

Math 134 Project

Rabbits vs. Foxes

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1 Rabbits vs. Foxes

1.1 Biological Meaning

In this project, we will study growth rate of populations of rabbits and foxes by following the Lotka Volterra predator-prey model, in which the presence of predators decreases the population of prey, and the presence of prey increases the population of predators. This is modeled by the system of equations

$$\begin{aligned}\dot{R} &= aR - bRF \\ \dot{F} &= -cF + dRF\end{aligned}$$

In the above system of equations, R represents the number of rabbits in the modeled population, and F represents the number of foxes. Then \dot{R} and \dot{F} represent the growth rate of the respective species.

Before beginning a mathematical analysis, let us first consider the biological interpretation of the Lotka Volterra predator-prey model. In the given equation, a represents the birth rate of the rabbits, and c represents the death rate of the foxes. In interactions between the two species, the growth rate of the rabbit population declines since rabbits will be eaten by foxes, which is represented by the $-bRF$ term, and thus the fox population will increase, which is represented by the dRF term.

However, this model makes some unrealistic assumptions. Firstly, it assumes that the two species are isolated in the sense that any effects of migration or other external influences are disregarded. Furthermore, it assumes that the sole cause of rabbit death is being eaten by foxes and that the rabbits have unlimited resources. Indeed, according to this equation, if there are no foxes in the environment, the growth rate of the rabbits will be

$\dot{R} = aR$ and so $R = e^{at}$. That is, the rabbit population will increase towards infinity exponentially.

Additionally, the model assumes that the fox population will only grow if the foxes are able to eat rabbits. If $R = 0$, then

$\dot{F} = -cF$ and so $F = e^{-ct}$. That is, in the absence of rabbits, the fox population will decrease exponentially to 0.

1.2 Nondimensionalization

Show that the model can be recast in dimensionless form as

$$x' = x(1 - y) \tag{1}$$

$$y' = \mu y(x - 1) \quad (2)$$

Definiton: Nondimensionalization is the removal of units from an equation involving physical quantities by a substitution of variables

We begin by factoring out aR from \dot{R} and cF from \dot{F} to give

$$\dot{R} = (1 - \frac{b}{a}F) \quad (3)$$

$$\dot{F} = cF(\frac{d}{c}R - 1) \quad (4)$$

Next, we define dimensionless variables $x = \frac{R}{R_0}$, $y = \frac{F}{F_0}$, and $\tau = \frac{t}{T}$. Rearranging these newly defined terms and plugging into equations (3) and (4) gives

$$\frac{R_0}{T} \frac{dx}{d\tau} = axR_0(1 - \frac{b}{a}F_0y), \quad \frac{F_0}{T} \frac{dy}{d\tau} = cF_0y(\frac{d}{c}xR_0 - 1)$$

For the first equation, we define T and F_0 such that they cancel out any parameters that are not dimensionless. By taking $T = \frac{1}{a}$ and letting $F_0 = \frac{a}{b}$, we achieve the desired result

$$\frac{dx}{d\tau} = x(1 - y)$$

For the next equation, substituting in $T = \frac{1}{a}$ and letting $R_0 = \frac{c}{d}$ gives

$$\frac{dy}{d\tau} = \frac{c}{a}y(x - 1)$$

setting $\mu = \frac{c}{a}$ the equation becomes $\frac{dy}{d\tau} = \mu y(x - 1)$ as desired

1.3 Conserved Quantity

Find a conserved quantity in terms of the dimensionless variables

Definiton: Conserved Quantity is a real-valued continuous function $E(x, y)$ that is constant along trajectories, i.e. $\frac{dE}{dt} = 0$, and nonconstant on every open set [2]

We solve for a conserved quantity by solving $\frac{dy}{dx}$ which will allow us to find quantities with zero total time derivatives. We accomplish this by separating the variables and then integrating both sides.

$$\frac{dy}{dx} = \frac{\mu y(x - 1)}{x(1 - y)} \Rightarrow \frac{(1 - y)dy}{\mu y} = \frac{(x - 1)}{x}$$

$$\begin{aligned}\frac{1}{\mu} \int \frac{1}{y} - 1 &= \int 1 - \frac{1}{x} \Rightarrow \frac{1}{\mu} (\ln |y| - y) + C_1 = x - \ln |x| + C_2 \\ \Rightarrow C &= x - \ln |x| - \frac{1}{\mu} (\ln |y| - y)\end{aligned}\tag{5}$$

Where C is a constant of integration. We see the right side of equation (5) is constant so the time derivative is zero proving it is a conserved quantity.

