

## Exercise 5: the evolution of aggressivity under limited dispersal

We now revisit the model of aggressivity evolution from day 1, but under limited dispersal.

A priori: how do you expect limited dispersal to affect the evolution of aggressivity?

Assume the population is subdivided into a large number of patches of size  $n = 2$ , with reproduction and death following a Moran process. Fecundity is determined by the payoff from repeated local interactions over a resource of value  $V$ .

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

## Exercise 5: life cycle under limited dispersal

Specifically, the life cycle proceeds as follows:

1. Individuals engage in repeated pairwise contests within patches. In each contest, they play either aggressive or docile with payoffs per interaction:
  - Docile vs. docile: share  $V$  equally.
  - Aggressive vs. docile: aggressive gets all.
  - Aggressive vs. aggressive: one wins  $V$  with probability  $1/2$ , both pay cost  $C > 0$ .
2. Individuals produce a large number of offspring. A focal individual with trait  $z_{\bullet}$  with a neighbour with trait  $z_1$  has fecundity  $f(z_{\bullet}, z_1) = 1 + \delta\pi(z_{\bullet}, z_1)$  is the average payoff received during contests and where  $\delta > 0$  is a parameter that tunes the strength of selection.
3. Offspring either disperse with probability  $m$  (in which case they land in a uniformly chosen patch, i.e. island model of dispersal) or stay with probability  $1 - m$ .
4. One adult per patch dies at random; offspring compete locally for the vacant spot.

## Exercise 5 (continued)

- a.** Write the individual fitness function  $w(z_\bullet, z_1)$  of a focal individual with trait  $z_\bullet$ , paired with a neighbour with trait  $z_1$ , when the rest of the population is resident at trait  $x$ .
- b.** Use  $w(z_\bullet, z_1)$  and the relatedness coefficient  $r_2^\circ$  (as derived during the lecture) to compute the selection gradient  $S(x)$ . Identify the singular strategy  $x^*$ , and assess its convergence stability (make use of the fact that  $\delta$  is small to make the algebra easier).

What is the effect of limited dispersal (i.e. small  $m$ ) on the singular strategy ?

- c.** Using the fact that under the Moran model when traits affect fecundity only :  $\partial r_2(y, x)/(\partial y)|_{y=x=x^*} = 0$  holds, calculate the coefficient of disruptive selection  $H(x^*)$ .

How does limited dispersal affect disruptive selection? Why?

## Exercise 6: the evolution of altruism for survival

We saw that altruism can evolve when individuals reduce their fecundity to increase that of their neighbours under limited dispersal.

Here, we ask: does selection on altruism change when it affects survival instead of fecundity?

Consider a population subdivided into patches of size  $n = 2$ , with reproduction and death following a Moran process and life-cycle:

1. Individuals interact within patches, providing a survival benefit  $b$  to their partner at a cost  $c$  to themselves.
2. Individuals reproduce with fixed fecundity.
3. Offspring disperse with probability  $m$ , or remain with probability  $1 - m$ .
4. One adult per patch dies. The probability of dying is determined by payoff. Offspring compete locally for the vacant spot.

## Exercise 6 (continued)

The evolving trait  $z \in [0, 1]$  is the amount invested into the partner's survival at a cost to oneself.

If a focal individual has trait  $z_\bullet$  and its neighbour  $z_1$ , their respective survival payoffs are:

$$P_\bullet = 1 + bz_1 - cz_\bullet, \quad P_1 = 1 + bz_\bullet - cz_1,$$

so that the probability that the focal survives is:

$$\frac{P_\bullet}{P_\bullet + P_1}.$$

## Exercise 6 (continued)

- a. Write the individual fitness  $w(z_{\bullet}, z_1)$  of a focal in a resident population.
- b. Using  $w(z_{\bullet}, z_1)$  and relatedness  $r_2^{\circ}$ , compute the selection gradient  $S(x)$ . What is the nature of directional selection on altruism in this case (positive, negative)? Why?
- c. Now suppose that altruism still reduces survival payoff  $(1 - cz_{\bullet})$ , but increases neighbour fecundity to  $1 + bz_1$ . Does this change directional selection on altruism?