Student Project: An Adaptive Predator-prey System

A simple **predator-prey model** can be written in normalized form as

$$\begin{aligned} N_1'(t) &= N_1(t)\left(1 - \frac{N_1(t)}{K} - c_{12}N_2(t)\right) \\ N_2'(t) &= N_2(t)\left(-r + c_{21}N_1(t)\right); \end{aligned} \tag{1}$$

where $N_1(t)$ and $N_2(t)$ are the sizes of the prey and predator populations, respectively, at time t. The constant K is the carrying capacity of the prey and r is the normalized death rate of the predator, assuming the prey's growth rate is $b = 1$. The term $c_{21}N_1N_2$ represents the gain in the growth rate of the predator due to its interaction with the prey, and $c_{12}N_1N_2$ is the corresponding loss in the growth rate of the prey. The constants c_{12} and c_{21} take into account the difference in the mean weight between the two species. For a really nice introduction to this model see Section 6.2 in [4].

Problem 1. Write system (1) in the form

$$\begin{aligned} N_1' = N_1 - \frac{(N_1)^2}{K} - c_{12}N_1N_2 &\equiv F(N_1, N_2) \\ N_2' = -rN_2 + c_{21}N_1N_2 &\equiv G(N_1, N_2), \end{aligned} \tag{2}$$

and compute the Jacobian matrix $J(N_1, N_2) = \begin{pmatrix} \frac{\partial F}{\partial N_1} & \frac{\partial F}{\partial N_2} \\ \frac{\partial G}{\partial N_1} & \frac{\partial G}{\partial N_2}. \end{pmatrix}$.

Problem 2. Show that the only points (N_1, N_2) where F and G are simultaneously equal to zero are $(0,0), (K,0)$, and $P = \left(\frac{r}{c_{21}}, \frac{Kc_{21}-r}{Kc_{12}c_{21}}\right)$. This means that if $K > \frac{r}{c_{21}}$, the system (1) will have three equilibrium solutions in the positive quadrant.

Problem 3. Use the Jacobian found in Problem 1 to show that $(0,0)$ is always a saddle point, and that if $K > \frac{r}{c_{21}}$ then $(K,0)$ is also a saddle point. What type of equilibrium is $(K,0)$ if $K < \frac{r}{c_{21}}$. Note that in this case, the point K is no longer in the positive quadrant.

Problem 4. If $K > \frac{r}{c_{21}}$, show that the interior critical point P is asymptotically stable. For what value of r does it bifurcate between a spiral sink and a sink?

The figure below shows a phase plane for the system (1), with parameters $r = 0.2, K = 10, c_{12} = 0.45$ and $c_{21} = 0.2$. In this particular case, all of the solutions with positive initial values converge to the interior critical point $P = (1,2)$ where the two populations coexist. With the above parameter values P can be clearly seen to be a *spiral* sink.

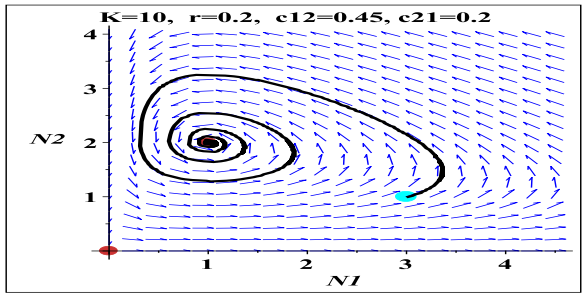

Figure 1: Trajectory of the predator-prey system starting at $N_1(0) = 3, N_2(0) = 1$.

