

On a principle of predatory exclusion

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Abstract

Suppose two prey species have the same rate of reproduction, and they are subjected to predation. Then the species more susceptible to predation dies out. So that in effect the predator introduces competition between the prey species.

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1 Introduction

We begin with the classical Lotka-Volterra model of the predator-prey interaction, which can be found in many textbooks

$$(1.1) \quad \begin{aligned} x'(t) &= ax(t) - bx(t)y(t) \\ y'(t) &= -cy(t) + dx(t)y(t). \end{aligned}$$

Here $x(t)$ and $y(t)$ give respectively the numbers of prey (rabbits) and predators (foxes) as functions of time t . Positive coefficients a, b, c and d are assumed to be constant. We assume the initial conditions $x(0)$ and $y(0)$ to be positive, which implies that solutions of (1.1) are positive functions. It is

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known, although perhaps not as widely as it should, that (1.1) is a Hamiltonian system in disguise. Namely, if we let $p(t) = \ln x(t)$ and $q(t) = \ln y(t)$, then we can rewrite (1.1) as

$$(1.2) \quad \begin{aligned} p'(t) &= a - be^{q(t)} \equiv H_q(p, q) \\ q'(t) &= -c + de^{p(t)} \equiv -H_p(p, q), \end{aligned}$$

with the Hamiltonian function $H(p, q) = aq - be^q + cp - de^p$. Along the solution curves of (1.2) $H(p(t), q(t)) = \text{constant}$. In the original variables

$$(1.3) \quad a \ln y - by + c \ln x - dx = \text{constant}.$$

The function $a \ln y - by + c \ln x - dx$ is unimodular, since it is a sum of two unimodular functions $c \ln x - dx$ and $a \ln y - by$. Hence its level curves, given by (1.3), are the familiar closed curves of the predator-prey interaction. Then $x(t)$ and $y(t)$ are periodic functions of t (whose period depends on the initial conditions, see J. Waldvogel [4]).

Let us now assume there are two types of rabbits, whose populations are given by $u(t)$ and $v(t)$ respectively, say females and males. They have the same reproduction rates, but males are more susceptible to predation (we understand that this assumption is correct). We thus consider the model

$$(1.4) \quad \begin{aligned} u'(t) &= au(t) - bu(t)y(t) \\ v'(t) &= av(t) - \alpha bv(t)y(t) \\ y'(t) &= -cy(t) + d(u(t) + v(t))y(t), \end{aligned}$$

with a constant $\alpha > 1$. Solution of (1.4) is uniquely determined by the initial conditions $u(0) = u_0 > 0$, $v(0) = v_0 > 0$ and $y(0) = y_0 > 0$.

Theorem 1.1 *For any (u_0, v_0, y_0) , $v(t)$ tends exponentially to zero, while $(u(t), y(t))$ tends to a solution of (1.1), as $t \rightarrow \infty$.*

We found this result to be rather unexpected. The conclusion is similar to the well-known principle of competitive exclusion, see e.g. [5], however there is no direct interaction between the two types of rabbits. One can say that in effect the rabbits do compete, although their competition happens through predation by the foxes. This phenomenon has been observed by ecologists, see R.D. Holt and J.H. Lawton, [2], [3], who referred to it as “apparent competition”.

We can also consider a “dual” situation, when $u(t)$ and $v(t)$ give populations of two types of foxes, preying on the rabbits

$$(1.5) \quad \begin{aligned} x'(t) &= ax(t) - b(u(t) + v(t))x(t) \\ u'(t) &= -cu(t) + \alpha du(t)x(t) \\ v'(t) &= -cv(t) + dv(t)x(t). \end{aligned}$$

Theorem 1.2 *If $\alpha > 1$, $v(t)$ tends exponentially to zero, while $(x(t), u(t))$ tends to a solution of (1.1), as $t \rightarrow \infty$.*

The proof is similar.

