

17 Predator-Prey Models

The logistic growth model (Chapter 11) focused on a single population. Moving beyond that one-dimensional model, we now consider the growth of two interdependent populations. Given two species of animals, interdependence might arise because one species (the “prey”) serves as a food source for the other species (the “predator”). Models of this type are thus called *predator-prey* models. While social scientists are primarily interested in human populations (in which interdependence hopefully takes other forms), there are several reasons for studying predator-prey models. Mathematically, some versions of this model generate *limit cycles*, an interesting type of equilibrium sometimes observed in dynamical systems with two (or more) dimensions. Substantively, given reinterpretation of the state variables, predator-prey models have a variety of useful social science applications. Finally, as we’ll see in Chapter xx, there is a deep mathematical connection between predator-prey models and the replicator dynamics of evolutionary game theory.

17.1 Logistic growth with a predator

We begin by introducing a predator population into the logistic growth model. Now that there are two species, we let P denote the size of the prey population, and Q denote the size of the predator population. The growth rate of the prey population is determined by the equation

$$\frac{\Delta P}{P} = r \left(1 - \frac{P}{K} \right) - s Q$$

where r , s , and K are parameters. In the absence of predators (when $Q = 0$), the growth of the prey population thus follows the logistic model (with K again interpreted as the carrying capacity of the environment). However, as indicated by the second term on the right-hand side of the equation, the prey growth rate falls as the predator population becomes larger. In turn, the growth rate of the predator population is determined by the equation

$$\frac{\Delta Q}{Q} = -u + v P$$

where u and v are parameters. In the absence of prey (when $P = 0$), the predator population would shrink at rate u . However, as indicated by the second term, the predator growth rate rises as the prey population becomes larger. We thus obtain the two-equation system

$$\begin{aligned} \Delta P &= [r(1 - P/K) - s Q] P h \\ \Delta Q &= (-u + v P) Q h \end{aligned}$$

where h denotes period length. One might well question the precise functional forms governing the population dynamics (and we return to this issue below). Nevertheless, this version of the predator-prey model provides a useful starting point, capturing the basic insight that more predators are bad for prey, while more prey is good for predators.

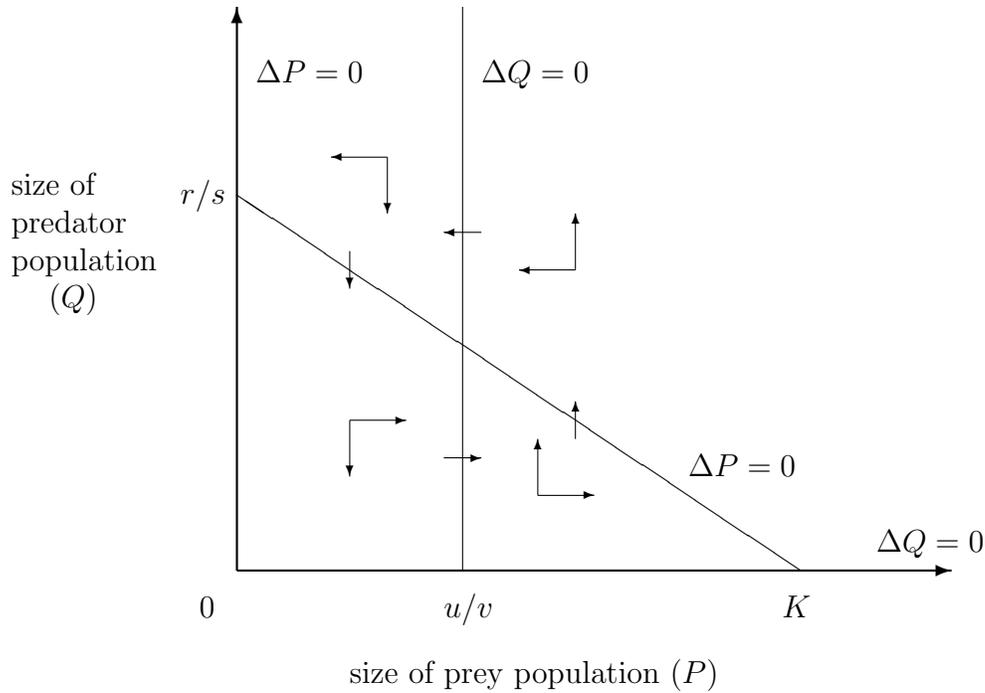
We can begin to analyze the model graphically. From the ΔP equation, we see that one P -nullcline follows the Q axis (at $P = 0$) while another is given by