1.4 Linearization

Now let us study our dimensionless equations by first finding their fixed points.

Definition: Fixed point A fixed point is a point at which there is no flow, that is, a point (x^*, y^*) such that \dot{x} and $\dot{y} = 0$.

By setting the first equation equal to 0, we get

$$x' = x(1 - y) = 0$$

So possible solutions are $x^* = 0, y^* = 1$

By substituting $x^* = 0$ into the second equation we get

$$y' = -\mu y^* = 0$$

and so $y^* = 0$. By substituting $y^* = 1$ into the second equation we get

$$y' = \mu(x^* - 1) = 0$$

and so $x^* = 1$.

Thus, the fixed points are $(x^*, y^*) = (0, 0)$ and $(1, 1)$

We will now use the Jacobian matrix A to linearize the system and check the stability of the fixed points. Let $f(x, y) = x', g(x, y) = y'$

$$A = \begin{pmatrix} \frac{\partial f}{\partial x} & \frac{\partial f}{\partial y} \\ \frac{\partial g}{\partial x} & \frac{\partial g}{\partial y} \end{pmatrix}$$

$$\text{Then } A = \begin{pmatrix} (1 - y) & -x \\ \mu y & \mu(x - 1) \end{pmatrix}$$

Let τ represent the trace of A, Δ represent the determinant of A. Evaluating at the fixed points:

$$A|_{(0,0)} = \begin{pmatrix} 1 & 0 \\ 0 & -\mu \end{pmatrix}, \tau = 1 - \mu, \Delta = -\mu < 0 \text{ so } (0, 0) \text{ is a saddle.}$$

$$A|_{(1,1)} = \begin{pmatrix} 0 & -1 \\ \mu & 0 \end{pmatrix}, \tau = 0, \Delta = \mu > 0 \text{ so } (0, 1) \text{ is a center.}$$

Definition: Robust fixed point A fixed point whose stability is not altered by small nonlinearities.

Robust cases: *Repellers* (or *sources*), *Attractors* (or *sinks*), *Saddles*.

Marginal cases: *Centers*, *Higher-order and non-isolated fixed points*.

The result for $(0, 0)$ is robust, but the fixed point at $(1, 1)$ warrants closer examination.

First let us check that $(1, 1)$ is a critical point of

$$E(x, y) = x - \ln(x) - \frac{1}{\mu}(\ln(y) - y)$$

Definition: Critical point is a point (x, y) such that $\nabla E = (\frac{\partial E}{\partial x}, \frac{\partial E}{\partial y}) \equiv 0$

In this case, $\nabla E = (1 - \frac{1}{x}, -\frac{1}{\mu}(\frac{1}{y} - 1))$

$$\nabla E|_{(1,1)} = (0, 0)$$

So indeed, $(1, 1)$ is a critical point of E .

Theorem: Consider the system $\dot{x} = \mathbf{f}(\mathbf{x})$, where $\mathbf{x} = (x, y) \in \mathbf{R}^2$, and \mathbf{f} is continuously differentiable. Suppose there exists a conserved quantity $E(\mathbf{x})$ and that \mathbf{x}^* is an isolated fixed point. If \mathbf{x}^* is a local minimum of E , then all trajectories sufficiently close to \mathbf{x}^* are closed.

