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## SEX, EVOLUTION OF

**JAN ENGELSTÄDTER**

*Institute for Integrative Biology, Zürich, Switzerland*

**FRANCISCO ÚBEDA**

*University of Tennessee*

The evolution of sex is one of the largest and most fertile areas of research in evolutionary biology. It encompasses multiple unresolved questions involving a number of evolutionary steps: the evolution of the recombination machinery, the evolution of meiosis, the differentiation into sexes, the differentiation of gametes produced by each sex, and, finally, the maintenance of sex despite its two-fold cost.

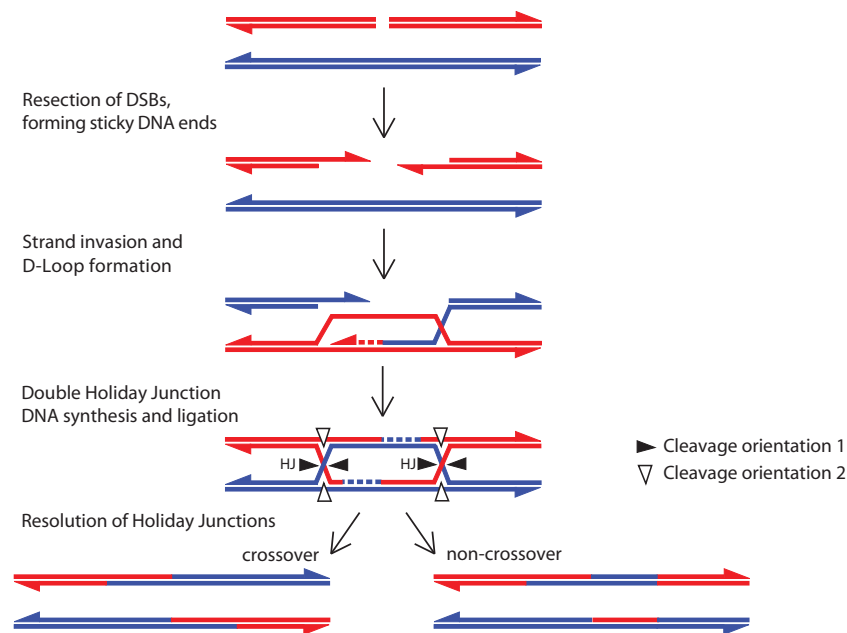
### A MOLECULAR MACHINERY-ENABLING RECOMBINATION

Sex and recombination through meiosis are confined to eukaryotes. However, a complex molecular machinery enabling homologous recombination between different DNA molecules was already present in prokaryotes long before the first eukaryotes evolved. The original function of this machinery lies in DNA repair, as was indicated by early experiments in *E. coli* showing that mutants deficient in genes involved in homologous recombination are highly sensitive to DNA damaging agents. Three types of DNA damage are repaired in bacteria through mechanisms that involve homologous recombination: double-strand breaks, stalled replication

forks, and single-stranded DNA arising from incomplete replication.

Recombinational repair of double-strand breaks (outlined in Fig. 1) is the most relevant mechanism with respect to the evolution of sex in eukaryotes, where double-strand breaks are induced during meiosis I to initiate crossovers. In bacteria, the key player in this process is the recombinase RecA, a DNA-dependent ATPase. Assisted by a host of other proteins, RecA binds to single-stranded DNA forming a helical filament, mediates the search for homology in other DNA molecules, and catalyzes strand invasion and branch migration. Homologues of RecA are found in virtually all organisms, in eukaryotes as Rad51 and the exclusively meiotically active Dmc1 and in the Archaea as RadA.

Even though the main function of the recombination machinery in bacteria is to repair DNA damage, it should be stressed that already in bacteria this machinery is sometimes employed to effect sexual processes. Three such mechanisms of recombination have been identified: conjugation (the exchange of plasmids), transduction (the transfer of DNA mediated by phages), and transformation (the uptake and integration of free DNA from the environment). While the evolution of former two processes is most parsimoniously explained as by-products of the action of autonomous genetic elements (plasmids and phages, respectively), the evolution of the ability to engage in transformation is more difficult to explain. Aside from fulfilling a similar function as sex in eukaryotes, i.e., to increase genetic variation, it has been suggested that transformation evolved to facilitate DNA repair or that it is simply a way of taking up nutrients.



