

Exercise sheet 4: Foraging

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

$$\frac{dn}{dt} = r \left(1 - \frac{n}{K}\right) n - n_c h(x) n. \quad (1)$$

We assume that the harvesting function is simply,

$$h(x) = x. \quad (2)$$

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

$$w(y, y_r, x) \propto y \hat{n}(y_r) - c(y), \quad (3)$$

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

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

is the individual cost of foraging.

- Calculate the equilibrium resource density, $\hat{n}(y_r)$, from eqs. (1) and (2).
- Calculate the selection gradient, which when there are interactions among relatives is given by

$$s(x) = \left. \frac{\partial w(y, y_r, x)}{\partial y} \right|_{y=y_r=x} + R_2 \left. \frac{\partial w(y, y_r, x)}{\partial y_r} \right|_{y=y_r=x}, \quad (5)$$

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

$$x^* = \frac{Kr}{c_0r + Kn_c(1 + R_2)}. \quad (6)$$

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

$$f_H(\pi_i) = 3 \log(1 + \pi_i) \quad (7)$$

if in high condition, and

$$f_L(\pi_i) = \frac{1}{2} \left(\exp(\pi_i) - 1 \right), \quad (8)$$

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 .