Exercise sheet 6

Sex, Ageing and Foraging Theory

Exercise 1: Competition for renewable resources among relatives

Here we model the evolution of foraging effort when individuals forage with relatives. We consider a scenario where each female lays its eggs in a single and unique patch (i.e. one patch per female) where eggs hatch and offspring exploit local resources. These resources follow Schaefer's model, i.e. the density of the resource in a patch where there are n_{c} offspring expressing foraging effort x changes in time according to

$$\frac{dn}{dt} = r\left(1 - \frac{n}{K}\right)n - n_{\mathrm{c}}h(x)n. \tag{1}$$

We assume that the harvesting function is simply,

$$h(x) = x. \tag{2}$$

After gathering resources offspring leave the patch and compete globally to become the adults of the next generations.

Assuming that the number of offspring per patch n_{c} is large, the fitness of a mutant individual with foraging effort y, when its local relatives on average express effort y_{r}, and the rest of the population express x, is proportional to

$$w(y, y_{\mathrm{r}}, x) \propto y\hat{n}(y_{\mathrm{r}}) - c(y), \tag{3}$$

where $\hat{n}(y_{\mathrm{r}})$ is the equilibrium density of the resource in a patch where individuals have foraging effort y_{r}, and

$$c(y) = \frac{c_0}{2}y^2, \tag{4}$$

is the individual cost of foraging.

a. Calculate the equilibrium resource density, $\hat{n}(y_{\mathrm{r}})$, from eqs. (1)-(2).

b. Calculate the selection gradient, which when there are interactions among relatives is given by

$$s(x) = \left.\frac{\partial w(y, y_{\mathrm{r}}, x)}{\partial y}\right|_{y=y_{\mathrm{r}}=x} + R_2 \left.\frac{\partial w(y, y_{\mathrm{r}}, x)}{\partial y_{\mathrm{r}}}\right|_{y=y_{\mathrm{r}}=x}, \tag{5}$$

where R_2 is the relatedness among offspring foraging together.

c. Show that the strategy x^* that selection favours (i.e. the strategy x^* such that $s(x^*) = 0$) is given by

$$x^* = \frac{Kr}{c_0 r + K n_\mathrm{c}(1 + R_2)}. \tag{6}$$

How does this strategy change with relatedness R_2? How does this strategy compare to the effort x_MSY that leads to maximum sustainable yield?

Exercise 2: Risk-sensitive foraging

In this exercise, we investigate the evolution of risk-sensitive foraging using computer simulations to explicitly consider the randomness in foraging outcome. We consider a population of fixed size N where individuals can be in either of two conditions: high (e.g. well-provisioned) or low (poorly-provisioned). We assume that this is determined at birth, with each individual being in high condition with probability p and low condition with probability $1 - p$. Individuals forage for resources and can choose among two foraging strategies: (i) a safe strategy; and (ii) a risk-taking strategy. An individual choosing the safe strategy always obtains a payoff of π_0 calories. An individual choosing the risk taking strategy obtains a payoff of π_0/a with probability a, or a payoff of 0 with probability $1 - a$ (so that the expected payoff is $a \times \pi_0/a + (1 - a) \times 0 = \pi_0$). Depending on their condition and payoff, individuals produce offspring. Specifically, an individual i with payoff π_i has fecundity

$$f_\mathrm{H}(\pi_i) = 3\log(1 + \pi_i) \tag{7}$$

if in high condition, and

$$f_\mathrm{L}(\pi_i) = \frac{1}{2}\Big(\exp(\pi_i) - 1\Big), \tag{8}$$

if in low condition. Adults die and offspring compete to become the adults of the next generation.

We model the evolution of risk taking behaviour by considering the evolution of two traits: x_H and x_L, the probability of choosing the risky strategy when in high and low condition, respectively. We assume both these strategies are genetically encoded and evolve by mutations of weak effects.

a. Assume that the expected payoff is $\pi_0 = 1$, and that the probability of successfully foraging under the risky strategy is $a = 0.5$. Complete the table below that associates payoff and fecundity according to condition with numerical values.

Payoff, π_i	Low condition f_L	High condition f_H
0		
1		
2		

b. Based on the table you completed, how do you think x_H and x_L are going to evolve?

c. Test your predictions using the individual based simulation program that implements the life cycle described above and that is available on the course website (lab-mullon.github.io/SAF).

d. So far, we have assumed that the payoff π_i an individual i obtains from foraging could be one of only three values: 0, π_0 or π_0/a. Next, we allow payoff π_i to be continuous and normally distributed.

(i) Plot fecundity in high and low condition, f_{H} and f_{L} (from eqs. (7)-(8)), as a function of payoff, π_i.

(ii) Change the simulation code you were given so that individual payoff π_i is now normally distributed, with parameters that depend on the foraging strategy taken. Specifically, assume that both the safe and risky strategies lead to the same expected payoff $\pi_0 = 1$, but that the variance is much greater under the risky strategy (e.g. the variance under the risky strategy is 1 and under the safe strategy is 0.1). Do you observe the same qualitative results as in the discrete version of the model?

Warning: Make sure that payoff is always positive, i.e. $\pi_i > 0$. In R, one can write x*(x>0) to get the positive part of a variable x.