

Solutions to exercise sheet 3

Sex, Ageing and Foraging Theory

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,

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

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

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

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

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

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

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

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

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

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

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

This can be rearranged to find

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

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^* .

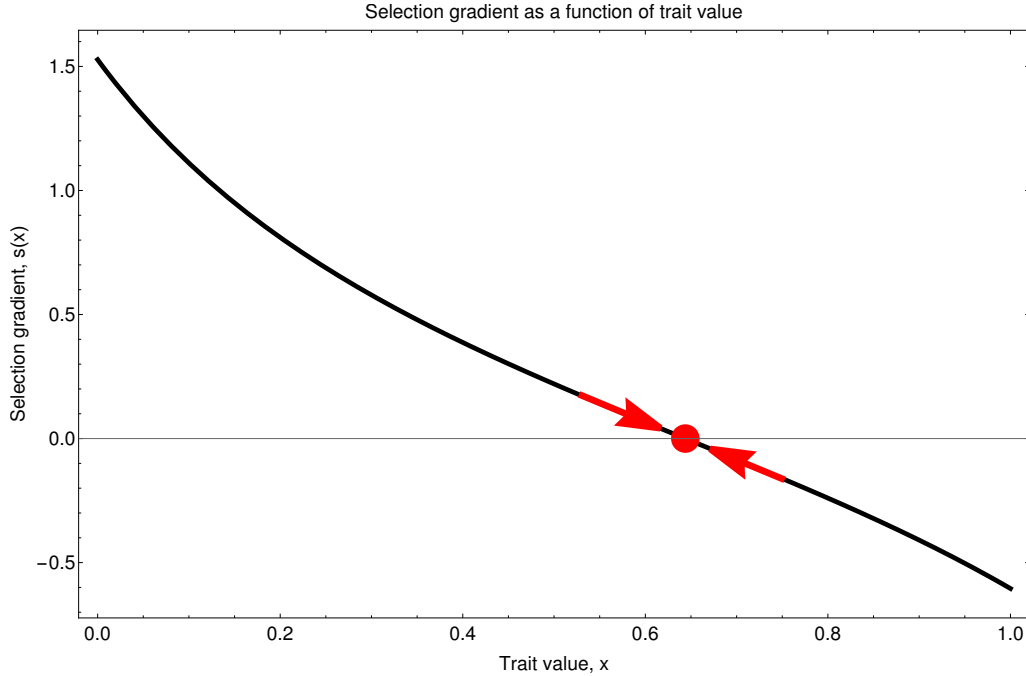


Figure 1: Selection gradient as a function of trait value.

- 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 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.

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 22 in the code calculates the fecundity of all individuals in the population using vector operations.
- b. See Figure 2.

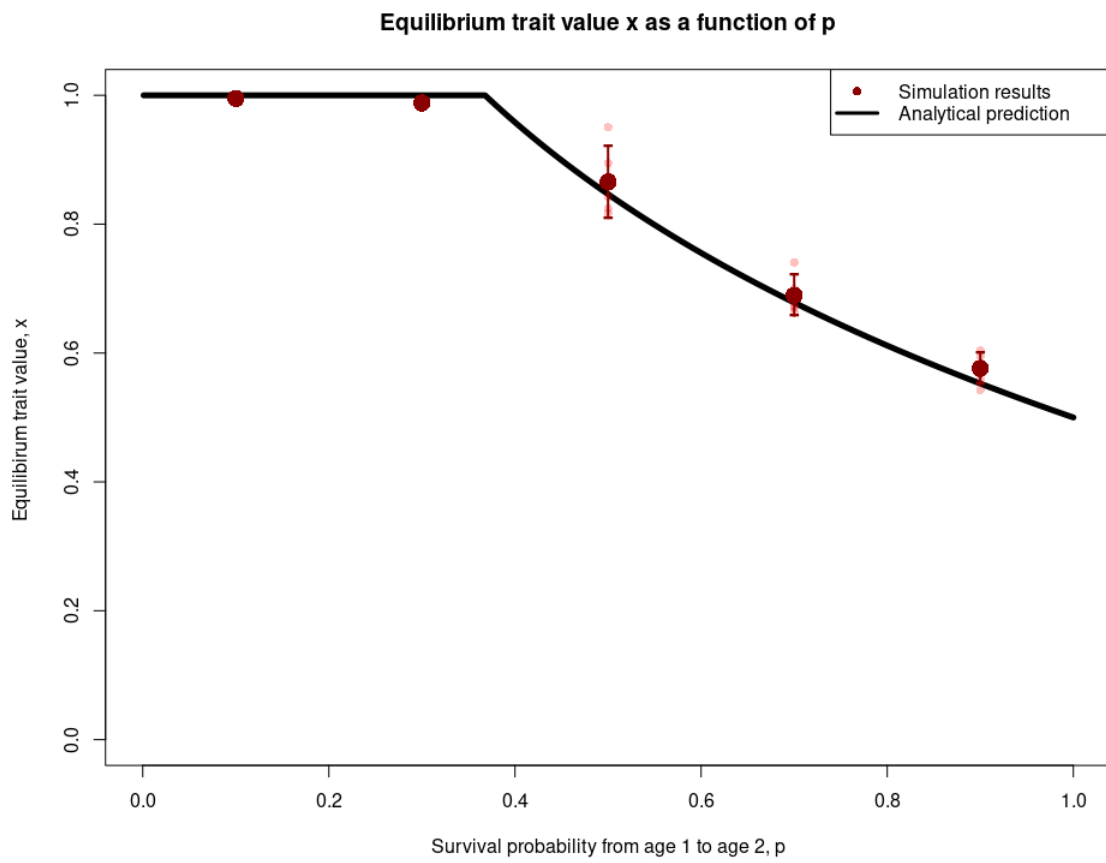


Figure 2: Equilibrium value of simulations with different values of p . Five replicates were run for each value.