Suppose it is known that increased interaction with the prey improves the predator's hunting ability; that is, the predator is able to adapt its behavior, or "learn". It seems logical to hypothesize that in this case the value of c_{12} and c_{21} should also be proportional to the amount of past interaction between the two species. The more contact the predators have had with the prey over the recent past, the more successful they should be at capturing them. One way to compute an average of past interaction is to use an integral with an *averaging kernel* k_T, and write:

$$\text{average interaction over the past} = \int_{-\infty}^{t} k_T(t-u)N_1(u)N_2(u)du,$$

where the averaging kernel $k_T(t)$ is a positive function on $(0, \infty)$ satisfying

$$\int_0^\infty k_T(u)du = 1 \text{ and } \int_0^\infty uk_T(u)du = T.$$

We will use the simplest averaging kernel of this type: $k_T(t) = \frac{1}{T}e^{-t/T}$. The larger the value of T, the longer the time period over which the adaptation takes place. A large negative exponent $-\frac{1}{T}$, with T small, makes the average more dependent on the *recent* past.

We will define an **adaptive predator-prey system**:

$$\begin{aligned} N_1'(t) &= N_1(t)\left(1 - \frac{N_1(t)}{K} - b_{12}N_2(t)\int_{-\infty}^{t} k_T(t-u)N_1(u)N_2(u)du\right) \\ N_2'(t) &= N_2(t)\left(-r + b_{21}N_1(t)\int_{-\infty}^{t} k_T(t-u)N_1(u)N_2(u)du\right); \end{aligned} \tag{3}$$

where the constants b_{12} and b_{21} are, respectively, the constants c_{12} and c_{21} each divided by the product of N_1 and N_2 at the interior critical point P. This serves to keep

the interior critical point the same for both the adaptive system and the nonadaptive system, so that the approach to the equilibrium can be compared.

Note that by defining a new function

$$Z(t) = \int_{-\infty}^{t} k_T(t-u) N_1(u) N_2(u) du,$$

we can write (3) as a system of three ordinary differential equations:

$$\begin{aligned} N_1'(t) &= N_1(t)\left(1 - \frac{N_1(t)}{K} - \frac{c_{12}}{n_1 n_2} N_2(t) Z(t)\right) \\ N_2'(t) &= N_2(t)\left(-r + \frac{c_{21}}{n_1 n_2} N_1(t) Z(t)\right) \\ Z'(t) &= \frac{1}{T}(N_1(t)N_2(t) - Z(t)); \end{aligned} \tag{4}$$

where we have used the product rule to differentiate the function $Z(t)$.

Problem 5. With $k_T(t) = \frac{1}{T} e^{-t/T}$, use the product rule for differentiation, and the fundamental theorem of calculus, to show that

$$Z'(t) = \frac{d}{dt}\left(\frac{1}{T} e^{-t/T} \int_{-\infty}^{t} e^{u/T} N_1(u) N_2(u) du\right) = \frac{1}{T}(N_1(t)N_2(t) - Z(t)).$$

At any equilibrium point (N_1, N_2, Z) of (4) the value of the integral $Z(t)$ remains constant at $N_1 \times N_2$. This means that if $(n_1, n_2, n_1 n_2)$ is an *interior* equilibrium, n_1 and n_2 must satisfy the two equations

$$1 - \frac{n_1}{K} - c_{12} n_2 = 0 \text{ and } -r + c_{21} n_1 = 0;$$

that is, $n_1 = \frac{r}{c_{21}}$ and $n_2 = \frac{1}{c_{12}}\left(1 - \frac{r}{c_{21} K}\right)$.

Problem 6. Writing the system (4) as

$$\begin{aligned} N_1' = F(N_1, N_2, Z) &= N_1 - \frac{N_1^2}{K} - \frac{c_{12}}{n_1 n_2} N_1 N_2 Z \\ N_2' = G(N_1, N_2, Z) &= -r N_2 + \frac{c_{21}}{n_1 n_2} N_1 N_2 Z \\ Z' = H(N_1, N_2, Z) &= \frac{1}{T}\left(N_1 N_2 - Z\right), \end{aligned} \tag{5}$$

find the Jacobian. It will be a 3×3 matrix containing the partial derivatives of F, G, and H with respect to each of the three variables N_1, N_2, and Z.

