Solutions to exercise sheet 2

Sex, Ageing and Foraging Theory

1 Evolution of ageing

1.1 Evolutionary analysis

a. According to the model, the lifetime reproductive success of a rare mutant expressing an allocation strategy y in a resident population expressing x is,

$$R_0(y, x) = K(x) \left[b(1 - e^{-y}) + p \times \alpha b(1 - e^{-(1-y)}) \right].$$ (1)

Using the fact that $R_0(x, x) = 1$ by definition, we have

$$K(x) = \frac{1}{b(1 - e^{-x}) + p \times \alpha b(1 - e^{-(1-x)})}.$$ (2)

Plugging this back into $R_0(y, x)$, we obtain,

$$R_0(y, x) = \frac{1 - e^{-y} + p \times \alpha(1 - e^{-(1-y)})}{1 - e^{-x} + p \times \alpha(1 - e^{-(1-x)})}.$$ (3)

b. Using the hints given in the exercise sheet and basic calculus, one finds that the selection gradient reads as

$$s(x) = \left. \frac{\partial R_0(y, x)}{\partial y} \right|_{y=x} = \frac{e^{-x} - \alpha p e^{-(1-x)}}{1 - e^{-x} + p \times \alpha(1 - e^{-(1-x)})}.$$ (4)

c. The problem of finding x^* such that $s(x^*) = 0$ reduces to solving

$$e^{-x^*} = \alpha p e^{-(1-x^*)}$$ (5)

for x^*. Applying $\ln(\cdot)$ to both sides of this equation (which we can do as both sides are positive) yields

$$-x^* = \ln(\alpha p) - 1 + x^*.$$ (6)

This can be rearranged to find

$$x^* = \frac{1 - \ln(\alpha p)}{2}.$$ (7)

To show that x^* maximises R_0 analytically, we take the derivative of $s(x)$ with respect to x, evaluate this

derivative at x^*, and check that it is negative. Doing this we get,

$$\left.\frac{ds(x)}{dx}\right|_{x=x^*} = -\left(\frac{e^{-x} - \alpha p e^{-(1-x)}}{1 - e^{-x} + p \times \alpha(1 - e^{-(1-x)})}\right)^2 - \frac{e^{-x} + \alpha p e^{-(1-x)}}{1 - e^{-x} + p \times \alpha(1 - e^{-(1-x)})} < 0, \quad (8)$$

which is indeed always negative.

Alternatively, one can plot $s(x)$ as a function of x and check that it is positive when approaching x^* from below and negative when approaching it from above (Figure 1), such that selection will push the trait value towards x^*.
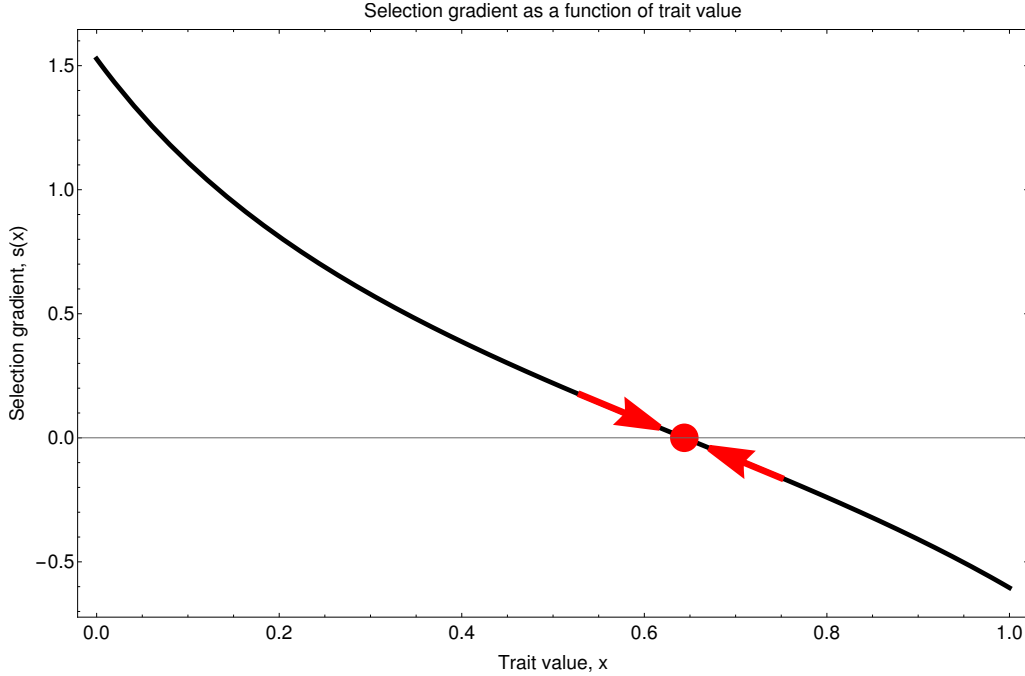

