoff, M., Fankhauser, C., Hardtke, C.S., Keller, L., Pannell, J.R., Reymond, A., Robinson-Rechavi, M., Xenarios, I., and P. Reymond (2017). Low number of fixed somatic mutations in a long-lived oak tree. Nature Plants 3:926-929.

Schön, I., Martens, K., & Van Dijk, P. (2009). Schön, I., Martens, K., & Van Dijk, P. (2009). Lost sex: The evolutionary biology of parthenogenesis. Dordrecht: Springer. Dordrecht: Springer.

Schurko, A.M., M. Neiman, and J.M. Logsdon. 2008. Signs of sex: What we know and how we know it. Trends in Ecology and Evolution 24:208-217.

Schweinsberg, M., R. A. Gonzalez Pech, R. Tollrian, and K. P. Lampert (2014). Transfer of intracolonial genetic variability through gametes in *Acropora hyacinthus* corals. Coral Reefs 33:77–87.

Silander, J.A. (1985) Microevolution in clonal plants, in *Population Biology and Evolution of Clonal Organisms* (J.B.C. Jackson, L.W. Buss and R.E. Cook, eds.), pp. 107-152. Yale University Press, New Haven.

Silvertown, J. (2008). The evolutionary maintenance of sexual reproduction: Evidence from the ecological distribution of asexual reproduction in clonal plants. International Journal of Plant Sciences 169: 157–168.

Slatkin, M. (1984) Somatic mutations as an evolutionary force, in *Evolution: Essays in Honour of John Maynard Smith* (P.J. Greenwood, P.H. Harvey, and M. Slatkin, eds.), pp. 19-30. Cambridge University Press, Cambridge.

Somme, L., C. Mayer, O. Raspé, A.-L. Jacquemart (2014) Influence of spatial distribution and size of clones on the realized outcrossing rate of the marsh cinquefoil (*Comarum palustre*). Annals of Botany 113: 477–487.

Stoeckel, S., Arnaud-Haond, S. and S. Krueger-Hadfield (2021). The combined effect of haplodiplonty and partial clonality on genotypic and genetic diversity in a finite mutating population. Journal of Heredity [special issue]

Sutherland, W.J., and Watkinson, A.R. (1986) Do plants evolve differently? Nature 320:305.

Tatarenkov, A., Bergstrom, L., Jonsson, R.B., Serrao, E.A., Kautsky, L. and K. Johannesson (2005). Intriguing asexual life in marginal populations of the brown seaweed *Fucus vesiculosus*. Molecular Ecology 14: 647-651.

Tiffney, B.H., and Niklas, K.J. (1985) Clonal growth in land plants: a paleobotanical perspective, in *Population Biology and Evolution of Clonal Organisms* (J.B.C. Jackson, L.W. Buss and R.E. Cook, eds.), pp. 35-66. Yale University Press, New Haven.

Tilquin, A. and H. Kokko (2016). What does the geography of parthenogenesis teach us about sex? Philosophical Transactions of the Royal Society B 371: 20150538.

van Oppen, M.J.H., Souter, P., Howells, E.J., Heyward, A., and Berkelmans, R. (2011) Novel genetic diversity through somatic mutations: fuel for adaptation in reef corals? Diversity 3:405-423.

Vandel, A. (1928) La parthénogénèse géographique: contribution à l'étude biologique et cytologique de la parthénogénèse naturelle. Bull Biol France Belgique 62:164–281.

Vrijenhoek, R.C. (1979) Factors affecting clonal diversity and coexistence. American Zoologist 19:787-797.

Welch, D.B.M., and Meselson, M. (2000) Evidence for the evolution of bdelloid rotifers without sexual reproduction or genetic exchange. Science 288:1211-1215.

Whitham, T.G., and Slobodchikoff, C.N. (1981) Evolution by individuals, plant-herbivore interactions, and mosaics of genetic variability: the adaptive significance of somatic mutations in plants. Oecologia 49:287-292.