A point (x, y, z) in $\mathbf{R}^3$ will be a critical point for the adaptive system iff $F(x, y, z) = G(x, y, z) = H(x, y, z) = 0$.

Problem 7. Show that the critical points of (4) are $(0, 0, 0), (K, 0, 0)$, and $P = \left(\frac{r}{c_{21}}, \frac{Kc_{21}-r}{Kc_{12}c_{21}}, \frac{r}{c_{21}}\frac{Kc_{21}-r}{Kc_{12}c_{21}}\right)$.

FROM HERE ON THE CONSTANTS WILL HAVE VALUES:

$$K = 10, \;\; r = 0.2, \;\; c_{12} = 0.45, \;\; c_{21} = 0.2.$$

Using these values, we will try to compare the *rate of approach* of solutions of the adaptive and non-adaptive systems to the interior critical point P, where $N_1 = 1$ and $N_2 = 2$. Remember that Z approaches the value $N_1 N_2$ as the trajectory approaches P. Figure (1) shows a trajectory of the non-adaptive system (with the above parameters) starting at the initial point $(3.0, 1.0)$ in the phase plane.

Check, using your solution to Problem 1, that the Jacobian for the non-adaptive system at the interior critical point $P = (n_1, n_2)$ will be

$$J(n_1, n_2) \equiv J(1, 2) = \begin{pmatrix} -\frac{n_1}{K} & -c_{12}n_1 \\ c_{21}n_2 & -r + c_{21}n_1 \end{pmatrix} = \begin{pmatrix} -0.1 & -0.45 \\ 0.4 & 0 \end{pmatrix};$$

therefore, the *characteristic polynomial* at P is

$$det(\lambda \mathbf{I} - \mathbf{J}) = det \begin{pmatrix} \lambda + 0.1 & 0.45 \\ -0.4 & \lambda \end{pmatrix} = \lambda^2 + 0.1\lambda + 0.18.$$

The eigenvalues (roots of the characteristic polynomial) are

$$\lambda \approx -0.05 \pm 0.4213\imath.$$

Close to the equilibrium point P, the non-adaptive system is approximated by the linear system with matrix J, so the solutions are given approximately by

$$\begin{pmatrix} N_1(t) \\ N_2(t) \end{pmatrix} = \begin{pmatrix} 1 \\ 2 \end{pmatrix} + \alpha_1 e^{\lambda_1 t}\vec{\mathbf{v}}_\mathbf{1} + \alpha_2 e^{\lambda_2 t}\vec{\mathbf{v}}_\mathbf{2}$$

where $(\lambda_i, \vec{\mathbf{v}}_\mathbf{i}), i = 1, 2$ are the two eigenpairs of $\mathbf{J}$ and α_1 and α_2 are constants. If both of the eigenvalues have negative real parts, we will define the **rate of approach to P for the non-adaptive system** to be $\max_{i=1,2}(Re(\lambda_i))$. Note that the closer the

negative real part of the eigenvalues is to zero, the more slowly the solution will approach P. In this case the trajectories will approach P at an exponential rate of $e^{-0.05t}$ when they are very close to P. It can also be seen that they spiral with a semi-period of $\frac{2\pi}{0.4213} \approx 15$ when they are close to P. The figure below shows a graph of the functions $N_1(t)$ and $N_2(t)$ starting from the initial point $(N_1(0), N_2(0)) = (3, 1)$.

