# Solutions to exercise sheet 4

Sex, Ageing and Foraging Theory

## 1 Two-fold cost of sex

a. Assuming $f^{\mathrm{A}} = f^{\mathrm{S}} = f$, leads to

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

$$n^{\mathrm{S}}_{t+1} = (1-r)\frac{1}{1+\gamma n^{\mathrm{T}}_{t}} f n^{\mathrm{S}}_{t} \ . \tag{2}$$

Dividing Eq. 1 by Eq. 2, we have

$$\frac{n^{\mathrm{A}}_{t+1}}{n^{\mathrm{S}}_{t+1}} = \left(\frac{1}{1-r}\right)\frac{n^{\mathrm{A}}_{t}}{n^{\mathrm{S}}_{t}} \ , \tag{3}$$

and since $0 < r < 1$, the factor $1/(1-r) > 1$ is always greater than 1. Hence, the ratio of asexuals to sexuals, $n^{\mathrm{A}}_{t}/n^{\mathrm{S}}_{t}$, increases with time. The number of asexuals must therefore increase with time relative to sexuals. In short, when sexual and asexual females have the same fecunfity, asexuals always outcompete sexuals. This is the "demographic cost of sexuality".

b. Assuming $f^{\mathrm{A}} = f$ and $f^{\mathrm{S}} = 3f$, we get

$$\frac{n^{\mathrm{A}}_{t+1}}{n^{\mathrm{S}}_{t+1}} = \left(\frac{1}{3(1-r)}\right)\frac{n^{\mathrm{A}}_{t}}{n^{\mathrm{S}}_{t}} \ . \tag{4}$$

Two outcomes are thus possibles depending on the sex ratio at birth. (1) When the sex ratio is high $r > 2/3$ (i.e. sexual females produce many sons), the factor $1/[3(1-r)] > 1$ is greater than 1 so as in the previous scenario, asexuals outcompete sexuals. (2) By contrast when the sex ratio is sufficiently low $r < 2/3$, the factor $1/[3(1-r)] < 1$ is less than 1 so asexuals decrease relative to sexuals.

c. With $f^{\mathrm{S}}(r) = 3f\sqrt{r/(1-r)}$ and $f^{\mathrm{A}} = f$, we obtain

$$\frac{n^{\mathrm{A}}_{t+1}}{n^{\mathrm{S}}_{t+1}} = \left(\frac{1}{3\sqrt{r(1-r)}}\right)\frac{n^{\mathrm{A}}_{t}}{n^{\mathrm{S}}_{t}} \ . \tag{5}$$

This again suggests two possible outcomes depending on the sex ratio. (1) If the sex ratio is not too biased, i.e. if $(3-\sqrt{5})/6 < r < (3+\sqrt{5})/6$, i.e., if sex ratio is not too far from $1/2$, sexuals outcompete asexuals (see calculation in Wolfram Alpha). (2) Otherwise, when the sex ratio is biased either towards females or males (i.e. if $r < (3-\sqrt{5})/6$ or $r > (3+\sqrt{5})/6$), then asexuals outcompete sexuals. This is because when sexual females produce many sons, asexuals can outcompete them by producing more daughters (as in question 1b). When sexual females produce few sons, it may be difficult for males to fertilise sexual females lowering their average fecundity thus favouring asexual females.

## 2 Consequences of asexuality

a. The function on line 22 models the addition of mutations across the $L$-locus genome. Mutations occur with probability $u$ per locus. To model this, we sample from a Bernoulli distribution with probability of success $u$ for each locus of each individual (i.e., sampling 0 or 1 with probability $1-u$ and $u$, respectively, and we do this $L$ times). For each individual and locus $i = 1, \dots, L$, we add the aforementioned sampled value for mutation ($M_i = 0$ or 1) to the allelic value before mutation ($x_i = 0$ or 1). If the locus before mutation was carrying the wild-type allele ($x_i = 0$) and no mutation occurred ($M_i = 0$), then the new allele is still wild type ($x_i + M_i = 0$). If a mutation occurred ($M_i = 1$), then the new allele is deleterious ($x_i + M_i = 1$). If the locus before mutation was carrying the deleterious allele ($x_i = 1$), then it remains deleterious whether or not a mutation has occurred (i.e. $1 + M_i = 1$ whether $M_i = 1$ or 0). To ensure this, we set values greater than 1 equal to 1, i.e., $x_i = 1$ if $x_i > 1$. For purposes of computational efficiency, we perform the operation described in this paragraph at all $L$ loci at the same time with vectorized operations (try running each line in the console of RStudio if you want to see this).