To check whether $(1, 1)$ is a minimum of E , we must calculate the Hessian matrix of E :

$$\mathbf{H}|_{(1,1)} = \begin{pmatrix} \frac{\partial^2 E}{\partial x^2} & \frac{\partial^2 E}{\partial x \partial y} \\ \frac{\partial^2 E}{\partial y \partial x} & \frac{\partial^2 E}{\partial y^2} \end{pmatrix}|_{(1,1)} = \begin{pmatrix} \frac{1}{x^2} & 0 \\ 0 & \frac{1}{\mu}(\frac{1}{y^2}) \end{pmatrix}|_{(1,1)} = \begin{pmatrix} 1 & 0 \\ 0 & \frac{1}{\mu} \end{pmatrix}$$

$(1, 1)$ is a local minimum of E if the determinant of the Hessian matrix evaluated at $(1, 1)$ is greater than 0 and the second partial derivative of E with respect to x is greater than 0.

$$\det \begin{pmatrix} 1 & 0 \\ 0 & \frac{1}{\mu} \end{pmatrix} = \frac{1}{\mu} > 0$$

$$\frac{\partial^2 E}{\partial x^2}|_{(1,1)} = 1 > 0$$

Indeed, $(1, 1)$ is a local minimum of E and so it satisfies the conditions of the theorem. Therefore, all trajectories sufficiently close to $(1, 1)$ are closed orbits. Finally, we can conclude that this model predicts cycles in the populations of both species.

Let us now examine a phase portrait of this system, which displays this cyclical behavior. We will study the behavior of this system only in the first quadrant, since it only make sense to study positive populations.

