THE ROSENZWEIG-MACARTHUR PREDATOR-PREY MODEL

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ABSTRACT. This is intended as lecture notes for 2nd ODE course, an application of the Poincaré-Bendixson Theorem. The model is derived and the behavior of its solutions is discussed.

1. THE MODEL

We derive and study the predator-prey model which Turchin [7] attributes to Rosenzweig and MacArthur [8]. Turchin's book is an excellent reference for predator-prey models. See also Hastings [2] and Murray [6].

Let x denote prey density (#/ unit of area) and y denote predator density (#/unit of area). A typical predator-prey model has the form

$$
\begin{aligned}
x' &= \text{birth rate} - \text{death rate not due to } y - \text{kill rate due to } y \\
y' &= -\text{death rate} + \text{reproduction rate}
\end{aligned}
$$

Models differ in the choices made for these. Logistic growth and death is a common choice made to model prey birth and death in the absence of predators. A linear death rate for predators is common. If predator density is not so large that they interfere with each other while searching for prey, then one often assumes that the death rate due to predators is linear in predator density. Also, it is common to assume that predator reproduction rate is proportional to the predator kill rate. Thus, we have

$$
\begin{aligned}
x' &= rx\left(1 - \frac{x}{K}\right) - yh(x) \\
y' &= y\left(-c + dh(x)\right)
\end{aligned}
$$

where $r, K > 0$ and $c, d > 0$. Note that $h(x)$ has units of 1/time:

$$
h(x) = \#\text{prey caught per predator per unit time}.
$$

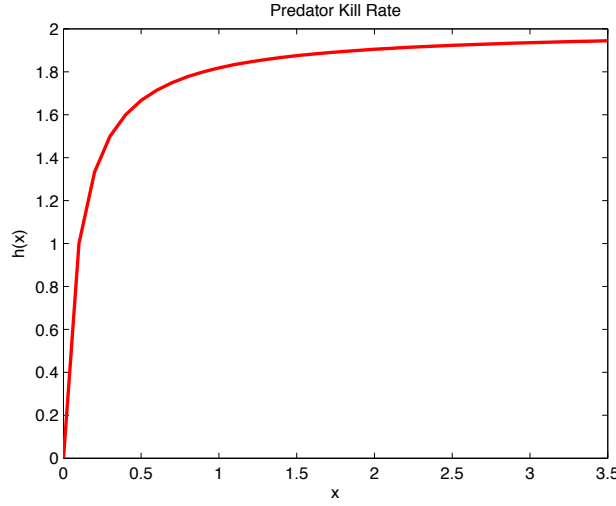It is the per predator kill rate.

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Figure 1.1. Predator kill rate.

The ecologist goes into the field and finds that in a fairly long time T, the average predator makes N kills in an environment with prey density x and therefore $h = \frac{N}{T}$. If the predator search rate is s units of area per unit time, and each prey requires time τ for the predator to handle (stalk,catch,eat,burp,clean teeth,sleep) before it is again ready to search for prey, then the average predator spends time $T - N\tau$ searching, covering area $s(T - N\tau)$, in which it encounters $xs(T - N\tau)$ prey, so $N = xs(T - N\tau)$ or

$$(1.1) \qquad h(x) = \frac{N}{T} = \frac{sx}{1 + s\tau x}$$

We have derived the Holling type II functional response [3, 7]. The maximum kill rate is $1/\tau$, reached at infinite prey density, and the prey density at which the kill rate is half maximum occurs at $x = 1/s\tau$. See Figure 1.1.

It leads to the system

$$
\begin{aligned}
x' &= rx\left(1 - \frac{x}{K}\right) - \frac{sxy}{1 + s\tau x} \\
y' &= -cy + d\frac{sxy}{1 + s\tau x}
\end{aligned}
$$

(1.2)

2. SCALING

If we let

$$u = x/X, \quad v = y/Y$$

where $X, Y > 0$ are to be determined we arrive at new differential equations for u and v, e.g.,

$$u' = x'/X = ru\left(1 - \frac{uX}{K}\right) - \frac{suYv}{1 + s\tau uX}$$

and

$$v' = y'/Y = -cv + s\frac{duvX}{1 + s\tau uX}$$

Choosing X, Y so

$$s\tau X = 1, \quad Y = dX$$

and setting $m = \frac{d}{\tau}$ and $k = K/X$ then our system becomes

$$u' = ru\left(1 - \frac{u}{k}\right) - \frac{muv}{1 + u}$$
$$v' = -cv + \frac{muv}{1 + u}$$