   The function in line 28 corresponds to the recombination between two given genomes, $\{x_i\}_i$ and $\{x_j\}_j$. First, both genomes are concatenated into one single vector (joint vector). Then, a new vector is returned by the function where each position $i$ is either the value at $i$-th position or at the $(i + L)$-th position of this concatenated vector with equal probabilities. In this concatenated vector, $i$-th position carries the information of the first parent ($x_i$) and $(i + L)$-th position carries the information of the second parent ($x_j$) at the same locus.

b. To understand the evolution of an asexual population, we can keep track of three quantities at each generation (Fig. 1): (1) the population size; (2) the minimum number of mutations found in a genome; and (3) mean number of mutations per genome in the population. The final plot in Fig. 1 (bottom right) shows the distribution of the number of deleterious mutations per genome in the population at generation 1000.

   Fig. 1 shows that asexuals rapidly accumulate deleterious mutations (as the minimum and mean numbers of mutations per genome increase). This in turn causes a decrease in population size. After $\sim 600$ generations, the population size stabilizes with $\sim 300$ asexual individuals. We observe that by generation 1000, over two thirds of individuals carry $50$ deleterious mutations (out of $L_{\text{loci}} = 50$ loci). Running the simulation for longer we would see that eventually, all individuals have deleterious mutations at all their 50 loci.

   As an illustration of Muller's ratchet, we observe in Fig. 1 (top right) that the minimum number of deleterious mutations in a genome just keeps increasing over time (i.e. it never goes down). This is due to the inability of asexual genomes to eliminate deleterious mutations with genetic recombination.

c. Fig. 2 shows the evolution of a sexual population. Although deleterious mutations still increase (due to genetic drift and the fact that mutations only go from wild-type to deleterious), the minimum number of deleterious mutation per genome does not only increase, i.e. it can sometime decrease from one generation to the next. This reflects that mutation can be purged from one generation to the next by sexual recombination. As a result the accumulation of deleterious mutations takes much longer in a sexual than in an asexual population (compare both histograms of Fig.1 and 2 at time $t = 1000$).

d. Fig. 3 shows evolution in asexuals with stronger selection, $s = 0.02$. We see that the population accumulates deleterious mutations and as a result rapidly crashes and even goes extinct. By contrast, a sexual population

