Practical exam 2022: Ageing and mutation accumulation

Sex, Ageing and Foraging Theory

Please send your report as a zipped folder containing: (i) an R code; and (ii) a single pdf document with your answers to charles.mullon@unil.ch by Tuesday 5th of April 2022 2pm. You can work in groups but the code and pdf document should be your own. Throughout, you are expected to give biological interpretations to your results and to support these interpretations with plots or figures when appropriate.

The goal is to study how mutation accumulation can lead to a decline of fecundity with age. We consider an initially monomorphic population at demographic equilibrium in which individuals can live for up to two years, and express a specific quantitative trait at each age: trait x_1 at age 1 and x_2 at age 2. Newborns establish (i.e. survive from age 0 to 1) with probability $K(x_1, x_2)$, which is such that the lifetime reproductive success of a resident is one. Established individuals survive from age 1 to age 2 with a fixed probability p. We assume that fecundity at ages 1 and 2 is a function of the trait expressed at that age:

$$\begin{aligned} m_1(x_1) &= b_0 \exp\left(-\frac{(x_1-\theta_1)^2}{\omega}\right) \\ m_2(x_2) &= b_0 \exp\left(-\frac{(x_2-\theta_2)^2}{\omega}\right), \end{aligned} \tag{1}$$

where θ_1, θ_2, $\omega > 0$ and $b_0 > 0$ are all constant parameters of the model.

Both traits x_1 and x_2 evolve via mutations that occur during reproduction with probability u, independently on each trait. When a trait mutates, its new value is sampled from a Gaussian distribution centered on the parental value with standard deviation σ.

1 Mathematical analysis

a. Plot $m_1(x_1)$ and $m_2(x_2)$ as functions of x_1 and x_2 for various parameter values (θ_1, θ_2, $\omega > 0$ $b_0 > 0$). From these plots, what should selection lead to for x_1 and x_2? What is the effect of the parameter ω?

b. Calculate the lifetime reproductive success $R_0(y_1, y_2, x_1, x_2)$ of a rare mutant expressing trait values y_1 and y_2 in a resident population expressing trait values x_1 and x_2. Then, compute the selection gradients, $s_1(x_1, x_2)$ and $s_2(x_1, x_2)$, acting on traits x_1 and x_2 respectively,

$$\begin{aligned} s_1(x_1,x_2) &= \left.\frac{\partial R_0(y_1,y_2,x_1,x_2)}{\partial y_1}\right|_{y_1=x_1,y_2=x_2} \\ s_2(x_1,x_2) &= \left.\frac{\partial R_0(y_1,y_2,x_1,x_2)}{\partial y_2}\right|_{y_1=x_1,y_2=x_2}. \end{aligned} \tag{2}$$

How do $s_1(x_1, x_2)$ and $s_2(x_1, x_2)$ compare to one another? Considering the three forces of evolution (selection, mutation and genetic drift), discuss the implications of your results for the evolution of age-specific fecundity and thus for ageing in this model.

c. Assuming that the population is fixed for $x_1 = \theta_1$ and $x_2 = \theta_2$, compute lifespan from birth $L_0(x_1, x_2)$ and lifespan conditional on establishment, $L_1(x_1, x_2)$. How do these two quantities depend on adult survival between ages 1 and 2, p?

2 Individual-based simulations

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

a. (i) Line 30 in the code has been left uncommented. Explain what this line does. (ii) Explain what the *if* statement on line 37 does. (iii) What does the sampling on line 39 correspond to biologically?

b. Run the simulation program with the following parameters: $N = 100$ (fixed population size), $b_0 = 100$, $u = 0.005$, $\omega = 0.01$, $\sigma = 0.1$ and $T_{\mathrm{f}} = 20000$ (number of generations) for three different survival probabilities: $p = 0.1$; $p = 0.5$; $p = 0.9$. Make ten replicates in each case, and record the average fecundities at age 1 and 2 over the last 10000 generations for each replicate. Store these average fecundities for all three values of p in a matrix (this should be a 6×10 matrix). Then, create three plots side-by-side (one per value of p) showing the mean fecundities at age 1 and age 2 averaged over the ten replicates, along with error bars showing the *between-replicates* standard deviations in mean age-specific fecundities (use the same scale for the y-axis of the three plots to help interpretation). Discuss your results. In particular, what is the effect of p on age-specific fecundity at mutation-selection-genetic drift equilibrium? Do your results agree with the predictions you made in the first exercise (in 1b)?

c. **Challenge question:** Extend the simulation program to model a population with four age classes, where fecundity at each age class also depends on a single, age-specific trait under stabilising selection (so each individual carries four traits), i.e., such that the fecundity $m_a(x_a)$ of an individual at age-class $a = 1, 2, 3, 4$ depends on the trait x_a it expresses in the following way

$$m_a(x_a) = b_0 \exp\left(-\frac{(x_a - \theta_a)^2}{\omega}\right). \tag{3}$$

Assume that individuals survive between age-classes with the same probability p (except when the final age-class is reached) and that $\theta_a = 0$ for all a. Repeat the analysis performed in the previous question for $n_a = 4$ age-classes and briefly comment on your results.