Finally, by scaling time $t = rs$ and using the chain rule $\frac{du}{ds} = \frac{du}{dt}\frac{dt}{ds} = r\frac{du}{dt}$ and redefining $\bar{m} = m/r$ and $\bar{c} = c/r$, we have the system

$$\frac{du}{ds} = u\left(1 - \frac{u}{k}\right) - \frac{\bar{m}uv}{1 + u}$$
$$\frac{dv}{ds} = -\bar{c}v + \frac{\bar{m}uv}{1 + u}$$

Now, lets return to our original variables x, y, time t, and drop the bars over certain parameters, so we arrive at the system:

$$x' = x\left(1 - \frac{x}{k}\right) - \frac{mxy}{1 + x}$$
(2.1)
$$y' = -cy + \frac{mxy}{1 + x}.$$

3. POSITIVITY AND BOUNDEDNESS OF SOLUTIONS

System 2.1 is continuously differentiable in a neighborhood of the first quadrant $Q = \{(x, y) : x, y \geq 0\}$ and therefore solutions of initial value problems with nonnegative initial conditions exist and are unique. In this brief section, we will show that Q is invariant. That is, solutions satisfying $x(0), y(0) \geq 0$ satisfy $x(t), y(t) \geq 0$ for all t. Furthermore, we show that solutions are bounded in the future and therefore are defined for all $t \geq 0$.

Notice that 2.1 has the form

$$\begin{aligned}
x' &= xP(x,y) \\
y' &= yQ(x,y).
\end{aligned}$$

If $(x(t), y(t))$ is a solution of such a system, then $x'(t) = x(t)p(t)$ where $p(t) = P(x(t), y(t))$ so by the integrating factor trick

$$\frac{d}{dt}\left(e^{-\int_0^t p(s)ds}x(t)\right) = 0$$

Consequently,

$$x(t) = e^{\int_0^t p(s)ds}x(0)$$

From this, we see that if $x(0) = 0$ then $x(t) = 0$ for all t and if $x(0) > 0$, then $x(t) > 0$ for all t. Similarly, for y. This proves (much more) than the invariance of Q; it also proves the invariance of the interior of Q and the boundary of Q.

As for boundedness of solutions, we prove the following:

Lemma 3.1. *There exists $R_0 > 0$ such that for all $R \geq R_0$, the right triangle $T(R)$ with sides $x = 0$, $y = 0$ and $x + y = R$ is positively invariant.*

Since every initial point $(x(0), y(0)) \in Q$ satisfies $(x(0), y(0)) \in T(R)$ for some $R \geq R_0$, this shows that all solutions starting in Q are bounded for $t \geq 0$ since $(x(t), y(t)) \in T(R)$, $t \geq 0$.

Proof. We need only show that solutions cannot leave $T(R)$ through the hypotenuse $x + y = R$ of our triangle. We show that $\frac{d}{dt}(x(t) + y(t)) = x'(t) + y'(t) < 0$ if $x(t) + y(t) = R$. Or, equivalently, $x' + y' < 0$ if $x + y = R$ (no t needed). For $x + y = R$, we have

$$x' + y' = x(1 - x/k) - cy = x(1 - x/k) - c(R - x) \equiv F(x), \ 0 \leq x \leq R.$$

The maximum of the parabolic function $F(x)$ on $0 \leq x$, obtained by setting its derivative to zero, is at $\bar{x} = \frac{k}{2}(1 + c)$ so

$$F(x) \leq F(\bar{x}) = -cR + (1 + c)\frac{k}{2}(1 + c) - \frac{1}{k}\left(\frac{k}{2}(1 + c)\right)^2 < 0$$

if R is chosen large enough. $\qquad\square$

4. EQUILIBRIA AND THEIR STABILITY

Equilibrium equations are

$$0 = x\left(1 - \frac{x}{k} - \frac{my}{1+x}\right)$$

(4.1) $$0 = y\left(-c + \frac{mx}{1+x}\right).$$

This leads to equilibria:

$$(0,0), \ (k,0),$$

which always exist, and a coexistence equilibrium $(\bar{x}, \bar{y})$, where

(4.2) $$\frac{m\bar{x}}{1+\bar{x}} = c \text{ and } c\bar{y} = \bar{x}(1 - \bar{x}/k)$$

which has positive components if and only if

(4.3) $$\frac{mk}{1+k} > c.$$

The reader should check these assertions using $\bar{x} = \frac{c}{m-c}$.

