

## 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  $P$  predators. We assume that the number of predators is regulated by factors other than the availability of this particular prey (e.g. we consider a generalist predator that feeds on many different prey species) and hence  $P$  is constant. Without predation, the population follows the logistic model of growth. On the Holling type III functional response, see e.g. P. Yodzis: Introduction to theoretical ecology (Harper & Row, 1989), pp. 14-20.

In a population of several types with different body sizes, denote the trait value and population density of strategy  $i$  by  $x_i$  and  $N_i$ , respectively. The population dynamics of  $n$  competing strategies are given by

$$\frac{dN_i}{dt} = \left[ r(x_i) - \sum_{j=1}^n \alpha(x_i - x_j)N_j - \frac{\beta P \sum_{j=1}^n N_j}{c^2 + \left( \sum_{j=1}^n N_j \right)^2} \right] N_i \quad (2)$$

Here  $r(x_i)$  is the intrinsic growth rate of strategy  $i$ , which measures how fast a population with trait value  $x_i$  can grow in absence of competition (i.e., at very low

densities). Because large size is costly in terms of reproduction or survival, we assume that  $r(x)$  is a decreasing function. The competition coefficient,  $\alpha(x_i - x_j)$ , is a decreasing function of the *difference* in size: This is because large size by itself does not help winning a contest; being *larger* than the opponent does. The last term is the natural extension of the Holling type III functional response to several strategies.

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

$$\alpha(x_i - x_j) = c \left[ 1 - \frac{1}{1 + v \exp(-k(x_i - x_j))} \right]$$

*Remark.* The key to this project is to understand the population dynamics of eq. (1). When the population dynamics have multiple attractors, a PIP must be developed for each attractor separately (cf. Tube Theorem).

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 population is on different attractors. With catastrophic bifurcations in the population dynamics, you should be able to obtain evolutionary cycles.

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