Coupled Conservation Laws: Predator-Prey

Mathematical Modelling Week 7
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Predator-Prey ODE System

Recall the classic ODE model for a predator-prey system: Let $u_1(t)$ denote the number of prey of a certain species at time t. Left on their own we'll assume the prey would grow according to some logistic law like $u_1' = \alpha_1 u_1(1 - u_1/m)$, or even more simply as

$$u_1'(t) = \alpha_1 u_1(t)$$

where α_1 is the growth rate. Let $u_2(t)$ denote the number of predators of a certain species (which of course prey on the u_1 species). Without the prey species the predators would die out, say according to

$$u_2'(t) = -\alpha_2 u_2(t)$$

for some constant $\alpha_2 > 0$. However, the presence of the prey species boosts the growth of the predators, and this can be simply modelled as $u_2'(t) = -\alpha_2 u_2(t) + \beta_2 u_1(t) u_2(t)$. This last term models the boost as being jointly proportional to the number of predators and prey. The presence of the predators, however, has a detrimental effect on the prey population. This effect is modelled by adding a term $-\beta_1 u_1(t) u_2(t)$ to the right side of the prey equation.

All in all the classic predator-prey ODE system is

$$u_1' = \alpha_1 u_1 - \beta_1 u_1 u_2 \quad (1)$$

$$u_2' = -\alpha_2 u_2 + \beta_2 u_1 u_2 \quad (2)$$

It's not hard to draw a phase portrait of this system. It has a single fixed point in the first quadrant; solutions spiral in closed loops about the fixed point.

A Spatially Distributed Model

In the last homework we saw how including spatial variation and boundary conditions can alter the conclusions of a biological model. We can incorporate space into the predator-prey ODE model too, and it gives a nice illustration of a coupled pair of conservation laws.

First, assume that the spatial domain is $0 < x < H$ for some H. Assume the prey diffuse with diffusivity κ_1 and the predators with diffusivity κ_2. Let $u_1(x,t)$ denote the prey density and $u_2(x,t)$ the predator density. If neither predators nor prey were created or destroyed both u_1 and u_2 would satisfy the diffusion equation with corresponding diffusivity. However, we can employ the reasoning that led to the ODE model to arrive at an analogous PDE model,

$$\frac{\partial u_1}{\partial t} - \kappa_1 \frac{\partial^2 u_1}{\partial x^2} = \alpha_1 u_1 - \beta_1 u_1 u_2 \quad (3)$$

$$\frac{\partial u_2}{\partial t} - \kappa_2 \frac{\partial^2 u_2}{\partial x^2} = -\alpha_2 u_2 + \beta_2 u_1 u_2 \quad (4)$$

with all constants positive. Of course we should also impose appropriate boundary and initial conditions.

Diffusive Instability

All the conservation laws involving diffusion that we've looked at so far result in solutions which approach steady-state behavior (the travelling wave is essentially steady-state too). And in fact if the boundary conditions are insulating on a bounded domain then the steady-state solutions have been constant in space too. This isn't too surprising—diffusion smear everything out to a uniform concentration.

But in a coupled system of diffusive PDE's this need not always be the case. In certain cases a coupled system can give rise to *diffusion-driven instability*, in which the system doesn't settle down to a steady-state. Consider the coupled system

$$\frac{\partial u_1}{\partial t} - \kappa_1 \frac{\partial^2 u_1}{\partial x^2} = (k_0 + k_1 u_1) u_1 - a u_1 u_2 \quad (5)$$

$$\frac{\partial u_2}{\partial t} - \kappa_2 \frac{\partial^2 u_2}{\partial x^2} = b u_1 u_2 - c u_2^2. \quad (6)$$

This is a variation on the predator-prey model, proposed by Segel and Jackson in 1972 in the article "Dissipative Structure: An Explanation and and

Ecological Example," J. Theor. Biol, 37, 545-559. Here u_1 is the density of prey, u_2 the density of predators. In equation (5) the term $(k_0 + k_1 u_1)u_1$ governs the growth of the prey and $-au_1u_2$ models the effect of the predators on prey density. The bu_1u_2 term models the effect of prey density on predators and $-cu_2^2$ is a "combat" term governing how predators affect or prey on each other. If we rescale as $\bar{x} = x/x_c, \bar{t} = t/t_c$ with $x_c = \sqrt{\kappa_2/k_0}$, $t_c = 1/k_0$, and $\bar{u}_1 = \frac{c}{k_0}u_1$, $\bar{u}_2 = \frac{b}{k_0}u_2$ we arrive at the system

$$\frac{\partial u_1}{\partial t} - \kappa\frac{\partial^2 u_1}{\partial x^2} = (1 + ku_1)u_1 - \bar{a}u_1u_2 \quad (7)$$

$$\frac{\partial u_2}{\partial t} - \frac{\partial^2 u_2}{\partial x^2} = u_1u_2 - u_2^2. \quad (8)$$

where I dropped all the bars from the dependent and independent variables. Here $\bar{a} = a/c, \kappa = \sqrt{\kappa_1/\kappa_2}, k = k_1/b$.

It turns out (via some tedious but not-so-hard analysis) that this system will NOT approach a steady-state if $k < 1$, $k < a$, and $2\sqrt{\kappa} < (k-\kappa)/\sqrt{a-k}$, but rather solutions will oscillate forever, even with homogeneous Neumann boundary conditions!

The intuitive explanation is this: The condition $2\sqrt{\kappa} < (k-\kappa)/\sqrt{a-k}$ forces κ to be small (play around with it, convince yourself). As a result, concentrations of prey diffuse rather slowly. Due to random variations in local density, a small peak develops in the prey u_1 density, and the term $(1+ku_1)u_1$ spurs further local growth. This spurs the predator growth due to the term u_1u_2 in equation (8), and so the $\bar{a}u_1u_2$ term then kicks in to moderate prey growth. But because the predators diffuse more rapidly than the prey (if $\kappa << 1$ the prey are much less mobile than the predators) any build-up of predators quickly diffuse and prey growth continues unhindered. Eventually, however, the predator density will increase (and continue diffusing), but not before a large peak has developed in u_1. The high predator density finally moderates the prey density peak and the whole thing repeats.

Another interpretation in which this kind of nonlinear coupling is important is chemistry. Specifically, we interpret u_1 as the concentration of an *activator*, that is, a substance which catalyzes its own production, and u_2 as the concentration of an *inhibitor* whose production is also catalyzed by u_1, but which itself tends to inhibit the production of u_1.