Figure 1: Selection gradient as a function of trait value.

d. Looking at eq. (7) with $\alpha = 1$, we see that the optimal allocation strategy x^* decreases when p increases, and that in particular $x^* = 0.5$ when $p = 1$ (see black line in fig. 2). In other words, as the probability p to survive to age 2 increases, selection favours investing an increasing share of one's resources into fecundity at age 2 (i.e. x^* increases). When $p = 1$ (so individuals always survive from age 1 to age 2) and $\alpha = 1$ (so one unit of resources invested into fecundity at age 1 or at age 2 yields the same fecundity benefit), selection on fecundity at age 1 and 2 has the same force. So the optimal allocation strategy x^* is to dedicate half of one's resource to reproduction at age 1 and the other half at age 2. As a result, individuals of age 1 and 2 have the same fecundity, i.e., no senescence has evolved. However it is very unlikely if not impossible for survival to be certain (i.e. for $p = 1$). There is always a chance of death by accident (i.e. $p < 1$). In this case, selection favours more resources into fecundity at age 1 and therefore leads to the evolution of senescence (with individuals at age 2 having lower fecundity).

e. Using eq. (7) to plot optimal allocation strategy x^* against α reveals that as α increases above 1, selection favours investing more resources into fecundity at age 2. This is because when $\alpha > 1$, one unit of resources invested at age 2 yields greater fecundity returns than at age 1. Selection then favours spending a larger amount of resources on reproduction at age 2 because the fecundity increases rapidly with age. From an

2

evolutionary point of view, this illustrates that the reduction in the strength of selection in older age-classes (due to extrinsic mortality) can be offset by larger effects of traits on fecundity at a later age. Biologically, this typically happens in species where fecundity is proportional to size and individuals keep growing throughout their lives.

1.2 Individual-based simulations

The simulation program describes a population of constant size, where deceased individuals are immediately replaced by a new one. Individuals are characterised by their age, stored in vector **A**, and their trait value, stored in vector **P**. At each time step, we first calculate the fecundity of individuals in the population, stored in vector **Fec** (line 22). Then, all individuals of age 2 die and each individual of age 1 dies with probability $1 - p$. For those that survive (with complementary probability p), we update their age from 1 to 2 in vector **A** (line 56). We then replace each dead individual by a new individual of age 1 as follows. First, a parent is sampled randomly from the population with a probability proportional to its fecundity (line 30). The new individual has the parent's trait value, which then mutates with probability u (line 34). Its trait value is stored in place of that of the dead and its age is set to 1. At the end of each time step, the mean trait value is stored in vector **R**. At the end of the simulation, this vector is returned.

This simulation program assumes that individuals always produce enough offspring to keep the population at a constant size, such that density-dependent survival of the newborns can be neglected since it does not depend on the trait. This allows simulations to run much faster with little effect on the evolutionary outcome, as shown by the excellent fit between analytical results and simulation results presented in Figure 2.

a. Line 23 in the code calculates the fecundity of all individuals in the population using vector operations.

b. See Figure 2.

2 Evolution of iteroparity and semelparity

2.1 Evolutionary analysis

a. The probability, $l_a(y, x)$, that a mutant y (in a resident population expressing reproductive effort x) survives up to age $a \geq 1$ is given by

$$l_a(y, x) = K(x)p_a(y)^{a-1} = K(x)\left(c(1 - y^\gamma)\right)^{a-1},\tag{9}$$

where $K(x)$ is the probability p_0 that an individual survives from age 0 to 1 and is such that the resident population is at demographic equilibrium (i.e. such that $R_0(x, x) = 1$).

b. The lifetime reproductive success of a mutant y (in a resident population expressing reproductive effort x) is by definition,

