Practical exam 2023: Ageing and mutation accumulation

Sex, Ageing and Foraging Theory

1 Mathematical analysis

a. The functions $m_1(x_1)$ and $m_2(x_2)$ have the same bell shape. As shown in Figure 1, selection is stabilising, favouring optimal trait value θ_1 at age 1 and θ_2 at age 2 (we have fixed $\theta = 0$ in Fig. 1). The parameter ω changes the width of the peak so that fecundity drops faster when the trait is further from the optimal when ω is smaller. In other words, selection is stronger when ω is smaller.

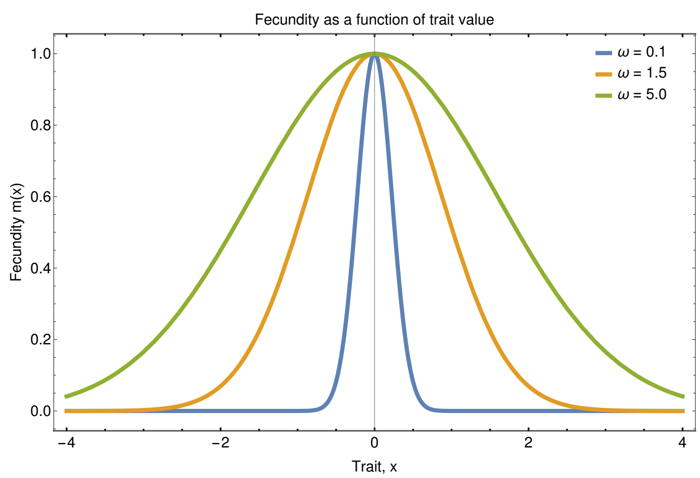


Figure 1: Fecundity as a function of trait value.

b. The lifetime reproductive success of a mutant expressing trait values y_1 and y_2 in a resident population expressing trait values x_1 and x_2 is

$$R_0(y_1, y_2, x_1, x_2) = K(x_1, x_2)\left[m_1(y_1) + p \times m_2(y_2)\right]. \quad (1)$$

where $K(x_1, x_2)$ is such that $R_0(x_1, x_2, x_1, x_2) = 1$, i.e.,

$$K(x_1, x_2) = \frac{1}{m_1(x_1) + p \times m_2(x_2)}. \quad (2)$$

So substituting eq. (2) into eq. (1), we get

$$R_0(y_1, y_2, x_1, x_2) = \frac{m_1(y_1) + p \times m_2(y_2)}{m_1(x_1) + p \times m_2(x_2)}. \quad (3)$$

The selection gradients acting on x_1 and x_2 can then be expressed as,

$$\begin{aligned} s_1(x_1) &= K(x_1,x_2) \times \left.\frac{\partial m_1(y_1)}{\partial y_1}\right|_{y_1=x_1} = -K(x_1,x_2) \times \frac{2(x_1-\theta_1)}{\omega} m_1(x_1) \\ s_2(x_2) &= K(x_1,x_2) \times p \times \left.\frac{\partial m_2(y_2)}{\partial y_2}\right|_{y_2=x_2} = -K(x_1,x_2) \times p \times \frac{2(x_2-\theta_2)}{\omega} m_2(x_2). \end{aligned} \tag{4}$$

Since the fecundity functions m_1 and m_2 have the same shape, the only relevant difference between the selection gradients s_1 and s_2 is that s_2 is proportional to the probability p of surviving to age 2. Since $0 \leq p \leq 1$, the strength of selection on the trait relevant for fecundity at age 2 is always lower (or equal when $p = 1$) than the strength of selection on the trait relevant for fecundity at age 1. At mutation-selection-drift balance, the evolved trait value at age 2 x_2 should therefore be further away from its optimum θ_2 than x_1 from θ_1, especially when p is small. As a result, we expect fecundity at age 2 to be lower than fecundity at age 1.

c. When $x_1 = \theta_1$ and $x_2 = \theta_2$, we have $m_1(\theta_1) = m_2(\theta_2) = b_0$. Using this and eq. (2), we have

$$K(\theta_1,\theta_2) = \frac{1}{b_0 + p \times b_0}. \tag{5}$$

Lifespan from birth in a population monomorphic for $x_1 = \theta_1$ and $x_2 = \theta_2$ is then given by

$$L_0(\theta_1,\theta_2) = K(\theta_1,\theta_2)(1-p) + 2K(\theta_1,\theta_2)p = \frac{1}{b_0}, \tag{6}$$

