15. Eco-evo: Fitness can be non-linear

Until now, we have made a very simple, but also very over-simplifying assumption: We have assumed that the fitness r_i of a type i is a constant number independent of the frequencies x_i of the various types. Yet we know many situations where this is not true. For example, the fitness of a rabbit depends very much on the frequency of the predators in its area, and also on the frequency of other rabbits that might be easier for the predators to catch!

The important point here is that simplistic slogans such as "*Survival of the Fittest!*" often rely on the unjustified assumption that "fitness" is a constant, measurable number determined only by the genomic makeup of a type. But fitness simply *is* the specific growth rate of a type, and the only way we can measure it is by observing that type's growth in a specific context.

Genetics may play a role in determining fitness, but we can only ever <u>measure</u> fitness ecologically!

And of course, ecology depends on details of how *this* type interacts with *this* context, so fitness cannot be constant, linear or even particularly simple! In practice, fitness depends highly nonlinearly on the *games* an organism plays with its environment …

Frequency-dependent selection

First, let's formulate a definition of general, nonlinear selection. Recall that the definition of *linear* selection looked like this:

$$\dot{x}_i = x_i(r_i - R); \quad R = \sum_{i=1}^{n} x_i r_i \qquad \textbf{(Linear selection)}$$

The only change we now need to make is to allow the fitness values r_i to depend explicitly upon the frequencies x_i:

$$\dot{x}_i = x_i(r_i(\boldsymbol{x}) - R); \quad R = \sum_{i=1}^{n} x_i r_i(\boldsymbol{x}) \qquad \textbf{(Frequency-dependent selection)}$$

If we set $n = 2$ in these equations, we obtain the simple 2-type situation. In this case, we immediately see that the dynamics of frequency-dependent selection is far more interesting and fun than boring old constant selection:

$$\dot{x}_1 = x_1(r_1(\boldsymbol{x}) - R); \quad \dot{x}_2 = x_2(r_2(\boldsymbol{x}) - R); \quad R = x_1 r_1(\boldsymbol{x}) + x_2 r_2(\boldsymbol{x}); \quad x_1 + x_2 = 1$$

? Using the last equation to replace x_2 by $1 - x_1$, show that our frequency-dependent selection equations become: $\dot{x}_1 = x_1(1 - x_1)\big(r_1(\boldsymbol{x}) - r_2(\boldsymbol{x})\big)$.

Again replacing x_2 by $1 - x_1$, we can replace the rates r_1, r_2 by functions of x_1:

$$\dot{x}_1 = x_1(1 - x_1)\big(r_1(x_1) - r_2(x_1)\big)$$

? This equation defines dynamics on the interval $[0,1]$. Sketch this interval as a horizontal axis and draw arrows on it to represent dynamics that flow from all points of the interval to a single stable fixed point within the interval. Now find two functions $r_1(x_1), r_2(x_1)$ with the property that they together generate these dynamics.

2-player games

OK, so we can see that frequency-dependent selection might generate fun dynamics, but can we find some realistic situation that produces frequency-dependent selection? In the 1970's, John Maynard Smith invented *evolutionary game theory*. His idea was that the difference between the types in a population might be *behavioural*: maybe type 1 uses a very different strategy from type 2 for its ecological interactions (with environment and other individuals), and this strategy might be important for its evolutionary survival!

Example: HD (*Hawks and Doves*): In the HD game, two dogs meet in a forest at a place where a tasty sandwich is lying on the ground, whose nutritional benefit is $b = 4$. Each dog has a choice between two strategies: *H* (hawk: attack) and *D* (dove: be nice). If the first dog adopts strategy *H*, and the second adopts *D*, the first dog will gain the sandwich benefit b, and the second dog gets nothing. On the other hand, if *both* dogs adopt strategy *H*, they will probably both pay the cost $c = 2$ of getting injured; on average, each dog will get the sandwich half of the time and so gain benefit $b/2$. If both play strategy *D*, each will again get the sandwich half the time (benefit $b/2$), and will pay no injury cost.

We represent the HD game as a *payoff matrix A*, and its strategies as two *basis vectors h*, *d*:

$$A_{HD} = \begin{pmatrix} \frac{b-c}{2} & b \\ 0 & \frac{b}{2} \end{pmatrix} = \begin{pmatrix} 1 & 4 \\ 0 & 2 \end{pmatrix}; \quad h \equiv \begin{pmatrix} 1 \\ 0 \end{pmatrix}; \quad d = \begin{pmatrix} 0 \\ 1 \end{pmatrix}$$

The payoff matrix tells us how each individual will benefit on average from using some strategy to interact with other individuals in the HD game. For example, we can represent the four possible HD interactions between individuals like this:

… receives payoff from:	Hawk	Dove
Hawk	$\begin{pmatrix} 1 \\ 0 \end{pmatrix} = \begin{pmatrix} 1 & 4 \\ 0 & 2 \end{pmatrix}\begin{pmatrix} 1 \\ 0 \end{pmatrix}$	$\begin{pmatrix} 4 \\ 2 \end{pmatrix} = \begin{pmatrix} 1 & 4 \\ 0 & 2 \end{pmatrix}\begin{pmatrix} 0 \\ 1 \end{pmatrix}$
Dove		

A hawk meeting a dove will always do well, getting a payoff of 4, whereas the dove gets nothing. On the other hand, the hawk strategy is much less useful in a population containing only hawks, since the hawk then only receives an average payoff of 1. In fact, it may well be that hawks die out from injuries, whereas a population of doves can survive.