$$R_0(y, x) = \sum_{a=1}^{\infty} m_a(y, x)l_a(y, x) = \frac{b_0 y}{1 - c(1 - y^\gamma)}K(x).\tag{10}$$
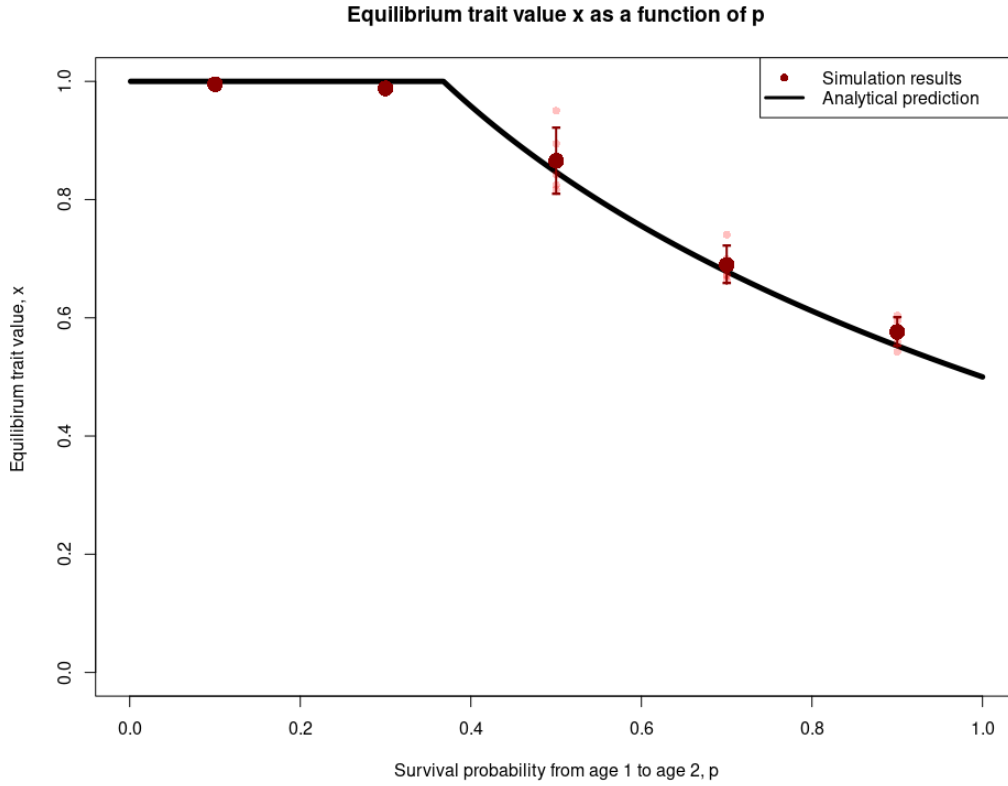
3

Equilibrium trait value x as a function of p

Figure 2: Equilibrium value of simulations with different values of p. Five replicates were run for each value.

Because $R_0(x, x) = 1$, we must have

$$K(x) = \frac{1 - c(1 - x^\gamma)}{b_0 x}, \tag{11}$$

Substituting eq. (11) into (10), we get,

$$R_0(y, x) = \frac{y}{x} \times \frac{1 - c(1 - x^\gamma)}{1 - c(1 - y^\gamma)}. \tag{12}$$

c. Using eq. (12) and basic calculus, the selection gradient is

$$s(x) = \left. \frac{\partial R_0(y, x)}{\partial y} \right|_{y=x} = \frac{1}{x} - \frac{c\gamma x^{\gamma-1}}{1 - c(1 - x^\gamma)}. \tag{13}$$

By plotting eq. (13) against x, we see that when $\gamma \leq 1$, the selection gradient $s(x)$ is always positive. This means that evolution will always favour $x^* = 1$ (semelparity) in this case. By contrast, the selection gradient can switch from positive to negative when $\gamma > 1$, so that iteroparity can be favoured (see Figure 3).

This is because γ controls the strength of trade-off between reproduction and survival (to see this, you can plot m_a and p_a in a monomorphic population against x for different values of γ). When γ is small, investing a few resources into survival causes a sharp drop in fecundity. There is therefore no incentive to do so and thus selection favours semelparity. When γ is large, investing a few resources into survival entails only a

4

small cost in fecundity. It therefore makes sense to attempt at surviving for another season and reproduce, leading to the evolution of iteroparity.

d. From eq. (13), solving the equilibrium condition, $s(x^*) = 0$ for x^* gives

$$x^* = \left(\frac{1-c}{c(\gamma - 1)} \right)^{\frac{1}{\gamma}} \tag{14}$$

for the optimal reproductive effort. Such optimal strategy decreases with extrinsic mortality parameter c. This is because if there is a high chance of dying between reproductive episodes, then it is more advantageous to reproduce fewer times.

The lifespan $L_0(y, x)$ of a mutant y (in a resident population expressing reproductive effort x) is defined as the expected age of death of such a mutant. By definition, this is given mathematically by,

$$L_0(y, x) = \sum_{a=1}^{\infty} a \times l_a(y, x)(1 - p_a(y, x)), \tag{15}$$

where $l_a(y, x)(1 - p_a(y, x))$ is the probability to survive up to age a and then die at that age (i.e. not survive to age $a + 1$).

