Exercise sheet 3: Costs and benefits of sex

Sex, Ageing and Foraging Theory

March 21, 2023

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

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

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

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

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

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 value of sex ratio at birth, r, such that sexual females exclude asexual females, i.e. such that $n^{\mathrm{A}}_{t}/n^{\mathrm{S}}_{t} \to 0$.

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 a cost as they do not have 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 the wild type to the deleterious allele occurs with a probability u per locus. We assume that a deleterious allele can never mutate back to the wild type, capturing the notion that there are many more possible deleterious alleles but only one wild-type allele.

The life cycle is as follows. (1) First, each adult individual either engages 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

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

when there are n_t adults in the population. (5) Finally, all the adults die and the surviving 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?

Exercise 3: Evolution of sex

Previously, you investigated evolution at L loci under purifying selection in: a population composed of asexual individuals (specifically where the probability σ of reproducing sexually was fixed to zero for all individuals, $\sigma = 0$); and a populations of sexuals (where $\sigma = 1$ for all individuals). Here, we extend this model to investigate when asexuality can and cannot invade a population of sexuals. To do so, we allow for the probability σ of reproducing sexually to also evolve, i.e. each individual i now has a probability σ_i of reproducing sexually. Each haploid individual is thus characterised by $L+1$ genetic loci: (1) one locus coding for the probability σ of reproducing sexually where two alleles segregate, one for sexual ($\sigma = 1$) and one for asexual reproduction ($\sigma = 0$); and (2) L loci under purifying selection, at each of which a wild type and deleterious mutation can segregate (as in Ex sheet 4).

The life cycle is composed of five steps. (1) First, each adult female i either reproduces sexually with probability σ_i or asexually with probability $1-\sigma_i$ according to her allele at the locus for sexual reproduction. If a female reproduces sexually, it mates at random with a male in the population. (2) Each female produces a Poisson-distributed number of offspring with mean f_0. Before mutation, an offspring produced asexually is an exact copy of its parent (e.g. if the parent has the allele for $\sigma = 0$ and 3 deleterious alleles at the L loci under purifying selection, its offspring also has the allele for $\sigma = 0$ and 3 deleterious alleles), while an offspring produced via sexual reproduction is a recombined version of its mother and father, assuming each locus segregates independently (i.e.,

at each locus, the inherited allele is a copy of the mother with probability $1/2$ or of the father with probability $1/2$). (3) Mutation from the neutral allele to the deleterious allele occurs with probability u at each of the L loci under purifying selection (we assume there is no constant mutation at the locus for sexual reproduction). (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 that the probability ω_i that an offspring i with k_i deleterious mutations survives to adulthood is,

$$\omega_i = \frac{(1-s)^{\left(k_i/K\right)^{\epsilon}}}{1+\gamma n_t}, \tag{9}$$

when there are n_t adults in the population. There are two extra parameters compared to eq. (8) of Ex sheet 4 to capture epistasis (see item (b) below). When $\epsilon = 1$ and $K = 1$, we recover eq. (8) of Exercise Sheet 4. Finally, (5) all adults die and the surviving offspring of sexual females becomes an adult male with probability r, or an adult sexual female with probability $1-r$, so that r is the sex ratio at birth (all offspring of asexual females are also asexual females).

An individual-based simulation program for the life-cycle above has been made available on the course website (lab-mullon.github.io/SAF). We start with 1000 sexual individuals that have no deleterious mutations (i.e. each individual carries the allele for $\sigma = 1$ and the wild-type allele at the L loci under purifying selection). We let the simulation run for 100 generations, which is enough time for the population to reach a distribution of deleterious mutations that no longer changes very much over time. In the 200-th generation, a random sexual female becomes asexual, i.e. we change the allele σ_i from 1 to 0 for some random i. We let the simulation run for another 200 generations to observe if the asexual lineage invades the sexual resident population.

a. Familiarise yourself with this program. Discuss the biological interpretation of line 133.

b. Plot the survival probability ω_i as a function of the number k_i of deleterious mutations for different strengths of epistasis (e.g. with $\epsilon = 0$, 0.5, 1, 10, and 75) for a fixed value of $K = 50$. Do these plots again but for different K (e.g. with $K = 10$, 50, 100) with a fixed value of $\epsilon = 75$. Interpret these plots and use them to conjecture on the implications of epistasis for the maintenance of sexual reproduction.

c. Run the simulation under no epistasis, $\epsilon = 1$ (and $K = 50$). Do this a few times recording relevant information about the population each replicate (remember it is a stochastic simulation so it is good to a have a few replicates). Run the simulations also with high epistatic effects, $\epsilon = 75$. Do the results differ when $\epsilon = 1$ and $\epsilon = 75$? Does this fit with your expectations formulated in part (b)?

d. Reduce the number L of loci under purifying selection from 200 to 100. Re-run simulations under strong epistasis, $\epsilon = 75$. What can you conclude from these simulations about the effects of the number of loci on the maintenance of sexual reproduction? Why?