**FIGURE 1** Double-strand break repair mechanism for the initiation of recombination. The blunt ends of the double-stranded DNA are partially digested, revealing single-stranded 3' DNA ends. One of these strands then invades the homologous DNA molecule, forming a D-loop structure. Branch migration and ligation leads to the formation of two holiday junctions. These holiday junctions are resolved producing either crossover or noncrossover products.

## MEIOSIS AND THE ALTERNATION OF GENERATIONS

Most eukaryotes are characterized by a life cycle termed the “alternation of generations,” in which a diploid phase of cell division alternates with a haploid phase. The transition between the diploid and the haploid phase is mediated by meiosis, a form of cell division that reduces the genomic content of cells by one-half. Meiosis starts with a cell that contains two chromosome sets inherited from two gametes (diploid cell) and results in four cells with one chromosome set each. Because of random segregation of chromosomes and crossover events between chromosomes during pairing, meiosis produces haploid cells with unique combinations of genes. Syngamy (or fertilization), on the other hand, mediates the transition from a haploid generation back to a diploid generation. In plants, the haploid generation can contain a multicellular phase before gametes are produced. In animals, the haploid generation is reduced to the production of gametes.

Compared to a genetic system of clonal reproduction, the alternation of generations life cycle has two characteristics that may explain its evolution. The first is the diploid phase. Spending a prolonged time in the diploid phase may be advantageous because it allows the masking of deleterious recessive alleles. The second

characteristic is recombination, the shuffling of alleles coming from two different haploid genomes during meiosis.

From a purely population genetics perspective, all that recombination does is to reduce statistical associations—the linkage disequilibrium (LD)—between alleles at different loci. Thus, the problem of why recombination is so prevalent in natural populations boils down to the questions of what forces generate LD and under what conditions is there selection to destroy LD. LD can be generated by a number of population genetic factors, including epistasis (nonindependent fitness effects of mutations at different loci), random genetic drift (changes in gene frequencies due to random sampling in finite populations), migration, and sexually antagonistic selection. Selection can operate on recombination rates in two ways that in combination determine whether or not recombination is advantageous. First, there is a direct effect stemming from the fitness of sexually produced offspring: when LD and epistasis are of opposite sign, there will be selection for recombination (because the offspring will then be disproportionately fit), but when LD and epistasis are of the same sign, there will be selection against recombination. Second, when LD is negative (i.e., there is an excess of genotypes of intermediate fitness), recombination can be favored because by bringing LD closer to

zero the genetic variance in the population is increased, thus increasing the efficiency of natural selection.

Based on these population genetic principles, many hypotheses have been proposed to account for the advantage of recombination. For example, the deterministic mutational theory posits that negative LD is produced through deleterious mutations with negative epistasis, and recombination is then selected for because it allows a more efficient purging of these mutations. According to a second theory, negative LD is produced by the interplay between random genetic drift and selection (the Hill–Robertson effect), which has been shown to result in strong selection for recombination even in large populations, especially when many loci are considered. Finally, sex and recombination can be favored through antagonistic coevolution between hosts and parasites (the Red Queen hypothesis). In this scenario, both LD and epistasis will fluctuate over time, and depending on how hosts and parasites interact with each other genetically, there can be selection for or against recombination. A number of excellent review articles on these and other hypotheses for the evolutionary advantage hypothesis are available.

### MATING TYPES

Mating types are the different types of gametes that can fertilize other gametes in a sexually reproducing organism. Most species show two different mating types (male and female, + and –,  $a$  and  $\alpha$ ), but some species of fungi can present several thousands.

This differentiation into mating types might be the outcome of selection to facilitate finding mates. In order for gametes to fertilize other gametes, they need to attract and/or be attracted by other gametes. Evolutionary models show that there may be selection for some cells to specialize in attracting gametes (by producing pheromones), while others specialize in becoming attracted (by expressing pheromone receptors).