$$Q = (r/s)(1 - P/K)$$

which is a downward-sloping line in (P, Q) space. The prey population is growing at points below this nullcline (because $\Delta P > 0$ implies $Q < (r/s)(1 - P/K)$) and is shrinking at points above this nullcline. From the ΔQ equation, we see that one Q -nullcline follows the P axis (at $Q = 0$) while another is given by

$$P = u/v$$

which is a vertical line in (P, Q) space. The predator population is growing at points to the right of this nullcline (because $\Delta Q > 0$ implies $P > u/v$), and is shrinking at points to the left of this nullcline. Without choosing numerical values for the parameters, we can draw the generic phase diagram below.



This diagram reveals three steady states. The two at $(P^* = 0, Q^* = 0)$ and $(P^* = K, Q^* = 0)$ are clearly unstable. The introduction of a few prey would cause the system to move away from the origin (where neither species is present); the introduction of a few predators would cause it to move away from the one-dimensional steady state (where the prey population has reached the capacity constraint). In contrast, the stability of the interior steady state at

$$\left(P^* = \frac{u}{v}, Q^* = \frac{r}{s} \left(1 - \frac{u}{vK} \right) \right)$$

cannot be immediately determined from the phase diagram. The arrows indicate that trajectories will “spiral” around this steady state. But without some additional analysis, it is not yet clear whether trajectories will spiral inward (converging to the steady state) or outward (moving away from the steady state).

17.2 A numerical example

To develop a numerical example, we now assume the parameter values $K = 1$, $r = 1.3$, $s = 0.5$, $u = 0.7$, $v = 1.6$, and $h = 1$. Further assuming the initial condition $(P_0 = 1, Q_0 = 1)$, the time paths and phase diagram are plotted on the next page. Given our numerical assumptions, we see that the oscillations dampen over time, eventually converging to the steady state $(P^* = 0.4375, Q^* = 1.4625)$. On the phase diagram, this behavior is reflected by the inward spiral of the trajectory. For reasons made apparent by this diagram, trajectories are sometimes called *orbits*, and a phase diagram with a trajectory is sometimes called an *orbit diagram*.

When we previously encountered oscillations (in Chapter 11), we raised the concern that they were merely artifacts of the discrete-time formulation of the model. But having moved from one- to two-dimensional models, it is important to recognize that the oscillations observed here would remain even if the model was recast in continuous time. To illustrate, we repeat the preceding example, this time setting period length very short ($h = .01$) to approximate continuous-time behavior. The time path and phase diagram are shown on the following page. Clearly, the oscillations dampen more rapidly in the continuous-time model.¹ Nevertheless, even in the continuous-time model, we see that the trajectory initially “overshoots” and then spirals inward toward the steady state.

For this example, the stability of each of the three steady states can be assessed more formally using the approach discussed in Chapter 11. Our two-equation system can be rewritten in the form

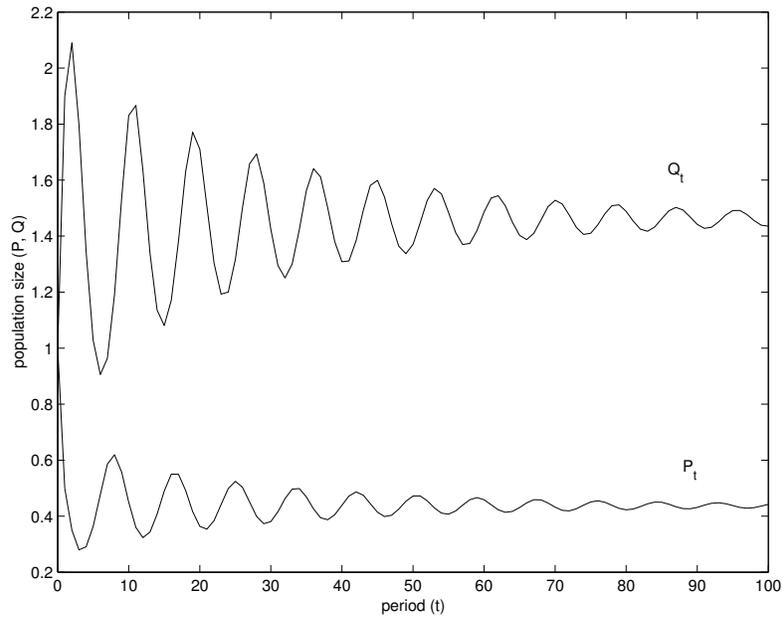
$$\begin{aligned} P_{t+1} &= g_1(P_t, Q_t) \\ Q_{t+1} &= g_2(P_t, Q_t) \end{aligned}$$