2 Proof of the Theorems 1.1 and 1.2.

We need two lemmas, dealing with a perturbed version of the Lotka-Volterra equations

$$(2.1) \quad \begin{aligned} x'(t) &= ax(t) - bx(t)y(t) \\ y'(t) &= -cy(t) + dx(t)y(t) + f(t)y(t). \end{aligned}$$

Lemma 2.1 *Assume that the given continuous function $f(t)$ is positive for all $t > 0$, and the integral $\int_0^\infty f(t) dt$ converges. Then both components of any positive solution of (2.1) are uniformly bounded for all $t > 0$.*

Proof: Letting $p(t) = \ln x(t)$ and $q(t) = \ln y(t)$, we rewrite (2.1) as

$$(2.2) \quad \begin{aligned} p'(t) &= a - be^{q(t)} \\ q'(t) &= -c + de^{p(t)} + f(t). \end{aligned}$$

We shall use the Lyapunov function $H(p, q) = be^q - aq + de^p - cp$. Then we see from (2.2) that $p' = -H_q$ and $q' = H_p + f(t)$. Then the derivative of H along the trajectories of (2.2) is

$$(2.3) \quad \frac{d}{dt}H(p, q) = -H_p H_q + H_q (H_p + f(t)) = f(t) (be^{q(t)} - a).$$

Clearly, we can find a positive constant C , so that

$$(2.4) \quad be^q - a < 2[be^q - aq + de^p - cp] + C = 2H + C,$$

for all real p and q . Using this in (2.3),

$$\frac{dH}{dt} < f(t)(2H + C).$$

Integrating

$$(2.5) \quad \frac{1}{2} \ln |2H(p(t), q(t)) + C| < \int_0^t f(s) ds + \frac{1}{2} \ln |2H(p(0), q(0)) + C| \\ < C_1 \quad \text{for all } t > 0,$$

for some positive constant C_1 . From (2.5) we conclude a bound from above on $H(p, q)$, and hence on p and q , and the lemma follows. $\diamond$

Lemma 2.2 *In the conditions of the preceding lemma, any positive solution of (2.1) tends to a solution of (1.1), as $t \rightarrow \infty$.*

Proof: Integrate (2.3)

$$H(p(t), q(t)) = H(p(0), q(0)) + \int_0^t f(t) (be^{q(t)} - a) dt.$$

Since $q(t)$ is bounded and $f(t)$ is positive, we see that $H(p(t), q(t))$ tends to a finite limit as $t \rightarrow \infty$. Hence the solutions of (2.1) approach the curves $H(p, q) = \text{constant}$, which correspond to the solutions of (1.1). $\diamond$

Similarly we prove the following lemma for another perturbation of the Lotka-Volterra system

$$(2.6) \quad \begin{aligned} x'(t) &= ax(t) - bx(t)y(t) - f(t)x(t) \\ y'(t) &= -cy(t) + dx(t)y(t). \end{aligned}$$

Lemma 2.3 *Assume that the given continuous function $f(t)$ is positive for all $t > 0$, and the integral $\int_0^\infty f(t) dt$ converges. Then any positive solution of (2.6) tends to a solution of (1.1), as $t \rightarrow \infty$.*

Proof of the Theorem 1.1. Our goal is to show that $v(t) \rightarrow 0$ as $t \rightarrow \infty$. Multiplying the first equation in (1.4) by e^{-at} , and denoting $U(t) = e^{-at}u(t)$, we have

$$U'(t) = -bU(t)y(t).$$

Letting $V(t) = e^{-at}v(t)$, we rewrite similarly the second equation in (1.4)

$$V'(t) = -\alpha bV(t)y(t).$$

Dividing,

$$(2.7) \quad \frac{dV}{dU} = \alpha \frac{V}{U}.$$

Integrating (2.7), and returning to the original variables,

$$(2.8) \quad v(t) = \gamma e^{-(\alpha-1)at} u^\alpha(t), \quad \text{with } \gamma = \frac{v(0)}{u^\alpha(0)}.$$

We can then rewrite our system (1.4) as a system of two equations

$$(2.9) \quad \begin{aligned} u'(t) &= au(t) - bu(t)y(t) \\ y'(t) &= -cy(t) + d \left(u(t) + \gamma e^{-(\alpha-1)at} u^\alpha(t) \right) y(t), \end{aligned}$$