while lifespan conditional on establishment is

$$L_1(\theta_1,\theta_2) = 1 - p + 2p = 1 + p. \tag{7}$$

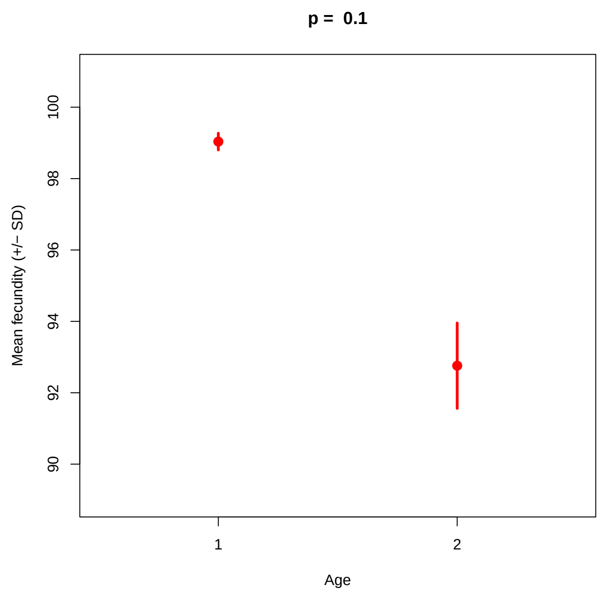
Lifespan conditional on establishment, $L_1(\theta_1,\theta_2)$, thus increases linearly with p up to a maximum of 2 when $p = 1$, i.e. where all individuals survive to age 2 then die. By contrast, lifespan from birth, $L_0(\theta_1,\theta_2)$, is independent from p. In fact, $L_0(\theta_1,\theta_2)$ only depends on b_0, which controls the intensity of competition for establishment. Lifespan from birth, $L_0(\theta_1,\theta_2)$, only depends on b_0 because the population is at a demographic equilibrium. As a result, establishment of an offspring is only possible when an adult has died. In turn this means that even if p increases, the increase in conditional lifespan $L_1(\theta_1,\theta_2)$ is compensated by the decrease in recruitment probability experienced by newborns.

2 Individual-based simulations

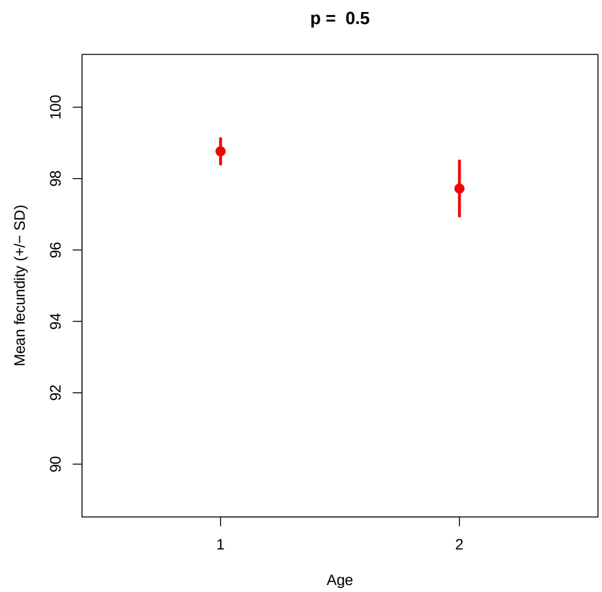
a. (i) Line 30 in the code computes the fecundity of the i^{th} individual in the population as a function of its age and age-specific trait value. (ii) The *if* statement on line 37 tests whether individual i survives this timestep. (iii) On line 39, a parent is sampled from the population with a probability proportional to its fecundity.

b. Increasing p reduces the difference between fecundity at age 1 and age 2 because it makes selection at age 2 more efficient (Figure 2), in agreement with the selection gradients computed in the first exercise.

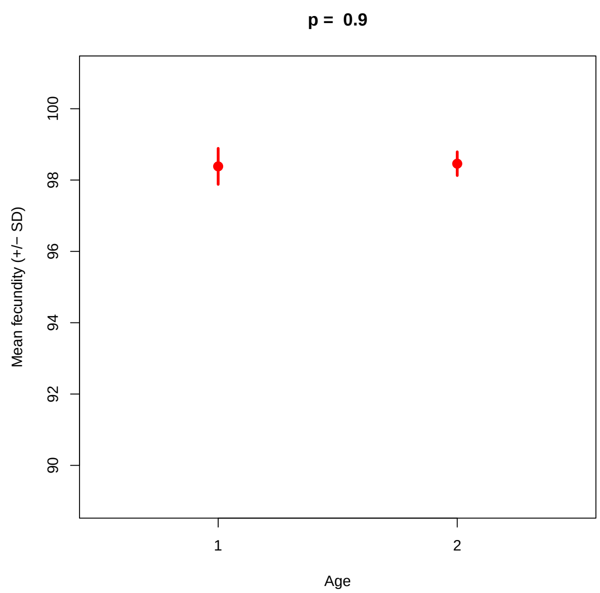
c. **Challenge question:** The same pattern emerges with four age-classes as with two: mean age-specific fecundity decreases with increasing age (Figure 3).