¹Comparing the two time-path diagrams, note that each period in the first diagram is divided into $1/h$ ($= 100$) periods in the second diagram. But the horizontal axes of both diagrams correspond to the same amount of real time.

```

>> K = 1; r = 1.3; s = .5; u = .7; v = 1.6; h = 1;
>> P = 1; Q = 1; y = [P Q];
for t = 1:(100/h);
    dP = (r*(1-P/K)-s*Q)*P*h; dQ = (-u+v*P)*Q*h; P = P+dP; Q = Q+dQ; y = [y; P Q];
end
>> plot(0:100, y) % time paths

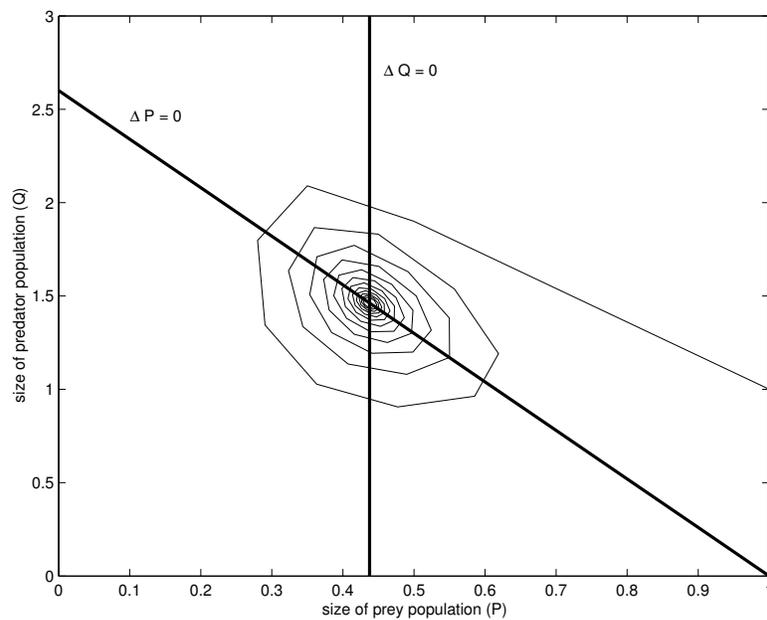
```



```

>> P = 0:.1:1; nullP = (r/s)*(1-P/K); plot(y(:,1),y(:,2),P,nullP,[u/v u/v],[0 3])
>> % phase diagram with trajectory

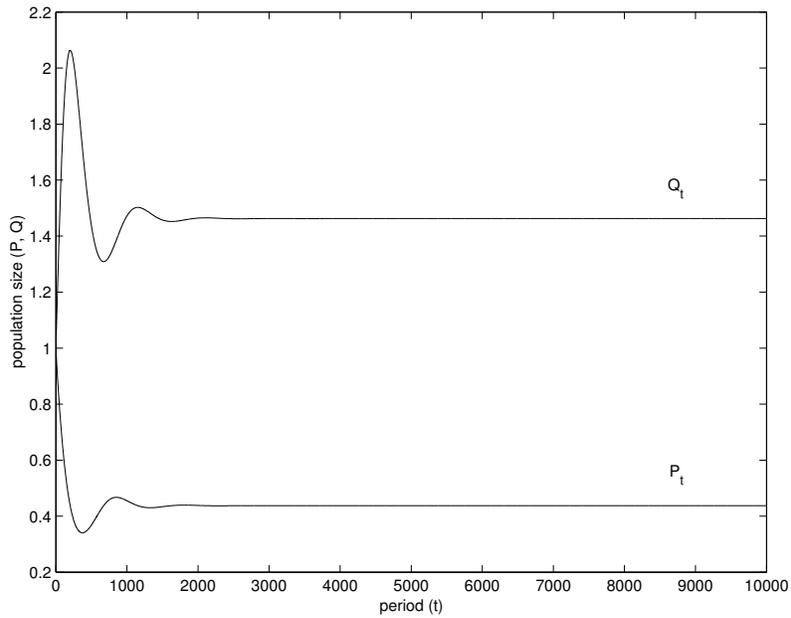
```



```

>> K = 1; r = 1.3; s = .5; u = .7; v = 1.6; h = .01;
>> P = 1; Q = 1; y = [P Q];
for t = 1:(100/h);
    dP = (r*(1-P/K)-s*Q)*P*h; dQ = (-u+v*P)*Q*h; P = P+dP; Q = Q+dQ; y = [y; P Q];
end
>> plot(0:(100/h), y) % time paths

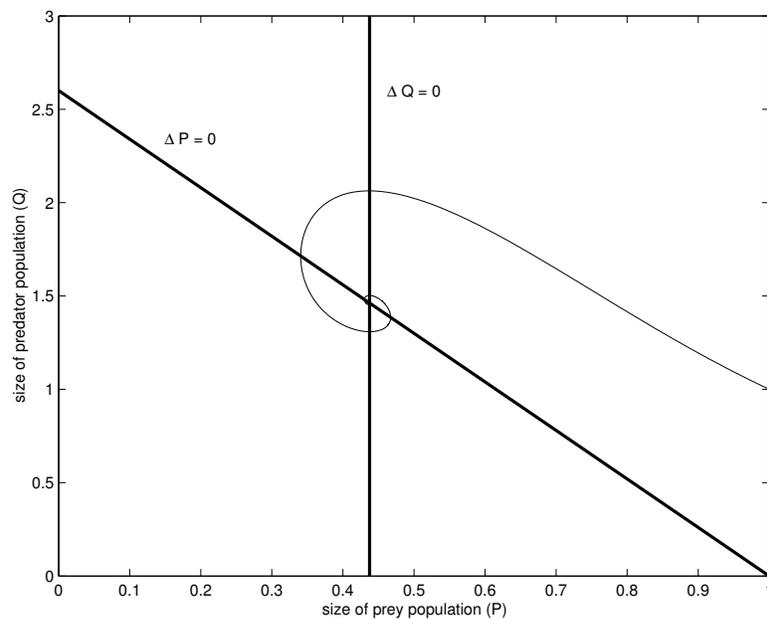
```



```

>> P = 0:.1:1; nullP = (r/s)*(1-P/K); plot(y(:,1),y(:,2),P,nullP,[u/v u/v],[0 3])
>> % phase diagram with trajectory