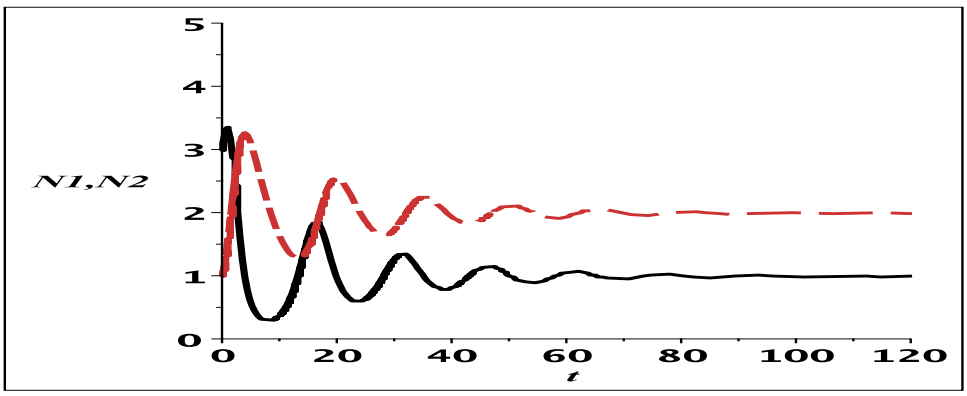

Figure 2: The functions $N_1(t)$ and $N_2(t)$ (dashed) as t goes from 0 to 120.

For the adaptive system we can do the same thing, using the Jacobian found in Problem 6:

$$J(n_1, n_2, n_1 \cdot n_2) = \begin{pmatrix} -\frac{n_1}{K} & -c_{12}n_1 & -c_{12} \\ c_{21}n_2 & 0 & c_{21} \\ \frac{n_2}{T} & \frac{n_1}{T} & -\frac{1}{T} \end{pmatrix} = \begin{pmatrix} -0.1 & -0.45 & -0.45 \\ -0.4 & 0 & 0.2 \\ \frac{2}{T} & \frac{1}{T} & -\frac{1}{T} \end{pmatrix}.$$

If the real parts of the three eigenvalues are all negative we will define the **rate of approach to P for the adaptive system** to be $\max_{i=1,2,3}(Re(\lambda_i))$.

This is a problem where you really want to have a CAS to find eigenpairs for a given matrix. In Maple, the instructions

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with(LinearAlgebra):
A:=<<a11,a21,a31>|<a12,a22,a32>|<a13,a23,a33>>:
v,e:=Eigenvectors(A);
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will return the three eigenpairs of the matrix $\mathbf{A}$. Be sure to notice that the matrix $\mathbf{A}$ is entered in **column** form.

In the adaptive case, the characteristic polynomial at P will be equal to

$$det(\mathbf{J} - \lambda\mathbf{I}) = det \begin{pmatrix} -0.1-\lambda & -0.45 & -0.45 \\ -0.4 & -\lambda & 0.2 \\ \frac{2}{T} & \frac{1}{T} & -\frac{1}{T}-\lambda \end{pmatrix},$$

and it will be a cubic polynomial in λ. Expand the matrix by cofactors and show that the characteristic polynomial is:

$$-p(\lambda) = \lambda^3 + \left(0.1 + \frac{1}{T}\right)\lambda^2 + \left(0.18 + \frac{0.8}{T}\right)\lambda + \frac{0.52}{T}. \tag{6}$$

Letting $f(\lambda) = -p(\lambda)$, we want to determine when the real part of each of the three roots is negative. If that is true then trajectories that start close enough to P will tend to P as $t \to \infty$. The cubic will either have three real roots or one real root and two complex conjugate roots. Note that there can be no positive real roots because all of the terms in the cubic are positive if $\lambda > 0$.

