## **Coevolution in a Predator-Prey System**

In this project, we study the coevolution of predators with their prey. The ecological model is the standard Lotka-Volterra model

$$\frac{dN}{dt} = rN\left(1 - \frac{N}{K}\right) - \beta PN$$

$$\frac{dP}{dt} = \gamma\beta PN - dP$$
(1)

where N and P are respectively the population densities of prey and predator, r and K are respectively the intrinsic growth rate and the carrying capacity of prey in absence of predation,  $\beta$  is the catch rate,  $\gamma$  is the conversion factor of consumed prey into predator offspring, and d is the predator death rate.

Predators of a given trait value can most efficiently catch and handle prey of a certain "matching" trait value (for example, predators of a certain size cannot catch prey that are too large for them and are also inefficient with too small prey). We scale the prey and predator trait values ( $x_1$  and  $x_2$ , respectively) such that the best "matching" occurs for  $x_1 = x_2$ , and assume that the catch rate is a Gaussian function of the difference between the two traits,

$$\beta(x_1, x_2) = \exp\left(-\frac{(x_1 - x_2)^2}{2\sigma_{\beta}^2}\right)$$
(2)

Further, we assume that the prey carrying capacity depends on the trait value according to

$$K(x_1) = \exp\left(-\frac{x_1^2}{2\sigma_K^2}\right)$$
(3)

i.e., too small or too large prey has a lower carrying capacity. In the absence of predation, this results in stabilising selection on prey size with optimum at  $x_1=0$ . Predation, however, may induce disruptive selection in the prey.

Due to the rarity of mutations, there is either a mutant prey or a mutant predator but not both at a time. When a mutant prey with trait value  $y_1$  enters the resident predatorprey system at a low density (such that it does not perturb the equilibrium of the resident predator-prey system), its dynamics is given by

$$\frac{dN_{mut}}{dt} = rN_{mut} \left(1 - \frac{\hat{N}}{K(y_1)}\right) - \beta(y_1 - x_2)\hat{P}N_{mut}$$
(4)

where the equilibrium densities  $\hat{N}$  and  $\hat{P}$  are determined by the resident prey and predator according to equations (1)-(3). Similarly, when a mutant predator with trait value  $y_2$  appears, its dynamics is given by

$$\frac{dP_{mut}}{dt} = \gamma \beta (x_1 - y_2) N P_{mut} - dP_{mut}$$
(5)

(a) In the full model, two traits (prey size and predator size) are evolving even in a monomorphic resident population. Therefore, we need to construct an isocline plot to find the monomorphic evolutionary singularity. Convergence stability is also more difficult than for a single trait. Use the canonical equation to see whether the singularity at  $x_1^* = 0$ ,  $x_2^* = 0$  is convergence stable. Establish whether the singularity is a fitness maximum or fitness minimum for the prey and for the predator.

(b) Fix the predator trait at  $x_2 = 0$  and assume that only the prey evolves. Construct PIPs for the prey. Can you find evolutionary branching? What happens if you fix the prey at  $x_1 = 0$  and let only the predator evolve?

(c) Generalise the above model assuming that prey with different size utilise partly different resources, and therefore do not compete so much as those of identical size. The competition coefficient between the resident prey  $x_1$  and its mutant  $y_1$  is a Gaussian function of the difference,

$$a(y_1, x_1) = \exp\left(-\frac{(y_1 - x_1)^2}{2\sigma_a^2}\right)$$
(6)

which attains its maximum  $\alpha(0) = 1$  when the mutant is identical to the resident  $(1/\sigma_a = 0 \text{ corresponds to a constant competition coefficient, <math>a(y_1, x_1) \equiv 1$ , as in the model above). The mutant prey feels competition only by the resident and therefore spreads according to the equation

$$\frac{dN_{mut}}{dt} = rN_{mut} \left( 1 - \frac{\alpha(y_1 - x_1)\hat{N}}{K(y_1)} \right) - \beta(y_1 - x_2)\hat{P}N_{mut}$$
(7)

Without predation (P = 0), this generalised model is the same as the Lotka-Volterra competition model studied in the lectures.

Investigate the evolution of prey in this model holding the predator trait constant at  $x_2 = 0$ , and compare the results to (b) and also to the Lotka-Volterra competition model in the lectures. If time permits, investigate the joint evolution of  $x_1$  and  $x_2$  in the generalised model.