```



where

$$\begin{aligned}g_1(P, Q) &= P + [r(1 - P/K) - sQ]Ph \\g_2(P, Q) &= Q + [-u + vP]Qh\end{aligned}$$

Recall that the elements of the Jacobian matrix can be found using calculus or non-calculus methods. Using calculus (to obtain the result more quickly),

$$\begin{aligned}J &= \begin{bmatrix} \partial g_1 / \partial P & \partial g_1 / \partial Q \\ \partial g_2 / \partial P & \partial g_2 / \partial Q \end{bmatrix}_{(P^*, Q^*)} \\ &= \begin{bmatrix} 1 + [r(1 - 2P^*/K) - sQ^*]h & -sP^*h \\ vQ^*h & 1 + (-u + vP^*)h \end{bmatrix}\end{aligned}$$

Given the parameter values from our example, we can assess stability by evaluating the Jacobian matrix at each steady state and then computing its eigenvalues.

```
>> K = 1; r = 1.3; s = .5; u = .7; v = 1.6; h = 1;
>> P = 0; Q = 0; J = [1+(r*(1-2*P/K)-s*Q)*h, -s*P*h; v*Q*h, 1+(-u+v*P)*h];
eig(J) % eigenvalues for steady state at (P = 0, Q = 0)

ans =
    0.3000
    2.3000

>> P = 1; Q = 0; J = [1+(r*(1-2*P/K)-s*Q)*h, -s*P*h; v*Q*h, 1+(-u+v*P)*h];
eig(J) % eigenvalues for steady state at (P = 1, Q = 0)

ans =
   -0.3000
    1.9000

>> P = .4375; Q = 1.4625; J = [1+(r*(1-2*P/K)-s*Q)*h, -s*P*h; v*Q*h, 1+(-u+v*P)*h];
eig(J) % eigenvalues for interior steady state

ans =
    0.7156 + 0.6565i
    0.7156 - 0.6565i

>> abs(ans) % computing the absolute value of complex eigenvalues

ans =
    0.9711
    0.9711
```

For each of the first two steady states, we see immediately that the dominant eigenvalue is greater than one, indicating instability. For the interior steady state, the

eigenvalues are complex, and so we must compute their absolute values. The interior steady state is stable because both eigenvalues have absolute values less than one.

