CHAPTER 3

Nonlinear Models of Interactions

3.1. A Simple Predator–Prey Model

3.1.1. The prey population peaks first, with the predator population peaking slightly later. Similarly, the prey population bottoms out slightly before the predator population. This is biologically reasonable, since when the prey population peaks, there will be a slight time lag as the predator population grows to its peak through consuming the prey. Any changes in prey population size should be reflected in the predator population size slightly later.

3.1.2. a. The peaks on the graph of $P_t = \cos t$ lead those on the graph of $Q_t = \sin t$ (by a time interval of $\pi/2$), similar to those of the prey and predator.

b. The plotted points lie on a circle centered at the origin, starting on the x-axis when $t = 0$ and proceeding counterclockwise around the circle.

c. Because the oscillations in the first figure get smaller as time increase (i.e., they are damped), the spiral in the second figure goes inward.

3.1.3. For increased s, the equilibrium value of the prey, P^*, appears unchanged, though that of the predator, Q^*, is reduced. Since larger s means the predator-prey interaction is harming the prey population more, this is a bit surprising, since the prey population size is all that is ultimately reduced. On further reflection, this is not unreasonable biologically, as a result of 'feedback' to the predator.

As v is increased, the equilibrium P^* is reduced, and Q^* increased. Since larger v means the prey benefits more from the predator-prey interaction, it is reasonable that Q^* would be larger, resulting in smaller P^*.

3.1.4. The effect of increasing s and v on the stable equilibrium is discussed in the last problem, so here we describe only the movement toward or away from the equilibrium.

If s or v is increased by a small amount, simulations often show qualitatively-similar damped oscillations of populations toward an equilibrium, with counterclockwise motion in the phase plane. If either parameter is increased excessively, orbits become more likely to leave the phase plane, signifying extinction. This is reasonable since increasing either of the parameters increases the effect of the predator-prey interaction, which seems likely to destabilize things. Large increases in the parameters can also lead to growing population oscillations (still with counterclockwise orbits), which also result in ultimate extinction.

3.1.5. The oscillatory behavior appears for most values of r, indicating their origin in the predator-prey interaction. For instance, when $r = .3$, which would not produce oscillations in the one-population logistic model, the predator-prey oscillations seem to take even longer to damp out than for the original value of r.

3.1.6. With the other parameters as in the text, $r = 2.1$ results in what appears to be a stable equilibrium, despite the fact that in the logistic model it leads to a 2-cycle. This illustrates that a predator-prey interaction can have a stabilizing effect on otherwise complex dynamics. A real-world example of this involves deer populations and hunters. (Can you find parameter values for which the logistic model is chaotic, yet the predator-prey model has an apparently stable equilibrium?)

3.1.7. The parameter w represents the size of the prey population that can be protected in the refuge. If $P > w$, then $P - w$ is the part of the prey population not in the refuge, which is therefore subject to the predator-prey interaction. The given interaction terms thus describe the predation appropriately. If $P < w$, however, the terms are not correct. Replacing the $P - w$ with $\max(0, P - w)$ would be better.

3.1.8. The introduction of a refuge typically results in a larger equilibrium value of the prey. If the refuge is small, the equilibrium value for the predator may increase. For a larger refuge, typically the equilibrium value of the predator is reduced. Oscillations may also tend to damp out faster. Using the model parameters of the text with $w = 0, .1, .2, .3$ gives good examples. Be careful to only consider orbits where P stays larger than w.

3.1.9. $P(1 - e^{-vQ})$, $\sqrt{PQ}$, and $P + Q$ all increase if either P or Q is increased. Only the first two of these are reasonable as interaction terms, though, since the there is no interaction between P and Q in $P + Q$.

3.1.10. In the absence of predators ($Q = 0$), this is the Ricker model of the prey. In the absence of prey ($P = 0$), the predators immediately die out. The factor e^{-sQ} in the formula for P is 1 when $Q = 0$ and decreases if Q is increased. Thus the larger Q_t is, the more this factor shrinks the size of P_{t+1}, as predation should. The factor $(1 - e^{-vQ})$ in the formula for Q is 0 when $P = 0$ and increases toward 1 as Q is increased. Thus Q_{t+1} will be larger for larger Q_t and fixed P_t, but will never exceed uP. This means the predator population can be at most a constant multiple of the prey population. These modeling equations are probably more reasonable in most situations than those used in the text, but they are a bit more complicated to analyze.

