The Evolution of Cannibalism - II

Adults of a cannibalistic species consume some resource *r* as well as conspecific juveniles. We assume that adults can morphologically or behaviourally adapt either to be efficient with capturing the resource or to be efficient with capturing juveniles but not both, such that the capture rate of the resource increases with a trait *x* whereas the capture rate of juveniles decreases with *x*. Strategy *x* is thus a measure of adaptedness to the resource. *x*=1 is a non-cannibalistic strategy which can consume only the resource, whereas *x*=0 is full cannibalism.

The population dynamics of the resource are given by

$$\frac{dr}{dt} = \alpha r\left(1 - \frac{r}{K}\right) - \beta_0 ur - \beta_1(x)vr \tag{1}$$

where *r* is the density of the resource, *u* and *v* are respectively the densities of juveniles and adults. In absence of the focal species, the resource grows logistically with parameters α and *K*. Juveniles eat the resource at a constant rate β_0. Adults eat the resource at rate $\beta_1(x)$, which is an increasing function of strategy *x*.

We assume that the dynamics of *r* is fast compared to that of *u* and *v*, so that $dr/dt \approx 0$ every time and we can assume that *r* is at its quasi-equilibrium value

$$\hat{r} = K\left(1 - \frac{\beta_0 u + \beta_1(x)v}{\alpha}\right) \tag{2}$$

whenever the density of juveniles and adults is respectively *u* and *v* in a population of strategy *x*.

The dynamics of juveniles (*u*) and adults (*v*) follow the equations

$$\begin{aligned} \frac{du}{dt} &= -\beta_2(x)uv + \gamma_1\beta_1(x)v\hat{r} + \gamma_2\beta_2(x)uv - \delta u - \varepsilon u \\ \frac{dv}{dt} &= \varepsilon u - \varsigma v \end{aligned} \tag{3}$$

The first term of the first equation is the loss of juveniles due to cannibalism by adults, who capture juveniles at rate $\beta_2(x)$ (a decreasing function of *x*). The second term adds the newborn juveniles produced by adults using the nutrients they gained from the resource, with a conversion factor γ_1 ($\hat{r}$ is to be substituted from eq. (1)). The third term is the production of newborns using nutrients from cannibalism, with conversion factor γ_2. δ is the natural death rate of juveniles. Finally, juveniles mature into adults at rate ε: Maturation removes juveniles (last term in the first equation of (3)) but adds adults (first term of the second equation). Adults die at a constant rate ς.

Finding the population dynamical equilibrium of a resident population with strategy *x* is straightforward from eqs. (3). Check when the equilibrium densities are positive, i.e., which resident strategies are viable. The stability of the equilibrium is somewhat more difficult to check, but it can be shown that the equilibrium, whenever positive, is stable (you can verify this numerically if you like).

Assume that a mutant strategy *y* appears at a low population density. Its dynamics are given by

$$\begin{aligned} \frac{du_{mut}}{dt} &= -\beta_2(x)u_{mut}v + \gamma_1\beta_1(y)v_{mut}\hat{r} + \gamma_2\beta_2(y)uv_{mut} - \delta u_{mut} - \varepsilon u_{mut} \\ \frac{dv_{mut}}{dt} &= \varepsilon u_{mut} - \varsigma v_{mut} \end{aligned} \tag{4}$$

The first term of the equation for mutant juveniles describes cannibalism by the residents (next to which cannibalism by mutants is negligible). The second term is birth given by mutant adults using the resource, where resource density is determined by the resident population (eq. (1)). The third term comes from mutant adults cannibalising resident juveniles.

Whether or not the mutant can invade can be determined by investigating the stability of the trivial equilibrium of eqs. (4), $u_{mut} = 0, v_{mut} = 0$: If the trivial equilibrium is unstable then mutants grow from a low population density. This can be done calculating the Jacobian of eqs. (4). There is however a simpler way to obtain a fitness proxy. Calculate the number of offspring surviving to adulthood per one adult mutant. If this number (the basic reproduction number, R_0) is greater than 1, then the mutant strategy spreads, otherwise the mutant dies out. One can use R_0 to obtain PIPs, singular strategies, and their stability properties just as one can use the invasion fitness.

To calculate R_0 of a mutant strategy *y* in the resident population of strategy *x*, notice that adults die exponentially at rate ς and therefore the expected lifetime of an adult is $1/\varsigma$. An adult mutant produces $\gamma_1\beta_1(y)\hat{r} + \gamma_2\beta_2(y)u$ mutant juveniles per unit of time (from the resource and from resident juveniles, respectively). Juveniles can mature into adults, die a natural death, or be victim to cannibalism by residents at exponential rates of ε, δ, and $\beta_2(x)v$, respectively. Hence the probability that maturation happens before natural death or cannibalism is $\varepsilon / \left(\varepsilon + \delta + \beta_2(x)v\right)$. Putting these together, one mutant adult, throughout its lifetime, produces

$$R_0 = \frac{1}{\varsigma}\left[\gamma_1\beta_1(y)\hat{r} + \gamma_2\beta_2(y)u\right]\frac{\varepsilon}{\varepsilon + \delta + \beta_2(x)v} \tag{5}$$

juveniles surviving into adulthood.

For the shape of $\beta_1(x)$ and $\beta_2(x)$, a possible choice is

$$\begin{aligned} \beta_1(x) &= b_1 x^p \\ \beta_2(x) &= b_2(1-x)^q \end{aligned} \tag{6}$$

Note that $\beta_1(0) = 0$, i.e., a fully cannibalistic strategy (x=0) cannot capture the resource. Similarly, $\beta_2(1) = 0$, which means that the strategy fully adapted to capturing the resource cannot cannibalize. With p=q=1, the capture rates are simply proportional to respectively x and (1-x). In this case, x can be interpreted as the fraction of time spent with searching for the resource, whereas (1-x) is time spent with cannibalism.

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 one of the parameter values, e.g. α, changes (bifurcation analysis).