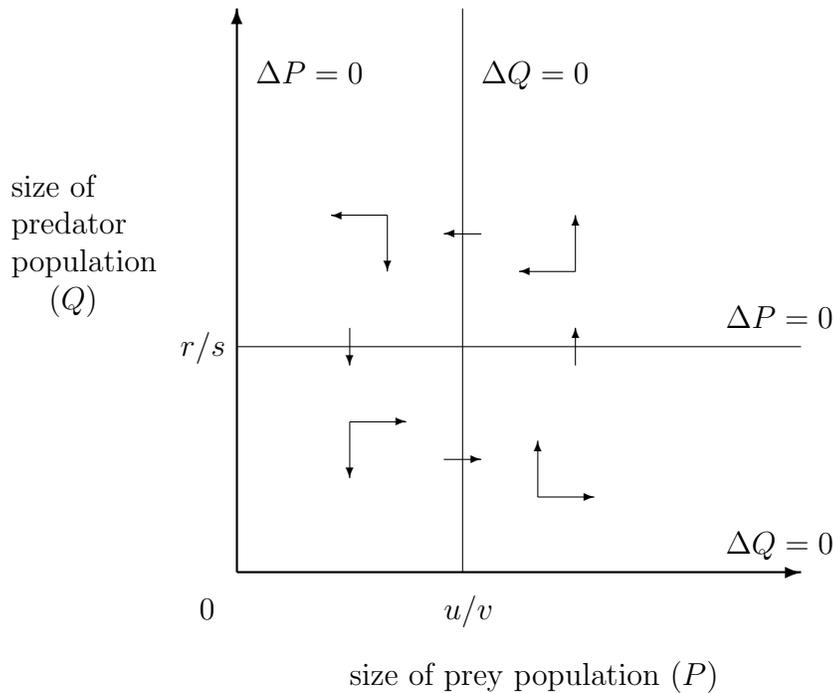
17.3 The original Lotka-Volterra model

We have assumed that the prey population faces a capacity constraint (given by parameter K). If there is no capacity constraint (so that K is infinite), the two-equation system becomes

$$\begin{aligned}\Delta P &= (r - s Q) P h \\ \Delta Q &= (-u + v P) Q h\end{aligned}$$

This special case is, in fact, the original predator-prey model. Developed independently in the 1920s by Alfred Lotka (who was modeling chemical reactions) and Vito Volterra (who was attempting to explain the dynamics of fish populations), it is often called the *Lotka-Volterra model*.

Removing the capacity constraint, the P -nullcline which had sloped downward is now horizontal in (P, Q) space. We can see from the phase diagram below that trajectories will spiral around the interior steady state at $(P^* = u/v, Q^* = r/s)$. But again, it is unclear from the diagram whether the trajectories will spiral inward (so that the steady state is stable) or outward (so that it is unstable).



For the continuous-time version of the Lotka-Volterra model, it is well known that the equilibria are cyclical. More precisely, starting from any initial condition, the trajectory will eventually return to this point (and the system continues along this “closed orbit” forever). This result does not hold for the discrete-time version (with $h > 0$) where orbits are not closed but instead spiral outward.² However, we can approximate continuous-time behavior by setting period length very small (say $h = 0.001$). To illustrate, we assume the other parameter values from above, along with the initial condition ($P_0 = 1, Q_0 = 3$). Time-path and phase diagrams are shown on the next page. While the phase diagram does not indicate elapsed time, we can see from the time-path diagram that one complete orbit takes about 7000 periods (corresponding to $7000/h = 7$ units of time). Had we chosen an initial condition closer to the interior steady state, it would lie on a “tighter” orbit around this steady state. Conversely, an initial condition further from this steady state would lie on a “wider” orbit. Thus, this model has a continuum of cyclical equilibria, arranged concentrically around the interior steady state.

When we first encountered cycles in Chapter 11, we viewed them as artifacts of the discrete-time formulation of the model. But in moving to two-dimensional models, cycles become possible even in continuous-time models.³ Recognizing that cycles are not artifactual, perhaps we should begin looking for social science applications of the predator-prey model. In fact, several authors have already suggested that this model could help explain the dynamics of interpersonal relationships. To sketch the simplest application, consider a couple (we’ll call them Chris and Pat) who are romantically involved. Reinterpreting the state variable of the Lotka-Volterra model, let P denote the affection of Pat for Chris, and Q denote the affection of Chris for Pat. The dynamics of Chris’ affection level seem straightforward: Chris becomes more affectionate when Pat’s affection level is high, and becomes less affectionate when Pat’s affection level is low. On the other hand, because the changes in Pat’s affection are inversely related to Chris’ affection level, we might say that Pat is “playing hard to get.” As we have already seen, the affection levels never converge to a steady state, but perpetually wax and wane over time.

