Exercise 1: the evolution of aggressivity

Many animals compete directly over food, mates or nesting sites. More aggressive individuals may obtain a larger share of a contested resource, but escalated fights are costly.

Consider a large, well-mixed, haploid and asexual population. The evolving trait $z \in X = [0, 1]$ is the probability of behaving aggressively during a contest. The resident population expresses x and a rare mutant expresses y.

How do the benefits of winning contests and the costs of escalated fights determine population size and invasion?

Exercise 1 (continued)

The population follows this life cycle:

1. Adults encounter resources many times and compete for them in randomly formed pairs. A resource has value $V > 0$. During each contest, an individual expressing phenotype z behaves aggressively with probability z, and behaves docilely otherwise. (i) If both are aggressive, they fight and one of them wins and obtains the resource. Each win with the same probability $1/2$, and both pay a cost $C > 0$ (in the same units as V). (ii) If one is aggressive and the other docile, the aggressive individual obtains the resource. (iii) If both are docile, they share the resource equally.

Exercise 1 (continued)

2. Payoffs accumulated across contests determine fecundity: $f(y,x) = f_0 + \delta P(y,x)$ (with $f_0 > 0, \delta > 0$), where $P(y,x)$ is the expected net payoff, measured in resource units, of an individual expressing phenotype y in a population monomorphic for x.
3. Each offspring recruits independently with probability $1/(1+\gamma N_t)$, where $\gamma > 0$.
4. Adults survive independently with probability $s \in [0,1)$.

Assume throughout that parameters ensure $f(y,x) > 0$.

Exercise 1 (continued)

For a rare mutant, nearly all its partners express the resident phenotype x.

a. Derive its expected payoff $P(y, x)$.

- Write the probability and payoff of each possible encounter
- Use this to calculate the expected payoff per encounter
- Compare the expected payoff of a mutant that always behaves aggressively, $P(1, x)$, with that of a mutant that is always docile, $P(0, x)$. Under what condition does aggressivity give the larger payoff? Interpret the result biologically.

Exercise 1 (continued)

b. Characterise resident demography.

- Write the recursion for the size N_t of a resident population expressing x.
- Find all demographic equilibria. Which one describes a persistent population? Denote it by $\hat{N}(x)$.
- How does aggressivity x influence population size ?

c. A rare mutant y appears after the resident population has reached $\hat{N}(x)$.

- Derive its invasion fitness $\rho(y, x)$.
- Verify that $\rho(x, x) = 1$.

Exercise 2: surviving before reproduction

In perennial plants, an adult may have to survive winter before it can flower again. Let $s(z) \in (0,1)$ be winter survival and $f(z) > 0$ expected seedling production conditional on survival.

The life cycle is:

1. Adults survive winter independently with probability $s(z)$.
2. Survivors remain as adults and have expected seedling production $f(z)$.
3. Each seedling recruits with probability $1/(1+\gamma N_t)$.

a. Write the recursion for resident population size. Find the equilibrium $\hat{N}(x)$ and the condition for population persistence.

Exercise 2 (continued)

b. A rare mutant has survival $s(y)$ and fecundity $f(y)$. Derive its invasion fitness $\rho(y,x)$ and verify that $\rho(x,x) = 1$.

c. Consider two possible mutants:

- a mutant whose survival is increased by a small proportion $\varepsilon > 0$, so that

$$s(y) = (1+\varepsilon)s(x), \qquad f(y) = f(x);$$

- a mutant whose fecundity is increased by the same proportion, so that

$$s(y) = s(x), \qquad f(y) = (1+\varepsilon)f(x).$$

Calculate the invasion fitness of each mutant. Which mutant has the greatest probability of invading? How would the comparison change if all adults reproduced before winter survival was realised?