We claim that all solutions of this system are bounded, for any $\gamma > 0$. Again, we appeal to its Hamiltonian-like nature. Letting $p(t) = \ln u(t)$ and $q(t) = \ln y(t)$, we rewrite (2.9) as

$$(2.10) \quad \begin{aligned} p'(t) &= a - be^q \\ q'(t) &= -c + d \left(e^p + \gamma e^{-(\alpha-1)at} e^{\alpha p} \right). \end{aligned}$$

We shall use a time-dependent Lyapunov function $H(t, p, q) = be^q - aq + de^p - cp + \frac{d\gamma}{\alpha} e^{-(\alpha-1)at} e^{\alpha p}$. In terms of H we can rewrite the equations in (2.10) as $p' = -H_q$ and $q' = H_p$ respectively. Then the derivative of H along the trajectories of (2.10) is

$$\frac{d}{dt} H(t, p, q) = H_t + H_p(-H_q) + H_q H_p = -\frac{(\alpha-1)ad\gamma}{\alpha} e^{-(\alpha-1)at} e^{\alpha p} < 0.$$

We conclude that $H(t, p, q)$ is bounded from above. The same is then true for the function $be^q - aq + de^p - cp$. Hence $p(t)$ and $q(t)$, and then $u(t)$ and $y(t)$ are bounded from above.

Since $u(t)$ is bounded, we see from (2.8) that $v(t)$ tends exponentially to zero. The rest of the proof now follows by Lemma 2.2. $\diamond$

Proof of the Theorem 1.2. We briefly outline the proof, since it is similar. Letting $U(t) = e^{ct}v(t)$ and $V(t) = e^{ct}v(t)$, we conclude as before

$$(2.11) \quad v(t) = c_0 e^{-\beta ct} u^{\frac{1}{\alpha}},$$

with $\beta = 1 - \frac{1}{\alpha} > 0$, and $c_0 = \frac{v(0)}{u^{\frac{1}{\alpha}}(0)}$. We now use (2.11) in the system (1.5), and in the resulting system for $x(t)$ and $u(t)$ we let $p(t) = \ln x(t)$, $q(t) = \ln u(t)$. As before we obtain a Hamiltonian-like system for $p(t)$ and $q(t)$. This time the Lyapunov function is $H(t, p, q) = be^q - aq + \alpha bc_0 e^{-\beta ct} e^{\frac{1}{\alpha}q} + \alpha de^p - cp$. We conclude the boundness of $x(t)$ and $u(t)$ from above, and then from (2.11) we see that $v(t)$ tends exponentially to zero. Using Lemma 2.3, we then conclude that $x(t)$ and $u(t)$ tend to a solution of (1.1). $\diamond$

3 Some extensions

For definiteness, we shall indicate some extensions for our first model (1.4), although similar extensions can be also made for the model (1.5).

Clearly, we can extend the model (1.4), to consider any number of rabbits, with the same reproduction rate a . Only one species of rabbits, the one least susceptible to predation, will survive.

We can also consider a more general model ($\alpha > 1$)

$$(3.1) \quad \begin{aligned} u'(t) &= au(t) - bu(t)y(t) \\ v'(t) &= a\theta v(t) - \alpha bv(t)y(t) \\ y'(t) &= -cy(t) + d(u(t) + v(t))y(t). \end{aligned}$$

We know that $v(t) \rightarrow 0$ as $t \rightarrow \infty$, when $\theta = 1$. We claim that the same is true, i.e. the conclusions of the Theorem 1.1 hold, when $1 < \theta < \alpha$. Indeed, rewriting the second equation in (3.1) as

$$(3.2) \quad v'(t) + (\alpha - \theta)av = a\alpha v(t) - \alpha bv(t)y(t)$$

suggests that we set $V = e^{(\alpha-\theta)at}v$, and rewrite (3.2) as

$$V'(t) = a\alpha V(t) - \alpha bV(t)y(t).$$

Dividing this by the first equation in (3.1), we have

$$\frac{dV}{du} = \alpha \frac{V}{u}.$$

Integrating, and returning to the original variables,

$$(3.3) \quad v = \gamma e^{-(\alpha-\theta)at} u^\alpha.$$

Then we complete the proof the same way as in the Theorem 1.1.

In case $\theta = \alpha$, the result no longer holds. Indeed, we see from (3.3) that $v = \gamma u^\alpha$, and hence u and v behave similarly as $t \rightarrow \infty$.

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