3.1.11. Behavior is qualitatively similar to model of text, at least for some parameter values (e.g., $r = 1.3$, $K = 1$, $s = .5$, $u = 5$, $v = 1.6$). Varying parameters produces interesting, yet reasonable results (e.g., changing to $s = 1.5$).

3.2. Equilibria of Multipopulation Models

3.2.1. If $u/v = 1$, the vertical line of the Q-nullcline joins the sloping line of the P-nullcline on the P-axis at $P = 1$. Then the only equilibria are $(0,0)$ and $(1,0)$. If $u/v > 1$, the vertical line lies even further to the right, and intersects the sloping line below the P-axis. The resulting equilibrium has $Q^* < 0$, so $(0,0)$ and $(1,0)$ are the only two biologically meaningful equilibria..

3.2.2. By problem 3.2.1, we need only discuss situations with $u/v < 1$. If u is increased, or v is decreased, the vertical line in the Q-nullcline moves right, causing the equilibrium at the intersection of it and the sloping line to move right and down. Thus P^* increases and Q^* decreases. Since increasing u means the predator dies more quickly, and decreasing v means the predator benefits

less from the predator-prey interaction, it is biologically reasonable that Q^* should decrease and therefor P^* should increase.

3.2.3. The nullclines are described in problem 3.2.1. For both $u/v = 1$ and $u/v > 1$ the region under the sloping line should have arrows pointing down and to the right. The region to the right of the vertical line should have arrows pointing up and to the left. The remaining region should have arrows pointing down and to the left. MATLAB experiments confirm this.

3.2.4. a. Yes; b. Yes, interpreting $\Delta P = 0$ as meaning the orbit must move vertically up or down; c. Yes, interpreting $\Delta Q = 0$ as meaning the orbit must move horizontally left or right; In (b) and (c), note that when an orbit jumps over a nullcline, the lines drawn don't change direction until they get to the next population values.

3.2.5. a. Pick a point with P and Q both large, then $1 - P < 0$, so $rP(1 - P) < 0$ and $-sPQ < 0$, so $\Delta P = rP(1 - P) - sPQ < 0$. Thus arrows point left.
b. Pick a point with P very small, so $-u + vP < 0$ and $\Delta Q = Q(-u + vP) < 0$. Thus arrows point down.
c. Pick a point with P very large, so $-u + vP > 0$ and $\Delta Q = Q(-u + vP) > 0$. Thus arrows point up.

3.2.6. a. The P-nullcline is composed of the Q-axis ($P = 0$) and the line $Q = (-r/sK)P + r/s$. The Q-nullcline is given by the P-axis ($Q = 0$) and $P = Q/(u(1 - e^{-vQ}))$, which can be graphed by computer for specific values of u and v, or analyzed using calculus. This last curve approaches the P-axis at $1/uv$, moving upward and to the right (concave down) , and is asymptotic to $Q = uP$ for large P and Q. For $1/uv < K$, the nullclines and direction arrows produce a figure qualitatively like Figure 3.4, with the vertical line replaced by one curving to the right.
b. Two equilibria are $(0,0)$, and $(K,0)$. Assuming $1/uv < K$, there is a third biologically meaningful one that is the solution to the two equations $Q = (-r/sK)P + r/s$ and $P = Q/(u(1 - e^{-vQ}))$. While these can be solved numerically for specific values of the parameters, there is not a simple formula for the solution.

3.2.7. a. Both predator and prey are follow the logistic model in the absence of the other, but the extra terms mean the predator benefits and prey is harmed from the predator-prey interaction.
b. The P-nullcline is as in Figure 3.4. The Q-nullcline is the P-axis ($Q = 0$) together with the line $P = (u/v)(Q - 1)$ which goes through $(0,1)$ and slopes upward. If $r/s > 1$, the two sloping lines of the nullclines intersect, and produce four regions. If $r/s \leq 1$, there are only three regions. Below $P = (u/v)(Q - 1)$ arrows point up; above it they point down. Above the line $Q = (r/s)(1 - P)$ arrows point to the left; below it they point to the right.
c. Equilibria are at $(0,0)$, $(1,0)$ and $((r - s)u/(ru + vs), (u + v)r/(ru + vs))$. The third equilibrium is only biologically meaningful if $r/s > 1$.
d. For $r/s > 1$ you might expect orbits to move counterclockwise around the third equilibrium, provided they begin close enough to it. Whether they spiral inward or outward is not yet clear.