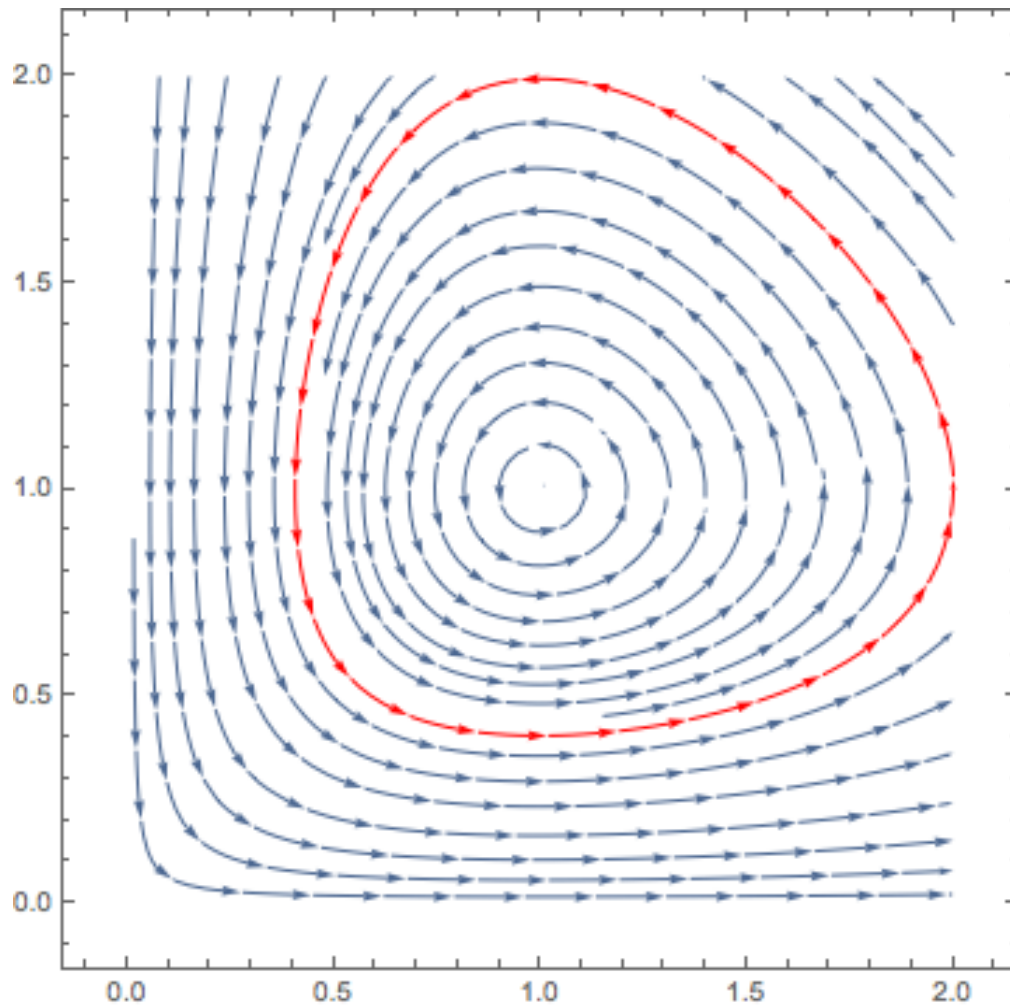


Figure 1

Indeed, as we previously calculated, the model predicts cycles in the populations of both species, with a center at $(1, 1)$. Thus this model predicts that neither population will ever die out, regardless of the initial conditions of the system.

One of the major drawbacks of this model is that solutions are not structurally stable. Pictured below is a graph of closed orbits that could be a potential solution to the Lotka Volterra model, taken from Murray (2002)

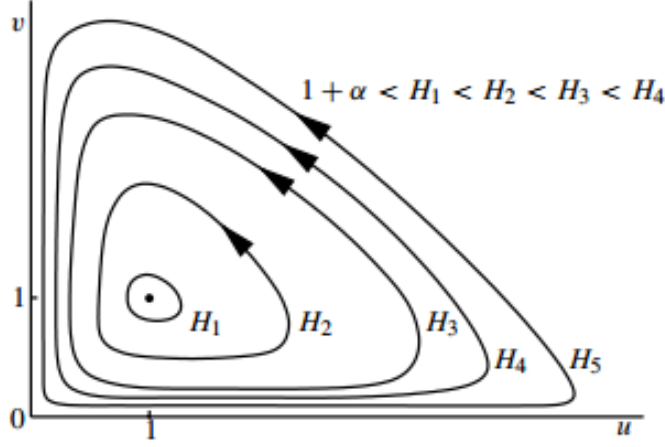


Figure 2

Suppose the initial conditions (u_0, v_0) are on the trajectory H_4 , which passes close to the axes. Any small perturbation near the axes will send the solution onto a trajectory that is not close to H_4 *everywhere*, and in fact a small perturbation may have a very large effect on the solution.

Another drawback we noted earlier is that according to this model, the rabbit population will grow unbounded in the absence of foxes. Suppose the population growth rates depend on both the rabbit and fox densities:

$$\dot{R} = Rf(R, F), \dot{F} = Fg(R, F)$$

Instead of $\dot{R} = aR - bRF$, a better approximation of the rabbit population might use logistic growth to model the rabbit population, such as

$$f(R, F) = a\left(1 - \frac{R}{K}\right) - Fh(F)$$

so that in the absence of foxes, the rabbit population will grow logistically.

In this modified equation, $h(F)$ is the **predation term**, or the function response of the predator to changes in prey density. We want this predation term to show some saturation effect, or to limit towards some number as the prey population approaches infinity. Some possible predation terms are

$$h(F) = \frac{A}{R+B}, \quad h(F) = \frac{A[1 - e^{-aR}]}{R}$$

where A, B , and a are positive constants.

Similarly, rather than modeling the fox population with $\dot{F} = -cf + dRF$, it would be more accurate to use a logistic model. One such possible form is

$$\dot{F} = Fg(R, F), \quad g(R, F) = k\left(1 - \frac{hF}{R}\right)$$

With this modified system of equations, oscillations in the model can go into a stable limit cycle oscillation.

Definition: Limit cycle solution is a closed trajectory in the predator-prey space that is not a member of a continuous family of closed trajectories, such as the solutions to our original model (Figure 1).

A **stable** limit cycle trajectory is such that any small perturbation from the trajectory decays to zero.