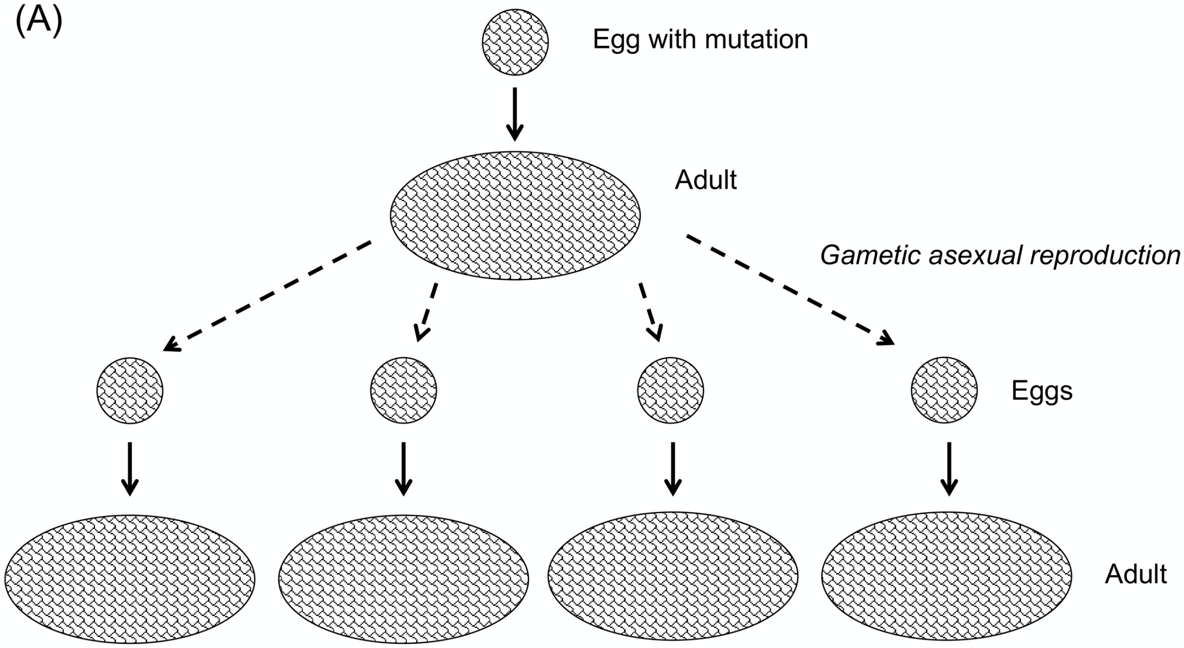
Whitton, J., Sears, C.J., Baack, E.J., and S.P. Otto (2008). The dynamic nature of apomixis in the angiosperms. Int. J. Plant Sci. 169:169-182.

Zhang, H., West, J.A., Zufall, R.A., and R.B.R. Azevedo. Amitosis confers benefits of sex in the absence of sex to Tetrahymena. bioRxiv 794735; doi: https://doi.org/10.1101/794735

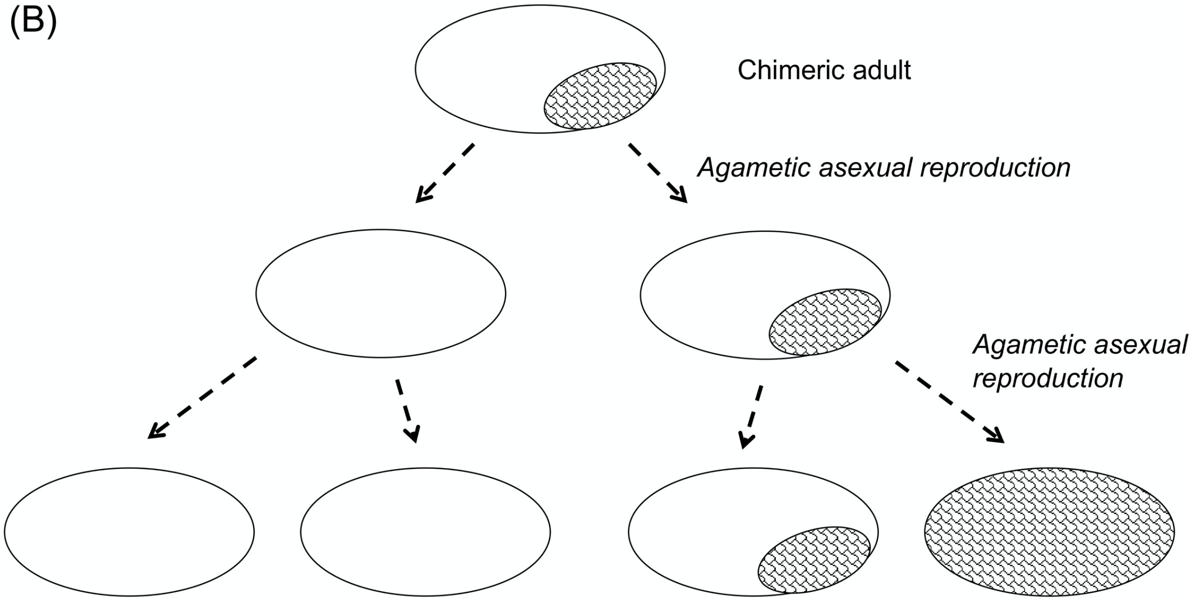
Figure Legend

Figure 1. Fate of mutations with asexual reproduction. (A) Gametic asexual reproduction – a mutation in an egg will be found in all of the cells of the adult that develops from that egg, so the mutation will be passed on to all future asexual progeny. (B) Agametic asexual reproduction – a mutation within a somatic cell will be found in all the descendant cells in that part of the soma of the individual; new individuals produced by agametic or vegetative reproduction from tissues containing the mutation will vary in the extent to which they carry the mutation. (We note that gametic asexual reproduction from a chimeric adult can also lead to variation in new individuals; this is not depicted in the figure.)

(A)


Egg with mutation
Adult
Gametic asexual reproduction
Eggs
Adult

(B)


Chimeric adult
Agametic asexual reproduction
Agametic asexual reproduction