Exercise sheet 2: Evolution of iteroparity and semelparity

Sex, Ageing and Foraging Theory

In this exercise sheet, 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 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.

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.