If (4.3) fails to hold, the predator goes extinct (the reader should verify this) and so hereafter, we assume that (4.3) holds.

The Jacobian matrix at equilibrium $(k,0)$ is given by

$$J = \begin{pmatrix} -1 & -\frac{mk}{1+k} \\ 0 & \frac{mk}{1+k} - c \end{pmatrix}$$

so, in view of (4.3), $(k,0)$ is a saddle point. For later use, we note the eigenvector corresponding to positive eigenvalue $\lambda = \frac{mk}{1+k} - c$ is $V = (-\frac{mk}{1+k}, 1+\lambda)$. The unstable manifold $W^u(k,0)$ is tangent to this vector at $(k,0)$, or, equivalently, tangent to the line $y = M(x-k)$ where the slope $M = -(1+\lambda)\frac{1+k}{mk}$.

The Jacobian at $(\bar{x}, \bar{y})$ is, on making use of (4.2), given by

$$J = \begin{pmatrix} 1 - 2\frac{\bar{x}}{k} - \frac{m\bar{y}}{(1+\bar{x})^2} & -c \\ \frac{m\bar{y}}{(1+\bar{x})^2} & 0 \end{pmatrix}$$

It has a positive determinant so stability depends only on the trace, which, using (4.2), we can rewrite as

$$\text{trace} = 1 - \frac{2\bar{x}}{k} - \frac{1}{(1+\bar{x})}(1 - \frac{\bar{x}}{k})$$

so

(4.4) $$(1+\bar{x})\text{trace} = (1 - \frac{2\bar{x}}{k})(1+\bar{x}) - (1 - \frac{\bar{x}}{k}) = \frac{2\bar{x}}{k}\left(\frac{k-1}{2} - \bar{x}\right)$$

We have proved the following:

Lemma 4.1. *Coexistence equilibrium $(\bar{x}, \bar{y})$ is a sink if $\bar{x} > \frac{k-1}{2}$ and a source if $\bar{x} < \frac{k-1}{2}$.*

The lemma can be made more explicit by inserting the value of $\bar{x} = \frac{c}{m-c}$. $(\bar{x}, \bar{y})$ is a sink if $k < \frac{m+c}{m-c}$ and a source if the reverse inequality holds. Regarding k as a bifurcation parameter, as it increases, the stability of $(\bar{x}, \bar{y})$ changes from a sink to a source as the real part of a complex conjugate pair of eigenvalues of the Jacobian change sign from negative to positive. A Hopf bifurcation occurs at $k = \frac{m+c}{m-c}$. Note that $k - 1$ may be negative!

The $x' = 0$ nullcline consists of $x = 0$ and the parabola $my = (1 - \frac{x}{k})(1 + x)$ which meets the x-axis at $x = k$ and $x = -1$ and has axis of symmetry given by $x = \frac{k-1}{2}$ where the parabola reaches maximum height.

The $y' = 0$ nullcline consists of $y = 0$ and the vertical line $x = \bar{x}$. Lemma 4.1 says that $(\bar{x}, \bar{y})$ is a sink if the vertical line $x = \bar{x}$ meets the parabola to the right of its peak and is a source if it meets the parabola on the left of its peak.

Finally, we want to locate the unstable manifold $W^u(k, 0)$ of the saddle point relative to the $x' = 0$ nullcline $my = (1 - \frac{x}{k})(1 + x)$, which meets the x-axis at the saddle point. The derivative of the nullcline, evaluated at the point $x = k$, is $\frac{dy}{dx}(x = k) = -\frac{k+1}{mk}$. Recall our calculation above revealed that the slope of the tangent line to $W^u(k, 0)$ is $M = -(1 + \lambda)\frac{1+k}{mk}$. Comparing this with the derivative of the nullcline (recall $\lambda > 0$) shows that the tangent line to $W^u(k, 0)$ is less (more negative) than the slope of the nullcline, ensuring that the branch of $W^u(k, 0)$ with $y > 0$ lies above the nullcline.
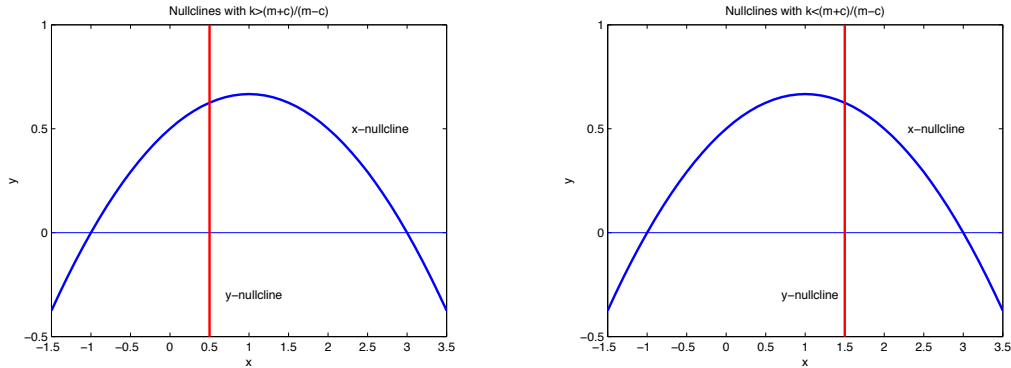