Another theory argues that mating types might be the result of selection to coordinate the inheritance of cytoplasmic genomes (for example, mitochondrial genes) so as to limit competition between unrelated cytoplasmic genomes. Fusion of isogamous gametes brings together cytoplasmic genes from different lineages that may compete to favor their own transmission to the next generation. Intragenomic conflict reduces the fitness of the organism and creates the context for the invasion of a nuclear gene that enforces the inheritance of cytoplasm from a single mother cell. However, if competitive genes are associated with an over-transmission cost, nuclear genes enforcing uniparental inheritance do not go to fixation. In such a

polymorphic population, nuclear genes that act to prevent its gametes from fusing with gametes produced by an individual that carries the same suppressor are at a selective advantage, and mating types may evolve.

If there is a selective pressure for mating types to evolve, how many mating types should evolve? While in most cases there are two mating types, some organisms can have thousands of mating types. With multiple mating types, the probability that a gamete finds another gamete of a compatible mating type becomes an important issue. The modus operandi of mating types is such that either gametes can fuse with gametes of a specific mating type or gametes can fuse with gametes of mating types other than their own. When gametes can fuse with gametes of a specific mating type, the probability of randomly finding a compatible mating type is at a maximum when the number of mating types is two (50% chance) and at a minimum when the number of mating types tends to infinity (0% chance). When gametes can fuse with gametes of mating types other than their own, the probability of randomly finding a compatible mating type is at a minimum when the number of mating types is two (50% chance) and at a maximum when the number of mating types tends to infinity (100% chance in the limit). The latter modus operandi is the most common in nature, which generates the paradoxical situation of most organisms having two mating types only when this is the number of mating types with the lowest probability of success.

### ANISOGAMY AND MOBILE GAMETES

Anisogamy refers to the production of gametes that differ, generally in size, as opposed to their being identical (isogamy).

One way to explain the evolution of this asymmetry is assuming that there is a tradeoff between productivity (more gametes are better than few gametes) and survival of zygotes (bigger zygotes have greater survival than smaller ones). This creates the context for the evolution of sexual antagonism, with one of the sexes acting as a cheater that withholds resources to produce more gametes and the other sex contributing the resources withheld by the first gamete to preserve zygotic viability. This sexual conflict results in males producing small gametes that are viable only because of the resources contributed by females.

The previous model, however, does not take into consideration how gamete density affects the probability of fertilization. When all gametes do not find a partner to fuse with and when small gametes have a higher

motility—thus increasing encountering rates with large gametes—there can be additional selective pressure for anisogamy. There are also scenarios in which gamete limitation in itself can be sufficient to select for anisogamy. Thus, anisogamy does not necessarily respond to the logic of sexual conflict; rather, it might be beneficial for both sexes.

Anisogamy creates a situation where in the extreme case that sperm do not contribute any resources to the zygote (and where there is also no other paternal contribution to offspring fitness), sex entails a twofold cost. This cost arises because under this assumption, asexual females can produce the same number of offspring as sexual females, but they avoid “diluting” their genome with paternal genetic material when producing offspring. Thus, in the absence of strong selection for sex through recombination, a clonally reproducing mutant is expected to spread rapidly in a sexual population of males and females.

## SECONDARY LOSS OF SEX

Most multicellular organisms—especially animals, the focus of this section—have a genetic system that involves obligate sex as well as male and female sexes (although not necessarily in separate individuals). Because of the twofold cost of sex, this near ubiquity of sex is even more difficult to explain than explaining how sex and recombination evolved in the first place. Some species, however, have re-evolved the ability to reproduce asexually, either partially or completely, thus offering important opportunities to investigate the evolutionary forces that maintain sex within populations and to test hypotheses for the advantage of recombination.

Partial loss of sexual reproduction is relatively common in multicellular organisms, and it is characteristic of several large taxa. Some groups of animals—for example, aphids, waterfleas, and monogonont rotifers—reproduce mainly asexually, but under certain conditions males and females are produced and mate (facultative sex or cyclic parthenogenesis). In other groups, sexual and obligatorily asexual individuals coexist, although often with different geographical distributions (geographical parthenogenesis).

By contrast, complete abandonment of sexual reproduction is rare among multicellular organisms. For example, there are fewer than 100 parthenogenetic vertebrate species. The genetic basis for parthenogenetic reproduction varies among groups and includes single mutations, hybridization (possibly the only cause of parthenogenesis in vertebrates), and maternally inher-

ited bacteria. Moreover, there is a great diversity in cytogenetic mechanisms by which offspring are produced asexually.

