

## Cycling Evolution under Predation and Asymmetric Competition

Consider a trait such as body size (or weapon size, etc.), which influences success in competitive contests with other members of the population. The evolution of such a trait is determined by two opposing forces: Being larger than the opponents is advantageous for winning the contests, thereby for obtaining resources and achieving high fecundity. On the other hand, large size entails some opponent-independent cost either in terms of resources used for maintenance or in reducing the chance for survival.

In this project, we explore the evolution of body size in an ecological model that admits multiple attractors. Assume that the population is subject to predation with Holling type III functional response. The dynamics of a monomorphic population is thus given by

$$\frac{dN}{dt} = [r - \alpha N]N - \frac{\beta P N^2}{c^2 + N^2} \quad (1)$$

where  $r$  is the intrinsic growth rate,  $\alpha$  is the competition coefficient and the last term is the loss to predation. The number of predators,  $P$ , is assumed to be constant (regulated by factors other than the availability of this particular prey, e.g. in case of a generalist predator that feeds on many different prey species). The function  $\beta N^2 / (c^2 + N^2)$  is the number of prey caught per predator per unit of time according to the Holling type III functional response (see e.g. P. Yodzis: Introduction to theoretical ecology, Harper & Row, 1989, pp. 14-20). Without predation, the population follows the logistic model of growth.

Because large size is costly in terms of reproduction or survival, we assume that the intrinsic growth rate depends on size according to some decreasing function  $r(x)$ . The competition coefficient depends on the *difference* in size: This is because large size by itself does not help winning a contest but being *larger* than the opponent does. We thus assume that  $\alpha(y-x)$ , the coefficient of competition exerted by strategy  $x$  onto strategy  $y$ , is a decreasing function of  $y-x$ . The population dynamics of a rare mutant strategy  $y$  in the equilibrium population of strategy  $x$  is thus given by

$$\frac{dN_y}{dt} = \left[ r(y) - \alpha(y-x)\hat{N} - \frac{\beta P \hat{N}}{c^2 + \hat{N}^2} \right] N_y \quad (2)$$

where  $\hat{N}$  is the equilibrium density of the resident population obtained from eq. (1).

When necessary for numerical work, assume that  $r(x)$  is a linearly or an exponentially decreasing function, and the competitive coefficient is of the form

$$\alpha(y-x) = c \left[ 1 - \frac{1}{1 + v \exp(-k(y-x))} \right] \quad (3)$$

*Remark.* The key to this project is to understand the population dynamics of eq. (1). For certain parameters and resident strategies, there may be two stable equilibria. When this is the case, a PIP must be developed for each attractor separately.

When investigating the adaptive dynamics of body size ( $x$ ) in this model,

(1) Construct an example such that evolution proceeds into different directions when the resident population is at different stable equilibria. Evolution may lead out of the domain of resident strategies where one or the other stable equilibrium exists, in which case the population converges to the remaining equilibrium. By switching between the two stable equilibria during evolution, you should be able to obtain evolutionary cycles.

(2) Construct an example of evolutionary branching, and investigate the adaptive dynamics of dimorphic populations in this example.