Solutions to exercise sheet 2

Sex, Ageing and Foraging Theory

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

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

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,

$$R_0(y,x) = \sum_{a=1}^{\infty} m_a(y,x)l_a(y,x) = \frac{b_0 y}{1-c(1-y^\gamma)}K(x). \tag{2}$$

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

$$K(x) = \frac{1-c(1-x^\gamma)}{b_0 x}, \tag{3}$$

Substituting eq. (3) into (2), we get,

$$R_0(y,x) = \frac{y}{x} \times \frac{1-c(1-x^\gamma)}{1-c(1-y^\gamma)}. \tag{4}$$

c. Using eq. (4) and basic calculus, the selection gradient is

$$s(x) = \left.\frac{\partial R_0(y,x)}{\partial y}\right|_{y=x} = \frac{1}{x} - \frac{c\gamma x^{\gamma-1}}{1-c(1-x^\gamma)}. \tag{5}$$

By plotting eq. (5) 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 1).

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 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. (5), solving the equilibrium condition, $s(x^*) = 0$ for x^* gives

$$x^* = \left(\frac{1-c}{c(\gamma-1)}\right)^{\frac{1}{\gamma}} \tag{6}$$

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,

$$L_0(y,x) = \sum_{a=1}^{\infty} a \times l_a(y,x)(1-p_a(y,x)), \tag{7}$$

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

$$L_0(x^*,x^*) = \frac{1}{b_0 x^*}. \tag{8}$$

Substituting for x^* (given by eq. 6) into eq. (8) reveals that lifespan decreases as c decreases. This is because higher extrinsic mortality c favours the evolution of higher reproductive efforts (eq. 6) and thus leads to reduced survival from one year to the next, which in turn means shorter lifespans.

Note: The definition of lifespan eq. (7) 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

$$L_1(y,x) = \sum_{a=1}^{\infty} a \frac{l_a(y,x)}{l_1(y,x)}(1-p_a(y,x)), \tag{9}$$

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

$$L_1(y,x) = \frac{L_0(y,x)}{K(x)}, \tag{10}$$

which would be most relevant where fecundity b_0 is high.

2 Individual based simulations

a. The 'if' statement on line 23 tests whether the individual survives to the next time step or not. If it survives nothing happens, and if it dies it is replaced by a juvenile. On line 25, the function 'sample' selects a parent for the offspring to be established and replace the dead individual. Each parent has a probability of being chosen proportional to its fecundity.