(a) Age-specific fecundities for $p = 0.1$

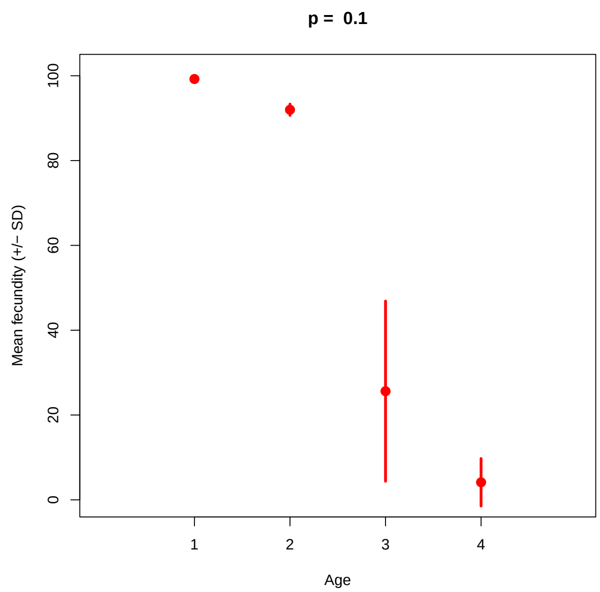


(b) Age-specific fecundities for $p = 0.5$

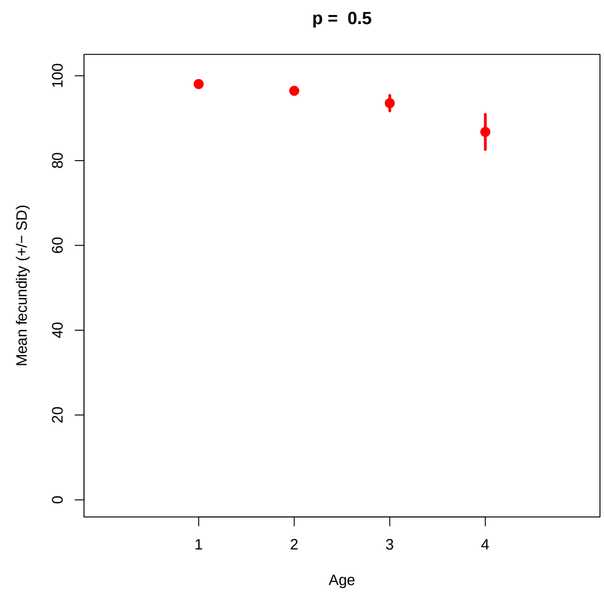


(c) Age-specific fecundities for $p = 0.9$

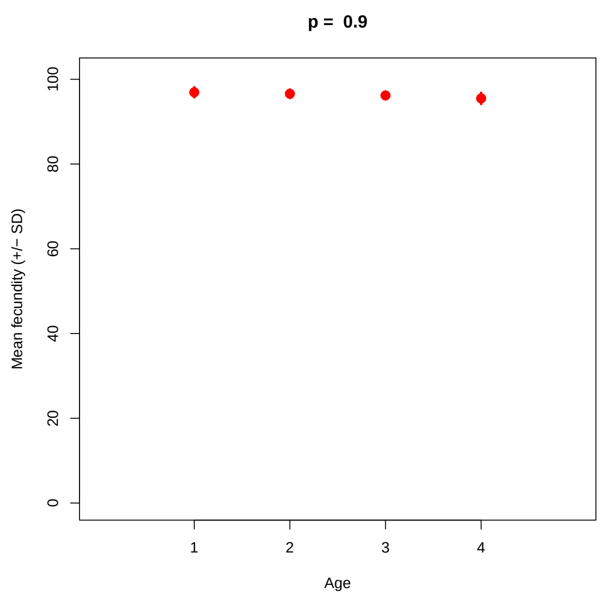
Figure 2: Mean age-specific fecundities ($\pm$ SD) at ages 1 and 2 for $p = 0.1;\ 0.5;\ 0.9$.



(a) Age-specific fecundities for $p = 0.1$



(b) Age-specific fecundities for $p = 0.5$



(c) Age-specific fecundities for $p = 0.9$

Figure 3: Mean age-specific fecundities ($\pm$ SD) at ages 1, 2, 3 and 4 for $p = 0.1;\ 0.5;\ 0.9$.