Using definition eq. (15) for our model and for a population monomorphic for x^* (i.e. $x = y = x^*$), we obtain,

$$L_0(x^*, x^*) = \frac{1}{b_0 x^*}. \tag{16}$$

Substituting for x^* (given by eq. 14) into eq. (16) reveals that lifespan decreases as c decreases. This is because higher extrinsic mortality c favours the evolution of higher reproductive efforts (eq. 14) and thus leads to reduced survival from one year to the next, which in turn means shorter lifespans.

Note: The definition of lifespan eq. (15) includes survival from birth to establishment (i.e. from age 0 to 1). In other words, this equation answers the question: what is the expected age that a newborn will die at? But in many species, the probability that an offspring dies before reaching age 1 (or another relevant stage) is extremely high. Think of species that produce offspring in extreme numbers where each offspring has a minute chance of survival (e.g. fish that release millions of eggs in the water). In these species, measuring lifespan conditional on successful establishment is more biologically meaningful. For instance, if establishment is at age 1, conditional lifespan would be

$$L_1(y, x) = \sum_{a=1}^{\infty} a \frac{l_a(y, x)}{l_1(y, x)} (1 - p_a(y, x)), \tag{17}$$

where $l_a(y, x)/l_1(y, x)$ gives the probability of reaching age a given survival till age 1. For our model, this would lead to

$$L_1(y, x) = \frac{L_0(y, x)}{K(x)}, \tag{18}$$

which would be most relevant where fecundity b_0 is high.

2.2 Individual based simulations

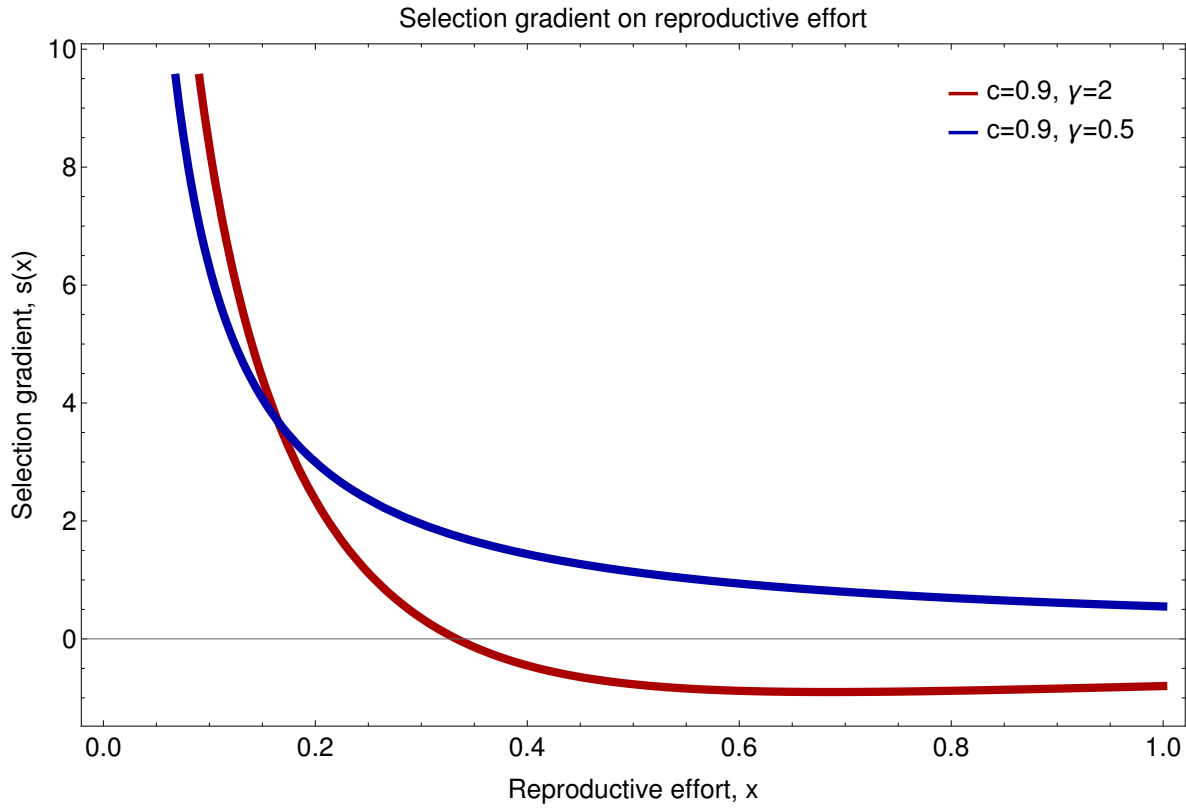a. A commented simulation program has been made available on the course website (https://lab-mullon.github.io/SAF).