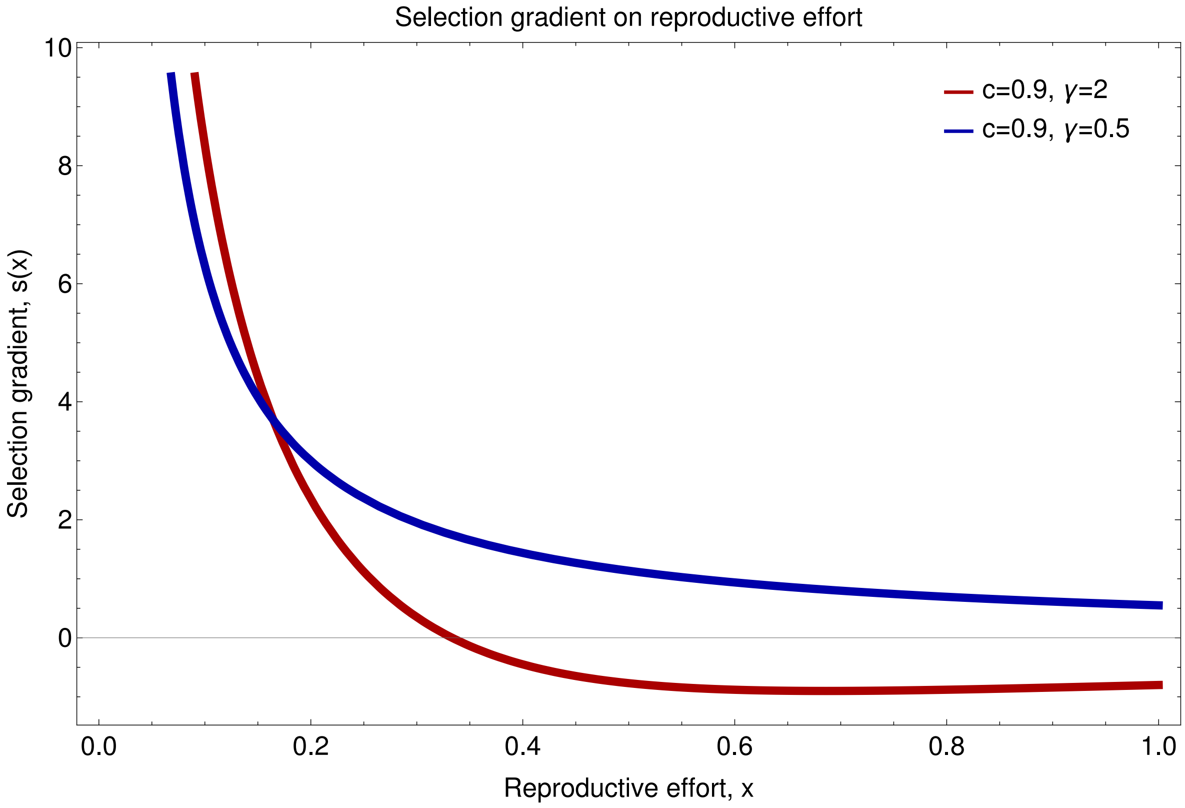

Figure 1: Selection gradient as a function of reproductive effort for values of γ above and below 1 ($b_0 = 1$ and $c = 0.9$).

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. (8). The simulation results match our evolutionary analysis (see Figure 2).

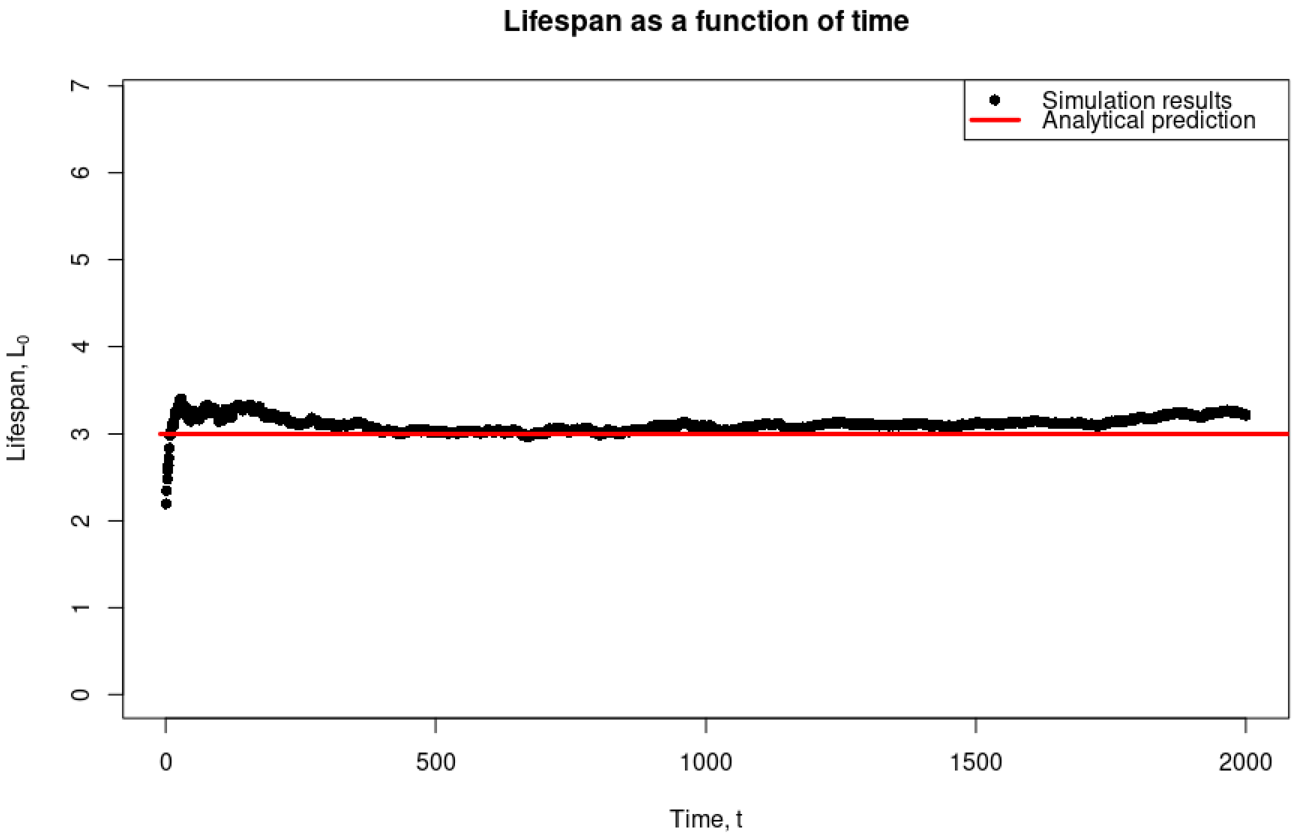

Figure 2: Lifespan as a function of time for $b_0 = 1$, $\gamma = 2$ and $c = 0.9$.
The black dots depict the simulation results while the red line depicts the mathematical prediction.