FIGURE 4.1. Nullclines when $\bar{x} < \frac{k-1}{2}$ (left) and $\bar{x} > \frac{k-1}{2}$ (right).

5. CASE 1: $\bar{x} < \frac{k-1}{2}$

We will prove the following result.

Theorem 5.1. *Assume that $\bar{x} < \frac{k-1}{2}$. Then there exists a periodic solution of* (2.1). *In fact, every solution starting in the interior of Q, except for the positive equilibrium, has a periodic orbit as its limit set.*

Proof. We will use the Poincaré-Bendixson theorem and the fact that $(\bar{x}, \bar{y})$ is an unstable source and hence cannot belong to an omega limit set of any solution other than itself. The unstable manifold $W^u = W^u(k, 0)$ of the saddle point $(k, 0)$ will play a key role in our argument. See Figure 5.1. The nullclines partition Q into 4 components which we number as Q_1, Q_2, Q_3, Q_4 in counterclockwise order about $(\bar{x}, \bar{y})$ with Q_1 being the upper right component above the red dotted $x' = 0$ nullcline and right of the yellow $y' = 0$ nullcline. As we noted above, the orbit of W^u with $y > 0$ emerges into Q_1 as it leaves $(k, 0)$. We argue that it must cross the yellow nullcline into Q_2, then cross the red nullcline into Q_3, again cross the lower part of the yellow nullcline into Q_4, and then meet the red nullcline as shown in Figure 5.1. The argument that it must leave each region in turn is similar in all cases so it will be given only for the initial crossing of the yellow $y' = 0$ nullcline. Indeed, if the trajectory were to remain in Q_1 for all $t \geq 0$, then since the solution is bounded by lemma 3.1 and its components are monotone functions of t, it must converge to an equilibrium in the closure of Q_1. The only possibility is $(\bar{x}, \bar{y})$ but it is a source so cannot be the limit. Consequently, the trajectory must meet the yellow nullcline as asserted.

We have traced the unstable manifold W^u as it crosses the yellow nullcline, then crosses the red nullcline, then the yellow nullcline, and finally meeting the red nullcline for a second time. Let Γ denote the Jordan curve consisting of this portion of W^u together with the portion of the red nullcline connecting it to the saddle $(k, 0)$ and let R denote the bounded component of the complement of Γ, the "inside of Γ". It is compact, positively invariant, and contains only one equilibrium $(\bar{x}, \bar{y})$. By the Poincaré-Bendixson theorem, for each $p \in R$ distinct from $(\bar{x}, \bar{y})$, the omega limit set of the trajectory through p must be a periodic orbit in R.

