Adaptive Dynamics Course
É. Kisdi, Oslo 2008

The Evolution of Cannibalism - I

A cannibalistic species spends a fraction of time x searching for resource R, whereas the remaining fraction of time, 1-x, is spent attacking those conspecific individuals which are searching for the resource. x=1 is a non-cannibalistic strategy which consumes only the resource, whereas x=0 is full cannibalism. We assume that the resource dynamics are logistic, and that the attack on foraging individuals has a Holling type II functional response with a handling time that depends on the strategy x. The latter reflects the assumption that the more time individuals spend attacking others, the better they learn the technique and hence they can handle the conspecific prey faster.

The population dynamics of the resource are given by

$$\frac{dR}{dt} = rR\left(1 - \frac{R}{K}\right) - \nu Rxn \tag{1}$$

where R is the density of the resource, n is the density of the focal species (note only a fraction x searches for the resource at any one time), and ν is the attack rate. We assume that the dynamics of R is fast compared to that of n, so that $dR/dt \approx 0$ every time and we can assume that R is at its quasi-equilibrium value

$$\hat{R} = K\left(1 - \frac{\nu}{r}xn\right) \tag{2}$$

whenever the focal species has density n.

The focal species grows according to the equation

$$\frac{dn}{dt} = \lambda \nu \hat{R}xn - \beta(1-x)n\frac{xn}{1+\beta T(x)xn} + \gamma\beta(1-x)n\frac{xn}{1+\beta T(x)xn} - \delta n \tag{3}$$

Here the first term is the offspring produced from the consumed resource, with conversion factor λ (cf. the last term of equation (1)). The second term is the loss to cannibalism. At any one time, $(1-x)n$ individuals are cannibalistic and they attack the remaining xn individuals at rate β. Due to the handling time ($T(x)$), a Holling type II function gives the number of individuals who fell prey to cannibalism. The third term is the number of offspring produced using the nutrients obtained via cannibalism, with a conversion factor γ. Finally the last term is due to external mortality (not due to cannibalism).

Assume that a rare mutant with strategy *y* enters the population of strategy *x*, which is at its population dynamical equilibrium $\hat{n}$. The number of mutants changes according to

$$\frac{dn_{mut}}{dt} = \lambda \nu \hat{R} y n_{mut} - \beta(1-x)\hat{n}\frac{y n_{mut}}{1+\beta T(x)\left[x\hat{n}+y n_{mut}\right]} + \\ + \gamma\beta(1-y)n_{mut}\frac{x\hat{n}}{1+\beta T(y)\left[x\hat{n}+y n_{mut}\right]} - \delta n_{mut} \tag{4}$$

Because the mutant is rare ($n_{mut} \ll \hat{n}$), n_{mut} can be neglected in the denominators and the equation simplifies to

$$\frac{dn_{mut}}{dt} = \left[\lambda \nu K\left(1-\frac{\nu}{r}x\hat{n}\right)y - \frac{\beta(1-x)\hat{n}y}{1+\beta T(x)x\hat{n}} + \frac{\gamma\beta(1-y)x\hat{n}}{1+\beta T(y)x\hat{n}} - \delta\right]n_{mut} \tag{5}$$

where $\hat{R}$ is substituted from equation (2). By choosing the units of population density and time, it may be assumed without loss of generality that $\beta = 1$ and $\delta = 1$. We can also denote combinations of parameters with a single symbol and use $a = \lambda \nu K$ and $d = \nu / r$. Equation (5) then simplifies to the final form

$$\frac{dn_{mut}}{dt} = \left[a\left(1-dx\hat{n}\right)y - \frac{(1-x)\hat{n}y}{1+T(x)x\hat{n}} + \frac{\gamma(1-y)x\hat{n}}{1+T(y)x\hat{n}} - 1\right]n_{mut} \tag{6}$$

For the handling time T we take

$$T(x) = T_{\max} x^{p} \quad (p \geq 0) \tag{7}$$

Different values of p correspond to different rates of learning how to attack and handle conspecific prey.

Study the adaptive dynamics of the time spent searching for the resource (*x*), or, equivalently, spent by cannibalism (1-*x*). Construct PIPs for various parameter values and try to find different types of singular strategies. Construct an isocline plot to investigate the coevolution of two resident strategies in an example with evolutionary branching. If time permits, explore how the number of monomorphic singularities and their stability properties change as the parameter values change (bifurcation analysis). Another possible extension is to study other trade-off functions next to eq. (7).