There is a standard test to determine which of the two cases will occur. If we write

$$f(\lambda) = \lambda^3 + p\lambda^2 + q\lambda + r,$$

and substitute $\lambda = x - \frac{p}{3}$, the cubic reduces to the form

$$x^3 + ax + b,$$

with the x^2 term missing. The new coefficients are

$$a = \frac{1}{3}(3q - p^2) \text{ and } b = \frac{1}{27}(2p^3 - 9pq + 27r).$$

It can then be shown that there will be three real roots iff $\frac{b^2}{4} + \frac{a^3}{27} \leq 0$. Since $b^2 > 0$, this can only occur if $a < 0$. The value of a in (6) is

$$a = q - \frac{p^2}{3} = \left(0.18 + \frac{0.8}{T}\right) - \frac{1}{3}\left(0.1 + \frac{1}{T}\right)^2 \approx 0.17667 + \frac{0.7333}{T} - \frac{0.3333}{T^2}$$

and this is positive at least if $T > 0.42$. So for all $T > 0.42$ we can assume that the characteristic polynomial has one negative real root and a pair of complex conjugate roots $\alpha \pm \beta\imath$. This means that the only way the critical point P can lose stability is if the real part α of the complex roots becomes positive.

Writing the cubic as a product of its factors,

$$\lambda^3 + p\lambda^2 + q\lambda + r = (\lambda - \lambda_1)(\lambda - \lambda_2)(\lambda - \lambda_3),$$

it is easily seen that the coefficient of λ^2 is $p = -(\lambda_1 + \lambda_2 + \lambda_3)$. Letting λ_1 and λ_2 be the complex roots $\alpha \pm \beta\imath$, and $\lambda_3 = c$, we see that

$$\lambda_1 + \lambda_2 + \lambda_3 = 2\alpha + c = -(0.1 + \frac{1}{T}) \rightarrow \alpha = \frac{-0.1 - \frac{1}{T} - c}{2}.$$

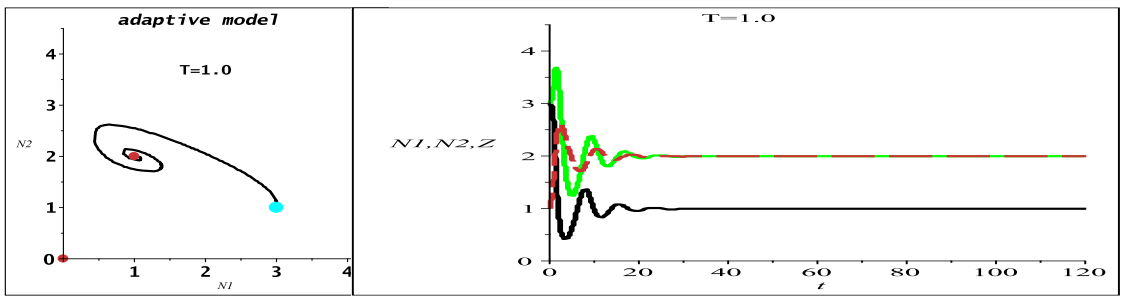
This means that α will be negative as long as $c > -\left(0.1 + \frac{1}{T}\right)$.

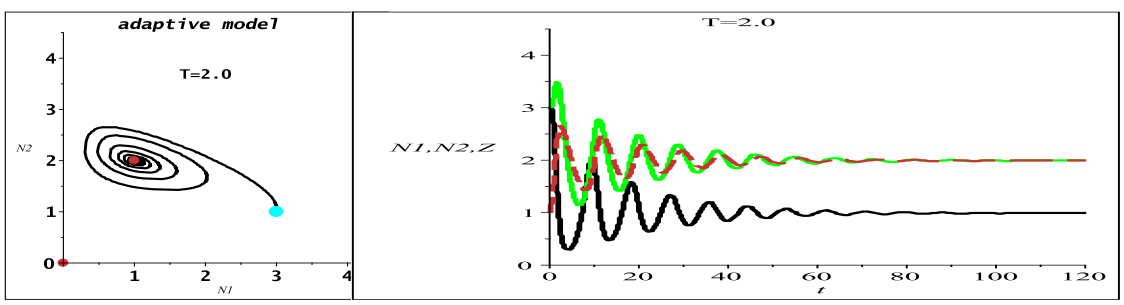
For several values of T, the table below shows the roots of (6) together with the value of $-0.1 - \frac{1}{T}$. It appears that a bifurcation occurs for $T \approx 4.444$. At the critical point P the real part of the complex roots becomes positive, and the point P is no longer asymptotically stable.