Moving beyond that (perhaps too-cute) example, researchers have suggested more sophisticated applications of dynamical systems models to interpersonal relationships (and social psychology more generally); some references are provided in the further reading section at the end of this chapter. Applications to other subfields would also seem possible. For instance, empirical studies indicate that protest activity is sometimes cyclical. One simple explanation closely follows the predator-prey model.

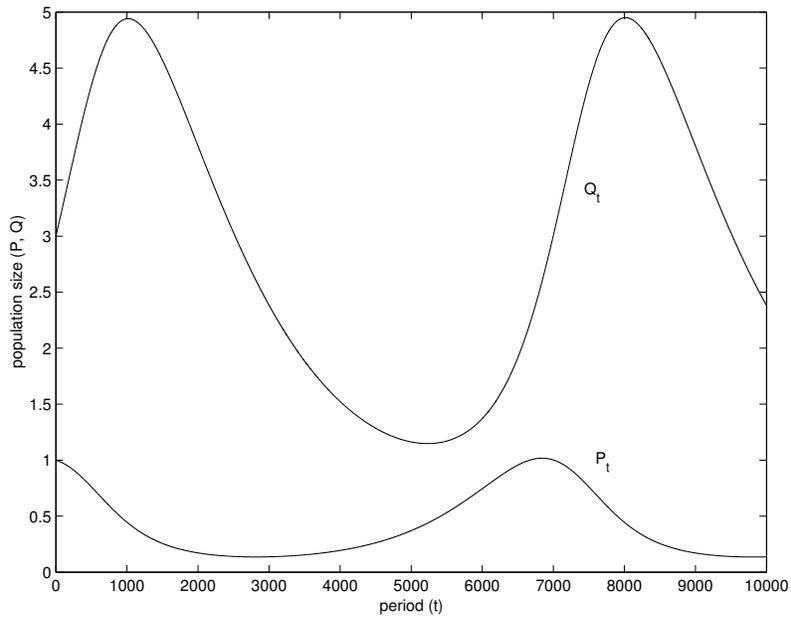
²Intuitively, because dynamics are updated more frequently as period length becomes smaller, the orbits make “sharper turns” in the continuous-time version of the model. This also explains the contrast between the orbit diagrams in the preceding section (which assumed $h = 1$ and $h = 0.01$).

³Indeed, as we have just discussed, cycles emerge only in the Lotka-Volterra model only when time is continuous. However, we’ll soon encounter other models in which cycles arise in both discrete-time and continuous-time versions.

```

>> r = 1.3; s = .5; u = .7; v = 1.6; h = .001;
>> P = 1; Q = 3; y = [P Q];
for t = 1:10000;
    dP = (r-s*Q)*P*h; dQ = (-u+v*P)*Q*h; P = P+dP; Q = Q+dQ; y = [y; P Q];
end
>> plot(0:10000,y) % time paths

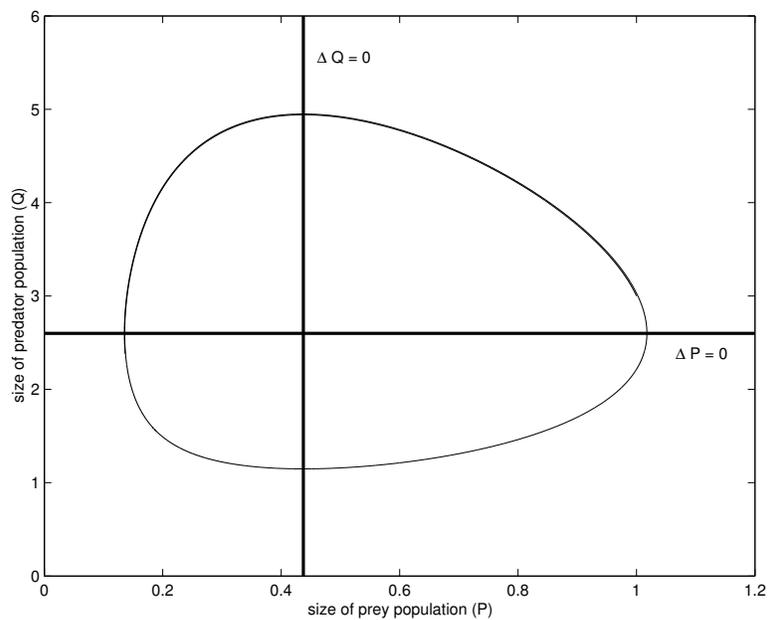
```



```

>> plot(y(:,1),y(:,2),[0 1.2],[r/s r/s],[u/v u/v],[0 6])
>> % orbit diagram

```



Letting P denote protest activity and Q denote police enforcement, the change in police enforcement is directly related to the level of protest activity, while the change in protest activity is inversely related to the level of police enforcement. (In this context, it is the protesters who are “playing hard to get.”) Again, the equilibrium outcome is not a steady state but a cycle in which protest activity perpetually rises and falls. While a more realistic model might incorporate other explanatory factors, the predator-prey model seems like a useful starting point. We suspect that many other sociological applications of the model are waiting to be discovered.

