Pest control may make the pest population explode

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To Larry Payne on his eightieth birthday

Abstract

We present an example of a predator-prey-like system with a prey-only state as a global attractor, and with the additional property that an attempt to control the prey by harvesting or poisoning both species produces solutions in which both populations blow up in finite time.

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One of the oldest models in population ecology is the predator-prey system

$$\begin{aligned} u_t &= u(a - bv) \\ v_t &= v(-c + du), \end{aligned}$$

which was discovered independently by A. J. Lotka [3] and V. Volterra [4, 5]. Volterra used this model to explain a measured increase in the shark population and decrease in the population of food fish during the decreased fishing activity caused by the first world war. The use of mathematical models for predicting the effect of human actions has continued since then. For example, the above model as well as more sophisticated models predict an increase in the average population of insect pests and a decrease of their natural enemies when one tries to control them by using insecticide. (See, e. g., Section 7 of [1]).

The purpose of this paper is to present a cautionary example which exhibits a more dire consequence of pest control. We shall show that a simple two-species predator-prey-like model has the property that the population always converges to a unique equilibrium state, but that if the death rate of the predator is increased ever so slightly, then there are initial conditions for which the populations of both species blow up in finite time. Our model has the following simple form

$$\begin{aligned} u_t &= u[1 + u(v-1)e^{-v} - 4v] \\ v_t &= v(ue^{-v} - 4) \end{aligned} \tag{1}$$

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with the initial conditions

$$u(0) = u_0 > 0, \quad v(0) = v_0 \geq 0.$$

We can think of u as the population of a prey species and v as that of a predator species. We see from the second equation that the predator always benefits from an increase in the prey population. The first equation shows that the prey is harmed by an increase of v whenever the population lies on the set

$$\{(u, v) : (2 - v)u \leq 4e^v\}.$$

The first equation also shows that outside this set, that is, for sufficiently small predator density and sufficiently large prey density, the pruning produced by increased predation actually benefits the prey.

We model a mechanism of control or harvesting by the perturbation

$$\begin{aligned} u_t &= u[1 + u(v - 1)e^{-v} - 4v] - \alpha u \\ v_t &= v(ue^{-v} - 4) - \beta v, \end{aligned} \tag{2}$$

where α and β are nonnegative constants. Our principal result is the following.

Theorem 1 . *If* $\alpha \geq 0$ *and* $\beta = 0$*, then every solution of the system* (2) *with* $u(0) > 0$ *approaches* $(\max\{1 - \alpha, 0\}, 0)$ *as* t *goes to infinity.*

If $\alpha \geq 0$ *and* $\beta > 0$*, there is a function* $\mu(v)$ *with the property that if the initial values* (u_0, v_0) *of* (u, v) *satisfy the inequality* $u_0 > \mu(v_0)$*, then both components of the solution of the system* (2) *blow up in finite time.*

Proof. We introduce the new dependent variables

$$\begin{aligned} U &= ue^{-v} \\ V &= v. \end{aligned} \tag{3}$$

The chain rule shows that if (u, v) is a solution of the system (2), then

$$\begin{aligned} U_t &= U(1 - \alpha - U + \beta V) \\ V_t &= V(U - 4 - \beta). \end{aligned} \tag{4}$$

When $\beta = 0$, the solution (U, V) of this problem with the initial values (U_0, V_0) is given by the explicit formula

$$\begin{aligned} &U = \frac{(1-\alpha)U_0 e^{(1-\alpha)t}}{1 - \alpha + U_0(e^{(1-\alpha)t} - 1)},\ V = \frac{V_0 e^{-4t}}{1-\alpha}[1 - \alpha + U_0(e^{(1-\alpha)t} - 1)], \quad \text{if } \alpha \neq 1, \\ &U = \frac{U_0}{U_0 t + 1},\ V = V_0(U_0 t + 1)e^{-4t}, \quad \text{if } \alpha = 1. \end{aligned}$$

Thus every solution (U, V) approaches $(\max\{1 - \alpha, 0\}, 0)$ as t goes to infinity. The inverse transformation

$$\begin{aligned} u &= Ue^V \\ v &= V \end{aligned} \tag{5}$$

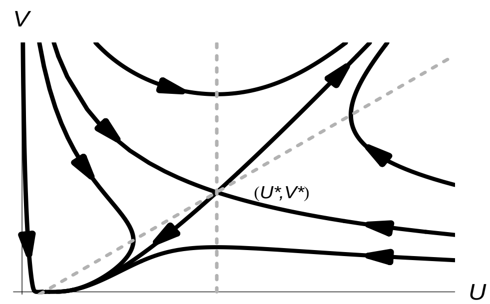

Figure 1: The phase plane of (4) with $\alpha = \beta = 0.5$. The dashed lines indicate the nullclines of the right-hand sides of (4).

of (3) shows that every solution (u, v) of (1) with $\beta = 0$ also approaches $(\max\{1-\alpha, 0\}, 0)$. Thus we have proved the first statement of the Theorem.

When $\beta > 0$, the system (4) has a saddle equilibrium point at (U^*, V^*) where

$$U^* := 4 + \beta \text{ and } V^* := \frac{3+\alpha+\beta}{\beta}.$$

The phase plane of the system (4) is as shown in Figure 1.