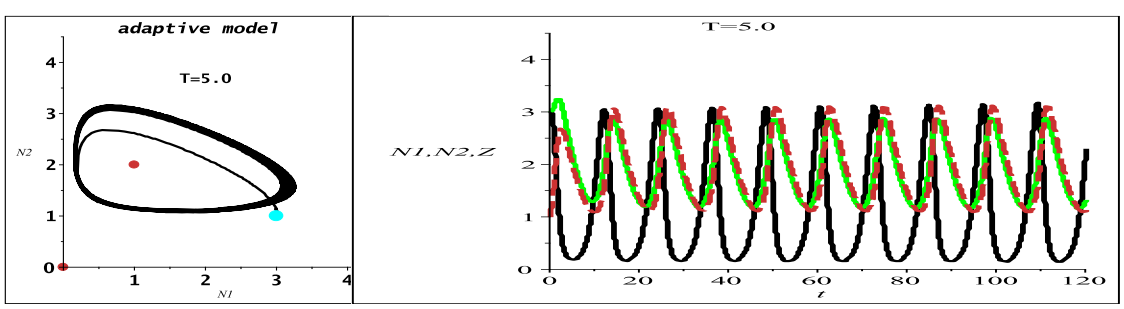
T	$\alpha \pm \beta\imath$	**c**	$-(0.1 + \frac{1}{T})$
0.1	$-0.4106 \pm 0.6259\imath$	-9.2788	-10.1
0.2	$-0.4188 \pm 0.6592\imath$	-4.2624	-5.1
0.5	$-0.3738 \pm 0.7933\imath$	-1.3524	-2.1
1.0	$-0.1841 \pm 0.8226\imath$	-0.7318	-1.1
2.0	$-0.0535 \pm 0.7242\imath$	-0.4931	-0.6
4.0	$-0.0030 \pm 0.6148\imath$	-0.3440	-0.36
4.444	$-2 * 10^{-6} \pm 0.6000\imath$	-0.3250	-0.3250
5.0	$0.0023 \pm 0.5843\imath$	-0.3046	-0.3

On the next page trajectories for $T = 1, 2,$ and 5 are shown, both in the (N_1, N_2)-plane and as time series $N_1(t), N_2(t)$, and $Z(t)$ over the t-interval $(0, 120)$. It seems clear that the populations move most quickly to the stable critical point when the time constant T is small. This suggests that quick adaptation is most effective at ending the cyclical behavior. With adaptation averaged over a long time period it appears that the populations enter into some type of long-term cyclical behavior.

For $T = 1, 2$, and 5, the figures below show the trajectory in the (N_1, N_2)-plane, together with graphs of $N_1(t), N_2(t)$, and $Z(t)$ over the t-interval $(0, 120)$. The dark curve is $N_1(t)$, the dashed (orange) curve is $N_2(t)$, and the light (green) curve is $Z(t)$. The initial conditions in each case are $N_1(0) = 3, N_2(0) = 1$, and $Z(0) = N_1(0) \cdot N_2(0) = 3$.







TOPICS FOR FURTHER STUDY

1. How does the value of the death rate r of the predator effect the behavior? If r is very small, the predators' average life span will be long, and they will be able to adapt over a longer time period. Changing r also changes the location of the critical point P, so you will need to recompute the nonadaptive system for different values of r in order to do a comparison.

2. How does the value of the carrying capacity K effect the behavior of the populations? Note that changing K also changes the location of the critical point P.

3. The cyclical trajectory observed in the adaptive model when $T \approx 4.444$ may be an example of a **Hopf bifurcation**. Learn everything you can about Hopf bifurcations and then see if you can prove that one occurs in this model.

4. Does the same type of bifurcation occur as the parameter r is varied?

References

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