Figure 3: Selection gradient as a function of reproductive effort for values of γ above and below 1 ($b_0 = 1$ and $c = 0.9$).

b. Simulations should match analytical predictions perfectly, unless γ is taken close to 1, at which point the simulations take a longer time to reach equilibrium because selection becomes very weak. To visualise this, you can plot the selection gradient $s(x)$ for $\gamma = 1$ and notice that it becomes very flat as x approaches 1.

c. Using the average reproductive effort in the simulated population at each timestep, we can compute the corresponding lifespan L_0 from eq. (16). The simulation results match our evolutionary analysis (see Figure 4).
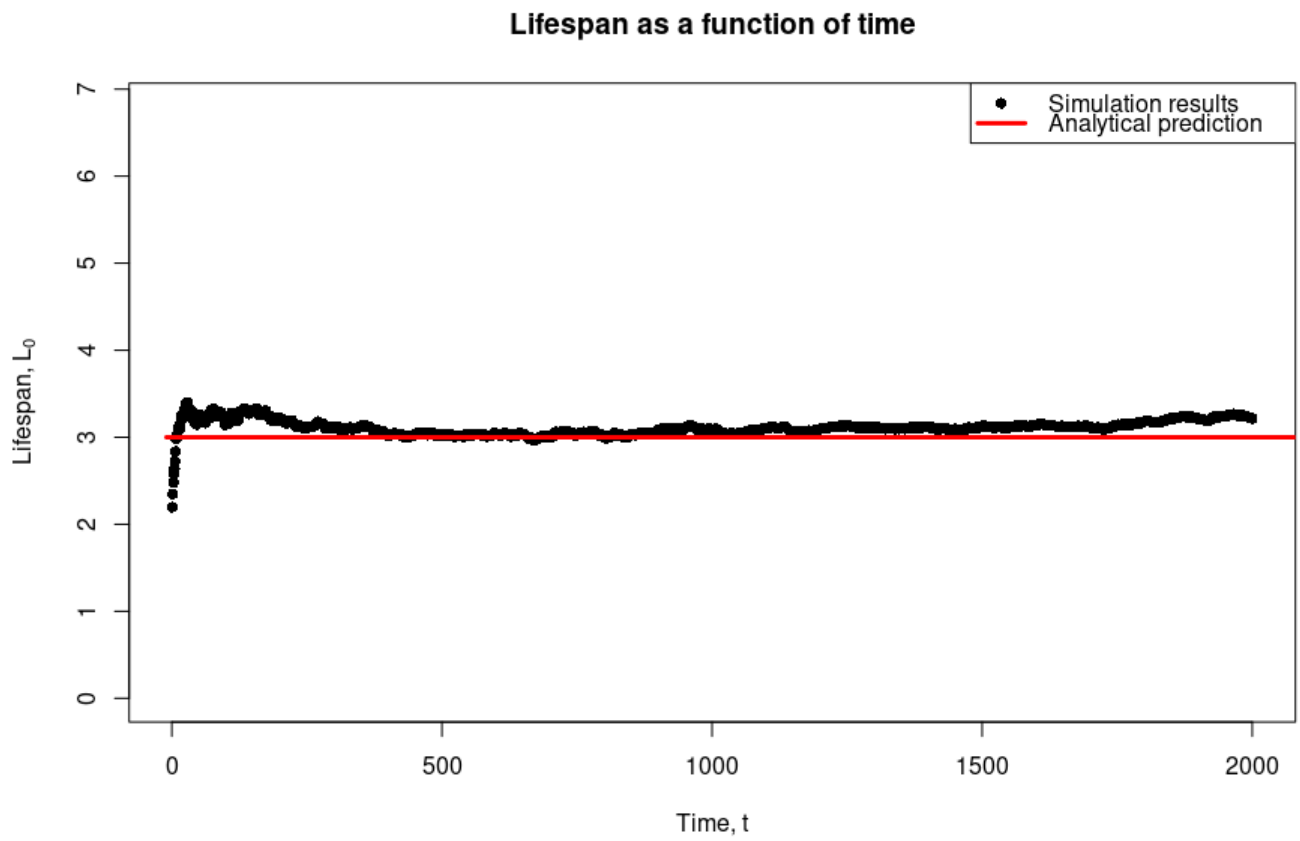
Figure 4: Lifespan as a function of time for $b_0 = 1$, $\gamma = 2$ and $c = 0.9$. The black dots depict the simulation results while the red line depicts the mathematical prediction.