Now we argue that every positive trajectory must enter R, and therefore have a periodic orbit as omega limit set. Indeed, arguing exactly as we did above for the trajectory W^u, it can be seen that every trajectory starting in the interior of Q must meet that red nullcline $x' = 0$ along that portion belonging to Γ. It then enters R and we are done. $\square$
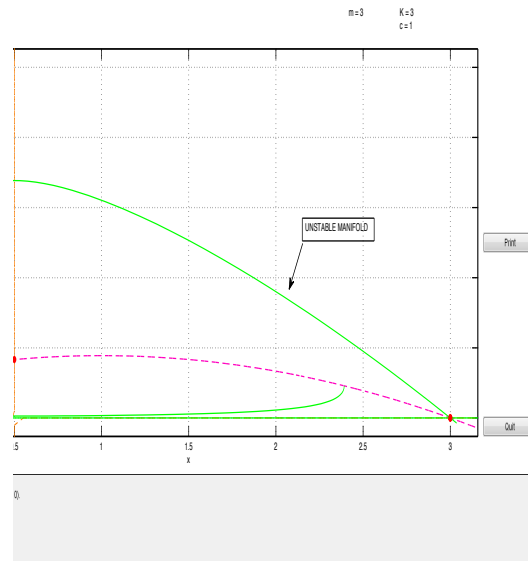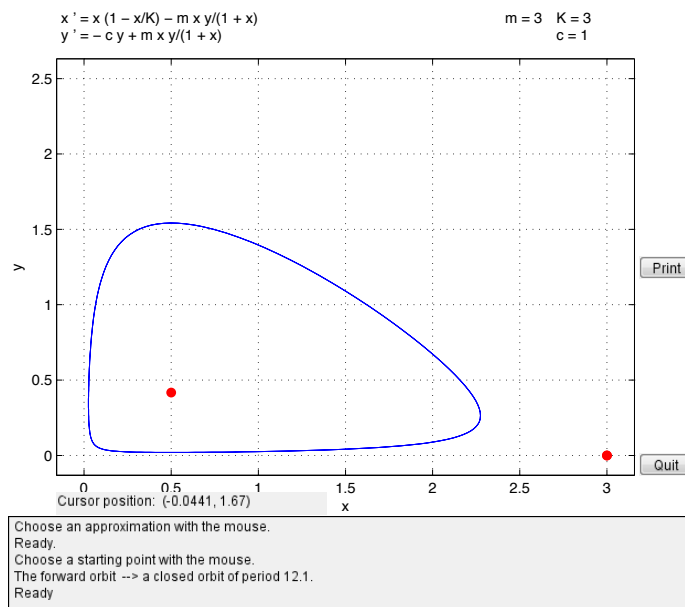
FIGURE 5.1. Unstable manifold of saddle point $(k, 0)$.

FIGURE 5.2. Periodic Orbit.

K. Cheng [1] has proved that the periodic orbit is unique and therefore that it is the omega limit set of every positive trajectory.

6. CASE 2: $\bar{x} > \frac{k-1}{2}$

In this case, we prove the following result.

Theorem 6.1. *Assume that $\bar{x} > \frac{k-1}{2}$. Then there are no periodic orbits of (2.1). In fact, every solution starting in the interior of Q converges to the positive equilibrium.*

Proof. We will use the Dulac criterion to show that no periodic orbit or homoclinic loop exist. Then, by the Poincaré-Bendixson theorem, for each p in the open first quadrant Q, the omega limit set of p must contain an equilibrium. If the omega limit set contains the sink $(\bar{x}, \bar{y})$, then it can contain no other point, by an assigned homework problem. If the omega limit set does not contain $(\bar{x}, \bar{y})$ then it contains the saddle $(k, 0)$ and no other equilibrium. According to the strong form of the Poincaré-Bendixson theorem, e.g. Theorem 6.19 in [5], the omega limit set is either the saddle point or it consists of the saddle point together with a non-empty set of homoclinic trajectories each of whose alpha and omega limit sets is the saddle point. The omega limit set cannot be the saddle point since then $\phi(t, p) \to (k, 0)$ as $t \to \infty$ so p would belong to the stable manifold of $(k, 0)$ which is the x-axis. The omega limit set cannot contain a homoclinic orbit whose alpha and omega limit set is the saddle point since such an orbit, together with the saddle point, constitutes a closed Jordan curve, forbidden by the Dulac criterion. Thus, we conclude that the omega limit set of every point p in the open first quadrant Q must be $\{(\bar{x}, \bar{y})\}$.

Following Hsu [4], we use the Dulac function $g(x, y) = \frac{1+x}{x} y^{\alpha-1}$ where α is to be determined. In the calculation below, we use subscripts x and y to denote partial derivatives with respect to these variables.

$$
\begin{aligned}
(gx')_x + (gy')_y &= y^{\alpha-1} \left(\frac{k-1}{k} - \frac{2x}{k} + \alpha \left(-c\frac{1+x}{x} + m \right) \right) \\
&= \frac{y^{\alpha-1}}{x} \left[\frac{2x}{k} \left(\frac{k-1}{2} - x \right) + \alpha(m-c)(x - \bar{x}) \right]
\end{aligned}
$$

The quadratic term in brackets has its maximum value at $x = x^* = \frac{k-1}{4} + \frac{\alpha k(m-c)}{4}$. We may choose $\alpha > 0$ so that $\frac{k-1}{2} < x^* < \bar{x}$ from which it follows that both terms in brackets are negative, making the maximum value negative. Consequently, $(gx')_x + (gy')_y < 0$ for points in Q with $x > 0$ and, by the Dulac criterion, there can be no periodic orbit or homoclinic loop in this region. $\square$

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