### **Exercise 1: survival—fecundity trade-off**

All organisms face trade-offs due to limited resources. One classical trade-off occurs between investment into survival and into reproduction, both major components of fitness.

Can such a trade-off favour diversification, with different types specialising in either survival or reproduction?

Consider a well-mixed population of constant size N with the following life cycle:

- 1. Adults produce a large number of offspring.
- 2. Adults survive with a certain probability; otherwise they die.
- 3. Offspring compete randomly for the vacant breeding spots.

The evolving trait z increases the survival probability, which is  $s_{\max}z$  where  $0 < s_{\max} < 1$  is a parameter for the maximum survival. Fecundity is a decreasing function of survival, f(z) > 0, with f'(z) < 0.

## Exercise 1 (continued)

- **a.** Define the invasion fitness  $\rho(y,x)$  of a rare mutant trait y in a resident population expressing trait x.
- **b.** Let  $f(z) = f_{\text{max}}(1-z^2)$  where  $f_{\text{max}} > 0$  is a parameter. For this specific trade-off:
  - Find the singular strategy  $x^*$ .
  - Determine whether  $x^*$  is convergence stable.
  - Determine whether x\* is uninvadable or whether evolutionary branching is possible.
- **c.** For an arbitrary smooth decreasing function f(z), can evolutionary branching occur? (hint: recall the necessary condition of negative trait dependent selection for polymorphism)

#### Exercise 2: the evolution of aggressivity

Many animals compete directly over resources such as mates, food, or nesting sites. In such contests, individuals may differ in aggressivity. When a more aggressive individual meets a less aggressive one, the latter tends to retreat. But when two aggressive individuals meet, the contest escalates into a costly fight.

Can such interactions favour social polymorphism, with both aggressive and docile individuals coexisting?

# Exercise 2: the evolution of aggressivity

Consider a well-mixed population of constant size N, with the following life cycle:

- 1. Individuals engage in repeated pairwise contests over a resource of value V (e.g. in calories).
- 2. In each contest, an individual expresses either aggressive or docile behaviour (with probability z and 1-z, resp.).
- 3. When two docile individuals meet, they share the resource equally. When a docile and an aggressive individual meet, the aggressive one obtains the full resource. When two aggressive individuals meet, one wins the resource with probability 1/2, but both pay a cost C>0 (e.g. in calories) from fighting.
- 4. Individuals reproduce with fecundity that increases with the resources accumulated minus any fighting costs, and then die.
- 5. Offspring compete randomly for the vacant breeding spots.

The evolving trait  $z \in [0,1]$  is the probability of behaving aggressively during a contest.

## Exercise 2 (continued)

- a. Derive the expected payoff  $\pi(y,x)$  of a mutant with aggressivity probability y in a resident population with trait x. Use this to characterise its fecundity  $f(y,x)=1+\delta\pi(y,x)$  where  $\delta>0$  is a parameter that tunes the strength of selection.
- **b.** Define the invasion fitness  $\rho(y,x)$  of a rare mutant in a resident population. Assuming weak selection (i.e. that  $\delta$  is small) :
  - Find the singular strategy  $x^*$  and determine whether it's convergence stable.
  - Determine whether  $x^*$  is uninvadable, or whether evolutionary branching is possible.
- c. Suppose expressing a mix of behaviours carries a cost of flexibility:

$$f(y,x) = 1 + \delta[\pi(y,x) - c_f y(1-y)],$$

where  $c_f > 0$  is a flexibility cost parameter. What is the effect of this cost on the possibility of evolutionary branching?