17.4 Another version of the predator-prey model

While the Lotka-Volterra model is well known (and a perennial favorite of textbook authors), it raises technical and substantive concerns that may undermine its empirical usefulness. The technical concern arises because each closed orbit is only weakly stable (that is, on the “borderline” between stability and instability). Following a small shock, the system neither returns to its original equilibrium nor continues to diverge from it. Rather, the system is simply “bumped” onto a new closed orbit where it remains indefinitely (unless hit by a subsequent shock). Weak stability might not seem problematic *per se*. However, in models with a continuum of weakly stable equilibria, small respecifications of the dynamics can have large qualitative effects, dramatically altering the number and stability of equilibria. In the parlance of dynamical systems, such models are not *structurally stable*. This calls into question the robustness of any predictions derived from the model.⁴

Substantively, reflection on the interaction between predator and prey species might suggest alternative (more realistic) specifications of the model. Generalizing our first model, suppose that predator-prey dynamics are given by

$$\begin{aligned}\Delta P &= \left[r P \left(1 - \frac{P}{K} \right) - s f(P) Q \right] h \\ \Delta Q &= [-u Q + v f(P) Q] h\end{aligned}$$

where the function $f(P)$ reflects the number of prey consumed per predator. Our first model implicitly assumed that this function is linear (with $f(P) = P$). When the prey population is small relative to the predator population, this linearity assumption may be reasonable. However, when there is an abundance of prey, each predator will stop eating once it is sated. In that context, it seems more reasonable to assume that

⁴Perhaps the technical concern is even more apparent in a different context. Consider a one-dimensional threshold model in which thresholds are uniformly distributed between 0 and 1, so that the threshold curve is given by $F(x) = x$. Graphically, the threshold curve lies along the 45-line, and hence every outcome x between 0 and 1 is a weakly stable steady state. Clearly, small respecifications of the threshold distribution could have a large qualitative effect (perhaps inducing a unique stable equilibrium as opposed to the initial continuum of equilibria).

$f(P)$ is a constant (which is independent of P). To address this issue, biologists have suggested several specifications of this function. Perhaps the simplest is

$$f(P) = \frac{P}{a + P}$$

where a is a new parameter. Given this specification, note that $f(P)$ is concave (increasing at a decreasing rate) and essentially constant when P is large (with $f(P) \approx 1$). The two-equation system becomes

$$\begin{aligned}\Delta P &= \left[r \left(1 - \frac{P}{K} \right) - \frac{sQ}{a + P} \right] P h \\ \Delta Q &= \left[-u + \frac{vP}{a + P} \right] Q h\end{aligned}$$

Moving toward a graphical analysis of the model, we see from the first equation that $\Delta P = 0$ implies $P = 0$ or

$$\begin{aligned}Q &= (r/s) \left(1 - \frac{P}{K} \right) (a + P) \\ &= (r/s) \left[a + \left(1 - \frac{a}{K} \right) P - \frac{1}{K} P^2 \right]\end{aligned}$$

Thus, this P -nullcline (which sloped downward in our first model) is now quadratic. From the second equation, we see that $\Delta Q = 0$ implies $Q = 0$ or

$$P = \frac{au}{v - u}$$

Thus, this Q -nullcline remains a vertical line in (P, Q) space. As before, the interior equilibrium is given by the intersection of these nullclines.

