Exercise sheet 3: Ageing and antagonistic pleiotropy

Sex, Ageing and Foraging Theory

In this exercise sheet, we will analyse a simple model to illustrate **antagonistic pleiotropy**, a mechanism that has been proposed to explain the evolution of ageing and that was discussed during the lecture.

1 Evolutionary analysis

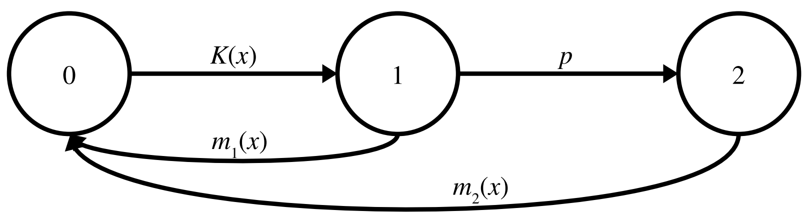

Figure 1: Life cycle.

We consider a monomorphic population at demographic equilibrium in which individuals can live for up to two years (Figure 1). Newborns establish in the population with probability $K(x)$ (which is such that the lifetime reproductive success of a resident is one), and established individuals survive from age 1 to age 2 with a fixed probability p. Individuals acquire a fixed amount of resources at birth, which they allocate to reproduction at age 1 and 2 in proportions x and $1-x$, respectively. Fecundities at age 1 and 2, $m_1(x)$ and $m_2(x)$, increase with resources allocated at that age according to,

$$m_1(x) = b(1-e^{-x}) \text{ and } m_2(x) = \alpha b(1-e^{-(1-x)}), \tag{1}$$

where $b > 0$ is a constant scaling the number of offspring produced, and $\alpha > 0$ controls how fecund age-class 2 is compared to age 1. When $\alpha = 1$, investing a resource unit to reproduction at age 1 and age 2 results in the same change in terms of fecundity. When $\alpha > 1$ (resp. $\alpha < 1$), investing a resource unit to reproduction at age 2 results in a greater (resp. lower) increase in fecundity than at age 1.

a. Using the information given above, compute the lifetime reproductive success of a rare mutant expressing an allocation strategy y in a resident population expressing x.

b. Compute the selection gradient acting on the allocation strategy x, $s(x)$ Hints:

$$\frac{d}{dy}\left(e^{u(y)}\right) = \frac{du(y)}{dy} \times e^{u(y)}, \tag{2}$$

and $e^{-1} = 1/e$.

c. Using natural log $\ln(x)$ and its properties, prove that $s(x)$ cancels for

$$x^* = \frac{1 - \ln(\alpha p)}{2}. \tag{3}$$

Does this x^* maximise or minimise R_0? Support your answer with either graphical or analytical arguments.

d. Set $\alpha = 1$. How does x^* change with p? In particular, what happens when $p = 1$? Make a plot of x^* as a function of p and give a biological interpretation of your results.

e. How does changing α away from one affect your results? Explain the implications of your findings for the evolution of ageing.

2 Individual-based simulations

An individual-based simulation program of the model studied above has been made available on the course website (https://lab-mullon.github.io/SAF). Download this program and familiarise yourself with it.

a. Line 22 in the code has been left uncommented. Explain what this line does. Note that R allows for term-by-term vector operations as shown in the code snippet below:

```
vec1 = c(1,2,3)
vec2 = c(2,2,2)

vec1*vec2 = c(2,4,6)
vec1+vec2 = c(3,4,5)
exp(vec1)*vec2 = c(2.00,5.44,14.78,40.17)
```

b. Run simulations for $nt = 3000$ time steps with $\alpha = 1$, $b = 10$, $u = 0.01$ (mutation rate), $\sigma = 0.01$ (size of mutations), $n = 500$ (population size), for $p = 0.1,\ 0.3,\ 0.5,\ 0.7,\ 0.9$. Store the mean of the evolving trait x obtained over the last 1000 generations of each simulation, and make a plot showing these values as dots together with a curve of your analytically predicted equilibrium x^* (from question 1.c) as a function of p. This may take a while depending on your computer.

c. **(Optional)** To go a step further, you can run several replicates (i.e. run simulations multiple times for each value of p) and plot their average with error bars showing between-replicates standard deviation.