Parthenogenetic species exhibit a “twiggy” distribution in phylogenetic trees; i.e., they do not form large and old clades. Two groups of parthenogenetic animals—the bdelloid rotifers and darwinulid ostracods—have long thought to be exceptions to this rule. Bdelloid rotifers, however, have recently been shown to engage in extensive horizontal gene transfer, incorporating genetic material from a wide range of organisms into their genome. This process may also involve homologous replacement of genes from related organisms. Similarly, recent observation of males in one species of darwinulids has cast doubts on this group’s status of ancient asexuals. However, it is not clear at present whether or not sex does indeed occur within this group, and if so, how common it is.

The twiggy distribution of asexuals is typically explained through adverse long-term consequences of the absence of recombination. According to this view, asexual species arise occasionally, but because of their reduced rate of adaptation and an accumulation of deleterious mutations, these asexual species become extinct quickly. However, this notion has not been rigorously tested to date, and alternative explanations for the scattered distribution of parthenogenetic species in phylogenetic trees exist. In particular, reduced rates of speciation in asexual species could produce similar phylogenetic distributions. Whether or not sexual or asexual species should be expected to have higher speciation rates is an unresolved question whose answer depends on the importance of factors like adaptation, geographical isolation, and random genetic drift in the process of speciation.

Another key factor are the rates of transition from sexual to asexual reproduction and vice versa. The former rate is expected to be small in many groups because of a variety of genetic and developmental constraints on evolving parthenogenetic reproduction. On the other hand, re-evolving sex once it has been lost for a long time is often considered impossible. Newly developed statistical methods make it possible in principle to simultaneously estimate extinction, speciation, and transition rates of sexual vs. asexual species from phylogenetic trees, but it remains to be seen whether the available data are sufficient to allow reliable estimates.

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## SINGLE-SPECIES METAPOPOPULATIONS

SEE METAPOPOPULATIONS

# SINGLE-SPECIES POPULATION MODELS

KAREN C. ABBOTT

Iowa State University

Anthony R. Ives

University of Wisconsin–Madison

In ecology, as in other sciences, models are used for three main purposes. They can provide a way to organize ideas and develop hypotheses about how real systems work, they can provide a qualitative understanding of a particular system, and they can make predictions. Simple models are best for conceptual explorations and hypothesis development, whereas detail rich, system-specific models are needed to make predictions. Simple single-species models provide a means to study populations whose dynamics are predominantly determined by intraspecific interactions. But just as importantly,

single-species models also provide many of the building blocks used in multispecies models.

## CONCEPTUAL FRAMEWORK

The main challenge to modeling ecological systems is their complexity. Unlike simple dynamical models, such as those for planets revolving around stars, ecological models are never designed to capture precisely the dynamics of a system. Instead, they are caricatures that nonetheless contain the salient features of reality. Thus, it makes sense not to think about the best model for a particular ecological system but instead to think about what model is best for a given question; different questions about the same system will require different models. For example, models can be used to ask whether it is possible for a single species, in isolation from other species, to show perpetually cyclic fluctuations in abundance, or whether competition is sufficiently strong to cause population cycles in a specific species of interest. Models could also be used to predict the abundance of a species in 3 years. The models most appropriate for each of these tasks will be different even if our species of interest remains the same.

This entry focuses primarily on the use of models as thought experiments to understand what is possible in real ecological systems. It discusses simple models that might equally apply to a wide range of systems, without applying realistically to any of them. At their core, all single-species models are equations that dictate how population abundances change through time, but these equations can look and behave quite differently from one another depending on the biological assumptions on which they are based. To model a particular population, the first step is to figure out what assumptions are appropriate for the situation at hand.

Individuals require resources in order to survive and reproduce, and thus to contribute to population growth. What these resources are depends on the species of interest and can include such things as soil nutrients like carbon and nitrogen, food plants, or prey animals. Given these dependences, how is it possible to model just a single species without also modeling its required resources? This rests on the assumption that either the resources never change in availability, or that they are replenished at the rate they are consumed. The key assumption of single-species models is that we can capture the processes that govern the dynamics of a species from information on that species alone. Single-species models, then, might be most appropriate for populations that do not have strong interactions with other species that have dynamics of their own. However, even information about interactions