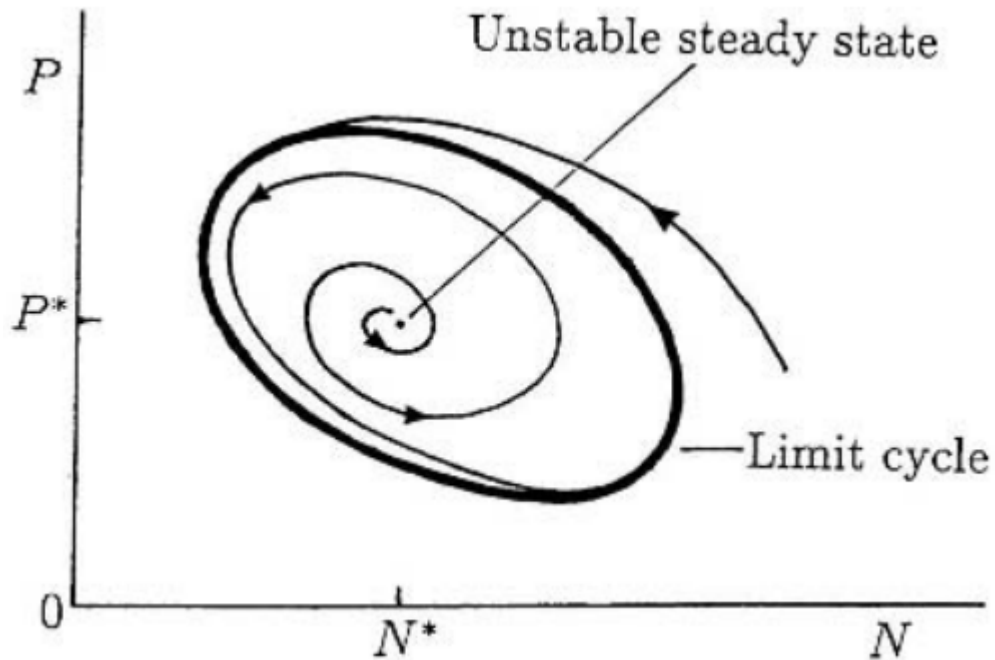


Figure 3

Figure 3 [1] above shows a typical closed predator-prey trajectory with a limit cycle. N refers to the prey and P refers to the predators. Any perturbation from the limit cycle decays to zero. This remedies the previous model's problem of small perturbations leading to large discrepancies in the solution.

1.5 Appendix

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(* The following mathematica code solves for the fixed points of the system and creates
a phase portrait for each one *)
CritPoints = Solve[{x (1 - y) == 0, y (x - 1) == 0}, {x, y}];
Clear[f, J, x, y]
f[x_, y_] := {x (1 - y), y (x - 1)}
J[f_] := Module[{A = Table[0, 2, 2]}, A[[1, 1]] = D[f[x, y][[1]], {x}];
  A[[1, 2]] = D[f[x, y][[1]], {y}];
  A[[2, 1]] = D[f[x, y][[2]], {x}];
  A[[2, 2]] = D[f[x, y][[2]], {y}];
  Return[A]
For[i = 1, i <= Length[CritPoints], i++, A1 = J[f] /. Flatten[CritPoints][[i]];
  f1[x_, y_] = A1[[1, 1]] x + A1[[1, 2]] y;
  g1[x_, y_] = A1[[2, 1]] x + A1[[2, 2]] y;
  Print[StreamPlot[{f1[x, y], g1[x, y]}, {x, -5, 5}, {y, -5, 5}, StreamScale -> Automatic,
    StreamPoints -> {{{2, 1}, Red}, Automatic}]]]
StreamPlot[{x (1 - y), y (x - 1)}, {x, 0, 2}, {y, 0, 2}, StreamScale -> Automatic,
  StreamPoints -> {{{2, 1}, Red}, Automatic}]
```

1.6 References

- [1] Murray, J. D. *Mathematical Biology: I. An Introduction, Third Edition*. 3rd ed. Vol. 17. Berlin: Springer-Verlag, 2003. Print. pg. 79-93.

- [2] Strogatz, Steven H. *Nonlinear Dynamics and Chaos: With Applications to Physics, Biology, Chemistry, and Engineering*. 2nd ed. Boulder, CO: Westview, a Member of the Perseus Group, 2015. Print.