Exercise sheet 4: Costs of sex and asexuality

Sex, Ageing and Foraging Theory

Exercise 1: Two-fold cost of sex

In this exercise, we investigate the two-fold cost of sex with a model following the demographic dynamics of a population that consists of three types of individuals: asexual females, sexual females and males. We assume that generations are non-overlapping and that at each generation, the following occurs. (1) Asexual females reproduce clonally while sexual females and males mate randomly. (2) Asexual and sexual females give birth to a number of offspring depending on their type (sexual or asexual). (3) Sexual offspring become male with probability r and female with probability $1-r$. (4) Sexual and asexual offspring survive to maturity according to adult density (density dependent competition) and adults of the previous generation die. The surviving offspring finally become the adults of the next generation.

To track the dynamics of the population, we write n_t^{A} and n_t^{S} for the numbers of asexual and sexual females at generation t, respectively. As the sex ratio (i.e., the proportion of males) at birth is fixed at r, the number of males, n_t^{M}, can be expressed in terms of the number of sexual females:

$$n_t^{\mathrm{M}} = \frac{r}{1-r} n_t^{\mathrm{S}}. \tag{1}$$

The total population size, n_t^{T}, which is the sum of asexual females, sexual females and males, is then given by

$$n_t^{\mathrm{T}} = n_t^{\mathrm{A}} + n_t^{\mathrm{S}} + n_t^{\mathrm{M}} = n_t^{\mathrm{A}} + \frac{1}{1-r} n_t^{\mathrm{S}}. \tag{2}$$

at generation t.

We assume that the number of offspring produced by a female is Poisson-distributed, with mean f^{A} for an asexual female and mean f^{S} for a sexual female. We also assume that each offspring survives to adulthood with a probability

$$p_0 = \frac{1}{1+\gamma n_t^{\mathrm{T}}}, \tag{3}$$

which decreases with the total number of adults n_t^{T} in the current generation to capture density-dependent competition.

Under the assumption that the fecundity of sexual females is not limited by either sperm quantity or finding a mate, we get from the above that the number of asexual and sexual females in the next generation $t+1$ are

$$n_{t+1}^{\mathrm{A}} = \frac{1}{1+\gamma n_t^T} f^{\mathrm{A}} n_t^{\mathrm{A}} \tag{4}$$

$$n_{t+1}^{\mathrm{S}} = (1-r)\frac{1}{1+\gamma n_t^{\mathrm{T}}} f^{\mathrm{S}} n_t^{\mathrm{S}} \ . \tag{5}$$

a. Assuming equal fecundity between asexuals and sexuals, $f^{\mathrm{A}} = f^{\mathrm{S}} = f$, calculate the ratio of asexual to sexual females,

$$\frac{n_{t+1}^{\mathrm{A}}}{n_{t+1}^{\mathrm{S}}}. \tag{6}$$

What happens to this ratio after a long time (i.e., when t becomes large)? Interpret your results biologically (e.g. do sexual and asexuals eventually coexist?). How does this long-term outcome depend on fecundity f and sex ratio at birth r?

b. Let us assume that sexuals are three times more fecund than asexuals, i.e., that $f^{\mathrm{S}} = 3f$ while $f^{\mathrm{A}} = f$. What happens to the long-term ratio of asexuals to sexuals in this case (eq. 6)? Find the values of fecundity, f, and sex ratio at birth, r, such that sexual females exclude asexual females, i.e. such that $n_t^{\mathrm{A}}/n_t^{\mathrm{S}} \to 0$.

c. So far we have assumed that finding a mate is costless to sexual females. More realistically, mate finding is an energetically and time consuming task, especially when the number of males is scarce. To capture this in our model, plug into eq. (5) the following fecundity function for sexuals, which depends on the sex ratio r at birth,

$$f^{\mathrm{S}}(r) = 3f\sqrt{\frac{r}{1-r}}. \tag{7}$$

According to eq. 7, fecundity decreases as the proportion of males among sexuals decreases. Asexual females, meanwhile, do not suffer such cost as they do not to find a mate. Therefore they have a constant fecundity f. Calculate the long-term ratio of asexuals to sexuals (eq. 6) with these modifications. Discuss the effects of the sex-ratio at birth, r, on the outcome of the model.

Exercise 2: Consequences of asexuality

This exercise investigates *Muller's ratchet*, i.e. the accumulation of deleterious mutations in asexual populations due to their inability of purging them (owing to the absence of chromosomal segregation and recombination). We simulate a population of hermaphrodite haploid individuals with L loci (i.e., genes). At each locus, there can be either a wild type allele (i.e., positively selected) or a deleterious allele (i.e., negatively selected). A mutation from wild type to deleterious occurs with a probability u per locus. We assume that a deleterious allele can never mutate back to wild type, capturing the notion that there are many more possible deleterious alleles but only one wild type.

The life cycle is as follows. (1) First, each adult individual either engage in sexual reproduction with probability σ, or clonal (asexual) reproduction with probability $1-\sigma$. If an individual reproduces sexually, it mates at random with another sexual. (2) Each individual then produces a Poisson-distributed number of offspring with mean f_0, regardless of the way they reproduce. Before mutation, an offspring produced asexually is an exact copy of its parent (e.g. if the parent has 3 deleterious alleles, its offspring also has 3 deleterious alleles), while an offspring produced via sexual reproduction is a recombined version of its two parents, assuming each locus segregates independently (i.e., at each locus, the inherited allele is a copy of parent 1 with probability $1/2$ and of parent 2 with probability $1/2$). (3) Mutation then occurs at each locus independently (with probability u). (4) An offspring survives with a probability that depends on density-dependent competition and on the number of deleterious mutations it carries. Specifically, we assume each deleterious mutation reduces the survival probability by a factor $(1-s)$. Overall, the probability that an offspring with k deleterious mutations survives is

$$\frac{(1-s)^k}{1+\gamma n_t}, \tag{8}$$

when there are n_t adults in the population. (5) Finally, all the adults die and offspring become the adults of the next generation.

An individual-based simulation program for the life-cycle above has been made available on the course website (lab-mullon.github.io/SAF). Familiarise yourself with this program.

a. Look at the code lines 22 and 28. What does the code do at these lines? What is the biology being modelled there?

b. Run the simulation for a completely asexual population ($\sigma = 0$). How does the population evolve? What happens to the number of deleterious mutations?

c. Run the simulation for a completely sexual population ($\sigma = 1$). What happens to the number of deleterious mutations? Why?

d. Increase the effect of deleterious mutations to $s = 0.02$. What happens to an asexual population? And to a sexual population? Why?