It is easily seen that the sector

$$\Sigma := \{(U, V) : 0 < U - U^* < \beta(V - V^*)\}$$

is a positively invariant set, and that U_t and V_t are positive on this set. We see from Figure 1 that every trajectory which lies above the stable manifold of (U^*, V^*) enters the set Σ. Because there are no equilibria other than (U^*, V^*) in the closure of the set Σ, and because U and V are increasing functions of t, they must have limits as t approaches infinity, and at least one of these limits must be infinity. We conclude that V increases to infinity along every trajectory in Σ. Therefore, we can solve for U in terms of V to obtain the equation

$$U - U^* = \rho(V)(V - V^*) \tag{6}$$

for any particular trajectory. The fact that the trajectory is in Σ means that

$$0 < \rho(V) < \beta.$$

We see by differentiating the relation (6) with respect to t and using the system (4) that ρ satisfies the differential equation

$$\begin{aligned}\frac{d\rho}{dV} &= \frac{1}{V - V^*}\left[\frac{U_t}{V_t} - \rho\right] \\ &= \frac{1}{V - V^*}\left[(\beta - \rho)\left(1 - \frac{V^*}{V} + \frac{U^*}{\rho V}\right) - \rho\right].\end{aligned}$$

A simple calculation shows that

$$\frac{d\rho}{dV} \geq \frac{\beta}{8(V - V^*)} \qquad \text{when } V \geq 2V^* \text{ and } 0 < \rho \leq \frac{\beta}{4}.$$

It follows that along any trajectory in Σ

$$U - U^* \geq \frac{\beta}{4}(V - V^*) \tag{7}$$

for all sufficiently large V. We plug this fact into the second equation of the system (4) to see that V must become infinite at a finite time. Because of the inequality (7) and because $U - U^* < \beta(V - V^*)$, U must blow up at the same time as V.

Because every solution which starts to the right of the stable manifold enters the sector Σ, we have shown that every such solution blows up in finite time. The stable manifold is the union of two curves. One of these lies in the the sector $\{(U, V) : U - U^* < \min\{0, \beta(V - V^*)\}\}$ where $U_t > 0$ and $V_t < 0$. The other lies in the sector $\{(U, V) : U - U^* > \max\{0, \beta(V - V^*)\}\}$ where $U_t < 0$ and $V_t > 0$. Thus its slope is negative, and it can be written as the graph $U = \nu(V)$, where ν decreases from ∞ at 0 to 0 at ∞. We can summarize the above result by saying that any solution of (4) whose initial conditions (U_0, V_0) satisfy the inequality $U_0 > \nu(V_0)$ blows up in finite time.

By using the transformation (5) and its inverse (3) we find that if the initial values (u_0, v_0) of the system (2) satisfy the inequality $u_0 > \nu(v_0)e^{v_0}$, then both u and v blow up at a finite time. This is the second statement of the Theorem with $\mu(v) := \nu(v)e^v$. Thus Theorem 1 is established. $\square$

Remark. Proposition 1.1 of [2] gives the same result for the system which is obtained from (4) by replacing the second equation by $V_t = V(U - 4 - \beta - c_2 V)$ where $0 < c_2 < \beta$.

Because of the applications to population ecology, we have restricted our attention to non-negative solutions. However, the explicit solution of the system (4) with $\beta = 0$ shows that all solutions with $U_0 > 0$ converge to $(\max\{1 - \alpha, 0\}, 0)$ and all solutions with $U_0 \leq 0$ approach the origin regardless of the sign of V_0. We obtain the same statement about the system (2) by applying the transformation (5).

The same ideas and the same transformation (3) applied to the system

$$\begin{aligned} u_t &= u[-1 + uve^{-v} - 4v] - \beta u \\ v_t &= v(ue^{-v} - 4) - \beta v \end{aligned} \tag{8}$$

show that when $\beta = 0$ all the solutions of this system approach the origin, while the system with $\beta > 0$ has solutions which blow up in finite time. Since the perturbing vector field points directly toward the origin, this result seems somewhat paradoxical. An explanation can be found in the phase plane diagram of Figure 2. While all the trajectories of the equation with $\beta = 0$ go to the origin, many of them do so along somewhat convoluted paths. In particular, at the points of the curve

$$u = [4 + (v - 1)^{-1}]e^v \tag{9}$$

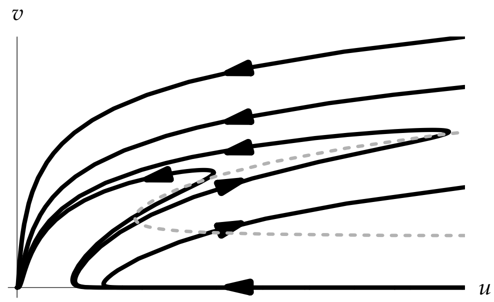

Figure 2: The phase planes of (8) when $\beta = 0$. The dashes indicate the curve (9) along which the flow is in the outward radial direction.

with $v > 1$, the right-hand side of (8) is the vector field $((v-1)^{-1}u, (v-1)^{-1}v)$. Therefore the trajectory at any point of this curve moves directly away from the origin. When $\beta > 0$ the perturbing vector field cancels this vector field at the point of the curve where $(v-1)^{-1} = \beta$. Thus this point becomes a saddle point, which leads to solutions which blow up in finite time.

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References

[1] M. KOT, *Elements of Mathematical Ecology*, Cambridge U. Press, 2001.

[2] Y. YOU, T. NAGYLAKI AND W.-M. NI, On diffusion-induced blowups in a mutualistic model, *Nonlinear Analysis* **45**, (2001), pp. 329–342.

[3] A. J. LOTKA, *Elements of Physical Biology*, Williams & Wilkins, Baltimore, 1925.

[4] V. VOLTERRA, Fluctuation in the abundance of a species considered mathematically, *Nature* **118**, (1926), pp. 558-560.

[5] V. VOLTERRA, Variazioni e fluttuazioni del numero d'individui in specie animali conviventi, *Atti R. Accad. Naz. dei Lincei, Memorie. Ser. VI*, **2**, (1927), pp. 31-113.