For the continuous-time version of this model, it can be shown that trajectories spiral inwards toward the (stable) interior equilibrium if

$$K < a \left(1 + \frac{2u}{v - u} \right)$$

Conversely, trajectories spiral outward from the (unstable) interior equilibrium if

$$K > a \left(1 + \frac{2u}{v - u} \right)$$

In this latter case, there is a unique cyclical equilibrium. This sort of equilibrium is sometimes called a *limit cycle* because trajectories converge to this cycle in the limit as time becomes infinite. Crucially, in contrast to the Lotka-Volterra model, there

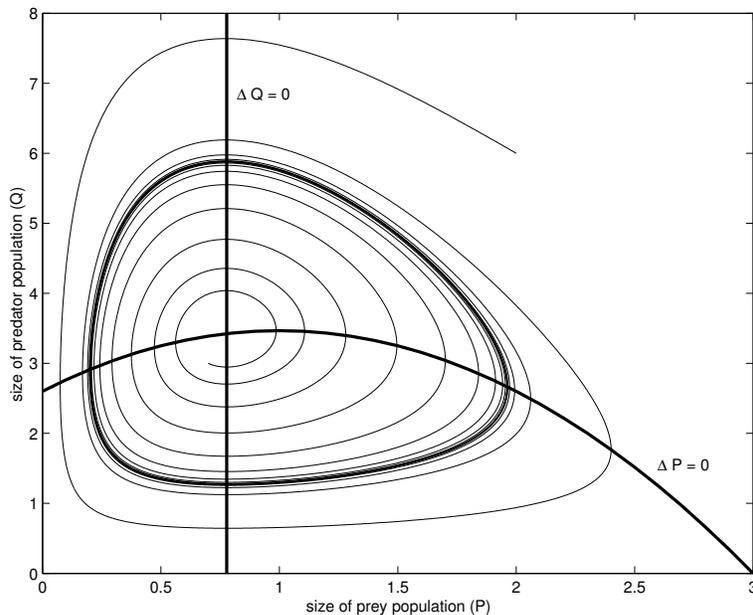
is not a continuum of equilibria. Rather, every trajectory converges to the unique limit cycle in the long run.

To illustrate, we consider an example with the parameter values $r = 1.3$, $s = 0.5$, $u = .7$, $v = 1.6$, $a = 1$, and $K = 3$. Because these values imply

$$K = 3 < a \left(1 + \frac{2u}{v - u} \right) = 2.5555$$

we know that the equilibrium is a limit cycle (when h is sufficiently small). The diagram below shows the orbits resulting from the initial conditions $(P_0 = .7, Q_0 = 3)$ and $(P_0 = 2, Q_0 = 6)$. Note that the orbit spirals outward toward the limit cycle in the first case, while the orbit spirals inward toward the limit cycle in the latter case.

```
>> r = 1.3; s = .5; u = .7; v = 1.6; a = 1; K = 3; h = .01;
>> P = .7; Q = 3; y1 = [P Q]; for t = 1:10000; dP = (r*(1-P/K)-(s*Q)/(a+P))*P*h;
dQ = (-u+(v*P)/(a+P))*Q*h; P = P+dP; Q = Q+dQ; y1 = [y1; P Q]; end;
>> P = 2; Q = 6; y2 = [P Q]; for t = 1:10000; dP = (r*(1-P/K)-(s*Q)/(a+P))*P*h;
dQ = (-u+(v*P)/(a+P))*Q*h; P = P+dP; Q = Q+dQ; y2 = [y2; P Q]; end;
>> P = 0:.1:3; nullP = (r/s)*(1-P/K).*(a+P);
>> plot(y1(:,1),y1(:,2),y2(:,1),y2(:,2),P,nullP,[a*u/(v-u), a*u/(v-u)], [0 8])
>> % phase diagram with two trajectories
```



17.5 Further reading

Our discussion of the logistic model with a predator follows the treatment in Allman and Rhodes (*Mathematical Models in Biology*, 2004, Chap 3). Original formulations of the Lotka-Volterra model are found in Lotka (*J Am Chem Soc* 1920) and Volterra (1926, 1931). For more advanced readers, Hofbauer and Sigmund (*Evolutionary Games and Population Dynamics*, 1998) offer an extended treatment of a generalized version of the predator-prey model. Strogatz (1994) discusses this model (Chapter 6.4) as well as the dynamics of “love affairs” (Chapter 5.3). A related analysis of interpersonal relationships is given by Felmeé and Greenberg (*J Math Soc* 1999). A more extended treatment of this topic is provided by Gottman et al (*The Mathematics of Marriage*, MIT, 2002). Other applications of dynamical systems in social psychology are presented by Nowak and Vallacher (*Dynamical Social Psychology*, Guilford, 1998). See Oliver and Myers (*Mobilization* 2003) for discussion of formal models of protest movements. The version of the predator-prey model developed in Section 17.4 follows Holling (*Mem Ent Soc* 1973), and is discussed by Hofbauer and Sigmund (*The Theory of Evolution and Dynamical Systems* 1988, p 155). Also see also May (*Science* 1972) for variations on the Lotka-Volterra model.