Adaptive Dynamics Course S.A.H. Geritz & É. Kisdi Vienna 2007

## **Evolutionary Arms Race and Disarmament**

Consider a trait such as body size, 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 (or weapon size or a similar trait) in a simple Lotka-Volterra type model.

When the intrinsic growth rate (r(x)) decreases with the trait value x, the smallest possible value of x is the "optimal" strategy, which produces the fastest growth and the highest equilibrium density. Whenever evolution leads to a larger trait value  $x^*$ , *evolutionary arms race* occurs, i.e., the trait increases because being *larger* than others is advantageous even if being *large* is costly (just like in human arms races). In the examples below, you will also discover the possibility of mutual disarming when two strategies coevolve, along with other interesting coevolutionary phenomena.

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

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

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  $r(x_i)$  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. When necessary for numerical work, assume the form

$$\alpha(x_{i} - x_{j}) = a + c \left[ 1 - \frac{1}{1 + v \exp(-k(x_{i} - x_{j}))} \right]$$

which has a sigmoidal shape and saturates for  $x_i - x_j \rightarrow \pm \infty$ : if the difference in size is big, the larger contestant will almost certainly win any fights, and hence increasing

its size further has hardly an effect on the outcome of competition. Note however that with a > 0, individuals feel some competition from smaller individuals even if the size difference is big. This is because the resource may be exploited also without a fight, i.e., a small individual may find and consume a resource item without being noticed and challenged by anybody else.

To explore the adaptive dynamics of size (x), start by investigating the monomorphic evolutionary singularities analytically. When exploring polymorphic evolution (numerically when necessary), focus on the following three points:

(i) Assume  $r(x) = \beta - bx$  and  $\alpha(x_i - x_j)$  as above, first with *a*=0. Choose parameters such that the population undergoes evolutionary branching. Construct the isocline plot for dimorphic evolution, and study the effect of increasing *a* on the pattern of coevolution of two strategies.

(ii) Assume  $r(x) = b(\sqrt{x^2 + d} - x) - \beta$ , a convex decreasing function with parameters b = 10, d = 3.5,  $\beta = 0.6$  and  $\alpha(x_i - x_j)$  as above with a = 0, c = 2, v = 0.7 and k = 0.24. Show that there are several monomorphic evolutionary singularities, but eventually the population will settle on a monomorphic ESS even if it first becomes dimorphic via evolutionary branching.

(iii) Assume  $r(x) = \beta - bx$  and  $\alpha(x_i - x_j)$  as above with *a*=0. Construct an example such that an initially monomorphic population stays monomorphic, but an initially dimorphic population can evolve higher levels of polymorphism.