? Suppose we have a population that contains 75% hawks and 25% doves. The frequency vector is then $x = (0.75, 0.25)^T$, and the typical payoff for a hawk or dove is given by the product $A_{HD}x$. What is this typical payoff for a hawk? For a dove?

? Now calculate the typical payoff for a hawk and for a dove in a population with the frequency vector $x = (0.25, 0.75)^T$. Does this make sense compared to your previous calculation for a hawk-dominated population?

You can see that the typical payoff for a hawk or a dove is highly frequency-dependent – the 'fitness' of a dove is much higher in a dove population than in a hawk-dominated population!

The replicator equation

You have just seen that for an individual using strategy i to play the game with payoff $A = (a_{ij})$ in a population with type frequencies $x = (x_j)$, the typical payoff is $\sum_{j=1}^n a_{ij}x_j$. But this is just the net benefit that this individual has in its daily life from interacting with other. *Average payoff is the source of this individual's replicative success r_i*, so we can insert this success, or fitness, into the frequency-dependent selection equation:

$$\left.\begin{array}{ll} \dot{x}_i = x_i\left(\sum_{j=1}^n a_{ij}x_j - R\right); & R = \sum_{i,j=1}^n x_i a_{ij}x_j \\ \text{or:} \quad \dot{x} = x\,(A \cdot x - R) & R = x^T \cdot A \cdot x \end{array}\right\} \quad \textbf{(Replicator equation)}$$

Josef Hofbauer and Karl Sigmund used the replicator equation in the 1990's to describe the dynamics of infinite populations of n strategy-types playing a 2-player game.

? Set up a general payoff matrix A_C and the replicator equation for the game of Chicken, in which two teenagers drive their cars straight towards each other at high speed on

a narrow road. Each teenager chooses one of two possible strategies: C (chicken out and leave the road) or D (drive straight ahead). The loser is the one who chickens out first – in this case the other driver gets the prestige benefit b. If neither chickens out, both are injured with a cost c; and if both chicken out, they share the benefit.

n-strategy games

The examples we've looked at so far have two possible strategies, but in general there may be n different strategies for playing a game. In this case, the payoff matrix contains $(n \times n)$ entries for playing each strategy against each of the others. A simple example is rock-scissors-paper (RSP), in which three strategies cyclically dominate each other – that is, rock beats scissors, scissors beat paper and paper beats rock. This situation does indeed occur naturally in some species of lizard. Its payoff matrix might look like the left-hand one below, which we can simplify to an equivalent form by adding an arbitrary constant to each column (this is always allowed for payoff matrices in the replicator equation):

$$
\begin{array}{c}
 \\
R \\
S \\
P
\end{array}
\begin{array}{c}
\begin{array}{ccc} R & S & P \end{array} \\
\begin{pmatrix} 4 & 2 & 1 \\ 3 & 1 & 3 \\ 5 & 0 & 2 \end{pmatrix}
\end{array}
\quad \longrightarrow \quad
A_{RSP} = \begin{pmatrix} 0 & 1 & -1 \\ -1 & 0 & 1 \\ 1 & -1 & 0 \end{pmatrix}
$$

? Write down the replicator equation for the game A_{RSP}.

Predator-prey dynamics

The bridge between evolution and ecology is illustrated by the fact that the replicator equation is equivalent to the Lotka-Volterra equations. To see that this is true, consider Vito Volterra's 2-species predator-prey equations for prey species y_1 and predator species y_2:

$$
\left. \begin{aligned}
\dot{y}_1 &= y_1 \left(a - b\, y_2 \right) \\
\dot{y}_2 &= y_2 \left(-c + d\, y_1 \right)
\end{aligned} \right\}
\qquad \textbf{(Predator-prey equation)}
$$

These equations describe a combined population that can grow arbitrarily large – it is not normalised to a total size of 1. For this reason, we first define a new variable describing the total population $y_3 \equiv y_1 + y_2$, then define:

$$
x \equiv \frac{1}{1 + y_3} \cdot \begin{pmatrix} y_1 \\ y_2 \\ 1 \end{pmatrix}
$$

? Verify that the sum of these populations $\sum_{i=1}^{3} x_i$ is equal to 1.

? (*Easy but lengthy*) Show that substituting the payoff matrix $A = \begin{pmatrix} 0 & -b & a \\ d & 0 & -c \\ 0 & 0 & 0 \end{pmatrix}$ in the replicator equation $\dot{x} = x \left(A \cdot x - x^T \cdot A \cdot x \right)$ recovers the predator-prey equations.

Alfred Lotka discovered the general form of predator-prey equations for n chemical species:

$$
\dot{y} = y \left(r - B \cdot y \right), \text{ or: } \quad \dot{y}_i = y_i \left(r_i - \sum_{j=1}^{n} b_{ij} y_j \right) \quad \textbf{(Lotka-Volterra equations)}
$$

Exercises

1. Build a julia RSP-simulation on S_3 to simulate competition between the three subtypes of a certain lizard species.

Summary

- The replicator equation $\dot{x} = x \left(Ax - R \right)$, where $R = x^T \cdot A \cdot x$ and A is a payoff matrix, is equivalent to the Lotka-Volterra equations $\dot{y} = y \left(r - B \cdot y \right)$.