# The Evolution of Resource Use

Consider a population living off two different resources with densities $R_1$ and $R_2$, respectively. The evolving trait, *x*, is the proportion of time spent searching for resource type 1, and $1-x$ is the proportion of time spent searching for resource type 2. Generalist consumers have intermediate values of *x*, i.e., search for both resources for some of their time, whereas specialists have *x* near to 0 or near to 1. The aim of the project is to study resource specialisation via the adaptive dynamics of *x*.

The resources enter the system at constant rates $a_1$ and $a_2$, respectively, as in a simple flow culture, and decay or leave the system at rates $b_1$ and $b_2$. The dynamics of the resources are given by

$$\begin{aligned} \frac{dR_1}{dt} &= a_1 - b_1 R_1 - c_1 R_1 xn \\ \frac{dR_2}{dt} &= a_2 - b_2 R_2 - c_2 R_2 (1-x) n \end{aligned} \tag{1}$$

where *n* is the number of consumers, and hence *xn* is the number of consumers searching for resource 1 and (1-*x*)*n* is the number of consumers searching for resource 2 at one given time.

A single individual acquires $xc_1R_1$ of resource 1 and $(1-x)c_2R_2$ of resource 2 per unit of time. The rate of offspring production is some function of acquisition of the two resources, $f\left(xd_1c_1R_1, (1-x)d_2c_2R_2\right)$, where $d_1$ and $d_2$ represent the nutritional values of the resources. The per capita death rate is constant $\mu$. These assumptions lead to the following equation of population dynamics:

$$\frac{dn}{dt} = nf\left(xd_1c_1R_1, (1-x)d_2c_2R_2\right) - \mu n \tag{2}$$

To simplify the system, we assume that the dynamics of the resources are fast compared to that of the consumer, so that $dR_1/dt \approx 0,\ dR_2/dt \approx 0$ every time. Then we can substitute $R_1$ and $R_2$ in equation (2) by their quasi-equilibrium values obtained from equations (1),

$$\begin{aligned} \hat{R}_1 &= a_1 \big/ \left(b_1 + c_1 xn\right) \\ \hat{R}_2 &= a_2 \big/ \left(b_2 + c_2 (1-x) n\right) \end{aligned} \tag{3}$$

to arrive at

$$\frac{dn}{dt} = nf\left(xd_1c_1\,a_1/\left(b_1+c_1xn\right),(1-x)d_2c_2\,a_2/\left(b_2+c_2(1-x)n\right)\right)-\mu n \tag{4}$$

Notice that many parameters occur only in one combination of parameters: renaming these combinations simplifies the equation into

$$\frac{dn}{dt} = nf\left(\beta_1 x/(1+\gamma_1 xn),\beta_2(1-x)/(1+\gamma_2(1-x)n)\right)-\mu n \tag{5}$$

where $\beta_i = d_i c_i a_i / b_i$ and $\gamma_i = c_i / b_i$ for $i = 1, 2$.

When a mutant strategy *y* is introduced at a low initial density, it grows according to

$$\frac{dn_y}{dt} = n_y f\left(yd_1c_1\hat{R}_1,(1-y)d_2c_2\hat{R}_2\right)-\mu n_y \tag{6}$$

(cf. equation (2)). Substituting the quasi-equilibrium resource abundances as determined by the resident population of strategy *x* and introducing the notations of equation (5), the mutant dynamics are

$$\frac{dn_y}{dt} = n_y f\left(\beta_1 y/(1+\gamma_1 xn),\beta_2(1-y)/(1+\gamma_2(1-x)n)\right)-\mu n_y \tag{7}$$

For the function $f$ we take

$$f(p,q) = \left(p^\alpha + q^\alpha\right)^{\frac{1}{\alpha}} \tag{8}$$

Different values of $\alpha$ correspond to the classification of resources in the following table (plot the function to get a visual impression):

**Table 1.**
Classification of resources

| **Parameter range:** | **Resource type:** |
|---|---|
| $\alpha > 1$ | Antagonistic |
| $\alpha = 1$ | Perfectly substitutable |
| $0 < \alpha < 1$ | Complementary |
| $-\infty < \alpha < 0$ | Hemi-essential |
| $\alpha = -\infty$ | Essential |

The aim of this project is to study the evolution of strategy *x*, i.e., of the partitioning of foraging time for two different resources, for various values of $\alpha$. Start with $\alpha = 1$ (substitutable resources) and find the singular strategies and their stability properties. This can be done analytically, but illustrate the results by PIPs. Then change the value of $\alpha$ and observe how the stability properties of the singular strategy change (bifurcation analysis). Find an example for evolutionary branching. Construct the isocline plot and explore the coevolution of two strategies in an example with evolutionary branching.