

Exercise 1 (continued): is intermediate aggressivity uninvadable?

Yesterday we found that, when $V = C = 1$, gradual evolution converges towards the intermediate strategy $x^* = \frac{1}{2}$.

Recall that

$$P(y, x) = \frac{1-x}{2} + y \left(\frac{1}{2} - x \right), \quad f(y, x) = f_0 + \delta P(y, x),$$

and

$$\rho(y, x) = s + (1-s) \frac{f(y, x)}{f(x, x)}.$$

g. Evaluate $\rho(y, x^*)$ for an arbitrary $y \in [0, 1]$.

- Can any mutant invade the singular resident?
- Calculate $H(x^*)$. What does this tell us about selection at the singular strategy?

Exercise 1 (continued): can aggressivity diversify?

Suppose now that expressing a mix of aggressive and docile behaviour requires sensory, cognitive or physiological machinery. Individuals therefore pay a cost of behavioural flexibility.

Fecundity becomes: $f(y, x) = f_0 + \delta [P(y, x) - c_f y(1 - y)]$, $c_f \geq 0$.

The cost is zero for individuals that are consistently docile or consistently aggressive, and is largest for individuals expressing the intermediate strategy $y = 1/2$.

The demographic life cycle is unchanged, so

$$\rho(y, x) = s + (1 - s) \frac{f(y, x)}{f(x, x)}.$$

Exercise 1 (continued)

h. Characterise gradual evolution.

- Show that $S(x) = (1 - s)\delta(1 - 2c_f)(1/2 - x)/f(x, x)$.
- Find x^* and calculate $S'(x^*)$. For which values of c_f is x^* convergence stable?
- Calculate $H(x^*)$. For which values of c_f is x^* an evolutionary branching point?
- Explain biologically why a cost of behavioural flexibility can favour diversification into more consistent behavioural types.

Exercise 4: can investment in cooperative defence diversify?

Many animals jointly defend a feeding territory against competitors or predators. Stronger defence allows both individuals to obtain more food, but defending the territory requires time and energy that could otherwise be devoted to reproduction.

Consider a large, well-mixed, haploid and asexual population. Adults repeatedly form random pairs to defend a shared feeding territory. The evolving trait $z \in X = [0, 1]$ is the amount of effort an individual invests in territorial defence.

Can evolution favour diversification with individuals that invest little and individuals that invest strongly?

Exercise 4 (continued)

The population follows this life cycle:

1. Adults repeatedly form random pairs and jointly defend a feeding territory.
2. If the two individuals invest y and x , their total investment $y + x$ generates a benefit $B(y + x)$ for each individual. The focal individual also pays the cost $C(y)$ of its own investment. Its expected net payoff is therefore $P(y, x) = B(y + x) - C(y)$.
3. Payoff accumulated across interactions determines fecundity:
$$f(y, x) = f_0 + \delta P(y, x), \quad f_0 > 0, \quad \delta > 0.$$

Exercise 4 (continued)

Assume that

$$B(z) = \frac{6}{5}z - \frac{1}{5}z^2, \quad C(z) = \frac{11}{10}z - \frac{3}{10}z^2.$$

Both the benefit generated by defence and its individual cost increase with investment, but their marginal effects decrease.

The demographic life cycle continues as follows:

4. Each offspring recruits independently with probability $1/(1 + \gamma N_t)$, where $\gamma > 0$.
5. Adults survive independently with probability $s \in [0, 1)$.
6. Recruited offspring and surviving adults form the population at time $t + 1$.

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

Exercise 4 (continued): gradual evolution and diversification

- a. Derive invasion fitness $\rho(y, x)$ from the life cycle and verify that $\rho(x, x) = 1$.
- b. Characterise gradual evolution.
 - Show that $S(x)$ is proportional to $[B'(2x) - C'(x)]$.
 - Find the singular phenotype x^* and determine whether x^* is convergence stable.
- c. Characterise selection at the singular phenotype. Show that $H(x^*)$ is proportional to $[B''(2x^*) - C''(x^*)]$. Is selection stabilising or disruptive? Is x^* an evolutionary branching point? Interpret biologically the types that may emerge.