Exercise sheet 2: Evolution of life-histories and ageing

Sex, Ageing and Foraging Theory

1 Evolution of iteroparity and semelparity

In this first part, we will be modelling the evolution of iteroparity and semelparity through the division of resources into reproduction *versus* survival. We consider a population in which individuals acquire the same total amount of resources each year, and split it between reproduction and survival in proportions x and $1-x$, respectively. The proportion x of resources dedicated to reproduction is called the **reproductive effort**. We assume this effort remains constant throughout an individual's life (i.e. does not change with age). When $x = 1$, all resources are allocated to reproduction and the individual dies after having reproduced only once. This leads to a **semelparous** life cycle in this model. By contrast, when $0 < x < 1$ individuals can survive from one breeding season to the next and thus reproduce multiple times, leading to an **iteroparous** life cycle.

We are interested in the evolution of reproductive effort and understanding when this evolution gives rise to a semelparous or iteroparous life-cycle. To do this, let us consider a rare mutant with reproductive effort y in a resident population with effort x. We assume that an individual's fecundity at age a, $m_a(y)$ is,

$$m_a(y) = b_0 y, \tag{1}$$

where $b_0 > 0$ is a constant; while its probability $p_a(y)$ of surviving from age a to $a+1$ is,

$$p_a(y) = c\,(1 - y^\gamma) \tag{2}$$

for $a \geq 1$, where $0 \leq c \leq 1$ is a constant that controls the strength of extrinsic mortality (i.e. the risk of dying due to external factors, irrespective of reproductive effort y), and γ controls the intensity of the trade-off between survival and reproduction. When an individual dies, it is replaced by a juvenile sampled among the newborns so that the population is kept at constant size (this can be thought of as equivalent to assuming that the survival of newborns till age 1, p_0, depends negatively on population size).

1.1 Evolutionary analysis

a. Compute the probability of surviving from age zero to age a of a mutant, $l_a(y, x)$.

b. Compute the mutant reproductive success, $R_0(y, x)$ (Hint: recall that $\sum_{k=0}^{\infty} q^k = \frac{1}{1-q}$ when $0 < q < 1$).

c. Compute the selection gradient $s(x)$ acting on reproductive effort. Plot this gradient against $x \in [0, 1]$ for various values of γ, fixing $b_0 = 1$ and $c = 0.9$. Different behaviours are observed when $\gamma \leq 1$ and $\gamma > 1$.

Plot two examples representative of these different behaviours on the same graph, and interpret these results. What are the consequences for the evolution of iteroparity and semelparity?

d. Focus on the case where iteroparity can evolve, and compute the reproductive effort value x^* at which the selection gradient cancels (i.e. where such that $s(x^*) = 0$). Calculate the lifespan of an individual in a population monomorphic for this level of reproductive effort. How is it affected by different values of extrinsic mortality (c) ? Give a biological interpretation of your results.

1.2 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. Lines 23 and 25 in the code have been left uncommented. Explain what each of these lines do.

b. Run simulations for $nt = 2000$ time steps with the following parameter values $c = 0.90$, $b_0 = 1$, $u = 0.01$ (mutation rate), $\sigma = 0.01$ (size of mutations), $n = 500$ (population size). Use various values of γ, both above and below 1. **Do not use values too close to 1** (for instance, use $\gamma = 0.50$ and $\gamma = 2$ for the below and above 1 cases, respectively), otherwise the simulations will take a very long time to reach their equilibrium. Do your simulation results confirm the results you obtained using evolutionary analysis?

c. Set $\gamma = 2$ and run simulations for a few different values of c. Using the simulation output, make a plot of mean individual lifespan in the simulated population as a function of time and check whether it matches your evolutionary analysis results.

2 Evolution of ageing

In this part of the 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.

2.1 Evolutionary analysis

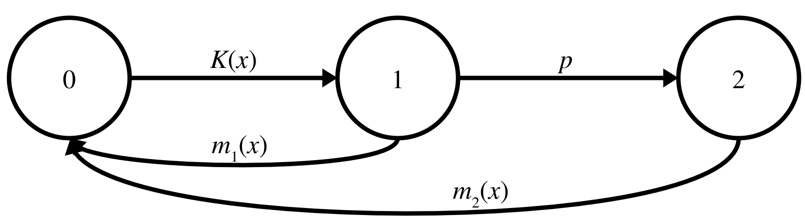

Figure 1: Life cycle.

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,

$$m_1(x) = b(1-e^{-x}) \text{ and } m_2(x) = \alpha b(1-e^{-(1-x)}), \tag{3}$$

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:

$$\frac{d}{dy}\left(e^{u(y)}\right) = \frac{du(y)}{dy} \times e^{u(y)}, \tag{4}$$

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

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

$$x^* = \frac{1-\ln(\alpha p)}{2}. \tag{5}$$

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.

2.2 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)
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```
vec1+vec2 = c(3,4,5)
exp(vec1)*vec2 = c(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.