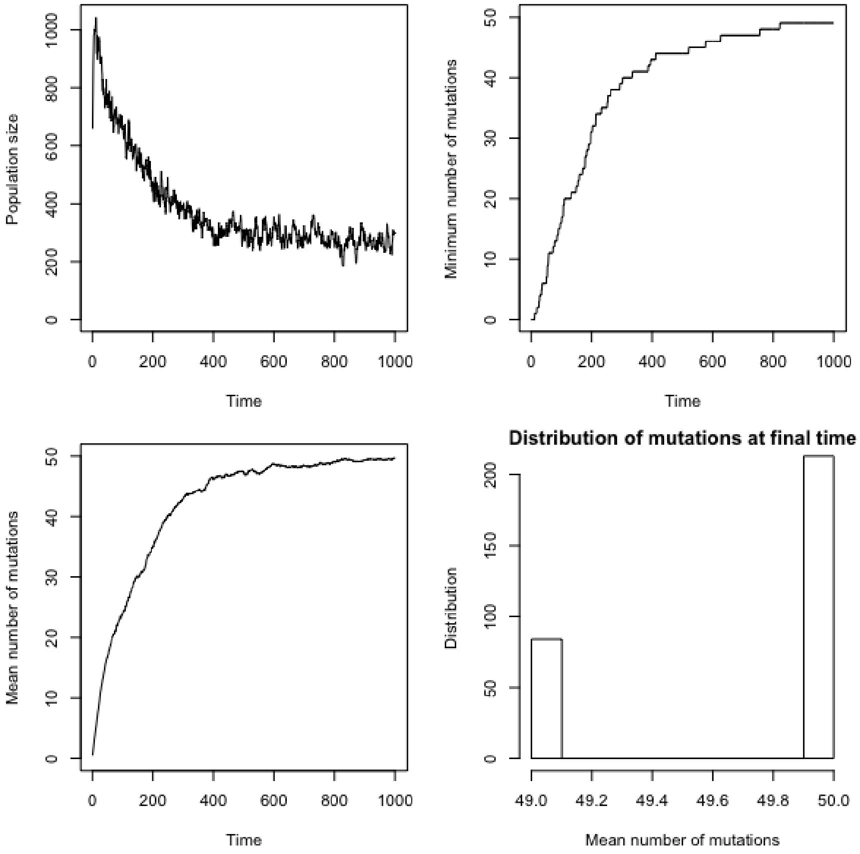

Figure 1: Evolution in asexuals with $s = 0.01$. Time is measured in units of life-cycle.

is able to purge these mutations and thus avoid extinction (see Fig. 4)

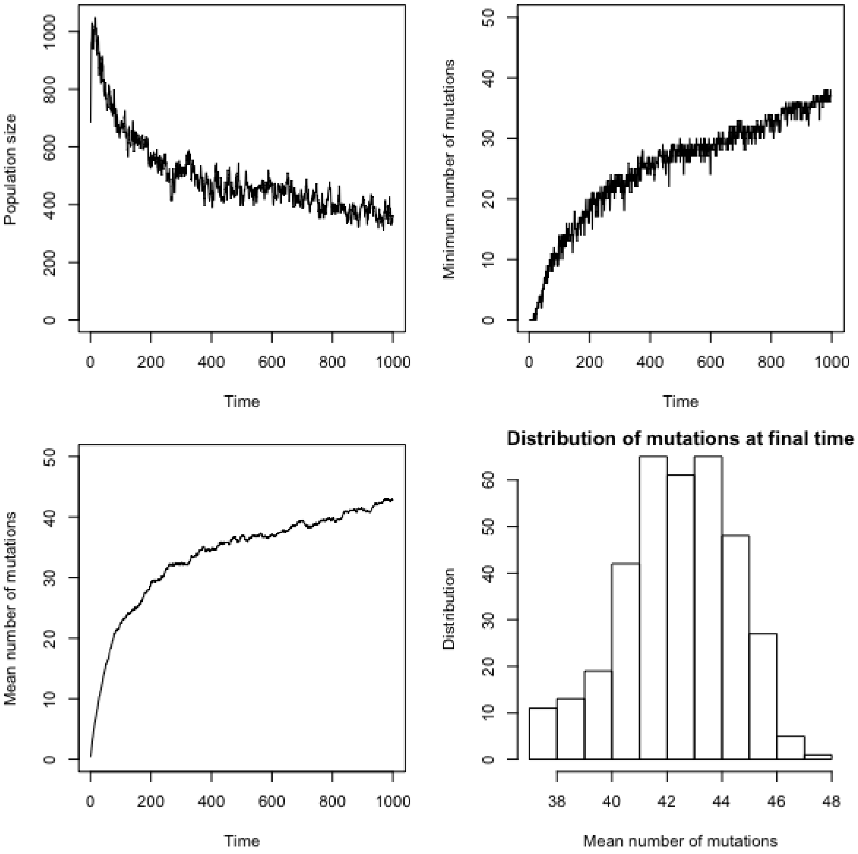

Figure 2: Evolution in sexuals with $s = 0.01$.

