Exercise sheet 4

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

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

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 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 a 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 a high and low condition, f_{H} and f_{L} (from eqs. 7 and 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.