3.3. Linearization and Stability

3.3.1. At $(0,0)$, linearization produces $\begin{pmatrix} p_{t+1} \\ q_{t+1} \end{pmatrix} \approx \begin{pmatrix} 2.3 & 0 \\ 0 & .3 \end{pmatrix} \begin{pmatrix} p_t \\ q_t \end{pmatrix}$. The eigenvalues are 2.3 and .3, so the equilibrium is a saddle and unstable. This is biologically reasonable, since small prey populations with no predators will move away from this equilibrium, while small predator populations with no prey will move toward it.

At $(1,0)$, $\begin{pmatrix} p_{t+1} \\ q_{t+1} \end{pmatrix} \approx \begin{pmatrix} -.3 & -.5 \\ 0 & 1.9 \end{pmatrix} \begin{pmatrix} p_t \\ q_t \end{pmatrix}$. The eigenvalues are $-.3$ and 1.9, so the equilibrium is a saddle and unstable. This is biologically reasonable since if there are no predators, we expect a nearby orbit to move toward this equilibrium, while if there are some predators, it might move away.

Numerical experiments confirm these results.

3.3.2. a. Equilibria are $(0,0)$, $(1,0)$, and $(.05, .19)$.

b. The first two appear to be saddles (so unstable) and the last as unstable.

c. Linearization at $(0,0)$ produces $\begin{pmatrix} p_{t+1} \\ q_{t+1} \end{pmatrix} \approx \begin{pmatrix} 1.8 & 0 \\ 0 & .9 \end{pmatrix} \begin{pmatrix} p_t \\ q_t \end{pmatrix}$. The eigenvalues are 1.8 and .9, so the equilibrium is a saddle and unstable.

Linearization at $(1,0)$ produces $\begin{pmatrix} p_{t+1} \\ q_{t+1} \end{pmatrix} \approx \begin{pmatrix} .2 & -4 \\ 0 & 2.9 \end{pmatrix} \begin{pmatrix} p_t \\ q_t \end{pmatrix}$. The eigenvalues are .2 and 2.9, so the equilibrium is a saddle and unstable.

Linearization at $(.05, .19)$ produces $\begin{pmatrix} p_{t+1} \\ q_{t+1} \end{pmatrix} \approx \begin{pmatrix} .96 & -.2 \\ .38 & 1 \end{pmatrix} \begin{pmatrix} p_t \\ q_t \end{pmatrix}$. The eigenvalues are $.98 \pm \sqrt{.0756}i$, with absolute value approximately 1.0178, so the equilibrium is unstable.

3.3.3. a. Equilibria are $(0,0)$, $(1,0)$, and $(1.167, -2.667)$, so only the first two are biologically meaningful.

b. The first appears to be a saddle (so unstable) and the second appears to be stable.

c. Linearization at $(0,0)$ produces $\begin{pmatrix} p_{t+1} \\ q_{t+1} \end{pmatrix} \approx \begin{pmatrix} 2.6 & 0 \\ 0 & .3 \end{pmatrix} \begin{pmatrix} p_t \\ q_t \end{pmatrix}$. The eigenvalues are 2.6 and .3, so the equilibrium is a saddle and unstable.

Linearization at $(1,0)$ produces $\begin{pmatrix} p_{t+1} \\ q_{t+1} \end{pmatrix} \approx \begin{pmatrix} -.6 & -.1 \\ 0 & .9 \end{pmatrix} \begin{pmatrix} p_t \\ q_t \end{pmatrix}$. The eigenvalues are $-.6$ and .9, so the equilibrium is stable.

3.3.4. The surface of a bump, or mountain top, with the high point being the unstable equilibrium; the surface of a bowl or depression, withe the low point being the stable equilibrium.

3.3.5. Substituting $P_t = P^{\#} + p_t$ and $Q_t = Q^{\#} + q_t$ into the model equations, and then discarding all terms of degree greater than 1, leaves both constant terms and terms of degree 1. The constants prevent the model from being expressed as a simple matrix equation. Rather than getting a linear approximation, we get an affine one.

3.3.6. a. Initial populations of the form $(P_0, 0)$, with P_0 small, will move away from the origin, since in the absence of predators, the prey behaves logistically. Initial populations of the form $(0, Q_0)$ will move toward the origin, since in the absence of prey, the predators will die out. Thus the origin must be a saddle equilibrium.