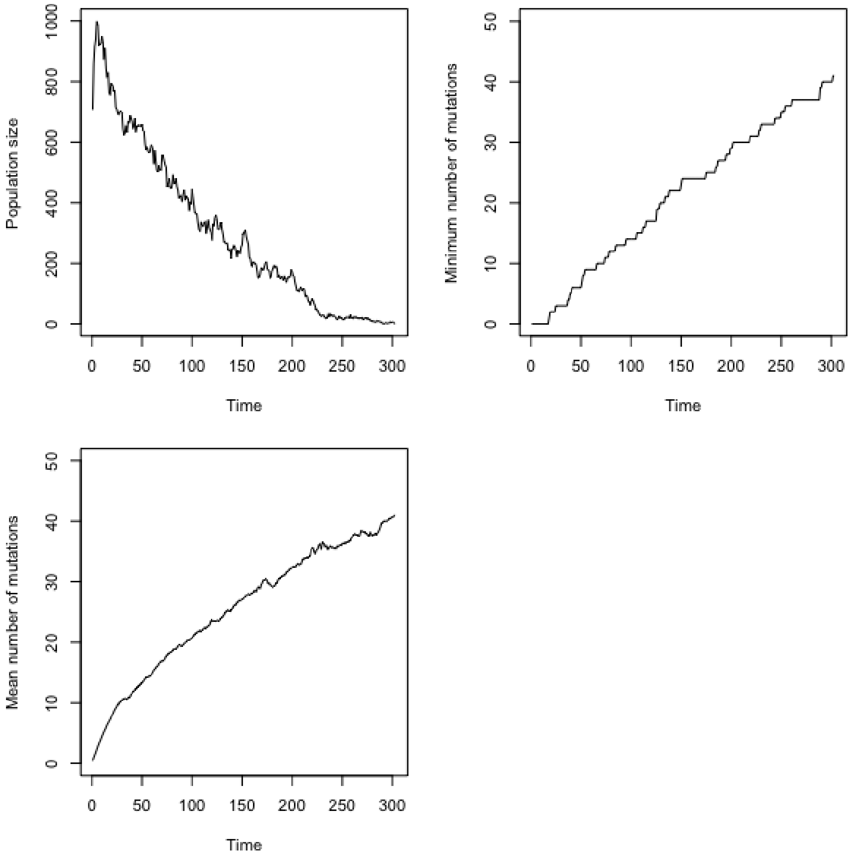

Figure 3: Evolution in asexuals under strong selection $s = 0.02$.

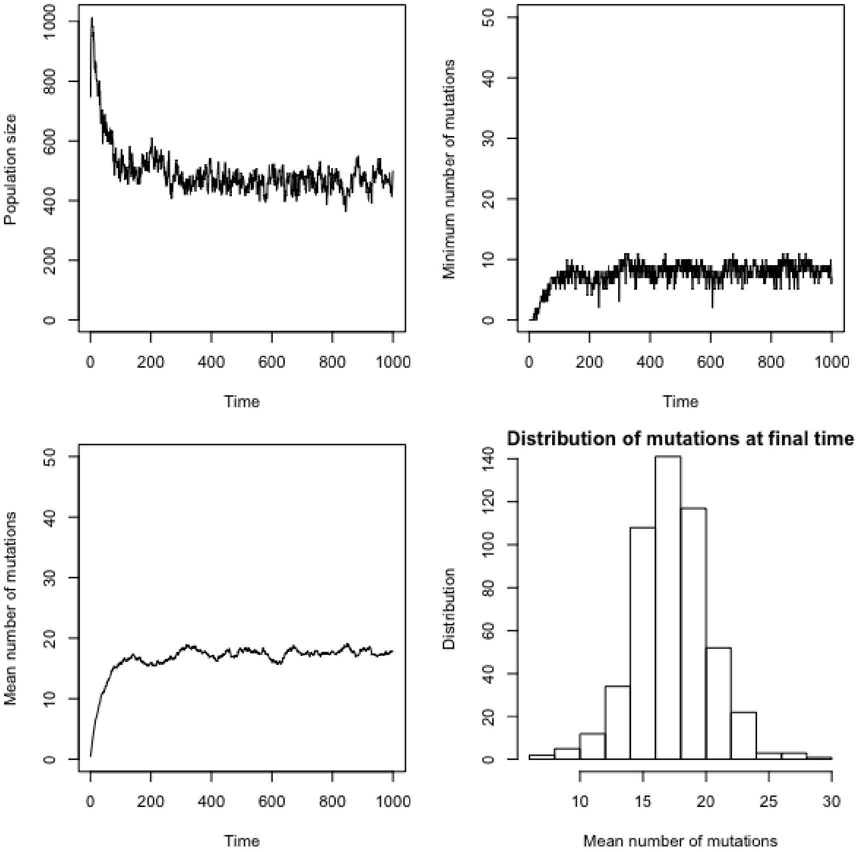

Figure 4: Evolution in sexuals under strong selection $s = 0.02$.